PROCEEDINGS

OF THE

DE VIS SYMPOSIUM

BRISBANE
31 MARCH, 1990

MEMOIRS OF THE
QUEENSLAND MUSEUM

VOLUME 28
PART 1

CONTENTS

INTRODUCTION

This volume contains the published proceedings of the first major scientific conference to be held at the new Queensland Museum, that moved in 1986 to the south bank of the Brisbane River. Appropriately the conference concerned the history of Australia's unique vertebrate fauna. Moreover, it was dedicated to Charles Walter de Vis (1829-1915), first Director of the Queensland Museum. In his time de Vis undertook prolific and pioneering work on a variety of Australia's vertebrate animals, both living and extinct, thereby founding the Queensland Museum's century-long tradition of leading research in vertebrate biology and phylogeny.

The conference extended over three days (May 12th to 14th, 1987) and served as a forum for original contributions in vertebrate palaeontology and allied sciences (functional anatomy and embryology). The crowded program comprised well over thirty scientific papers, supplemented by numerous posters and exhibits. Field excursions were made to the classic Pleistocene localities on the Darling Downs (led by Mr Andrew Rozenfelds and Mr Ian Sobbe) or to examine the prolific sources of Tertiary and Pleistocene vertebrates at Riversleigh in northern Queensland (led by Dr Michael Archer and Mr Henk Godthelp).

The symposium was officially opened by the Hon. B.D. Austin, MLA, then State Minister for Tourism and National Parks, and by Dr Alan Bartholomai, Director of the Queensland Museum. There followed an introductory presentation by Dr Glen Ingram (Queensland Museum) on the life and scientific achievements of C.W. de Vis. The first session was then given over to the astonishing series of discoveries recently made by Dr Michael Archer and his colleagues (University of New South Wales) in the Tertiary and Pleistocene rocks of Riversleigh, northern Queensland. It is safe to predict that those discoveries, which include entirely new and hitherto unsuspected types of mammals, will entail major revision of existing views on the origin of Australia's fauna. The remainder of the scientific program included presentations on a wide range of taxonomic groups and reflected an equally diverse array of research interests — including biogeography, faunal analysis, functional anatomy, systematics and taphonomy.

The contents of the scientific program are reflected faithfully in the papers comprising this volume. Some contributions correspond almost *verbatim* with the spoken delivery at the conference; other participants have presented much fuller written papers. And, as at any scientific conference, some participants spoke about new discoveries that had barely emerged from the preliminary stages of their research. The editors have persuaded most of those participants to provide written abstracts of their presentations, and these are included in this volume so as to convey the fullest flavour of the meeting.

The sheer diversity of subjects in this volume should come as a pleasant surprise to many vertebrate biologists outside Australia. Indeed, the editors share the hope that this diversity will dispel the curious notion that Australia's fossil vertebrates comprise little more than Pleistocene marsupials. This present volume, with topics as varied as Devonian fishes, Triassic amphibians and Cretaceous ichthyosaurs, should serve to correct such misunderstandings.

An official reception was hosted by the Queensland Museum's Board of Trustees, and supported by the Royal Society of Queensland. The symposium also opened its doors to a wider audience when Dr John Long (Western Australian Museum) delivered a public lecture on the exquisitely preserved fossil fishes of the Devonian Gogo Formation in Western Australia. At the symposium dinner the inaugural Queensland Museum Medal was presented by Dr Alan Bartholomai to Dr Michael Archer, formerly curator of mammals at the Queensland Museum and currently Associate Professor in the School of Biological Science at the University of New South Wales. This award was made in recognition of Dr Archer's outstanding contributions to vertebrate palaeontology and mammalogy.

Two prizes were generously sponsored by the Fossil Collectors' Association of Australasia (FCAA) and the Association of Australasian Palaeontologists (AAP). In awarding the FCAA prize, for the best presentation by an amateur palaeontologist, the judges found it impossible to distinguish between the merits of Mr John Barrie (a study of the Pleistocene snake *Wonambi*) and Mr Ian Sobbe (a study of tooth-marks on Pleistocene mammal bones from the Darling Downs) who shared the joint award. The AAP prize, for the best presentation by a student, was awarded to Mr Michael Leu (Department of Earth Sciences, Macquarie University) for his work on lacustrine sharks from the Permian of central Queensland.

The success of the de Vis symposium which provided such a fertile medium for the exchange of scientific information and ideas was agreed unanimously. Consequently it was resolved that this symposium should not be an isolated event, but should serve as the foundation for a regular series of Australian conferences on vertebrate biology and phylogeny. Dr Michael Archer (University of New South Wales) and Dr Alex Ritchie (Australian Museum, Sydney) promptly volunteered to arrange a second symposium in Sydney. That second symposium (titled the 1989 Conference on Australasian Vertebrate Evolution, Palaeontology & Systematics) took place in Sydney, in May 1989. A third symposium will take place in Alice Springs, Northern Territory, in 1991, and a fourth is foreshadowed for Adelaide, South Australia, in 1993. These events, past and future, are eloquent testimony to the enthusiasm and excitement that was generated by the de Vis symposium in May 1987.

The editors would like to thank many individuals and organizations for their efforts and contributions. Foremost is, of course, the Queensland Museum — members of its staff, its Board of Trustees and its Director, Dr Alan Bartholomai. Sponsors and supporters of the symposium included the Ian Potter Foundation, the Fossil Collectors' Association of Australasia, the Association of Australasian Palaeontologists, and the Royal Society of Queensland. In addition a grateful acknowledgement is extended to the referees of the papers included in this volume. Publication of the symposiums proceedings was facilitated by considerable assistance from the Queensland Museum, and by funding from a National Heritage Grant from the Federal Department of The Arts, National Parks and Sport.

THE WORKS OF CHARLES WALTER DE VIS, ALIAS 'DEVIS', ALIAS 'THICKTHORN'

GLEN J. INGRAM

Ingram, G.J. 1990 3 31: The works of Charles Walter de Vis, alias 'Devis', alias 'Thickthorn'. *Mem. Qd Mus.* **28**(1): 1-34. Brisbane. ISSN 0079-8835.

Charles Walter de Vis (born Devis), 1829-1915, was an important Australian biologist. He was an English immigrant whose Australian career began after his fiftieth birthday. From 1880 to 1911, he wrote 353 articles and papers under the surnames of 'Devis' and 'de Vis', and the pen-name of 'Thickthorn'. In these publications, he described 551 new fossil and extant taxa of animals and one fossil plant from Australasia and Africa. Some of his work has been disparaged. But, in most cases, the poor standard of this work can be excused because of the inadequate libraries and the inadequate collections of comparative material in colonial Queensland. Despite shortcomings, de Vis's contributions were important and significant in the development of our understanding of the faunas, past and present, of Australia and New Guinea. In this, he should be celebrated as a pioneering Australian scientist.

☐ *Devis, de Vis, Thickthorn, biography, bibliography.*

Glen J. Ingram, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 24 January, 1988.

Charles Walter de Vis (né Devis), 1829-1915, is an important figure in Australian natural history. From 1880 to 1911, he described 551 new fossil and extant taxa of animals and one fossil plant from Australasia and Africa (see Appendix 1). De Vis's output was prodigious. Not counting republications, 353 articles and papers appeared under his names of 'de Vis', 'Devis', and 'Thickthorn' (see Appendix 2). Even more startling is that all but three of these publications were written after his 50th birthday. The three exceptions (1865, 1868, 1870) were written before he came to Australia and while he was the Curator of the Queen's Park Museum at Manchester, England. De Vis's life has been documented by Johnston (1916), Whitley (1948), Whittell (1954), Ingram (1986a,c,d), Turner (1986), Turner and Wade (1986), and Mather (1986). Amongst others, his work has been reviewed or commented upon by Boulenger (1885), McCulloch and Ogilby (1919), Chisholm and Chaffer (1956), Bartholomai (1966), Covacevich (1971), Rich and van Tets (1982), Cogger (1985) and Ingram (1987). I am concerned with de Vis's writings and their quality, after he settled in Queensland in 1870.

De Vis's Australian publications fall into two distinct periods: the 'Thickthorn' period from January, 1880, to March, 1882, and the 'Queensland Museum' period from May, 1882, to November, 1911.

THICKTHORN

'Thickthorn' was the pen-name of Charles Walter Devis (he was not then 'de Vis') for articles and letters he wrote for the newspapers, the *Queenslander* and *Brisbane Courier*. These communications were based on observations of birds, marsupials, and reptiles from around Rockhampton, although he wrote once about ghosts (1880d). Thickthorn's prose was spirited and in the tradition of the natural theological style (Ingram, 1986a,c). The following example illustrates the style:

> 'If the love and discrimination of the beautiful be humanizing — if ever wise Government seek to elevate the mental horizon of the governed by bringing the eye into contact with the conceptions of the painter and sculptor — surely the pencil and chisel of nature working in their happiest moods must stir within the most grovelling mind its latent admiration for the ideal, and wean it from those grosser sensualities which are ultimately pernicious, if not fatal to society [1880f].'

Concurrently, Devis, without pseudonym, wrote more severely empirical articles. These were mainly about geology and minerals. One of the articles (1880g) — 'Is the Queensland coast rising or sinking?' — created a controversy. The debate was heated and it continued for several weeks until the Editor said, 'We begin to tire of this subject, or some of our readers most certainly do so' (Queenslander, January 1, 1881, p. 18).

In the penultimate article from this period (1882a), Devis used the name 'de Vis' for the first time in print. He assumed this surname for the rest of his life.

QUEENSLAND MUSEUM

De Vis's newspaper articles attracted much attention, including that of the Trustees of the Queensland Museum (Chisholm, 1922). He was appointed the Curator of the museum in February, 1882, and remained in charge until March, 1905, when he retired at the age of 75 (Mather, 1986). His last paper (1911h) was published in the *Annals of the Queensland Museum* when he was 82. He died on 30 April, 1915.

This period marked most of de Vis's publishing life; it is on these works that his reputation stands or falls.

Popular articles

From May, 1882, to May, 1890, de Vis mostly succeeded in having his monthly reports to the Trustees published in the newspapers. In them, he detailed what had been accessioned and he listed the donors to the museum. Also, he elaborated on any exciting discoveries. These articles served two purposes: rewarding donors by putting their names in print and focusing public attention on the museum.

Most evidence suggests de Vis was successful with the public. The museum was very popular (Kohlstedt, 1983); there was a marked expansion in the collections (Turner and Wade, 1986); and his popular writings as well as his more scientific works were readily published. Curiously, Brenan (in Chisholm, 1922) said de Vis was too retiring to make the museum popular, and Mack (1956) said de Vis would have have been happier in a secluded room rather than building up the collections.

Scientific articles

De Vis's scientific contribution was mostly taxonomic. While associated with the museum, he described 549 new taxa (Appendix 1). Of fossils, he described a species of plant, a trace fossil attributed to a species of worm, a species of fish, three genera and 12 species of reptiles, 11 genera and 46 species of birds, and one family, 11 genera, and 31 species of mammals. Of the living world, he described one crustacean, a subspecies of spider, 12 genera, 194 species, and one subspecies of fish, seven species of frogs, seven genera, 71 species, and one subspecies of reptiles, 14 genera, 103 species, and three subspecies of birds, and one genus and 15 species of mammals. (The preceding figures differ, in part, from Ingram, 1986d; at that time I was unaware that there were more of de Vis's papers to find. Also, *nomina nuda* presented a problem).

About 22% of these taxa are regarded as valid today. This does not appear to be a very good rate of success. Cogger (1985) stated the general feeling when writing of de Vis's work on snakes:

> 'His work was characterized by inadequate descriptions and poor research; it seemed that almost every specimen which fell into his hands acquired a new name.'

Similarly, Miller (1966) said of de Vis:

> 'He evidently proceeded on the general belief that all fossils should be designated as separate species, whether or not they differed significantly from their modern relatives.'

Turner and Wade (1986), however, said that de Vis did not describe all fossils available to him as new. In fact, in all groups he worked, his Curator's reports (see citations in Appendix 2) show that he identified most specimens as already known. Certainly de Vis described many new taxa that would not be justified by modern standards. However, he was a product of his time (van Tets and Rich, this volume). De Vis belonged to what has been called the 'traditional school' of taxonomy by Serventy (1950). That school believed in 'small' species and 'narrow' genera and they had little interest in subspecies. The basic taxonomic unit was the individual. As Serventy (1950) noted, the idea of geographical variation, with the subspecies as a geographical component of the species, was a later development in taxonomy.

The claim that de Vis's descriptions and research were poor is true. But this must be put in the context of the 19th Century in the Colony of Queensland. Library facilities were inadequate and, more important, comparative collections of animals were lacking (Diggles, 1873, 1875). Most of the research had been done in Europe and the important collections resided there. Even if authoritative books were available, they were no substitute for comparative collections. Any researcher in the colonies was disadvantaged by these conditions. De Vis was no exception. The quality of his research compares favourably with that of more acclaimed contemporaneous taxonomists. This can be illustrated by comparing de Vis's work with that of Sir William Macleay (1820-1891) of the Colony of New South Wales. Both's work presented similar problems; Goldman *et al.* (1969) noted that some of Macleay's species were ignored in subsequent taxonomic revisions because his original descriptions were inadequate.

In recognising entities in nature, de Vis was as skilful as Macleay. With reptiles, for example, de Vis described 71 species of which 25 (34%) are regarded as valid (Appendix 1). Macleay described 66 species of which 14 (22%) are regarded as valid (data taken from Goldman *et al.*, 1969, and Cogger *et al.*, 1983).

There have also been criticisms of where de Vis published. Turner and Wade (1986) noted that there has been concern about his publishing in newspapers. But de Vis did not consider publications in newspapers as scientifically valid (de Vis, 1907a). Further, most of his 'scientific' publications in newspapers had nothing to do with him. As a matter of course and in the public interest, the Linnean Society of New South Wales and the Royal Society of Queensland sent abstracts of papers read at their meetings for publication in newspapers. That these are now regarded as valid descriptions for taxonomy, and thus 'scientific', results from the modern rules and regulations of the *International Code of Zoological Nomenclature*, not from standards of his time. Mathews (1925) mentioned that de Vis published in obscure places, such as parliamentary papers. From 1890 to 1898, de Vis produced reports for Sir William MacGregor on the material MacGregor had had collected while Administrator and Lieutenant Governor of British New Guinea. MacGregor included de Vis's reports as part of the 'Annual Report on British New Guinea'. These were published by the Houses of Parliament to which they were submitted by law. De Vis did not consider these to be scientific publications (Ingram, 1987). Again, it is the rules and regulations of nomenclature that make these publications valid and give them priority over subsequent papers in respectable scientific journals. De Vis was not always successful with subsequent publication, but that he tried is a source of confusion in the taxonomic literature because of the multiple versions (Ingram, 1987).

Probably what contributed most to de Vis's bad reputation was the attack by Boulenger (1885) writing from the British Museum. Of de Vis's papers he said:

> 'Their author is no doubt stimulated by the desire of promoting herpetological knowledge in his country, but, through his incompetence and want of care, he will do much harm.'

And further:

> '. . . he has no excuse, and one can only wonder at his daring to write on subjects of which he is so manifestly ignorant.'

One can only wonder at the extent of Boulenger's vitriol. Boulenger was an excellent taxonomist. He was, no doubt, offended by the standard of de Vis's work compared to his own. But was he also putting the Colonial, de Vis, in his place? I find it difficult to discover why just de Vis was singled out. De Vis did make mistakes in observations on his material: some of these are particularly galling (McCulloch and Ogilby, 1919; Ingram and Covacevich, 1988). If his type material is missing, one cannot be sure just what the mistake was. Even so, Boulenger must have been possessed of a healthy arrogance to draw-and-quarter de Vis in public.

CONCLUSION

With hindsight, and with the advantage of being separated from de Vis by 70 years, we can evaluate his work. His contribution was important and significant in the development of our understanding of the faunas, past and present, of Australia and New Guinea. His contribution to palaeontology was particularly important (Johnston, 1916; Turner, 1986; Turner and Wade, 1986). In all his achievements, despite shortcomings, he should be celebrated as a pioneering Australian scientist.

Perhaps the fitting epitaph is one given by Iredale (1950). He was writing of de Vis's work on New Guinean birds, but his comments could be considered apt for all the groups de Vis worked.

> 'DE VIS, C.W. Curator of the Queensland Museum, to whom fell the task of determining the wonderful bird collections made by MacGregor and his assistants. Though not a professed ornithologist, he made an excellent job of this difficult problem, much better than has been allowed by some extra-limital 'ornithologists', and he deserves great credit.'

ACKNOWLEDGEMENTS

Many thanks to Donna Case, Lucille Crevola-Gillespie, and Lenore Wedgwood who spent many long hours combing newspapers for articles by de Vis. Many thanks to Kathleen Buckley, Victoria Coops and Kevin Lambkin for their help with bibliographic work. Many thanks to Gerald Allen, Alan Bartholomai, Peter Jell, Jeffrey Johnson, Wayne Longmore, Roland McKay, Ralph Molnar, Robert Raven, and Stephen Van Dyck for finding the modern identities of many of de Vis's name-bearing specimens. Many thanks to Robert Raven, Paul Merefield, and Neale Hall for transferring the data-base across operating systems. Particular thanks are due to Jeanette Covacevich, Peter Jell, Wayne Longmore, and Robert Raven for their encouragement and support for what has been a tedious but necessary task.

LITERATURE CITED

AKIHITO, PRINCE AND MEGURO, K. 1975. Description of a new gobiid fish, *Glossogobius aureua*, with notes on related species of the genus. *Japanese Journal of Ichthyology* **22**(3): 127–142.

1980. On the six species of the genus *Bathygobius* found in Japan. *Japanese Journal of Ichthyology* **27**(3): 215–236.

ALLEN, G.R. 1975. 'Damselfishes of the South Seas'. (T.F.H. Publications: Hong Kong). 240 pp.

ALLEN, G.R. AND EMERY, A.R. 1985. A review of the pomacentrid fishes of the genus *Stegastes* from the Indo-Pacific, with description of two new species. *Indo-Pacific Fishes* **3**: 1–31, pl. 1-3.

ALLEN, G.R. AND HEEMSTRA, P.C. 1976. *Cheilodactylus rubrolabiatus*, a new species of morwong (Pisces: Cheilodactylidae) from Western Australia, with a key to the cheilodactylid fishes of Australia. *Records of the Western Australian Museum* **4**(4): 311–325.

ALLEN, G.R. AND TALBOT, F.H. 1985. Review of the snappers of the genus *Lutjanus* (Pisces: Lutjanidae) from the Indo-Pacific, with the description of a new species. *Indo-Pacific Fishes* **11**: 1–87, pl. 1–10.

AMADON, D. 1951. Taxonomic notes on the Australian butcher-birds (family Cracticidae). *American Museum Novitates* **1504**: 1–33.

ARCHER, M. 1977. *Kooboor notabilis* (de Vis), an unusual koala from the Pliocene Chinchilla Sand. *Memoirs of the Queensland Museum* **18**(1): 31-35, pl. 14.

1981. A review of the origins and radiations of Australian mammals. p. 1435–1488. *In* Keast, A. (ed.), 'Ecological biogeography of Australia'. Vol. 3, ix p. 1435–2142. (Junk: The Hague).

ARCHER, M. AND DAWSON, L. 1982. Revision of marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and thylacoleonid evolution in the late Cainozoic. p. 477-494. *In* Archer, M. (ed.), 'Carnivorous marsupials'. Vol. 2, iv p. 397–804. (Royal Zoological Society of New South Wales: Sydney).

ARCHER, M., PLANE, M.D. AND PLEDGE, N.S. 1978. Additional evidence for interpreting the Miocene *Obdurodon insignis* Woodburne and Tedford, 1975, to be a fossil platypus (Ornithorhynchidae: Monotremata) and a reconsideration of the status of *Ornithorhynchus agilis* de Vis, 1885. *Australian Zoologist* **20**(1): 1–27.

BARTHOLOMAI, A. 1963. Revision of the extinct macropodid genus Sthenurus Owen in Queensland. *Memoirs of the Queensland Museum* **14**(3): 51–76.

1966. The type specimens of some of de Vis' species of fossil Macropodidae. *Memoirs of the Queensland Museum* **14**(5): 115-126, pl. 16–19.

1967. *Troposodon*, a new genus of fossil Macropodinae. *Memoirs of the Queensland Museum* **15**(1): 21–33.

1968. A new fossil koala from Queensland and a reassessment of the taxonomic position of the problematical species *Koalemus ingens* de Vis. *Memoirs of the Queensland Museum* **15**(2): 65–71, pl. 9.

1975. The genus *Macropus* Shaw (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* **17**(2): 195–235, pl. 7-26.

1976. The genus *Wallabia* Trouessart (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* **17**(3): 373–377, pl. 53.

BARTHOLOMAI, A. AND MARSHALL, L.G. 1973. The identity of the supposed dasyurid marsupial, *Sarcophilus prior* de Vis, 1883, with comments on other reported 'Pliocene' occurrences of *Sarcophilus*. *Memoirs of the Queensland Museum* **16**(3): 369–374, pl. 26.

BEN-TUVIA, A. 1986. Taxonomic status of *Upeneichthys lineatus* (Bloch) in Australian and New Zealand waters. p. 590-594. *In* Uyeno, T., Arai, R., Taniuchi, T. and Matsuura, K. (eds), 'Indo-Pacific fish biology: Proceedings of the Second International Conference on Indo-Pacific Fishes'. (Ichthyological Society of Japan: Tokyo).

BERGMANS, W. 1979. Taxonomy and zoogeography of *Dobsonia* Palmer, 1898, from the Louisiade Archipelago, the D'Entrecasteaux Group, Trobriand Island and Woodlark Island (Mammalia, Megachiroptera). *Beaufortia* **29**(355): 199-214.

BONNET, P. 1958. Bibliographia Araneorum. Vol. 2, pt 4, p. 3027-4230. Douladoure: Toulouse.

BOULENGER, G.A. 1885. Remarks on Mr. de Vis' recent contributions to the herpetology of Australia. *Annals and Magazine of Natural History* (5)**16**(95): 386-387.

1887. 'Catalogue of lizards in the British Museum (Natural History)'. 2 ed. Vol. 3. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae. xii 575 pp, 40 pls. (British Museum (Natural History): London).

BROWN, W.C. 1953. Results of the Archbold Expeditions. No. 69. A review of New Guinea lizards allied to *Emoia baudini* and *Emoia physicae*. *American Museum Novitates*. **1627**: 1–25.

BURGESS, W.E. 1978. 'Butterfly fishes of the world: A monograph of the family *Chaetodontidae*'. (T.F.H. Publications: Neptune City). 832 pp.

BUSTARD, H.R. 1970. *Oedura marmorata* a complex of Australian geckos (Reptilia: Gekkonidae). *Senckenbergiana Biologica* **51**(1/2): 21–40.

CANTWELL, G.E. 1964. A revision of the genus *Parapercis*, family Mugiloididae. *Pacific Science* **18**(3): 239–280.

CHISHOLM, A.H. (1922). Bird seeking in Queensland. Part 2 [3]. Queensland Naturalist 3(6): 115–124.

CHISHOLM, A.H. AND CHAFFER, N. 1956. Observations on the Golden Bower-bird. *Emu* **56**(1): 1–39, pl. 1–5.

CHOAT, J.H. AND RANDALL, J.E. 1986. A review of the parrotfishes (family Scaridae) of the Great Barrier Reef of Australia with description of a new species. *Records of the Australian Museum* **38**: 175-228, pl. 1.

COGGER, H.G. 1966. The status of the "elapid" snake *Tropidechis dunensis* de Vis. *Copeia* **1966**(4): 893-894.

1985. Australian proteroglyphous snakes - an historical overview. p. 141-154. *In* Grigg, G., Shine, R. and Ehmann, H. (eds), 'Biology of Australasian frogs and reptiles'. (Surrey Beatty and Sons: Norton). xvi 527 pp.

COGGER, H.G., CAMERON, E.E. AND COGGER, H.M. 1983. Amphibia and reptilia. *Zoological Catalogue of Australia* 1:1-313.

COLLETTE, B.B. AND RUSSO, J.L. 1984. Morphology, systematics, and biology of spanish mackerels (*Scomberomorus*, Scombridae). *FisheryBulletin* **82**(4): 545-692.

CONDON, H.T. 1975. 'Checklist of the birds of Australia'. Part 1. Non-passerines. (Royal Australasian Ornithologists Union: Melbourne). xx 311, 2 maps.

COOPER, W.T. AND FORSHAW, J.M. 1977. 'The birds of paradise and bower birds.' (Collins: Sydney). xii 304 pp.

CORBEN, C.J. AND INGRAM, G.J. 1987. A new barred river frog (Myobatrachidae: *Mixophyes*). *Memoirs of the Queensland Museum* **25**(1): 233-237

COVACEVICH, J. 1971. Amphibian and reptile type-specimens in the Queensland Museum. *Memoirs of the Queensland Museum* **16**(1): 49-67.

COVENTRY, A.J. AND RAWLINSON, P.A. 1980. Taxonomic revision of the elapid genus *Drysdalia* Worrell 1961. *Memoirs of the National Museum of Victoria* **41**: 65-78, pl. 12.

CROWLEY, L.E.L.M., IVANTSOFF, W. 1988. A new species of Australian *Craterocephalus* (Pisces: Atherinidae) and redescription of four other species. *Records of the Western Australian Museum* **14**(2): 151-169.

CROWLEY, L.E.L.M., IVANTSOFF, W. AND ALLEN, G.R. 1986. Taxonomic position of two Crimson-Spotted Rainbowfish, *Melanotaenia duboulayi* and *Melanotaenia fluviatilis* (Pisces: Melanotaeniidae), from Eastern Australia, with special reference to their early life-history stages. *Australian Journal of Marine and Freshwater Research* **37**(3): 385-398.

DAWSON, L. 1982. Taxonomic status of fossil thylacines (*Thylacinus*, Thylacinidae, Marsupialia) from Late Quarternary deposits in eastern Australia. p. 527-536. *In* Archer, M. (ed.), 'Carnivorous marsupials'. Vol. 2. iv p. 397-804, (Royal Zoological Society of New South Wales: Sydney).

1983. The taxonomic status of small fossil wombats (Vombatidae: Marsupialia) from the Quaternary deposits, and of related modern wombats. *Proceedings of the Linnean Society of New South Wales* **107**(2): 99-121.

DE BEAUFORT, L.F. AND BRIGGS, J.C. 1962. 'The fishes of the Indo-Australian Archipelago'. Vol. 11. Scleroparei, Hypostomides, Pediculati, Plectognathi, Opisthomi, Discocephali, Xenopterygii. xi 481 pp. (E.J. Brill: Leiden).

DE ROOIJ, N. 1915. 'The reptiles of the Indo-Australian Archipelago'. Vol. 1. Lacertilia, Chelonia, Emydosauria. xiv 384 pp. (E.J. Brill: Leiden).

DE VIS, C.W., OR DEVIS, C.W., OR THICKTHORN, see Appendix 2.

DIGGLES, S. 1873. Two new Australian birds. [In Anon.] *Brisbane Courier*, December 2, p. 3. Republished 1873, *Queenslander*, December 6, p. 6.

1875. Birds of Australia. I. *Queenslander*, March 13, p. 7.

ESCHMEYER, W.N., RAMA-RAO, K.V. AND HALLACHER, L.E. 1979. Fishes of the scorpionfish subfamily Choridactylinae from the western Pacific and the Indian Ocean. *Proceedings of the California Academy of Sciences* **41**(21): 475-500.

FLETCHER, J.J. 1896. On the dates of publication of the early volumes of the Society's Proceedings. *Proceedings of the Linnean Society of New South Wales* (2)**10**(4): 533-536.

FORD, J. 1982. Origin, evolution and speciation of birds specialized to mangroves in Australia. *Emu* **82**(1): 12-23.

1983. Speciation in the Ground-thrush complex *Zoothera dauma* in Australia. *Emu* **83**(3): 141-151.

FOWLER, H.W. 1928. The fishes of Oceania. *Memoirs of the Bernice P. Bishop Museum* **10**: 1-540, pl. 1-49.

1931. The fishes of Oceania — Supplement 1. *Memoirs of the Bernice P. Bishop Museum* **11**: 311-381.

1933. The fishes of the families Banjosidae, Lethrinidae, Sparidae, Girellidae, Kyphosidae, Oplegnathidae, Gerridae, Mullidae, Emmelichtyhyidae, Sciaenidae, Sillaginidae, Arripidae, and Enoplosidae collected by the United States Bureau of Fisheries steamer "Albatross," chiefly in Philippine seas and adjacent waters. *United States National Museum Bulletin* **100**(12): 1-465.

FOWLER, H.W. AND BEAN, B.A. 1929. The fishes of the series Capriformes, Ephippiformes, and Squamipennes, collected by the United States Bureau of Fisheries steamer "Albatross," chiefly in Philippine seas and adjacent waters. *United States National Museum Bulletin* **100**(8): 1-352.

GAFFNEY, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates* **2720**: 1-38.

GOLDMAN, J., HILL, L. AND STANBURY, P.J. 1969. Type specimens in the Macleay Museum, University of Sydney. II. Amphibians and reptiles. *Proceedings of the Linnean Society of New South Wales* **93**(3): 427-438.

GOMON, M.F. AND PAXTON, J.R. 1985. A revision of the Odacidae, a temperate Australian-New Zealand labroid fish family. *Indo-Pacific Fishes* **8**: 1-57, pl. 1-6.

GOODWIN, R.E. 1979. The bats of Timor: systematics and ecology. *Bulletin of the American Museum of Natural History* **163**(2): 73-122.

GORDON, G. 1983. Northern Nailtail Wallaby. p. 204. *In* Strahan, R. (ed.), 'Complete book of Australian mammals'. (Angus and Robertson: Sydney). xxi 530 pp.

GRANT, E. 1987. 'Fishes of Australia'. (E.M. Grant: Scarborough). 480 pp.

GREENWAY, J.C. 1967. Family Sittidae. p. 125-149. *In* Paynter, R.A.and Mayr, E. (eds), 'Checklist of birds of the world'. Vol. 12. ix 495 pp. (Museum of Comparative Zoology: Cambridge, Massachusetts).
GREER, A.E. 1974. The generic relationships of the scincid genus *Leiolopisma* and its relatives. *Australian Journal of Zoology Supplementary Series* **31**: 1–67
1979. *Eremiascincus*, a new generic name for some Australian sand swimming skinks (Lacertilia: Scincidae). *Records of the Australian Museum* **32**(7): 321–338
1983. The Australian scincid lizard genus *Calyptotis* de Vis: resurrection of the name, description of four new species, and discussion of relationships. *Records of the Australian Museum* **35**:29–59.
GREER, A.E. AND COGGER, H.G. 1985. Systematics of the reduce-limbed and limbless skinks currently assigned to the genus *Anomalopus* (Lacertilia: Scincidae). *Records of the Australian Museum* **37**(1): 11-54.
GROVES, C.P. 1982. The systematics of tree kangaroos (Dendrolagus; Marsupialia, Macropodidae). *Australian Mammalogy* **5**(3): 157–186.
HAND, S. 1987. A marsupial mosiac. p. 63–65. *In* Hand, S. and Archer, M. (eds), 'The antipodean arc.' (Angus and Robertson: North Ryde). 90 pp.
HARDY, G.S. 1982. Two new generic names for some Australian pufferfishes (Tetraodontiformes: Tetraodontidae), with species' redescriptions and osteological comparisons. *Australian Zoologist* **21**(1): 1–26.
1983. Revision of Australian species of *Torquigener* Whitley (Tetraodontiformes: Tetraodontidae), and two new generic names for Australian puffer fishes. *Journal Royal Society of New Zealand* **13**(1/2): 1–48.
HERRE, A.W. 1953. Check list of Philippine fishes. *United States Department of Interior, Fish and Wildlife Service. Research Report* **20**: 1–977.
HUTCHINS, J.B. 1976. A revision of the Australian frogfishes (Batrachoididae). *Records of the Western Australian Museum* **4**(1): 3–43.
INGRAM, G.J. 1986a. "Thickthorn" and his birds. *Sunbird* **16**(2): 25–32.
1986b. Annals of the Queensland Museum: Bibliography and index to new taxa. *Memoirs of the Queensland Museum* **22**(2): 313–318.
1986c. The writings of Thickthorn. *Wildlife Australia* **23**(1): 6–7.
1986d. Scales, feathers and fur. Vertebrate zoology. p. 151–171, 340–341. *In* Mather, P. (ed.), 'A time for a museum. The history of the Queensland Museum 1862-1986'. *Memoirs of the Queensland Museum* Vol. 24, 366 pp. (Queensland Museum: Brisbane).
1987. Avian type specimens in the Queensland Museum. *Memoirs of the Queensland Museum* **25**(1): 239–254.
1989. *Vanapina lineata* de Vis 1905 is a junior synonym of the New Guinean snake *Toxicocalamus longissimus* Boulenger 1896. *Copeia* **1989**(3): 748–750.
INGRAM, G.J. AND COVACEVICH, J. 1981. Frog and reptile type specimens in the Queensland Museum, with a checklist of frogs and reptiles in Queensland. *Memoirs of the Queensland Museum* **20**(2): 291–306.
1988. Revision of the genus *Lygisaurus* de Vis (Scincidae: Reptilia). *Memoirs of the Queensland Museum* **25**(2): 335–354.
1989. Revision of the genus *Carlia* (Reptilia, Scincidae) in Australia with comments on *Carlia bicarinata* of New Guinea. *Memoirs of the Queensland Museum* **27**(2): 443–490.
INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1963. Opinion 684. Eleven dubious specific names of birds: Suppressed under the plenary powers. *Bulletin of Zoological Nomenclature* **20**(6): 418–420.
IREDALE, T. 1950. 'Birds of Paradise and Bower Birds'. (Georgian House: Melbourne). xii 239pp, 33 pls.
IREDALE, T. AND TROUGHTON, E. LE G. 1934. A check-list of the mammals recorded from Australia. *Memoirs of the Australian Museum* **6**: 1–122.
JOHNSON, C.R. 1971. Revision of the callionymid fishes referable to the genus *Callionymus* from Australian waters. *Memoirs of the Queensland Museum* **16**(1): 103–140.
JOHNSTON, T.H. 1916. Presidential address. *Proceedings of the Royal Society of Queensland* **28**: 1–30.
JONES, G. 1985. Revision of the Australian species of the fish family Leiognathidae. *Australian Journal of Marine and Freshwater Research* **36**(4): 559–613.
JORDAN, D.S. AND SEALE, A. 1906. The fishes of Samoa. Description of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. *Bulletin of the Bureau of Fisheries* **25**: 173–455, pl. 33-53.
KAILOLA, P.J. 1983. *Arius graeffei* and *Arius armiger:* Valid names for two common Australo-Papuan fork-tailed catfishes (Pisces, Ariidae). *Transactions of the Royal Society of South Australia* **107**(3): 187–196.
KEAST, A. 1958. Variation and speciation in the Australian flycatchers (Aves: Muscicapinae). *Records of the Australian Museum* **24**(8): 73–108.
KLUGE, A.G. 1963. The systematic status of certain Australian and New Guinean gekkonid lizards. *Memoirs of the Queensland Museum* **14**(3):77–86.
1967. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Australian Journal of Zoology* **15**(5): 1007–1108.
1974. A taxonomic revision of the family Pygopodidae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **147**: 1–221.
KOHLSTEDT, S.G. 1983. Australian Museums of natural history: Public priorities and scientific initiatives in the 19th century. *Historical Records of Australian Science* **5**(4): 1–29.
KOUMANS, F.P. 1953. 'The fishes of the Indo-Australian Archipelago'. Vol. 10. Gobiodea. xii 423pp. (E.J. Brill: Leiden).
KUITER, R.H. AND RANDALL, J.E. 1981. Three look-alike Indo-Pacific labrid fishes, *Halichoeres margaritaceus, H. nebulosus* and *H. miniatus. Revue Francaise d'Aquariologie* **8**(1): 13–18.
LAURIE, E.M.O. AND HILL, J.E. 1954. 'List of the land mammals of New Guinea, Celebes and adjacent

islands 1758-1952'. (British Museum: London). 175 pp, 3 pls, 1 map.

LONGMAN, H.A. 1921. A new genus of fossil marsupials. *Memoirs of the Queensland Museum* 7(2): 63-80, pl. 4-7.

1924. Some Queensland fossil vertebrates. *Memoirs of the Queensland Museum* 8(1): 16-28, pl. 1-4.

LOVERIDGE, A. 1948. New Guinean reptiles and amphibians in the Museum of Comparative Zoology and United States National Museum. *Bulletin of the Museum of Comparative Zoology* 101(2): 305-430.

MACK, G. 1956. The Queensland Museum. *Memoirs of the Queensland Museum* 13(2): 107-124, pl. 3.

MACK, G. AND GUNN, S.B. 1953. De Vis' types of Australian snakes. *Memoirs of the Queensland Museum* 13(1): 58-70.

MACLEAY, W. 1884. Census of Australian snakes with descriptions of two new species. *Proceedings of the Linnean Society of New South Wales* (1)9(3): 548-568. (Published 29 November [Fletcher, 1896]).

MAHONEY, J.A. AND RIDE, W.D.L. 1975. Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968. *Western Australian Museum Special Publication* No. 6. 250 pp.

MARSHALL, L.G. 1981. The families and genera of Marsupialia. *Fieldiana Geology* (ns)8: 1-65.

MARSHALL, T.C. 1964. 'Fishes of the Great Barrier Reef'. (Angus and Robertson: Sydney). xvi 566, 64 bw pls, 72 colour pls.

MATHER, P. 1986. Charles Walter de Vis. p. 313-315. *In* Mather, P.(ed.), 'A time for a museum. The history of the Queensland Museum 1862-1986', *Memoirs of the Queensland Museum* Vol. 24, 366 pp. (Queensland Museum: Brisbane).

MATHEWS, G.M. 1925. 'The birds of Australia'. Supplements 4 & 5, Bibliography of the birds of Australia, parts 1 & 2. (London: H.F. & G. Witherby). viii 149 pp.

1930. 'Systema Avium Australasianarum'. Part 2, p. 427-1048. (British Ornithologists' Union: London).

1934. Nomenclatorial notes. *Ibis* (13)4(3): 640-641.

MAYR, E. 1941. 'List of New Guinea birds'. (American Museum of Natural History: New York). 260 pp, 1 map.

1962a. Eight dubious species of birds: Proposed use of the plenary powers to place these names on the Official Index. *Bulletin of Zoological Nomenclature* 19(1): 23-26.

1962b. Family Grallinidae. p. 159-160. *In* Mayr, E. and Greenway J.C. (eds), 'Checklist of birds of the world'. Vol. 15. x 315 pp. (Museum of Comparative Zoology: Cambridge, Massachusetts).

1967. Subfamily Pachycephalinae. p. 3-51. *In* Paynter, R.A. and Mayr, E. (eds), 'Checklist of birds of the world'. Vol. 12. ix 495 pp. (Museum of Comparative Zoology: Cambridge, Massachusetts).

MAYR, E. AND SERVENTY, D.L. 1938. A review of the genus *Acanthiza* Vigors and Horsfield. *Emu* 38(3): 245-292, pl. 38.

MCCULLOCH, A.R. 1929. A check list of the fishes recorded from Australia. *Memoirs of the Australian Museum* 5(1): 1-144, (2): 145-329, (3): 329-436.

MCCULLOCH, A.R. AND OGILBY, J.D. 1919. Some Australian fishes of the family Gobiidae. *Records of the Australian Museum* 12(10): 193-291, pl. 31-37.

MCKAY, G.M. 1988. Petauridae. *Zoological Catalogue of Australia* 5: 87-97.

MCKEAN, J.L. AND HITCHCOCK, W.B. 1969. The taxonomic status of *Acanthiza katherina* de Vis. *Emu* 69(2): 113.

MEES, G.F. 1964. Geographical variation and distribution of some birds from Western Australia. *Journal of the Royal Society Western Australia* 47(3): 91-96.

MENZIES, J.I. 1987. A taxonomic revision of Papuan *Rana* (Amphibia: Ranidae). *Australian Journal of Zoology* 35(4): 373-418.

MERCHANT, J.C. 1983. Agile Wallaby. p. 242. *In* Strahan, R. (ed.), 'Complete book of Australian mammals'. (Angus and Robertson: Sydney). xxi 530 pp.

MESTON, A. 1889. 'Report of the Government Scientific Expedition to Bellenden-Ker Range upon the flora and fauna of that part of the Colony'. Department of Agriculture: Brisbane). 127 pp.

MILLER, A.H. 1966. An evaluation of the fossil anhingas of Australia. *Condor* 68(4): 315-320.

MOLNAR, R.E. 1982a. A catalogue of fossil amphibians and reptiles in Queensland. *Memoirs of the Queensland Museum* 20(3): 613-633.

1982b. *Pallimnarchus* and other Cenozoic crocodiles in Queensland. *Memoirs of the Queensland Museum* 20(3): 657-673, pl. 1-2.

1982c. Longirostrine crocodilian from Murua (Woodlark), Solomon Sea. *Memoirs of the Queensland Museum* 20(3): 675-685, pl. 1-2.

MOODY, S. 1977. Redescription and taxonomic reassignment of *Calyptoprymnus verecundus* de Vis (Lacertilia). *Copeia* 1977 (4): 759-60.

MUNRO, I.S.R. 1958. The fishes of the New Guinea Region: A check-list of the fishes of New Guinea incorporating records of species collected by the Fisheries Survey Vessel "Fairwind" during the years 1948 to 1950. *Papua and New Guinea Agricultural Journal* 10(4): 97-369.

1960. Handbook of Australian fishes. No. 35. *Fisheries Newsletter* 19(10): 17-20.

1961a. Handbook of Australian fishes. No. 37. *Fisheries Newsletter* 20(2): 17-20.

1961b. Handbook of Australian fishes. No. 39. *Fisheries Newsletter* 20(6): 17-20.

1961c. Handbook of Australian fishes. No. 42. *Fisheries Newsletter* 20(12): 19-22.

MURDY, E.O. 1985. A review of the gobiid fish genera *Exyrias* and *Macrodontogobius*, with description of a new species of *Exyrias*. *Indo-Pacific Fishes* 10: 1-14, pl. 1-2.

NORMAN, J.R. 1934. 'A systematic monograph of the flatfishes (Heterosomata)'. Vol. 1. Psettodidae, Bothidae, Pleuronectidae. v 459 pp. (British Museum (Natural History): London).

OGILBY, J.D. 1910. On new or insufficiently described fishes. *Proceedings of the Royal Society of Queensland* 23(1): 1-55.

OLSON, S.L. 1975. The fossil rails of C.W. de Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* 75(2): 49–54, pl. 4–5.
1977. The identity of the fossil ducks described from Australia by C.W. de Vis. *Emu* 77(3): 127–131, pl. 5–6.
PARKER, S.A. 1984. The identity of *Sericornis tyrannula* de Vis. *Emu* 84(2): 108–110.
POSS, S.G. AND ESCHMEYER, W.N. 1978. Two new Australian velvetfishes, genus *Paraploactis* (Scorpaeniformes: Aploactinidae), with a revision of the genus and comments on the genera and species of the Aploactinidae. *Proceedings of the California Academy of Sciences* 41(18): 401–426.
RAND, A.L. AND GILLIARD, E.T. 1967. 'Handbook of New Guinea birds'. (Weidenfeld and Nicolson: London), x 612 pp, 76 bw pls, 5 colour pls.
RANDALL, H.A. AND ALLEN, G.R. 1977. A revision of the damselfish genus *Dascyllus* (Pomacentridae) with the description of a new species. *Records of the Western Australian Museum* 31(9): 349–385.
RANDALL, J.E. 1956. A revision of the surgeon fish genus *Acanthurus*. *Pacific Science* 10(2): 159–235.
RANDALL, J.E. AND BEN-TUVIA, A. 1983. A review of the groupers (Pisces: Serranidae: Ephinephelinae) of the Red Sea, with description of a new species of *Cephalopholis*. *Bulletin of Marine Science* 33(2): 373–426.
RANDALL, J.E. AND STROUD, G.J. 1985. On the varidity of the mugiloidid fish *Parapercis robinsoni* Fowler. *Japanese Journal of Ichthyology* 32(1): 93–99.
RANDALL, J.E. AND WHITEHEAD, P.J.P. 1985. *Epinephelus cyanopodus* (Richardson), a senior synonym of *E. hoedtii* (Bleeker), and comparison with related *E. flavocaeruleus* (Lacepede). *Cybium* 9(1): 29–39, pl. 1–2.
REINHART, R.H 1976. Fossil sirenians and desmostylids from Florida and elsewhere. *Bulletin of the Florida State Museum., Biological Sciences* 20(4): 187–300.
RICH, P.V. AND VAN TETS, G.F. 1981. The fossil pelicans of Australasia. *Records of the South Australian Museum* 18(13): 235–264.
1982. Fossil birds of Australia and New Guinea: Their biogeographic, phylogenetic, and biostratigraphic input. p. 235–384. *In* Rich, P.V. and Thompson, E.M. (eds), 'The fossil vertebrate record of Australasia'. (Monash Offset Printing Unit: Clayton). 759 pp.
RICH, P.V., VAN TETS, G.F., AND MCEVEY, A.R. 1982. Pleistocene records of *Falco berigora* from Australia and the identity of *Asturaetus furcillatus* de Vis (Aves: Falconidae). *Memoirs of the Queensland Museum* 20(3): 687–693.
RICH, P.V., VAN TETS, G.F., RICH, T.H.V., AND MCEVEY, A.R. 1987. The Pliocene and Quaternary flamingoes of Australia. *Memoirs of the Queensland Museum* 25(1): 207–225.
RIDE, W.D.L. 1964. A review of Australian fossil marsupials. *Journal of the Royal Society of Western Australian* 47(4): 97–131
RUSSELL, B.C. 1983. 'Annotated checklist of the coral reef fishes in the Capricorn-Bunker Group Great Barrier Reef Australia'. (Great Barrier Reef Marine Park Authority: Townsville). 184 pp.
1988. Revision of the labrid fish genus *Pseudolabrus* and allied genera. *Records of the Australian Museum. Supplement* 9: 1–77.
SALOMONSEN, F. 1967. Family Meliphagidae. p. 338-450. *In* Paynter, R.A. and Mayr, E. (eds), 'Checklist of birds of the world'. Vol. 12. ix 495 pp. (Museum of Comparative Zoology: Cambridge, Massachusetts).
SATO, T. 1978. A synopsis of the sparoid fish genus *Lethrinus*, with the description of a new species. *Bulletin of the University Museum, University of Tokyo* 15: 1–70.
SCARLETT, R.J. 1969. On the alleged Queensland moa, *Diornis queenslandiae* de Vis. *Memoirs of the Queensland Museum* 15(3): 207–212, pl. 15.
SCHODDE, R. 1978. The identity of five type-specimens of New Guinean birds. *Emu* 78(1): 1–6
SCHULTZ, L.P. 1966. Addenda. p. 147–165. *In* Schultz, L.P., Woods, L.P. and Lachner, E.A., Fishes of the Marshall and Marianas Islands. Vol. 3. Families from Kraemeriidae through Antennariidae. *United States National Museum Bulletin* 202: 1–176, pl. 124–148.
SCOTT, F., PARKER, F., AND MENZIES, J.I. 1977. A checklist of the amphibians and reptiles of Papua New Guinea. *Wildlife in Papua New Guinea* No. 77/3, 18 pp.
SCOTT, T.D. 1959. Notes on Western Australian fishes, No. 1. *Transactions of the Royal Society of South Australia* 82: 73–91.
SERVENTY, D.L. 1950. Taxonomic trends in Australian ornithology — with special reference to the work of Gregory Mathews. *Emu* 49(4): 257–267.
SHARPE, R.B. 1895. Aves. *Zoological Records* 31: Aves 1–55.
SHIMIZU, T. AND YAMAKAWA, T. 1979. Review of the squirrelfishes (subfamily Holocentrinae: order Beryciformes) of Japan. *Japanese Journal of Ichthyology* 26(2): 109–147.
SMITH-VANIZ, W.F. 1976. The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae). *Academy of Natural Sciences of Philadelphia. Monograph* No. 19, 196 pp.
1987. The saber-toothed blennies, tribe Nemophini (Pisces: Blenniidae): an update. *Proceedings of the Academy of Natural Sciences of Philadelphia* 139:1–52.
SMITH-VANIZ, W.F. AND SPRINGER, V.G. 1971. Synopsis of the tribe Salariini, with description of five new genera and three new species (Pisces: Blenniidae). *Smithsonian Contributions to Zoology* No. 73, 72 pp.
SPRINGER, V.G. AND GOMON, M.F. 1975. Revision of the blenniid fish genus *Omobranchus* with descriptions of three new species and notes on other species of the tribe Omobranchini. *Smithsonian Contributions to Zoology* No. 177, 135 pp.
STEPHENSON, W. 1953. Notes on the Australian Stomatopoda (Crustacea) in the collections of the Queensland Museum. *Memoirs of the Queensland Museum* 13(1): 40–49.

STORR, G.M. 1971. The genus Lerista (Lacertilia, Scincidae) in Western Australia. *Journal of the Royal Society of Western Australia* 54(3): 59–75.

1973. List of Queensland birds. *Western Australian Museum Special Publication*. No. 5, 177 pp.

1978. The genus *Egernia* (Lacertilia, Scincidae) in Western Australia. *Records of the Western Australian Museum* 6(2): 147–187.

1981. The genus *Furina* in Western Australia. *Records of the Western Australian Museum* 9(2): 119–123.

TATE, G.H.H. 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Bulletin of the American Museum of Natural History* 97(4): 187–430.

1952. Results of the Archbold Expeditions. No. 66. Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. *Bulletin of the American Museum of Natural History* 98(7): 563–616.

TAYLOR, W.R. 1964. Fishes of Arnhem Land. p. 45-307. *In* Specht, R.L. (ed.), 'Records of the American-Australian Scientific Expedition to Arnhem Land'. Vol. 4. Zoology. xvii 533 pp. (Melbourne University Press: Melbourne).

THICKTHORN, OR DE VIS, C.W., OR DEVIS, C.W., see Appendix 2.

THOMSON, J.M. 1954. The Mugilidae of Australia and adjacent seas. *Australian Journal of Marine and Freshwater Research* 5(1): 70–131, pl. 1-2.

TREWAVAS, E. 1977. The sciaenid fishes (Croakers or Drums) of the Indo-West-Pacific. *Transactions of the Zoological Society of London* 33(4): 253–541.

TROUGHTON, E. LE G. 1925. A revision of the genera Taphozous and Saccolaimus (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. *Records of the Australian Museum* 14(4): 313–341, pl. 47–48.

TURNER, S. 1982. A catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum* 20(3): 599–611.

1986. Vertebrate palaeontology in Queensland. *Earth Sciences History* 5(1): 50–65.

TURNER, S. AND WADE, M.J. 1986. The record in the rocks. Geology. p. 129–149, 337–340. *In* Mather, P. (ed.), 'A time for a museum. The history of the Queensland Museum 1862-1986'. *Memoirs of the Queensland Museum* Vol. 24, 366 pp. (Queensland Museum: Brisbane).

VARI, R.P. 1978. The terapon perches (Percoidei, Teraponidae). A cladistic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* 159(5): 175–340.

VAN DYCK, S. (this volume). *Belideus gracilis* - soaring problems for an old de Vis glider. *Memoirs of the Queensland Museum*.

VAN TETS, G.F. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* de Vis. *Transactions of the Royal Society of South Australia* 98(4): 213–224.

VAN TETS, G.F. AND RICH, P.V. 1980. A review of the de Vis fossil pigeons of Australia. *Memoirs of the Queensland Museum* 20(1): 89–93.

(this volume). An evaluation of de Vis' fossil birds. *Memoirs of the Queensland Museum*.

WALKOM, A.B. 1914. 'The Royal Society of Queensland. Index to papers in Volumes I to XXV inclusive'. (Royal Society of Queensland: Brisbane). 18 pp.

1916. Note on *Nilssonia mucronatum* (de Vis). *Memoirs of the Queensland Museum* 5: 233-232, pl. 24.

WATTS, C.H.S. AND ASLIN, H.J. 1981. 'The rodents of Australia'. (Angus and Robertson: Sydney). viii 321 pp. 16 pls.

WEBER, M. AND DE BEAUFORT, L.F. 1929. 'The fishes of the Indo-Australian Archipelago', Vol. 5. Acanthini, Allotriognathi, Heterosomata, Berycomorphi, Percomorphi. xiv 458 pp. (E.J. Brill:Leiden).

1931. 'The fishes of the Indo-Australian Archipelago'. Vol. 6. Percomorphi (continued). xii 448 pp. (E.J. Brill: Leiden).

WHITLEY, G.P. 1929. Studies in ichthyology. No. 3. *Records of the Australian Museum* 17(3): 101–143, pl. 30-34.

1948. Some founders of Australian fish science. *Australian Museum Magazine* 9(7): 242–246

1964. Presidential address. A survey of Australian ichthyology. *Proceedings of the Linnean Society of New South Wales* 89(1): 11–127.

WHITTELL, H.M. 1954. 'The literature of Australian birds: a history and a bibliography of Australian ornithology'. (Paterson Brokensha: Perth). *166 pp*, 788 pp, 32 pls.

WOODS, J.T. 1958. The extinct marsupial genus Palorchestes Owen. *Memoirs of the Queensland Museum* 13(4): 177–193.

1960. The genera Propleopus and Hypsiprymnodon and their position in the Macropodidae. *Memoirs of the Queensland Museum* 13(5): 199–212.

1968. The identity of the extinct marsupial genus *Nototherium* Owen. *Memoirs of the Queensland Museum* 15(2): 111–116, pl. 13–14.

FIG. 1. Left humerii of *Palvaranus brachialis* and *Varanus giganteus*. De Vis apparently did his own drawings. His palaeontological papers, unlike his other papers, were usually excellently illustrated. This has undoubtedly helped his reputation in that discipline. If the original fossils were subsequently lost, there still were the illustrations to go by. This lithograph appeared in de Vis (1885ao), where he described the fossil bones of the gian t lizard, *Notiosaurus dentatus* Owen. However, when he presented the paper earlier at the Royal Society on 13 March, he (1885af) thought the fossil represented a new genus and species, *Palvaranus brachialis*.

FIG. 2. MacGregor's Bird of Paradise. In the British journal *Ibis*, de Vis (1897a) described a new genus and species, *Macgregoria pulchra*, for this new bird of paradise. Sir William MacGregor had sent him three specimens that had been collected on Mt Scratchley between 11000 and 12200 feet, British New Guinea. The specimen illustrated was sent to England by de Vis to Dr P.L. Sclater for the lithograph for the paper. The specimen is now in the British Museum (Natural History); the other two are in the Queensland Museum (Ingram, 1987).

APPENDIX 1. NEW TAXA DESCRIBED BY CHARLES WALTER DE VIS.

The following is a list of all de Vis's taxa that I have found in his papers and articles listed in Appendix 2. After each taxon, de Vis's reference is cited, then a modern identification of the name-bearing specimen/s, and then a reference to who identified it/them. By giving an identity and identifier, I do not in any way suggest that these are correct and final. There will be debate about some of the identities for many years to come. I have not listed *nomina nuda* of which there are many: they are best left in obscurity. However, some of the names are arguably valid. Also, some of the names I have accepted have barely a description. The decision to accept has not been easy; the conditions for what is an indication are vague and skimpy in Section 13 of *International Code of Zoological Nomenclature.* If you do not find my decision acceptable, then use the next available use of the name, which, if there is one, is indicated after the reference in Appendix 2. Also, I have not listed names that have been cited by various authors as having been proposed by de Vis but were never published by him. These names properly take the authorship of the people who cited the names. Early fish workers are the main offenders when citing cabinet names or names from unpublished manuscripts of de Vis's (for example, Ogilby, 1910). However, this kind of offence has happened within other groups (Ingram, 1987).

TAXON	DE VIS	IDENTITY	IDENTIFIER
FOSSIL TAXA			
Plantae			
mucronatum, Pterophyllum	1911a:2	*Nilssonia mucronatum*	Walkom (1916)
Vermes			
berneyi, Nereites	1911b:12	Trace fossil	P. Jell (pers. comm.)
Pisces			
incussidens, Hybodus	1911d:18	*Hybodus ? incussidens*	Turner (1982)
Reptilia			
ampla, Pelocomastes	1897d:6	Testudines indeterminate	Gaffney (1981)
antiqua, Chelymys	1897d:4	Testudines indeterminate	Gaffney (1981)
arata, Chelymys	1897d:5	Chelidae	Gaffney (1981)
australiensis, Trionyx	1894h:125	Trionychidae	Gaffney (1981)
brachialis, Palvaranus (Fig. 1)	1885af:5	*Megalania prisca*	(1)
dirus, Varanus	1889as:98	*Megalania prisca*	Molnar (1982a)
emeritus, Varanus	1889as:98	*Varanus emeritus*	Molnar (1982a)
insculpta, Chelodina	1897d:5	*Chelodina*	Gaffney (1981)
murua, Chelone	1905b:30	Marine turtle	Molnar (1982c)
Pallimnarchus (2)	1885az:3	*Pallimnarchus*	Molnar (1982b)
Palvaranus (Fig. 1)	1885af:5	*Megalania*	(1)
papuensis, Gavialis	1905b:31	"*Gavialis*" *papuensis*	Molnar (1982c)
Pelocomastes	1897d:6	Testudines indeterminate	Gaffney (1981)
pollens, Pallimnarchus (2)	1885az:3	*Pallimnarchus pollens*	Molnar (1982b)
uberrima, Chelymys	1897d:3	Chelidae	Gaffney (1981)
Aves			
alacer, Necrastur	1892c:439	*Harpyopsis?*	Rich and van Tets (1982)
Archaeocycnus	1905a:11	Anatidae	Rich and van Tets (1982)
Asturaetus	1905a:6	*Falco*	Rich *et al. (1982)*
bifrons, Metapteryx	1892c:453	*Dromaius novaehollandiae*	Rich and van Tets (1982)
brachialis, Uroaetus	1889du:162	Buteoninae	Rich and van Tets (1982)
Chosornis	1889al:55	*Progura*	van Tets (1974)
conditus, Ibis	1905a:10	*Ocyplanus proeses*	Rich *et al. (1987)*
effluxus, Tribonyx	1892c:439	*Tribonyx mortierii mortierii*	Olson (1975)
effodiata, Nyroca	1905a:15	*Phaps chalcoptera/histrionica*	van Tets and Rich (1980)
elapsa, Anas	1888ba:1281	*Aythya australis*	Olson (1977)
exhumata, Biziura	1889al:57	*Biziura lobata*	Olson (1977)
eyrensis, Nettapus	1905a:16	*Anas castanea*	Olson (1977)
furcillatus, Asturaetus	1905a:6	*Falco berigora*	Rich *et al. (1982)*

gallinacea, Progura	1888ax:4	*Progura gallinacea*	van Tets (1974)
gorei, Palaeolestes	1911c:15	Not a bird?	van Tets and Rich (this volume)
gracilipes, Anas	1905a:14	*Anas castanea*	Olson (1977)
gracilipes, Dromaius	1892c:445	*Dromaius novaehollandiae*	Rich and van Tets (1982)
gracilis, Baza	1905a:7	*Accipiter*	van Tets and Rich (this volume)
grandiceps, Pelecanus	1905a:16	*Pelecanus conspicillatus*	Rich and van Tets (1981)
gregorii, Phalacrocorax	1905a:18	Phalacrocoracidae, Anhingidae *Ardeidae*	Rich and van Tets (1982)
lacertosus, Taphaetus	1905a:4	Gypaetinae?	Rich and van Tets (1982)
lacustris, Archaeocycnus	1905a:11	Anatidae	Rich and van Tets (1982)
laticeps, Plotus	1905a:17	*Anhinga laticeps*	Rich and van Tets (1982)
Lithophaps	1891k:121	*Phaps*	van Tets and Rich (1980)
mackintoshi, Porphyrio	1892c:440	*Tribonyx mortierii mortierii*	Olson (1975)
Metapteryx	1892c:453	*Dromaius*	Rich and van Tets (1982)
minor, Xenorhynchopsis	1905a:10	*Xenorhynchopsis minor*	Rich *et al.* (1987)
nanus, Chenopis	1905a:13	Anatidae	Rich and van Tets (1982)
nanus, Xenorhynchus	1888ba:1287	*Ciconia? nana*	Rich and van Tets (1982)
Necrastur	1892c:437	*Harpyopsis?*	Rich and van Tets (1982)
nobilis, Palaeopelargus	1892c:442	*Progura gallinacea*	van Tets (1974)
Ocyplanus	1905a:8	*Ocyplanus*	Rich *et al.* (1987)
Palaeopelargus	1892c:441	*Progura*	van Tets (1974)
parvus, Plotus	1888ba:1286	*Microcarbo melanoleucos*	Miller (1966)
patricius, Dromaius	1888ba:1290	*Dromaius novaehollandiae*	Rich and van Tets (1982)
peralata, Gallinula	1892c:440	*Tribonyx mortierii mortierii*	Olson (1975)
praeteritus, Chosornis	1889al:55	*Progura gallinacea*	van Tets (1974)
prior, Fulica	1888ba:1285	*Fulica atra*	Olson (1975)
proavus, Pelicanus	1892c:444	*Pelecanus proavus*	Rich and van Tets (1981)
proeses, Ocyplanus	1905a:8	*Ocyplanus proeses*	Rich *et al.* (1987)
proevisa, Leucosarcia	1905a:8	*Phaps chalcoptera/histrionica*	van Tets and Rich (1980)
Progura	1888ax:4	*Progura*	van Tets (1974)
queenslandiae, Dinornis	1884ah:27	*Pachyornis elephantopus*	Scarlett (1969)
reclusa, Nyroca	1888ba:1292	*Aythya australis*	Olson (1977)
reperta, Nyroca	1888ba:1292	*Aythya australis*	Olson (1977)
reperta, Porphyrio	1888ba:1283	*Tribonyx mortierii mortierii*	Olson (1975)
robusta, Nyroca	1888ba:1278	*Anas superciliosa*	Olson (1977)
strenua, Anas (Nettium)	1905a:15	*Anas castanea*	Olson (1977)
strenuipes, Gallinula	1888ba:1284	*Tribonyx mortierii mortierii*	Olson (1975)
subtenuis, Platalea	1892c:443	Not rallid	Olson (1975)
Taphaetus	1891l:123	Buteoninae	Rich and van Tets (1982)
tibialis, Xenorhynchopsis	1905a:10	*Xenorhynchopsis tibialis*	Rich *et al.* (1987)
ulnaris, Lithophaps	1891k:122	*Phaps chalcoptera/histrionica*	van Tets and Rich (1980)
validipes, Pelicanus	1894f:21	*Pelecanus conspicillatus*	Rich and van Tets (1981)
validipinnis, Dendrocygna	1888ba:1282	*Biziura lobata*	Olson (1977)
vetustus, Phalacrocorax	1905a:22	Phalacrocoracidae, Anhingidae	Rich and van Tets (1982)
Xenorhynchopsis	1905a:9	*Xenorhynchopsis*	Rich *et al.* (1987)
Mammalia			
aevorum, Synaptodon	1888bb:6	Probably not determinable	Ride (1964)
agilis, Ornithorhynchus	1885ah:2	*Ornithorhynchus anatinus*	Archer, Plane and Pledge (1978)
angustidens, Phascolomys	1891o:243	?*Lasiorhinus angustidens*	Dawson (1983)
Archizonurus	1889at:109	Marsupialia *incertae sedis*	Mahoney and Ride (1975)
australe, Chronozoon	1883be:395	Sirenia	Reinhart (1976)
Brachalletes	1883ak:8	Diprotodontidae	Marshall (1981)
brevirostris, Halicore	1905b:30	Dugongidae	Mahoney and Ride (1975)
celer, Prochaerus (3)	1886j:6	*Thylacoleo carnifex*	Archer and Dawson (1982)

charon, Sthenomerus	1883ap:15	Diprotodontidae	Mahoney and Ride (1975)
Chronozoon	1883be:395	Sirenia	Reinhart (1976)
dunense, Nototherium	1888ac:v	*Euryzygoma dunense*	Longman (1921)
dryas, Halmaturus	1895c:109	*Macropus (Prionotemnus) dryas*	Bartholomai (1975)
Euowenia	1891e:v	*Euowenia*	Marshall (1981)
faunus, Macropus	1895c:127	*Macropus faunus*	Bartholomai (1966)
grata, Owenia	1887l:6	*Euowenia grata*	Hand (1987)
indra, Halmaturus	1895c:112	*Wallabia indra*	Bartholomai (1976)
ingens, Koalemus	1889at:106	Diprotodontidae	Bartholomai (1968)
Koalemus (4)	1889ak:4	Diprotodontidae	Bartholomai (1968)
magister, Macropus	1895c:120	*Macropus magister*	Bartholomai (1966)
notabilis, Pseudochirus	1889at:113	*Kooboor notabilis*	Archer (1977)
odin, Halmaturus	1895c:111	unidentifiable	Bartholomai (1966)
oreas, Sthenurus	1895c:96	*Sthenurus oreas*	Bartholomai (1963)
oscillans, Triclis	1888ad:2	*Propleopus oscillans*	Woods (1960)
Owenia	1887l:6	*Euowenia*	Marshall (1981)
pales, Sthenurus	1895c:94	*Sthenurus pales*	Bartholomai (1963)
palmeri, Brachalletes	1883ak:8	Probably not determinable	Ride (1964)
pan, Macropus	1895c:124	*Macropus (Osphranter) pan*	Bartholomai (1975)
parvus, Palorchestes	1895c:84	*Palorchestes parvus*	Woods (1958)
prior, Sarcophilus	1883at:189	? *Vombatus prior*	Bartholomai and Marshall (1973)
Prochaerus (3)	1886j:6	*Thylacoleo*	Archer and Dawson (1982)
procuscus, Cuscus	1889at:111	Thylacoleonid?	Archer (1981)
Protemnodontidae	1883av:221	Macropodidae	Marshall (1981)
robusta, Euowenia	1891n:160	*Nototherium inerme*	Woods (1968)
rostralis, Thylacinus	1893c:v	*Thylacinus rostralis*	Dawson (1982)
securus, Archizonurus	1889at:109	Marsupialia *incertae sedis*	Mahoney and Ride (1975)
Simoprospus	1907a:4	*Zygomaturus*	Marshall (1981)
siva, Halmaturus	1895c:113	*Macropus (Prionotemnus) agilis siva*	Bartholomai (1975)
Sthenomerus	1883ap:15	Diprotodontidae	Marshall (1981)
Synaptodon	1888bb:6	Macropodidae	Marshall (1981)
thor, Halmaturus	1895c:102	*Macropus (Prionotemnus) thor*	Bartholomai (1975)
Triclis	1888ad:2	*Propleopus*	Longman (1924)
vinceus, Halmaturus	1895c:100	*Troposodon minor*	Bartholomai (1967)
vishnu, Halmaturus	1895c:114	*Wallabia indra*	Bartholomai (1976)
RECENT TAXA			
Crustacea			
miersii, Lysiosquilla	1882m:321	*Lysiosquilla maculata*	Stephenson (1953)
Araneae			
piscatorum, Nephila maculata	1911h:167	*Nephila maculata*	Bonnet (1958)
Pisces			
achates, Callionymus	1883ai:620	*Callionymus calauropomus*	Johnson (1971)
acutirostris, Therapon	1884bg:398	*Mesopristes argenteus*	Vari (1978)
aetatevarians, Scatophagus	1884cb:456	*Selenotoca multifasciata*	Taylor (1964)
albigena, Choerops	1885ac:876	*Choerodon albigena*	Grant (1987)
amabilis, Genyoroge	1884bu:145	*Lutjanus adetti*	Allen and Talbot (1985)
amabilis, Glypidodon	1884ae:452	*Glyphidodontops leucopomus*	Allen (1975)
amabilis, Platyglossus	1885ac:885	*Platyglossus amabilis*	McCulloch (1929)
annulatus, Gobius	1884cd:688	*Amblygobius albimaculatus*	Koumans (1953)
apicalis, Pomacentrus	1885ac:874	*Stegastes apicalis*	Allen and Emery (1985)
argentea, Equula	1884cc:542	*Leiognathus decorus*	Jones (1985)
argenteus, Autisthes	1884bg:398	*Terapon puta*	Vari (1978)
arion, Amphiprion	1884ae:450	*Amphiprion melanopus*	Allen (1975)
armatus, Mulloides	1884cb:458	*Mulloidichthys samoensis*	Fowler (1933)

armiger, Arius	1884ae:454	*Arius armiger*	Kailola (1983)
asina, Equula	1884cc:544	*Leiognathus fasciatus*	Jones (1985)
aurifer, Cossyphus	1884bu:146	*Lepidaplois vulpinus*	McCulloch (1929)
auriga, Caranx	1884cc:539	*Caranx oblongus*	Herre (1953)
aurora, Chaetodon	1884cb:453	*Chaetodon ulietensis*	Burgess (1978)
Autisthes	1884bg:398	*Terapon*	Vari (1978)
axillaris, Corvina	1884cc:538	*Argyrosomus hololepidotus*	Trewavas (1977)
axillaris, Gobiodon	1884ae:448	*Gobiodon verticalis*	Fowler (1928)
bankiensis, Trachycephalus	1884ae:456	*Caracanthus unipinna*	de Beaufort and Briggs (1962)
barbatus, Pelor	1884cc:547	*Inimicus caledonicus*	Eschmeyer *et al.* (1979)
belemnites, Salarias	1884cd:695	*Salarias chrysospilos belemnites (5)*	Whitley (1964)
bellona, Tetraroge	1884cb:460	*Centropogon australis*	McCulloch (1929)
brevipinnis, Heptadecanthus	1885ac:872	*Acanthochromis polyacanthus*	Herre (1953)
caloundra, Apistus	1885aw:3	*Apistops caloundra*	Grant (1987)
calvus, Salarias	1884cd:697	*Salarias irroratus*	McCulloch (1929)
canina, Corvina	1884cc:538	*Johnius vogleri*	Trewavas (1977)
carbonaria, Girella	1883aw:283	*Girella tricuspidata?*	Fowler (1933)
carpentariae, Engraulis	1882l:320	*Stolephorus carpentariae*	Grant (1987)
cavifrons, Eleotris	1884cd:693	*Carassiops compressus*	McCulloch (1929)
cavifrons, Homodemus	1884bg:396	*Maccullochella macquariensis*	McCulloch (1929)
cinerea, Synaptura	1883aw:288	*Synaptura nigra*	Whitley (1929)
cives, Caranx	1884cc:540	*Caranx speciosus*	Weber and de Beaufort (1931)
Cleidopus	1882n:367	*Cleidopus*	McCulloch (1929)
cobra, Ophichthys	1884ae:455	*Leiuranus semicinctus*	Fowler (1928)
coeca, Thalassophryne	1884cc:546	*Batrachomoeus dubius*	Hutchins (1976)
comes, Corvina	1884cc:538	*Johnius belangerii*	Trewavas (1977)
concinna, Percis	1884cc:546	*Parapercis nebulosa*	Randall and Stroud (1985)
concolor, Choerops	1885ac:876	*Choerodon cyanodus*	G. Allen (pers. comm.)
concolor, Eleotris	1884cd:692	*Mogurnda mogurnda adspersus*	McCulloch (1929)
concolor, Gobius	1884cd:689	*Exyrias puntang*	Murdy (1985)
convexus, Mugil	1885ac:869	*Liza argentea?*	Thomson (1954)
convexus, Pseudambassis	1884bg:394	*Ambassis castelnaui*	Munro (1961a)
coronata, Coris	1885ac:883	*Coris coronata*	McCulloch (1929)
crescens, Eleotris	1885ab:5	*Oxyeleotris lineolatus*	Koumans (1953)
cristata, Amphisile	1885ac:872	*Centriscus cristatus*	Marshall (1964)
cruentatus, Labrichthys	1885ac:879	*Pseudolabrus guentheri*	Russell (1988)
cruentus, Serranus	1884ae:446	*Epinephelus fasciatus*	Randall and Ben-Tuvia (1983)
Dactylophora	1883aw:284	*Dactylophora*	Allen and Heemstra (1976)
decipiens, Salarias	1884cd:694	*Omobranchus punctatus*	Springer and Gomon (1975)
decora, Equula	1884cc:543	*Leiognathus decorus*	Jones (1985)
dispar, Equula	1884cc:542	*Gazza minuta*	Jones (1985)
dux, Labrichthys	1883aw:287	*Pseudolabrus guentheri*	Russell (1988)
ecclipsifer, Caranx	1884cc:541	*Decapterus russelli*	Weber and de Beaufort (1931)
elphinstonensis, Therapon	1884av:57	*Leiopotherapon unicolor*	Vari (1978)
equinus, Platyglossus	1885ac:885	*Halichoeres margaritaceus*	Kuiter and Randall (1981)
expansus, Glyphidodon	1885ac:875	Unidentifiable	G. Allen (pers. comm.)
festivus, Gobius	1884cd:687	*Ctenogobius criniger*	Koumans (1953)
fitzroiensis, Synaptura	1882l:319	*Synaptura nigra*	Whitley (1929)
flava, Teuthis	1884cb:462	*Teuthis lineatus*	Herre (1953)
flavescens, Gobius	1884cd:689	*Stigmatogobius javanicus*	Koumans (1953)
flavidus, Gobiodon	1884ae:449	*Gobiodon rivulatus*	Fowler (1928)
flavipinnis, Pseudoscarus	1885ac:886	*Scarus ghobban*	Choat and Randall (1986)
flavirosea, Mesoprion	1884ae:446	*Lutjanus boutton*	Allen and Talbot (1985)

frenatus, Pomacentrus	1885ac:874	*Dischistodus perspicillatus*	Allen (1975)
furcatus, Salarias	1884cd:696	*Omobranchus rotundiceps rotundiceps*	Springer and Gomon (1975)
furtivus, Salarias	1885al:3	*Omobranchus rotundiceps rotundiceps*	Springer and Gomon (1975)
furvus, Salarias	1884cd:696	*Salarias fasciatus*	Herre (1953)
fuscus, Pseudoscarus	1885ac:887	*Scarus globiceps*	Choat and Randall (1986)
galeatus, Salarias (6)	1884bu:147	*Omobranchus anolius*	Springer and Gomon (1975)
galeatus, Salarias (6)	1885al:3	*Omobranchus anolius*	Springer and Gomon (1975)
geometricus, Serranus	1884bu:144	*Epinephelus fasciatus*	Randall and Ben-Tuvia (1983)
germanus, Chaetodon	1884cb:454	*Chaetodon pelewensis*	Burgess (1978)
gibbosus, Teuthis	1884cb:461	*Siganus corallinus*	Fowler and Bean (1929)
gloriamaris, Cleidopus	1882n:368	*Cleidopus gloriamaris*	Russell (1983)
goliath, Oligorus	1882g:??	*Promicrops lanceolatus*	Schultz (1966)
graphicus, Choerops	1885ac:878	*Choerodon graphicus*	Russell (1983)
griseus, Salarias	1884ae:450	*Salarias fasciatus*	Herre (1953)
hamiltoni, Tetraroge	1884cb:460	*Centropogon australis*	McCulloch (1929)
Harpage	1884ae:447	*Harpage*	Fowler (1928)
hasta, Neoniphon	1884cc:537	*Flammeo sammara*	Shimizu and Yamakawa (1979)
helenae, Salarias	1884cd:697	*Omobranchus punctatus*	Springer and Gomon (1975)
Hephaestus	1884bg:399	*Hephaestus*	Vari (1978)
Herops	1884bg:392	*Kuhlia*	Weber and de Beaufort (1929)
Homodemus	1884bg:395	*Maccullochella*	McCulloch (1929)
humilis, Dules	1884bg:396	*Kuhlia munda*	Weber and de Beaufort (1929)
humilis, Eleotris	1884cd:690	*Carassiops compressus*	McCulloch (1929)
imperialis, Lethrinus	1884bu:146	*Lethrinus chrysostomus*	Sato (1978)
inornata, Julichthys	1885ac:884	*Julichthys inornatus*	McCulloch (1929)
inornatus, Gobiodon	1884ae:449	*Gobiodon citrinus*	Fowler (1928)
insularum, Tetrodon	1884ae:456	*Tetractenos hamiltoni*	Hardy (1983)
Julichthys	1885ac:884	*Julichthys*	McCulloch (1929)
junonis, Priacanthus	1884bg:392	*Priacanthus macracanthus?*	Weber and de Beaufort (1929)
laevis, Tetrodon	1884ae:456	*Marilyna pleurostricta*	Hardy (1982)
laticeps, Eleotris	1884cd:692	*Glossogobius giuris*	Akihito and Meguro (1975)
latro, Cossyphus	1885ac:878	*Lepidaplois latro*	McCulloch (1929)
Leme	1883aw:286	*Taenioides*	Koumans (1953)
lichen, Aploactis	1884cb:461	*Paraploactis trachyderma*	Poss and Eschmeyer (1978)
lineata, Torresia	1885ac:881	*Choerodon lineatus*	Whitley (1964)
lineatus, Gobiodon	1884ae:449	*Gobiodon rivulatus*	Fowler (1928)
lineatus, Petroscirtes	1884cd:698	*Meiacanthus lineatus*	Smith-Vaniz (1987)
longibarba, Exocaetus	1884ae:454	*Exocoetus longibarba*	Munro (1958)
longicauda, Apogonichthys	1884bg:395	*Glossamia aprion aprion?*	Munro (1960)
longicauda, Eleotris	1884cd:691	*Butis butis (7)*	Koumans (1953)
longispina, Equula	1884cc:542	*Leiognathus leuciscus*	Jones (1985)
luctuosus, Homalogrystes	1882n:369	*Epinephelus cyanopodus*	Randall and Whitehead (1985)
lupus, Salarias	1885al:3	*Petroscirtes lupus*	Smith-Vaniz (1976)
maculatus, Labrichthys	1885ac:881	*Pseudolabrus guentheri*	Russell (1988)
maculosus, Heptadecanthus	1885ac:873	*Acanthochromis polyacanthus*	Herre (1953)
marginalis, Gobius	1884cd:686	*Bathygobius fuscus*	Akihito and Meguro (1980)
marginalis, Mugil	1885ac:870	*Mugil cephalus*	Thomson (1954)

mars, Serranus	1884bg:390	*Cephalopholis mars*	Munro (1961b)
masterii, Regalecus	1892f:110	*Regalecus glesne*	McCulloch (1929)
mentalis, Girella	1883aw:284	*Girella tricuspidata*	Fowler (1933)
mimus, Eleotris	1884cd:690	*Mogurnda mogurnda adspersus*	McCulloch (1929)
mordax, Leme	1883aw:286	*Taenioides cirratus?*	Koumans (1953)
mortoniensis, Pleuronectes	1882n:370	*Pseudorhombus arsius*	Norman (1934)
munda, Herops	1884bg:392	*Kuhlia munda*	Weber and de Beaufort (1929)
murrayensis, Pseudojulis	1885ac:882	*Halichoeres miniatus*	Kuiter and Randall (1981)
mysticalis, Serranus	1884bg:390	*Epinephelus mysticalis*	Munro (1961c)
naja, Ophichthys	1884ae:455	*Myrichthys colubrinus*	Fowler (1928)
nasutus, Mugil	1883ai:621	*Squalomugil nasutus*	Taylor (1964)
nebulosum, Onar	1885ac:875	*Pseudochromis fuscus*	McCulloch (1929)
Nesiotes	1884ae:453	*Pseudochromis*	Fowler (1931)
niger, Amblyopus	1884cd:698	*Leme purpurascens*	McCulloch (1929)
nigricauda, Genyoroge	1884bg:391	*Lutjanus fulvus*	Allen and Talbot (1985)
nigripes, Chaetodon	1884cb:453	*Chaetodon citrinellus*	Burgess (1978)
nigripinnis, Pseudambassis	1884bg:393	*Ambassis nigripinnis*	Munro (1961a)
niomatus, Pomacentrus (8)	1884ae:451	*Pomacentrus inornatus*	Fowler (1931)
nitens, Centropogon	1884cb:459	*Notesthes robusta*	McCulloch (1929)
notata, Plagusia	1883aw:288	*Paraplagusia guttata*	Weber and de Beaufort (1929)
notatus, Pomacentrus	1884ae:451	*Pomacentrus pavo*	Munro (1958)
novaebritanniae, Rhynchichthys	1884ae:447	*Flammeo argenteus*	Shimizu and Yamakawa (1979)
nudigena, Labrichthys	1885ac:881	*Halichoeres trimaculatus*	Russell (1988)
olivaceus, Choerops	1885ac:876	*Choerodon cyanodus*	G. Allen (pers. comm.)
Onar	1885ac:875	*Pseudochromis*	Herre (1953)
onyx, Pomacentrus	1884ae:451	*Dascyllus melanurus*	Randall and Allen (1977)
ornatus, Crossorhinus	1883aw:289	*Orectolobus ornatus*	Russell (1983)
ornatus, Lethrinus	1884cb:458	*Lethrinus nebulosus*	Fowler (1933)
ovalis, Equula	1884cc:543	*Leiognathus splendens*	Jones (1985)
pallidus, Glypidodon	1884ae:452	*Glyphidodontops glaucus*	Allen (1975)
pallidus, Pseudambassis	1884bg:393	*Ambassis agassizi*	Allen and Burgess (pers. comm.)
pauper, Gobius	1884cd:687	*Gobius pauper*	McCulloch (1929)
pauper, Salarias	1884cd:695	*Salarias fasciatus*	Herre (1953)
perguttatus, Serranus	1884ae:445	*Cephalopholis argus*	Herre (1953)
perporosus, Aristeus	1884cd:694	*Melanotaenia duboulayi*	Crowley *et al.* (1986)
perpulcher, Choerops	1885ac:877	*Choerodon cephalotes*	McCulloch (1929)
plebaeius, Scolopsis	1884bg:400	*Scolopsis plebaeius*	McCulloch (1929)
princeps, Gobius	1884cd:685	*Gobius princeps*	McCulloch (1929)
procaranx, Caranx	1884cc:540	*Selaroides leptolepis*	Herre (1953)
profunda, Equula	1884cc:544	*Secutor ruconius*	Jones (1985)
profundior, Helotes	1884bg:397	*Pelates sexlineatus?*	Vari (1978)
profundus, Pomacentrus	1885ac:873	Unidentifiable	G. Allen (pers. comm.)
punctatus, Atherinichthys	1885ac:869	*Craterocephalus mugiloides*	Crowley and Ivantsoff (1988)
punctatus, Platyglossus	1885ac:885	*Platyglossus punctatus*	McCulloch (1929)
punctularum, Gobiosoma	1884ae:449	*Scartelaos viridis*	Koumans (1953)
purpurascens, Leme	1884cd:698	*Leme purpurascens*	McCulloch (1929)
purpurascens, Nesiotes	1884ae:453	*Pseudochromis purpurascens*	Fowler (1931)
quandranus, Scatophagus	1884cb:455	*Scatophagus argus*	Taylor (1964)
queenslandiae, Micropteryx	1884cc:541	*Atule kalla*	Herre (1953)
queenslandiae, Porichthys	1882n:370	*Halophryne queenslandiae*	Hutchins (1976)
regia, Genyoroge	1884bu:145	*Lutjanus sebae*	Allen and Talbot (1985)
rex, Labrichthys	1885ac:880	*Pseudolabrus guentheri*	Russell (1988)
robustus, Eleotris	1884cd:692	*Culius robustus*	Whitley (1964)
rosea, Harpage	1884ae:448	*Harpage rosea*	Fowler (1928)
rubriniger, Upeneoides	1884cb:458	*Upeneichthys lineatus*	Ben-Tuvia (1986)
rudis, Apogon	1884bg:395	*Gronovichthys rudis*	Munro (1960)

sanguinolentus, Trochocopus	1883aw:287	*Trochocopus sanguinolentus*	McCulloch (1929)
semeremis, Platycephalus	1883aw:285	*Platycephalus haackeri?*	McCulloch (1929)
semimaculata, Dactylophora	1883aw:284	*Dactylophora nigricians*	Allen and Heemstra (1976)
serotinus, Enoplosus	1911g:29	*Enoplosus armatus*	Fowler (1933)
sexlineatus, Labrichthys	1885ac:880	*Pseudolabrus guentheri*	Russell (1988)
simplex, Apogon	1884bg:394	*Gronovichthys opercularis?*	Munro (1960)
simplex, Equula	1884cc:544	*Leiognathus splendens*	Jones (1985)
specularis, Polynemus	1883aw:285	*Polynemus multiradiatus*	Scott (1959)
specularis, Scolopsis	1882n:369	*Scolopsis specularis*	McCulloch (1929)
sphynx, Holacanthus	1884cb:457	*Holacanthus flavissimus*	Fowler and Bean (1929)
spinosior, Therapon	1884bg:397	*Amniataba percoides*	Vari (1978)
splendens, Gerres	1884bg:400	*Gerres splendens*	McCulloch (1929)
splendens, Mugil	1885ac:871	*Liza splendens*	McCulloch (1929)
stigmaticus, Gobius	1884cd:686	*Waiteopsis stigmaticus*	Whitley (1964)
strenua, Sphyraena	1883aw:287	*Sphyraena obtusata*	McCulloch (1929)
stricticeps, Percis	1884cc:545	*Parapercis xanthozona*	Cantwell (1964)
strigatus, Naseus	1884cc:539	*Zebrasoma veliferum*	Herre (1953)
strigipinnis, Pseudoscarus	1885ac:886	*Scarus globiceps?*	Choat and Randall (1986)
subfasciatus, Serranus	1884bg:389	*Epinephelus subfasciatus*	McCulloch (1929)
sublineata, Genyoroge notata	1884bg:391	*Lutjanus quinquelineatus*	Allen and Talbot (1985)
sublineatus, Salarias	1884cd:695	*Salarias fasciatus*	Herre (1953)
subniger, Pomacentrus	1885ac:873	*Stegastes nigricans*	Allen and Emery (1985)
tenuiceps, Heteroscarus	1885ac:883	*Odax acroptilus*	Gomon and Paxton (1985)
teuthopsis, Teuthis	1884cb:462	*Siganus corallinus*	Fowler and Bean (1929)
tigris, Cybium	1884cc:545	*Scomberomorus semifasciatus*	Collette and Russo (1984)
townleyi, Chaetodon	1884cb:454	*Parachaetodon ocellatus*	Burgess (1978)
Trachycephalus	1884ae:455	*Caracanthus*	de Beaufort and Briggs (1962)
trifasciatus, Pomacentrus	1884ae:452	*Dascyllus aruanus*	Randall and Allen (1977)
tulliensis, Hephaestus	1884bg:399	*Hephaestus fuliginosus*	Vari (1978)
unimaculatus, Choerops	1885ac:877	*Choerodon olivaceus*	McCulloch (1929)
ventralis, Julis	1885ac:884	*Thalassoma ventrale*	Whitley (1964)
venustus, Choerops	1884bu:147	*Choerodon venustus*	Russell (1983)
vestitus, Tetraroge	1884ae:446	*Gymnapistus vestitus*	Fowler (1931)
viperidens, Salarias	1884cd:697	*Petroscirtes variabilis*	Smith-Vaniz (1976)
viridipinnis, Serranus	1884bu:144	*Epinephelus grammatophorus?*	Munro (1961c)
watkinsoni, Gobius	1884cd:685	*Bathygobius fuscus*	Koumans (1953)
zebra, Acanthurus	1884ae:447	*Acanthurus triostegus*	Randall (1956)
ziczac, Pseudojulis	1885ac:882	*Halichoeres scapularis*	McCulloch (929)
Amphibia			
fenestrata, Hyla	1884bs:128	*Mixophyes fasciolatus*	Corben and Ingram (1987)
irrorata, Hyla	1884bs:128	*Litoria caerulea*	Ingram and Covacevich (1981)
lineatus, Limnodynastes	1884ab:3	*Limnodynastes peronii*	Boulenger (1885)
nobilis, Hyla	1884bs:129	*Rana daemeli*	Menzies (1987)
olivaceus, Limnodynastes	1884ap:66	*Limnodynastes convexiusculus*	Cogger *et al.* (1983)
peninsulae, Hyla	1884bs:130	*Litoria nasuta*	Cogger *et al.* (1983)
rothii, Hyla	1884ap:66	*Litoria rothii*	Cogger *et al.* (1983)
Reptilia			
ambigua, Hinulia	1888ah:817	*Eremiascincus richardsonii*	Greer (1979)
angulata, Denisonia	1905f:51	*Hoplocephalus bitorquatus*	Mack and Gunn (1953)
bancrofti, Denisonia	1911f:23	*Furina ornata*	Storr (1981)
bancrofti, Pseudelaps	1911f:25	*Pseudonaja nuchalis*	Cogger *et al.* (1983)
blackmanni, Heteropus	1885ai:168	*Carlia munda*	Ingram and Covacevich (1989)
branchialis, Amphibolurus	1884au:55	*Physignathus lesueurii*	Cogger *et al.* (1983)

brevicauda, Diporophora	1884bb:99	*Diporiphora bilineata*	Cogger *et al.* (1983)
bungana, Egernia	1888ah:814	*Egernia major*	Cogger *et al.* (1983)
caeruleocauda, Mocoa	1892a:98	*Emoia caeruleocauda*	Loveridge (1948)
Calyptoprymnus	1905f:46	*Cordylus*	Moody (1977)
Calyptotis	1885al:3	*Calyptotis*	Greer (1983)
cincta, Oedura	1888ah:810	*Oedura marmorata*	Bustard (1970)
cuneiceps, Emoa	1890l:498	*Emoia cuneiceps*	Scott *et al.* (1977)
crucifer, Micropechis	1905f:52	*Elaps lacteus*	Ingram and Covacevich (1981)
delicata, Mocoa	1888ah:820	*Lampropholis delicata*	Greer (1974)
domina, Hinulia	1888ah:818	*Sphenomorphus tenuis*	G.J. Ingram (this work)
dunensis, Trophidechis	1911l:21	*Dasypeltis scabra*	Cogger (1966)
englishi, Homolepida	1890l:499	*Lygosoma muelleri*	de Rooij (1915)
fenestrata, Denisonia	1905f:50	*Glyphodon tristis*	Mack and Gunn (1953)
flaviventer, Calyptotis	1885al:3	*Calyptotis scutirostrum*	Greer (1983)
foliorum, Lygisaurus	1884az:77	*Lygisaurus foliorum*	Ingram and Covacevich (1988)
fracticolor, Oedura	1884bv:160	*Oedura marmorata*	Cogger *et al.* (1983)
frontalis, Ophioscincus	1888ah:823	*Anomalopus frontalis*	Cogger *et al.* (1983)
frontalis, Platurus	1905f:48	*Laticauda colubrina*	Cogger *et al.* (1983)
guttata, Pseudechis	1905f:49	*Pseudechis guttatus*	Cogger *et al.* (1983)
inermis, Grammatophora	1888ah:812	*Amphibolurus nuchalis*	Cogger *et al.* (1983)
kentii, Neospades	1889be:238	*Myron richardsonii*	Mack and Gunn (1953)
laevis, Nephrurus (9)	1886g:??	*Nephrurus laevis*	Boulenger (1887)
lateralis, Heteropus	1885ai:168	*Carlia pectoralis pectoralis*	Ingram and Covacevich (1989)
latizonatus, Rhynchelaps	1905f:49	*Vermicella annulata*	Cogger *et al.* (1983)
lauta, Egernia	1888ah:813	*Egernia luctuosa*	Storr (1978)
lentiginosus, Anomalopus	1888ah:823	*Anomalopus leuckartii*	Greer and Cogger (1985)
lineata, Vanapina	1905f:49	*Toxicocalamus longissimus*	Ingram (1989)
longicauda, Egernia	1888ah:816	*Tiliqua gerrardii*	Cogger *et al.* (1983)
louisiadensis, Gymnodactylus	1892a:98	*Cyrtodactylus louisiadensis*	Cogger *et al.* (1983)
Lygisaurus	1884az:77	*Lygisaurus*	Ingram and Covacevich (1988)
Macrops	1884bb:97	*Amphibolurus*	Cogger *et al.* (1983)
maculatus, Heteropus	1885ai:169	*Carlia longipes*	Ingram and Covacevich (1989)
mestoni, Perochirus	1890d:1035	*Gehyra variegata*	Kluge (1963)
monilis, Oedura	1888ah:810	*Oedura monilis*	Cogger *et al.* (1983)
mortonensis, Pseudechis	1911f:24	*Pseudechis guttata*	Mack and Gunn (1953)
mundus, Heteropus	1885ai:172	*Carlia munda*	Ingram and Covacevich (1989)
Myophila	1884az:77	*Carlia*	Cogger *et al.* (1983)
nasalis, Distira	1905f:48	*Disteira major*	Cogger *et al.* (1983)
Neospades	1889be:238	*Myron*	Cogger *et al.* (1983)
nigra, Denisonia	1905f:50	*Drysdalia coronoides*	Coventry and Rawlinson (1980)
nuchalis, Diporophora	1884bb:98	*Diporiphora australis*	Cogger *et al.* (1983)
nuchalis, Macrops	1884bb:97	*Amphibolurus nuchalis*	Cogger *et al.* (1983)
orientalis, Miculia	1889ab:160	*Lerista orientalis*	Cogger *et al.* (1983)
ornata, Diporophora	1884bb:99	*Diporiphora australis*	Cogger *et al.* (1983)
ornatus, Hoplocephalus	1884bc:100	*Denisonia devisi*	Cogger *et al.* (1983)
pallidiceps, Emoa	1890l:497	*Emoia pallidiceps pallidiceps*	Brown (1953)
pectoralis, Heteropus	1884bz:6	*Carlia pectoralis pectoralis*	Ingram and Covacevich (1989)
pentalineata, Diporophora	1884bb:99	*Diporiphora bilineata*	Cogger *et al.* (1983)
plebeia, Delma	1888ah:825	*Delma plebeia*	Kluge (1974)
propinqua, Denisonia frontalis	1905f:51	*Suta suta*	Cogger *et al.* (1983)
queenslandiae, Tropidophurus	1890d:1034	*Tropidophorus queenslandiae*	Cogger *et al.* (1983)
revelata, Denisonia	1911f:22	*Hoplocephalus bitorquatus*	Mack and Gunn (1953)
robusta, Furina	1905f:51	*Simoselaps bertholdi*	Cogger *et al.* (1983)
rostralis, Denisonia	1911f:23	*Simoselaps warro*	Cogger *et al.* (1983)

rostralis, Heteropus	1885ai:171	*Carlia rostralis*	Ingram and Covacevich (1989)
rubricatus, Heteropus	1885ai:170	*Carlia longipes*	Ingram and Covacevich (1989)
rugosa, Egernia	1888ah:815	*Egernia rugosa*	Cogger *et al.* (1983)
spectabilis, Mocoa	1888ah:819	*Lampropholis challengeri*	Cogger *et al.* (1983)
sulcans, Hoplocephalus	1884bo:5	*Hoplocephalus bitorquatus*	Mack and Gunn (1953)
sutherlandi, Brachysoma	1884bt:139	*Pseudonaja nuchalis*	Cogger *et al.* (1983)
taenicauda, Diplodactylus	1886k:169	*Diplodactylus taenicauda*	Kluge (1967)
tigrina, Hinulia	1888ah:817	*Sphenomorphus tigrinus*	Cogger *et al.* (1983)
timidus, Ablepharus	1888ah:824	*Lerista muelleri*	Storr (1971)
tincta, Delma	1888ah:824	*Delma tincta*	Kluge (1974)
tryoni, Oedura	1884au:54	*Oedura tryoni*	Cogger *et al.* (1983)
Vanapina	1905f:48	*Toxicocalamus*	Ingram (1989)
verecundus, Calyptoprymnus	1905f:46	*Cordylus cordylus*	Moody (1977)
vertebralis, Heteropus	1888ah:821	*Carlia mundivensis*	Cogger *et al.* (1983)
vestigiatus, Hoplocephalus	1884bo:5	*Demansia vestigiatus*	(10)
vivax, Myophila	1884az:77	*Carlia vivax*	Ingram and Covacevich (1989)
warro, Cacophis	1884bt:139	*Simoselaps warro*	Cogger *et al.* (1983)
wilesmithii, Pseudechis	1911f:24	*Oxyuranus scutellatus*	Mack and Gunn (1953)
zellingi, Silubosaurus	1884au:53	*Egernia stokesii*	Cogger *et al.* (1983)
Aves			
albicauda, Rhipidura	1897c:375	*Rhipidura brachyrhyncha devisi*	Mayr (1941)
amabilis, Ptilonopus	1880i:172	*Ptilonopus regina*	Ingram (1986a)
Amalocichla	1892a:95	*Amalocichla*	Mayr (1941)
animosa, Climacteris	1895c:i	*Cormobates affinis*	Mathews (1934)
armiti, Paecilodryas	1894d:101	*Heteromyias albispecularis armiti*	Mayr (1941)
auricularis, Rhipidura	1890g:59	*Rhipidura albolimbata auricularis*	Mayr (1941)
belfordi, Melirrhophetes	1890g:60	*Melidectes belfordi belfordi*	Rand and Gilliard (1967)
bella, Charmosynopsis	1901d:pl.8	*Charmosyna pulchella bella*	Mayr (1941)
bivittata, Petroeca	1897c:376	*Petroica bivittata bivittata*	Mayr (1941)
brevicauda, Drymaedus	1894d:103	*Amalocichla incerta brevicauda*	Mayr (1941)
brevirostris, Drymaoedus	1897c:386	*Drymodes superciliaris brevirostris*	Mayr (1941)
brunnea, Gerygone	1897c:378	*Sericornis papuensis papuensis*	Mayr (1941)
canescens, Merula	1894d:105	*Turdus poliocephalus canescens*	Rand and Gilliard (1967)
caniceps, Poecilodryas	1897c:377	*Pachycephala schlegelli obscurior*	Mayr (1941)
cervinus, Acrocephalus	1897c:386	*Timeliopsis griseigula fulviventris*	Salomonsen (1967)
citrypura, Pachycephala	1880e:140	*Pachycephala pectoralis*	Ingram (1986a)
Cnemophilus	1890g:61	*Cnemophilus*	Mayr (1941)
collaris, Melirrhophetes	1894d:103	*Melidectes ochromelas batesi*	Mayr (1941)
concinna, Rhipidura	1892a:94	*Rhipidura albolimbata auricularis*	Mayr (1941)
Corymbicola	1889ai:600	*Prionodura*	Mathews (1930)
cuicui, Zosterops	1897c:384	*Microeca flavovirescens cuicui*	Mayr (1941)
cuneata, Geocichla	1889bf:242	*Zoothera lunulata cuneata*	Ford (1983)
Daphoenositta	1897c:380	*Daphoenositta*	Mayr (1941)
discolor, Colluricincla	1890g:60	*Colluricincla megarhyncha discolor*	Rand and Gilliard (1967)
divaga, Monarcha	1897c:374	*Chaetorhynchus pauensis*	Mayr (1941)
Eulacestoma	1894d:102	*Eulacestoma*	Mayr (1941)
fretorum, Pachycephala	1889be:237	*Pachycephala lanioides fretorum*	Mees(1964)
fuliginosa, Oreospiza	1897c:388	*Oreostruthus fuliginosus fuliginosus*	Rand and Gilliard (1967)
fusca, Acanthochoera	1897c:383	*Melidectes fuscus fuscus*	Mayr (1941)
goodenoviensis, Ninox	1890g:58	*Ninox theomacha goldii*	Mayr (1941)
griseiceps, Sittella	1894d:102	*Neositta papuensis albifrons*	Greenway (1967)
griseoceps, Micraeca	1894d:101	*Microeca griseoceps griseoceps*	Mayr (1941)
guisei, Ptilotis	1894d:103	*Ptiloprora guisei guisei*	Rand and Gilliard (1967)
gutturalis, Anthus	1894d:103	*Anthus gutturalis gutturalis*	Mayr (1941)
gutturalis, Sericornis	1889bf:244	*Oreoscopus gutturalis*	Storr (1973)

helenae, Parotia	1897c:390	*Parotia helenae*	Cooper and Forshaw (1977)
humeralis, Ibis (Falcinellus)	1898c:90	*Plegadis falcinellus*	Condon (1975)
insperata, Gerygone	1892a:94	*Gerygone ruficollis insperata*	Mayr (1941)
intermedia, Paradisea	1894d:105	*Paradisea raggiana intermedia*	Rand and Gilliard (1967)
katherina, Acanthiza	1905e:43	*Acanthiza katherina*	McKean and Hitchcock (1969)
kowaldi, Todopsis	1890g:59	*Ifrita kowaldi kowaldi*	Mayr (1941)
lacrimans, Ptilotis	1897c:382	*Meliphaga subfrenata salvadorii*	Salomonsen (1967)
laeta, Alcyone	1894d:100	*Ceyx lepidus solitarius*	Mayr (1941)
laeta, Zosterops	1897c:385	*Microeca papuana*	Mayr (1941)
laetiscapa, Rhipidura	1898c:83	*Rhipidura brachyrhyncha devisi*	Mayr (1941)
leucypura, Gerygone albogularis	1880c:650	*Gerygone olivacea*	Ingram (1986a)
Lobospingus	1897c:389	*Erythrura*	Mayr (1941)
longicauda, Graucalus	1890g:59	*Coracina longicauda longicauda*	Mayr (1941)
loralis, Poecilodryas	1897c:377	*Monachella muelleriana muelleriana*	Mayr (1941)
lorealis, Arses	1895a:i	*Arses telescophthalmus lorealis*	Keast (1958)
lurida, Ninox boobook	1887h:1135	*Ninox novaeseelandiae lurida*	Condon (1975)
Macgregoria (Fig. 2)	1897a:251	*Macgregoria*	Mayr (1941)
macgregoriae, Amblyornis	1890g:60	*Amblyornis macgregoriae macgregoriae*	Mayr (1941)
macgregorii, Cnemophilus	1890g:61	*Cnemophilus macgregorii macgregorii*	Cooper and Forshaw (1977)
maculata, Melipotes	1892a:94	*Melipotes fumigatus fumigatus*	Mayr (1941)
maculiceps, Sarganura	1898c:87	*Melanocharis versteri maculiceps*	Rand and Gilliard (1967)
manayoensis, Rhipidura	1894d:101	*Rhipidura hyperytha castaneothorax*	Mayr (1941)
mariae, Cnemophilus	1894d:104	*Loria loriae loriae*	Mayr (1941)
mestoni, Corymbicola,	1889ai:600	*Prionodura newtoniana*	Mathews (1930)
mestoni, Pachycephala	1905e:44	*Pachycephala pectoralis queenslandica*	Mayr (1967)
minor, Peltops	1894d:100	*Peltops blainvillii*	Mayr (1941)
miranda, Daphoenositta	1897c:380	*Daphoenositta miranda*	Rand and Gilliard (1967)
modesta, Acanthiza	1905e:43	*Acanthiza nana modesta*	Mayr and Serventy (1938)
modesta, Paecilodryas	1894d:101	*Pachycephala modesta modesta*	Rand and Gilliard (1967)
montana, Crateroscelis (11)	1897c:387	Unidentifiable	Mayr (1962a)
monticola, Munia	1897c:387	*Lonchura monticola*	Mayr (1941)
montium, Paramythia	1892a:95	*Paramythia montium montium*	Rand and Gilliard (1967)
moretoni, Malurus	1892a:97	*Malurus alboscapulatus moretoni*	Rand and Gilliard (1967)
murina, Gerygone	1897c:377	*Acanthiza murina*	Mayr (1941)
nanus, Cyclopsittacus	1898c:81	*Opopsitta gulielmiterti suavissima*	Mayr (1941)
Neneba	1897c:384	*Melanocharis*	Schodde (1978)
newtoniana, Prionodura	1883ag:562	*Prionodura newtoniana*	Mathews (1930)
nigrifrons, Rhipidura	1897c:374	*Monarcha guttula*	Mayr (1941)
nigripectus, Symmorphus	1894d:102	*Grallina bruijni*	Mayr (1962b)
nigropectus, Eulacestoma	1894d:102	*Eulacestoma nigropectus nigropectus*	Mayr (1941)
nitida, Poecilodryas	1897c:376	*Monarcha chrysomela praerepta*	Mayr (1941)
obscura, Ptilotis	1897c:383	*Meliphaga obscura obscura*	Salomonsen (1967)
oreas, Rhipidura	1897c:375	*Rhipidura rufiventris gularis*	Mayr (1941)
Oreospiza	1897c:388	*Oreostruthus*	de Vis (1898a)
Oreostruthus	1898a:388	*Oreostruthus*	Mayr (1941)
orientalis, Nasiterna	1898c:81	*Micropsitta bruijnii bruijnii*	Mayr (1941)
orientalis, Ptilopus bellus	1894d:104	*Ptilonopus rivoli bellus*	Mayr (1941)
ornatus, Melirrhophetes	1894d:103	*Melidectes torquatus emilii*	Mayr (1941)
pallida, Micraeca	1884bv:159	*Microeca leucophaea pallida*	Keast (1958)
pallidipes, Zosterops	1890g:60	*Zosterops griseotincta pallidipes*	Mayr (1941)
papuensis, Acanthiza	1894d:102	*Sericornis papuensis papuensis*	Mayr (1941)
papuensis, Merula	1890g:60	*Turdus poliocephalus papuensis*	Rand and Gilliard (1967)
Paramythia	1892a:95	*Paramythia*	Mayr (1941)
perstriata, Ptilotus	1898c:86	*Ptiloprora perstriata perstriata*	Rand and Gilliard (1967)

phasiana, Rhipidura	1884bv:158	*Rhipidura phasiana*	Ford (1982)
piperata, Ptilotus	1898c:86	*Rhamphocharis crassirostris piperata*	Mayr (1941)
prasina, Neneba	1897c:384	*Melanocharis striativentris*	Schodde (1978)
Prionodura	1883ag:561	*Prionodura*	Mathews (1930)
Ptiloprora	1894d:103	*Ptiloprora*	Mayr (1941)
pulchra, Macgregoria (Fig. 2)	1897a:251	*Macgregoria pulchra pulchra*	Cooper and Forshaw (1977)
punctata, Micraeca	1894d:101	*Microeca papuana*	Mayr (1941)
punctatus, Megalurus	1897c:385	*Megalurus timoriensis macrurus*	Mayr (1941)
robusta, Gerygone	1898c:84	*Crateroscelis robusta robusta*	Mayr (1941)
rosaulba, Strepera	1890g:59	*Cracticus lousiadensis*	Mayr (1941)
rufescens, Cracticus	1883ag:562	*Cracticus quoyi rufescens*	Amadon (1951)
Sarganura	1898c:87	*Melanocharis*	Rand and Gilliard (1967)
schistacea, Meliornis (11)	1897c:381	*Ptiloprora plumbea*	Schodde (1978)
sclateriana, Amalocichla	1892a:95	*Amalocichla sclaterina*	Mayr (1941)
sibila, Colluricincla	1888bd:6	*Collurincla boweri*	de Vis (1889bh)
sibisibina, Ptilotis	1897c:381	*Xanthotis flaviventer visi*	Mayr (1941)
sigillata, Paecilodryas	1890g:59	*Peneothello sigillatus sigillatus*	Rand and Gilliard (1967)
sigillifer, Lobospingus	1897c:389	*Erythrura trichroa sigillifer*	Mayr (1941)
sororcula, Pachycephala	1897c:380	*Pachycephala schlegelii obscurior*	Mayr (1941)
squamata, Acanthiza	1889bi:248	*Acanthiza reguloides squamata*	Mayr and Serventy (1938)
strenua, Pachycephala	1898c:85	*Pachycephalopsis poliosoma poliosoma*	Mayr (1941)
subcaudalis, Aeluroedus	1897c:390	*Ailuroedus buccoides stonii*	Mayr (1941)
subcyanea, Poecilodryas	1897c:377	*Peneothello cyanus subcyanus*	Mayr (1941)
sudestensis, Eopsaltria	1892a:96	*Pachycephala griseiceps sudestensis*	Mayr (1941)
sudestiensis, Geoffroyus	1890g:58	*Geoffroyus geoffroyi sudestensis*	Mayr (1941)
tyrannula, Sericornis (11)	1905c:42	*Sericornis pyrrhopygius*	Parker (1984)
vicaria, Paecilodryas	1892a:94	*Peneothello bimaculatus vicarius*	Mayr (1941)
vinitinctus, Melithreptus (12)	1884bq:5	*Melithreptus albogularis albogularis*	Salomonsen (1967)
viridiceps, Neopsittacus	1897c:371	*Neopsittacus pullicauda pullicauda*	Mayr (1941)
viridigaster, Oreopsittacus	1898c:81	*Oreopsittacus arfaki grandis*	Mayr (1941)
viridis, Monachella	1894d:101	*Tregellasia leucops albifacies*	Mayr (1941)
Mammalia			
annulicauda, Onychogalea	1884bv:157	*Onychogalea unguifera annulicauda*	Gordon (1983)
aroaensis, Dendrosminthus	1907c:11	*Mallomys rothschildi*	Laurie and Hill (1954)
banfieldi, Uromys	1907b:8	*Melomys cervinipes*	Watts and Aslin (1981)
bennettianus, Dendrolagus (13)	1886c:6	*Dendrolagus bennettianus*	Groves (1982)
Dendrosminthus	1907c:11	*Mallomys*	Tate (1951)
frontalis, Dromicia	1887h:1134	*Acrobates pygmaeus frontalis*	Iredale and Troughton (1934)
fulvus, Dendrolagus	1887s:7	*Dendrolagus lumholtzi*	Groves (1982)
fumosus, Taphozous	1905d:37	*Taphozous australis*	Troughton (1925)
gazella, Halmaturus	1884bl:5	*Thylogale stigmatica coxenii*	Tate (1952)
gillespiei, Phascolomys	1901e:pl.9	*Lasiorhinus krefftii*	Dawson (1983)
gracilis, Belideus	1883aa:ii	*Petaurus norfolcensis*	Van Dyck (this volume)
jardinii, Halmaturus	1884bl:5	*Macropus agilis jardinii*	Merchant (1983)
mongan, Pseudochirus	1887h:1130	*Pseudocheirus herbertensis*	McKay (1988)
nudicluniatus, Taphozous	1905d:39	*Taphozous saccolaimus*	Goodwin (1979)
pannietensis, Cephalotes	1905d:36	*Dobsonia pannietensis*	Bergmans (1979)
temporalis, Halmaturus	1884br:111	*Thylogale stigmatica wilcoxi*	Iredale and Troughton (1934)

FOOTNOTES: (1). De Vis (1885ao) changed his mind and did not use *Palvaranus brachialis* for his specimens. Instead, he identified them with *Notiosaurus dentatus* Owen. Molnar (1982a), listed *N. dentatus*, including de Vis's specimens, as *Megalania prisca*.

(2). In de Vis (1885az), the generic name was misspelt as *'Pallinnarchus'*. In the intended version of the paper, de Vis (1886b) corrected the spelling to *'Pallimnarchus'*.

(3). In de Vis (1886j), the name given is *Prochaerus ceter*. Subsequently, in the intended paper, de Vis (1887c) corrected the species name to *'celer'*. Also in this paper, the generic name is spelt as either *'Prochaerus'* and *'Prochoerus'*. Mahoney and Ride (1975) concluded that *'Prochaerus'* was the correct spelling.

(4). In de Vis (1889ak), the original spelling was *'Koallmus'*. De Vis (1889at) corrected this to *'Koalemus'* (see Mahoney and Ride, 1975).

(5). Whitley (1964) gave no justification for this subspecific status. Smith-Vaniz and Springer (1971) allocated the name-bearing specimen to the genus *Istiblennus* but gave no specific allocation.

(6). '. . . twice described as new; impossible to determine if the same or different specimens formed basis of descriptions' (Springer and Gomon, 1975).

(7). Koumans (1953) included the de Vis name in the synonymy of *Butis butis* (Hamilton Buchanan) but cited Ogilby (1910) as the author.

(8). Jordan and Seale (1906) said that *'niomatus'* was a printer's error and that *'inornatus'* was correct.

(9). In the intended paper (de Vis, 1886k), the name is misspelt as *'levis'*. As Boulenger (1887), and the original spelling in the abstract (de Vis, 1886g), indicated *'laevis'* was correct.

(10). Cogger *et al*. (1983) gave *Demansia atra* (Macleay) as the name for this taxon and listed *Hoplocephalus vestigiatus* (de Vis, 1884bt) as a junior synonym. However, the latter name originally appeared in de Vis (1884bo), which predates *Diemenia atra Macleay*, 1884 (13 September vs 29 November, respectively).

(11). Suppressed for the purposes of priority but not homonymy by the International Commission on Zoological Nomenclature (1963) after a submission by Mayr (1962a). This was a strange decision and a doubtful submission (Schodde, 1978; Parker, 1984; Ingram, 1987).

(12). The original spelling was *'viniticnta'* (de Vis, 1884bq). This is obviously a misprint. De Vis (1884bv) corrected it to *'vinitinctus'*.

(13). Originally spelt as *'bennetianus'* (de Vis, 1886c). De Vis (1886s, 1887a) gave the correct spelling of *'bennettianus'*. The species was named in honour of Dr G. Bennett.

APPENDIX 2
PUBLICATIONS OF CHARLES WALTER DE VIS.

The following is a list of all the publications of de Vis, alias 'Thickthorn', alias 'Devis' that I have located. Where available the date of publication is listed after the reference. The dates are taken from the actual articles and papers, but, when these have not been available, I have followed Fletcher (1896) for *Proceedings of the Linnean Society of New South Wales,* Walkom (1916) for *Proceedings of the Royal Society of Queensland* (for the few more exact dates for this journal, I have used Mathews [1930] or de Vis's date of acknowledgement of receipt in his Curator's reports), and Ingram (1986b) for *Annals of the Queensland Museum*. For parliamentary papers, the dates of publication are the earliest the papers were tabled in either House. With newspaper articles, the same article can occur in different newspapers on the same day. Because the *Brisbane Courier* was a morning newspaper I have listed it as the earliest publication in opposition to the *Daily Observer, Evening Observer,* and *Telegraph,* which were evening newspapers. I have agreed with Mahoney and Ride's (1975) argument that the *Abstract of Proceedings of the Linnean Society of New South Wales* satisfies the criteria for publication. I have not given dates of publication for these abstracts except on authority. Mahoney and Ride (1975) have discussed the difficulty of dating them and suggest a procedure; the reader is referred to their work. Also, I have followed them in listing as the earliest the publication of the abstracts in the *Sydney Morning Herald*. Most likely the *Abstract of Proceedings of the Linnean Society of New South Wales* was prior but this rarely can be shown. I have not listed abstracts that are only titles of papers.

1865. Ornithological notes from Manchester. *Zoologist* **23:** 9596-9597 (As 'C.W. Devis').

1868. Notes on the myology of Viverra civetta. *Journal of Anatomy and Physiology* **2:** 207-217. (As 'C.W. Devis').

1870. Elasticity of animal type. *Memoirs read before the Anthropological Society of London.* **3:** 81-105. (As 'C.W. Devis').

1880a. [In Anon.] The black cockatoo. *Queenslander,* January 31, p. 140-141. (As 'Thickthorn').

1880b. [In Anon.] The black cockatoo. *Queenslander,* March 27, p. 403. (As 'Thickthorn').

1880c. The white-throated gerygon. *Queenslander,* May 22, p. 650. (As 'Thickthorn').

1880d. Concerning ghosts. *Queenslander,* June 5, p. 716-717. Republished 1880, *Brisbane Courier,* June 5, p. 3. (As 'Thickthorn').

1880e. Thickheads are very common in Queensland. [In Anon.] *Queenslander,* July 31, p. 140. (As 'Thickthorn').

1880f. The wonga-wonga. *Queenslander,* August 7, p. 172. (As 'Thickthorn').

1880g. Is the Queensland coast rising or sinking? *Queenslander,* November 20, p. 653. Republished 1880, *Brisbane Courier,* November 25, p. 3. (As 'Chas. W. Devis').

1880h. The pardalote. [In Anon.] *Queenslander,* December 11, p. 747. (As 'Thickthorn').

1880i. Tin — historically and geologically considered. *Queenslander,* December 25, p. 812-813. (As 'Chas. W. Devis').
1881a. The upheaval of the Queensland coast. *Brisbane Courier,* January 5, p. 5. (As 'Chas. W. Devis').
1881b. In re hail *Queenslander,* February 12, p. 205. (As 'Chas. W. Devi's).
1881c. [In Anon.] Current notes on natural history. *Queenslander,* March 5, p. 298. (As 'Thickthorn').
1881d. [In Anon.] Double vision. *Queenslander,* April 23, p. 524. (As 'C.W. Devis').
1881e. Notes on zoology. *Queenslander,* April 23, p. 524. Republished 1881, *Brisbane Courier,* April 23, p. 3. (As 'Thickthorn').
1881f. [In Anon.] Magnesium deposits. *Queenslander,* April 30, p. 563. (As 'C.W. Devis').
1881g. About snakes. *Queenslander,* December 10, p. 748-749. Republished 1881, *Brisbane Courier,* December 14, p. 5. (As 'Thickthorn (Chas. W. Devis)').
1882a. Sleeping lizards. *Queenslander,* January 28, p. 108. (As 'C.W. De Vis').
1882b. About marsupials. *Queenslander,* March 18, p. 332-333. (As 'Thickthorn').
1882c. [In Anon.] The Museum. *Telegraph,* May 25, p. 2. Republished 1882, *Brisbane Courier,* May 26, p. 2.
1882d. [In Anon.] The Museum. *Telegraph,* June 7, p. 3. Republished 1882, *Brisbane Courier,* June 8, p. 2.
1882e. [In Anon.] Queensland Museum. *Brisbane Courier,* July 6, p. 3. Republished 1882, *Telegraph,* July 6, p. 6.
1882f. [In Anon.] The Queensland Museum. *Telegraph,* July 7, p. 3. Republished 1882, *Brisbane Courier,* July 8, p. 5.
1882g. Descriptions of three new fishes of Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for July 26, 1882, p.?. Republished 1882, *Southern Science Record* (1)2(8): 189 (Aug.). (Abstract of de Vis, 1882l).
1882h. Description of a species of squill *Lysiosquilla miersii,* from Moreton Bay. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for July 26, 1882, p.?. Republished 1882, *Southern Science Record* (1)2(8): 189 (Aug.). (Abstract of de Vis, 1882m).
1882i. [In Anon.] The Museum. This newspaper cutting is in the Minute Book for the meetings of the Board of Trustees, but I have been unable to locate it in the newspapers. It details the Curator's report, which would have been presented at the meeting of August 2nd. There is the possibility that it was printed but not published.
1882j. [In Anon.] Queensland Museum. *Brisbane Courier,* September 7, p. 5. Republished 1882, *Telegraph,* September 7, p. 2.
1882k. [In Anon.] Queensland Museum. *Brisbane Courier,* October 5, p. 6. Republished 1882, *Telegraph,* October 5, p. 3.
1882l. Description of three new fishes of Queensland. *Proceedings of the Linnean Society of New South Wales* (1)7(3): 318-320 (28 Oct.).
1882m. Description of a species of squill from Moreton Bay. *Proceedings of the Linnean Society of New South Wales* (1)7(3): 321-322 (28 Oct.).
1882n. Descriptions of some new Queensland fishes. *Proceedings of the Linnean Society of New South Wales* (1)7(3): 367-371 (28 Oct.).
1882o. [In Anon.] Queensland Museum. *Brisbane Courier,* November 9, p. 5. Republished 1882, *Telegraph,* November 9, p. 6.
1882p. Description of two new birds of Queensland. [In Anon.] *Sydney Morning Herald,* December 4, p. 11. Republished 1882, *Abstract of Proceedings of the Linnean Society of New South Wales* for November 29, 1882. p. i. Republished 1882, *Southern Science Record* (1)2(12): 296-297 (Dec.). (Abstract of de Vis, 1883ag).
1882q. [In Anon.] Queensland Museum. *Telegraph,* December 6, p. 2. Republished 1882, *Brisbane Courier,* December 7, p. 6.
1882r. On three new fishes from Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for 27 September, 1882, p. i. (Abstract of de Vis, 1882n).
1883aa. Description of a new *Belideus* from northern Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for 27 December, 1882, p. ii. Republished 1883, *Southern Science Record* (1)3(1): 27 (Jan.). (Abstract of de Vis, 1883ah).
1883ab. Two new Queensland fishes. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for 27 December, 1882, p. ii. Republished 1883, *Southern Science Record* (1)3(1): 27 (Jan.). (Abstract of de Vis, 1883ai).
1883ac. [In Anon.] Queensland Museum. *Telegraph,* January 3, p. 2. Republished 1883, *Brisbane Courier,* January 4, p. 5.
1883ad. On remains of an extinct marsupial. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for January 31, 1883, p. ii. Republished 1883, *Southern Science Record* (1)3(2): 64 (Feb.). (Abstract of de Vis, 1883ap).
1883ae. [In Anon.] Queensland Museum. *Brisbane Courier,* February 8, p. 5. Republished 1883, *Telegraph,* February 8, p. 2.
1883af. [In Anon.] Brisbane Museum. *Brisbane Courier,* March 7, p. 5. Republished 1883, *Telegraph,* March 7, p. 2.
1883ag. Description of two new birds of Queensland. *Proceedings of the Linnean Society of New South Wales* (1)7(4): 561-563 (Apr.).
1883ah. Description of a new Belideus from northern Queensland. *Proceedings of the Linnean Society of New South Wales* (1)7(4): 619-620 (Apr.).
1883ai. Description of two new Queensland fishes. *Proceedings of the Linnean Society of New South Wales* (1)7(4): 620-621 (Apr.).
1883aj. On tooth-marked bones of extinct marsupials. [In Anon.] *Sydney Morning Herald,* April 2, p. 8. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for March 28, 1883, p. ii. Republished 1883, *Southern Science*

Record (1)3(4): 119-120 (Apr.). Republished 1883, *Zoologischer Anzeiger* 6(140): 303 (4 Jun.). (Abstract of de Vis, 1883at).

1883ak. "On *Brachalletes palmeri*" an extinct marsupial. [In Anon.] *Sydney Morning Herald*, April 2, p. 8. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for March 28, 1883, p. ii (25 Apr.). Republished 1883, *Southern Science Record* (1)3(4): 120 (Apr.). Republished 1883, *Zoologischer Anzeiger* 6(140): 303 (4 Jun.). (Abstract of de Vis, 1883au).

1883al. [In Anon.] Queensland Museum. This newspaper cutting is in the Minute Book for the meetings of the Board of Trustees, but I have been unable to locate it in the newspapers. It details the Curator's report, which would have been presented at the meeting of April 11th. There is the possibility that it was printed but not published.

1883am. [In Anon.] Brisbane Museum. *Brisbane Courier*, May 2, p. 5. Republished 1883, *Telegraph*, May 2, p. 2.

1883an. Notes on a lower jaw of *Palorchestes azael*. [In Anon.] *Sydney Morning Herald*, June 1, p. 8. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for May 30, 1883, p. i. Republished 1883, *Southern Science Record* (1)3(6): 167 (Jun.). Republished 1883, *Zoologischer Anzeiger* 6(146): 446 (23 Aug.). (Abstract of de Vis, 1883av).

1883ao. [In Anon.] Queensland Museum. *Brisbane Courier*, June 6, p. 3. Republished 1883, *Telegraph*, June 6, p. 3.

1883ap. On remains of an extinct marsupial. *Proceedings of the Linnean Society of New South Wales* (1)8(1): 11-15 (19 Jun.).

1883aq. Appendix X. Circular to Schools of Arts. p. 6. In 'Annual Report of the Trustees of the Queensland Museum for the year 1882'. *Queensland Parliamentary Paper*. (Government Printer: Brisbane). 6 pp. (26 Jun.).

1883ar. Descriptions of new genera and species of fishes. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for June 27, 1883, p. i. Republished 1883, *Southern Science Record* (1)3(7): 190 (Jul.). Republished 1883, *Zoologischer Anzeiger* 6(149): 520 (24 Sep.). (Abstract of de Vis, 1883aw)

1883as. [In Anon.] Queensland Museum. *Brisbane Courier*, July 5, p. 3. Republished 1883, *Telegraph*, July 6, p. 2.

1883at. On tooth-marked bones of extinct marsupials. *Proceedings of the Linnean Society of New South Wales* (1)8(2): 187-190 (17 Jul.).

1883au. On Brachalletes palmeri an extinct marsupial. *Proceedings of the Linnean Society of New South Wales* (1)8(2): 190-193 (17 Jul.).

1883av. Notes on a lower jaw of Palorchestes azael. *Proceedings of the Linnean Society of New South Wales* (1)8(2): 221-224 (17 Jul.).

1883aw. Descriptions of new genera and species of Australian fishes. *Proceedings of the Linnean Society of New South Wales* (1)8(2): 283-289 (17 Jul.)

1883ax. On the myology of the frilled lizard (Chlamydosaurus kingii). [In Anon.] *Sydney Morning Herald*, July 27, p. 7. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for July 25, 1883, p. ii. Republished 1883, *Southern Science Record* (1)3(8): 208 (Aug.). Republished 1883, *Zoologischer Anzeiger* 6(150): 543 (8 Oct.). (Abstract of de Vis, 1883bd).

1883ay. [In Anon.] Queensland Museum. *Brisbane Courier*, August 9, p. 3. Republished 1883, *Telegraph*, August 10, p. 5.

1883az. On a fossil Calvaria. [In Anon.] *Sydney Morning Herald*, August 31, p. 3. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for August 29, 1883, p. ii. Republished 1883, *Zoologischer Anzeiger* 6(152): 591 (5 Nov.). (Abstract of de Vis, 1883be).

1883ba. [In Anon.] Queensland Museum. *Brisbane Courier*, September 6, p. 5. Republished 1883, *Daily Observer*, September 6, p. 2. Republished 1883, *Telegraph*, September 7, p. 3.

1883bb. On a fossil humerus. [In Anon.] *Sydney Morning Herald*, September 29, p. 9. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for September 26, 1883, p. iii. Republished 1883, *Southern Science Record* (1)3(10): 244 (Oct.). Republished 1883, *Southern Science Record* (1)3(11): 263 (Nov.). Republished 1883, *Zoologischer Anzeiger* 6(154): 639 (26 Nov.). (Abstract of de Vis, 1883bf).

1883bc. [In Anon.] Queensland Museum. *Brisbane Courier*, October 4, p. 3. Republished 1883, *Telegraph*, October 4, p. 3. Republished 1883, *Daily Observer*, October 4, p. 3.

1883bd. Myology of Chlamydosaurus kingii. *Proceedings of the Linnean Society of New South Wales* (1)8(3): 300-320, pl. 14-16 (19 Oct.).

1883be. On a fossil Calvaria. *Proceedings of the Linnean Society of New South Wales* (1)8(3): 392-395, pl. 17 (19 Oct.).

1883bf. On a fossil humerus. *Proceedings of the Linnean Society of New South Wales* (1)8(3): 404-408 (19 Oct.).

1883bg. [In Anon.] The Museum. *Brisbane Courier*, November 14, p. 5. Republished 1883, *Telegraph*, November 14, p. 2. Republished 1883, *Daily Observer*, November 14, p. 4.

1883bh. Some fishes of New Britain and the adjoining islands. [In Anon.] *Sydney Morning Herald*, December 1, p. 12. Republished 1883, *Abstract of Proceedings of the Linnean Society of New South Wales* for November 28, 1883, p. ii. Republished 1884, *Zoologischer Anzeiger* 7(160): 103 (18 Feb.). (Abstract of de Vis, 1884ae).

1883bi. [In Anon.] Queensland Museum. *Brisbane Courier*, December 6, p. 5. Republished 1883, *Telegraph*, December 7, p. 6.

1884aa. [In Anon.] Queensland Museum. *Brisbane Courier*, January 10, p. 3. Republished 1884, *Telegraph*, January 10, p. 3. Republished 1884, *Daily Observer*, January 10, p. 2.

1884ab. On some new batrachians from Queensland. [In Anon.] *Sydney Morning Herald*, February 5, p. 3. Republished 1884, *Abstract of Proceedings of the Linnean Society of New South Wales* for January 30, 1884, p. iv, Republished 1884, *Zoologischer Anzeiger* 7(164): 208 (7 Apr.). (Abstract of de Vis, 1884ap).

1884ac. [In Anon.] Queensland Museum. *Brisbane Courier*, February 7, p. 5. Republished 1884, *Telegraph*, February 7, p. 5. Republished 1884, *Daily Observer*, February 8, p. 3.

1884ad. The moa (Dinornis) in Australia. [In Anon.] *Brisbane Courier*, February 13, p. 5. Republished 1884, *Daily Observer*, February 13, p. 4. (Abstract of de Vis, 1884ah).

1884ae. Fishes from South Sea Islands. *Proceedings of the Linnean Society of New South Wales* (1)8(4): 445-457 (21 Feb.).

1884af. [In Anon.] The Museum. *Brisbane Courier*, March 10, p. 5. Republished 1884, *Telegraph*, March 10, p. 3. Republished 1884, *Daily Observer*, March 10, p. 2.

1884ag. Ceratodus post-Pliocene. [In Anon.] *Brisbane Courier*, March 12, p. 5. Republished 1884, *Daily Observer*, March 12, p. 3. (Abstract of de Vis, 1884ai).

1884ah. The moa (Dinornis) in Australia. *Proceedings of the Royal Society of Queensland* 1(1): 23-28, pl. 3-4 (before 25 Jun.).

1884ai. Ceratodus forsteri post-Pliocene. *Proceedings of the Royal Society of Queensland* 1(1): 40-43 (before 25 Jun.).

1884aj. [In Anon.] Queensland Museum. *Telegraph*, April 2, p. 3. Republished 1884, *Brisbane Courier*, April 3, p. 5. Republished 1884, *Daily Observer*, April 3, p. 3.

1884ak. On new Australian lizards. [In Anon.] *Brisbane Courier*, April 9, p. 6. (Abstract of de Vis, 1884aw).

1884al. On a new form of the genus Therapon [In Anon.] *Brisbane Courier*, April 9, p. 6. (Abstract of de Vis, 1884av).

1884am. [In Anon.] The Queensland Museum. *Brisbane Courier*, May 8, p. 6. Republished 1884, *Daily Observer*, May 8, p.2. Republished 1884, *Telegraph*, May 9, p. 5.

1884an. Two new lizards. [In Anon.] *Brisbane Courier*, May 14, p. 5. Republished 1884, *Daily Observer*, May 14, p. 2. (Abstract of de Vis, 1884az).

1884ao. Deglutition in the freshwater snake. [In Anon.] *Brisbane* Courier, May 14, p. 5. Republished 1884, *Daily Observer*, May 14, p. 2. (Abstract of de Vis, 1884ba).

1884ap. On some new batrachians from Queensland. *Proceedings of the Linnean Society of New South Wales* (1)9(1): 65-67 (23 May).

1884aq. [In Anon.] Queensland Museum. *Telegraph*, June 5, p. 5. Republished 1884, *Brisbane Courier*, June 6, p. 5. Republished 1884, *Daily Observer*, June 6, p. 2.

1884ar. Description of a new species of *Hoplocephalus* from the MacKenzie River. [In Anon.] *Brisbane Courier*, June 11, p. 5. Republished 1884, *Daily Observer*, June 11, p. 3. (Abstract of de Vis, 1884bc).

1884as. On new species of Australian lizards. [In Anon.] *Brisbane Courier*, June 11, p. 5. Republished 1884, *Daily Observer*, June 11, p. 3. (Abstract of de Vis, 1884bb)

1884at. On *Perameles bougainvillii, Q. and G.* [In Anon.] *Brisbane Courier*, June 11, p. 5. Republished 1884, *Daily Observer*, June 11, p. 3. (Abstract of de Vis, 1884bd).

1884au. On new Australian lizards. *Proceedings of the Royal Society of Queensland* 1(2): 53-56.

1884av. On a new form of the genus Therapon. *Proceedings of the Royal Society of Queensland* 1(2): 56-57.

1884aw. On an anomalous snake. *Proceedings of the Royal Society of Queensland* 1(2): 58.

1884ax. A possible source of isinglass. *Proceedings of the Royal Society of Queensland* 1(2): 58.

1884ay. Nest of Philemon corniculatus, Lath. *Proceedings of the Royal Society of Queensland* 1(2): 58.

1884az. On new Queensland lizards. *Proceedings of the Royal Society of Queensland* 1(2): 77-78.

1884ba. On deglutition in the fresh-water snake. *Proceedings of the Royal Society of Queensland* 1(2): 82-83.

1884bb. On new species of Australian lizards. *Proceedings of the Royal Society of Queensland* 1(2): 97-100.

1884bc. On a new species of Hoplocephalus. *Proceedings of the Royal Society of Queensland* 1(2): 100, pl. 15.

1884bd. Perameles bougainvillii, Q. & G. *Proceedings of the Royal Society of Queensland* 1(2): 101-102.

1884be. New Australian fishes in the Queensland Museum. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for May 28, 1884, p. ii. Republished 1884, *Zoologischer Anzeiger* 7(173): 432 (4 Aug.). (Abstract of de Vis, 1884bg).

1884bf. [In Anon.] Queensland Museum. *Brisbane Courier*, July 1, p. 5. Republished 1884, *Daily Observer*, July 2, p.2. Republished 1884, *Telegraph*, July 3, p. 2.

1884bg. New Australian fishes in the Queensland Museum. *Proceedings of the Linnean Society of New South Wales* (1)9(2): 389-400 (19 Jul.).

1884bh. On the new Australian fishes in the Queensland Museum. Part II. [In Anon.] *Sydney Morning Herald*, June 27, p.4. Republished 1884, *Abstract of Proceedings of the Linnean Society of New South Wales* for June 25, 1884, p. iv. Republished 1884, *Zoologischer* Anzeiger 7(177): 527 (29 Sep.). (Abstract of de Vis, 1884cb).

1884bi. New fishes in the Queensland Museum. No.3. [In Anon.] *Sydney Morning Herald*, August 2, p. 9 Republished 1884, *Abstract of Proceedings of the Linnean Society of New South Wales* for July 30, 1884, p. iii. Republished 1884, *Zoologischer Anzeiger* 7(178): 550 (6 Oct.). (Abstract of de Vis, 1884cc).

1884bj. [In Anon.] Queensland Museum. *Brisbane Courier*, August 9, p. 6. Republished 1884, *Telegraph*, August 11, p. 2.

1884bk. On new species of Hyla. [In Anon.] *Brisbane Courier*, August 16, p. 5. Republished 1884, *Daily*

Observer, August 16, p. 3. (Abstract of de Vis, 1884bs).
1884bl. On apparently new species of Halmaturus. [In Anon.] *Brisbane* Courier, August 16, p. 5. Republished 1884, *Daily Observer*, August 16, p. 3. (Abstract of de Vis, 1884br).
1884bm. New fishes in the Queensland Museum. No. IV. [In Anon.] *Sydney Morning Herald*, August 29, p. 5. Republished 1884, *Abstract of Proceedings of the Linnean Society of New South Wales* for August 27, 1884, p. iii. Republished 1884, *Zoologischer Anzeiger* 7(180): 598 (3 Nov.). (Abstract of de Vis, 1884cd).
1884bn. [In Anon.] Queensland Museum. *Brisbane Courier*, September 6, p. 5. Republished 1884, *Daily Observer*, September 6, p. 3. Republished 1884, *Telegraph*, September 8, p. 2.
1884bo. Descriptions of new snakes. [In Anon.] *Brisbane Courier*, September 13, p. 5. Republished 1884, *Daily Observer*, September 13, p. 3. (Abstract of de Vis, 1884bt).
1884bp. On new fish from Moreton Bay. [In Anon.] *Brisbane Courier*, September 13, p. 5. Republished 1884, *Daily Observer*, September 13, p. 3. (Abstract of de Vis, 1884bu).
1884bq. Notes on the fauna of the Gulf of Carpentaria. [In Anon.] *Brisbane Courier*, September 13, p. 5. Republished 1884, *Daily Observer*, September 13, p. 3. (Abstract of de Vis, 1884bv).
1884br. On apparently new species of Halmaturus. *Proceedings of the Royal Society of Queensland* 1(3): 107-112 (after Sep.).
1884bs. On new species of Hyla. *Proceedings of the Royal Society of Queensland* 1(3): 128-130 (after Sep.).
1884bt. Descriptions of new snakes with a synopsis of the genus Hoplocephalus. *Proceedings of the Royal Society of Queensland* 1(3): 138-140 (after Sep.).
1884bu. On new fish from Moreton Bay. *Proceedings of the Royal Society of Queensland* 1(3): 144-147 (after Sep.).
1884bv. Notes on the fauna of the Gulf of Carpentaria. *Proceedings of the Royal Society of Queensland* 1(3): 154-160 (after Sep., *vide* Mathews, 1930: 737).
1884bw. New fishes in the Queensland Museum. No. V. [In Anon.] *Sydney Morning Herald*, September, 27, p. 16. Republished 1884, *Abstract of Proceedings of the Linnean Society of New South Wales* for September 24, 1884, p. ii. Republished 1884, *Zoologischer Anzeiger* 7(181): 623 (17 Nov.). (Abstract of de Vis, 1885ac).
1884bx. [In Anon.] Queensland Museum. *Brisbane Courier*, October 4, p.5. Republished 1884, *Daily Observer*, October 4, p. 3. Republished 1884, *Telegraph*, October 6, p. 2.
1884by. [In Anon.] Queensland Museum. *Brisbane Courier*, November 8, p. 5. Republished 1884, *Daily Observer*, November 8, p. 3. Republished 1884, *Telegraph*, November 10, p. 2.
1884bz. A conspectus of the genus Heteropus. [In Anon.] *Brisbane Courier*, November 15, p. 6. Republished 1884, *Daily Observer*, November 15, p. 3. (Abstract of de Vis, 1885ai).
1884ca. On a small whale recently stranded near Southport. [In Anon.] *Brisbane Courier*, November 15, p. 6. Republished 1884, *Daily Observer*, November 15, p. 3. (Abstract of de Vis, 1885aj).
1884cb. New Australian fishes in the Queensland Museum. Part 2. *Proceedings of the Linnean Society of New South Wales* (1)9(3): 453-462 (29 Nov.).
1884cc. New fishes in the Queensland Museum. No.3. *Proceedings of the Linnean Society of New South Wales* (1)9(3): 537-547 (29 Nov.).
1884cd. New fishes in the Queensland Museum. No.4. *Proceedings of the Linnean Society of New South Wales* (1)9(3): 685-698 (29 Nov.).
1884ce. [In Anon.] Queensland Museum. *Brisbane Courier*, December 6, p. 6. Republished 1884, *Daily Observer*, December 6, p. 3. Republished 1884, *Telegraph*, December 9, p. 2.
1885aa. [In Anon.] Queensland Museum. *Brisbane Courier*, January 8, p. 6. Republished 1885, *Telegraph*, January 8, p. 2. Republished 1885, *Daily Observer*, January 8, p. 3.
1885ab. [In Anon.] Queensland Museum. *Brisbane Courier*, February 4, p. 5. Republished 1885, *Daily Observer*, February 4, p. 2. Republished 1885, *Telegraph*, February 5, p. 2.
1885ac. New fishes in the Queensland Museum. No.5. *Proceedings of the Linnean Society of New South Wales* (1)9(4): 869-887 (4 Mar.)
1885ad. [In Anon.] Queensland Museum. *Brisbane Courier*, March 5, p. 6. Republished 1885, *Daily Observer*, March 5, p. 3. Republished 1885, *Telegraph*, March 6, p. 2.
1885ae. A description of a species of *Eleotris*, from Rockhampton. [In Anon.] *Brisbane Courier*, March 14, p. 5. Republished 1885, *Daily* Observer, March 14, p. 3. (Abstract of de Vis, 1885ap).
1885af. Bones of a large extinct lizard. [In Anon.] *Brisbane Courier*, March 14, p. 5. Republished 1885, *Daily Observer*, March 14, p. 3. (Abstract of de Vis, 1885ao).
1885ag. [In Anon.] Queensland Museum. *Brisbane Courier*, April 7, p. 5. Republished 1885, *Telegraph*, April 8, p. 4. Republished 1885, *Daily Observer*, April 8, p. 3.
1885ah. On an extinct monotreme — *Ornithorhynchus agilis*. [In Anon.] *Daily Observer*, April 11, p. 2. Republished 1885, *Brisbane Courier*, April 13, p. 6. Republished in Mahoney and Ride (1975: 185). (Abstract of de Vis, 1885aq).
1885ai. A conspect of the genus Heteropus. *Proceedings of the Royal Society of Queensland* 1(4): 166-173 (May).
1885aj. A whale *(Ziphius layardi, Flower)* recently stranded near Southport. *Proceedings of the Royal Society of Queensland* 1(4): 174, pl. 19 (May).
1885ak. [In Anon.] Queensland Museum. *Brisbane Courier*, May 6, p. 3. Republished 1885, *Daily Observer*, May 6, p. 3. Republished 1885, *Telegraph*, May 7, p. 2.
1885al. On three species of Salarias and on a lizard, apparently hitherto undescribed [In Anon.] *Brisbane*

Courier, May 9, p. 3. Republished 1885, *Daily Observer*, May 9, p. 2. (Abstract of de Vis, 1885ar).

1885am. Report of the Curator to the Trustees of the Queensland Museum. p. 1-14. *In* 'Queensland Museum. (Report of Board of Trustees for the year 1884.)' *Queensland Parliamentary Paper*. (Government Printer: Brisbane). 14pp. Republished in de Vis (1885an).

1885an. Report of the Curator to the Trustees of the Queensland Museum. p. 4-35. *In* 'Report of the Board of Trustees of the Queensland Museum for the year 1884'. *Queensland Parliamentary* Paper. (Government Printer: Brisbane). 35 pp. Reprinted from de Vis (1885am).

1885ao. On bones and teeth of a large extinct lizard. *Proceedings of the Royal Society of Queensland* 2(1): 25-32, pl. 1-3.

1885ap. Description of a species of Eleotris from Rockhampton. *Proceedings of the Royal Society of Queensland* 2(1): 32-33.

1885aq. On an extinct monotreme, Ornithorhynchus agilis. *Proceedings of the Royal Society of Queensland* 2(1): 35-38, pl. 4.

1885ar. On a lizard and three species of Salarias, &c. *Proceedings of the Royal Society of Queensland* 2(1): 56-60

1885as. [In Anon.] Queensland National Museum. *Brisbane Courier*, June 3, p. 6. Republished 1885, *Daily Observer*, June 3, p. 3. Republished 1885, *Telegraph*, June 4, p. 5.

1885at. [In Anon.] Queensland Museum. *Brisbane Courier*, July 13, p. 5. Republished 1885, *Daily Observer*, July 13, p. 3. Republished 1885, *Telegraph*, July 15, p. 2.

1885au. [In Anon.] Queensland Museum. *Brisbane Courier*, August 8, p. 5. Republished 1885, *Daily Observer*, August 8, p. 3. Republished 1885, *Telegraph*, August 11, p. 2.

1885av. [In Anon.] Queensland Museum. *Daily Observer*, September 7, p. 3. Republished 1885, *Brisbane Courier*, September 8, p. 3.

1885aw. Notice of a fish apparently undescribed. [In Anon.] *Brisbane Courier*, October 5, p. 3. Republished 1885, *Daily Observer*, October 5, p. 3. (Abstract of de Vis, 1886a).

1885ax. [In Anon.] Queensland Museum. *Brisbane Courier*, October 5, p. 3. Republished 1885, *Daily Observer*, October 5, p. 3.

1885ay. [In Anon.] Queensland Museum. *Brisbane Courier*, November 7, p. 9. Republished 1885, *Daily Observer*, November 7, p. 6.

1885az. Remains of an extinct saurian. [In Anon.] *Brisbane Courier*, November 9, p. 2-3. Republished 1885, *Daily Observer*, November 9, p. 3. (Abstract of de Vis, 1886b).

1885ba. [In Anon.] Queensland Museum. *Brisbane Courier*, December 7, p. 6. Republished 1885, *Daily Observer*, December 7, p. 3.

1886a. Notice of a fish apparently undescribed. *Proceedings of the Royal Society of Queensland* 2(2): 144-145.

1886b. On remains of an extinct saurian. *Proceedings of the Royal Society of Queensland* 2(2): 181-191, pl. 10-15.

1886c. Notice of an apparently new species of Dendrolagus. [In Anon.] *Brisbane Courier*, January 11, p. 6. Republished 1886, *Daily Observer*, January 11, p. 3. (Abstract of de Vis, 1887a).

1886d. [In Anon.] Queensland Museum. *Brisbane Courier*, January 12, p. 6. Republished 1886, *Daily Observer*, January 12, p. 3.

1886e. [In Anon.] Queensland Museum. *Daily Observer*, February 6, p. 5. Republished 1886, *Brisbane Courier*, February 8, p. 6. Republished 1886, *Telegraph*, February 9, p. 2.

1886f. [In Anon.] Queensland Museum. *Brisbane Courier*, March 8, p. 5. Republished 1886, *Daily Observer*, March 8, p. 2. Republished 1886, *Telegraph*, March 12, p. 5.

1886g. On certain geckos in the Queensland Museum. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for March 31, 1886, p.iii. Republished 1886, *Zoologischer Anzeiger* 9(224): 352. (31 May). (Abstract of de Vis, 1886k).

1886h. [In Anon.] Queensland Museum. *Brisbane Courier*, April 5, p. 5. Republished 1886, *Daily Observer*, April 5, p. 3. Republished 1886, *Telegraph*, April 6, p. 2.

1886i. [In Anon.] Queensland Museum. *Brisbane Courier*, May 10, p. 6. Republished 1886, *Daily Observer*, May 10, p. 2. Republished 1886, *Telegraph*, May 11, p. 2.

1886j. A postpliocene artiodactyle. [In Anon.] *Brisbane Courier*, May 12, p. 6. Republished 1886, *Daily Observer*, May 12, p. 2. Republished in Mahoney and Ride (1975: 186). (Abstract of de Vis, 1887c).

1886k. On certain geckos in the Queensland Museum. *Proceedings of the Linnean Society of New South Wales (2)*1(1): 168-170 (25 May).

1886l. [In Anon.] Queensland Museum. *Brisbane Courier*, June 7, p. 5. Republished 1886, *Daily Observer*, June 7, p. 3.

1886m. [In Anon.] Queensland Museum. *Brisbane Courier*, July 5, p. 6. Republished 1886, *Daily Observer*, July 5, p. 3. Republished 1886, *Telegraph*, July 6, p. 2.

1886n. Annual report to the Trustees of the Queensland Museum. p. 1- 2. *In* 'Queensland Museum. (Report of Board of Trustees for the year 1885)'. *Queensland Parliamentary Paper*. (Government Printer: Brisbane). 14 pp.

1886o. On a femur, probably by *Thylacoleo*. [In Anon.] *Brisbane Courier*, August 9, p. 6. Republished 1886, *Daily Observer*, August 9, p. 2. (Abstract of de Vis, 1887d).

1886p. [In Anon.] Queensland Museum. *Brisbane Courier*, August 9, p. 5. Republished 1886, *Telegraph*, August 9, p. 2. Republished 1886, *Daily Observer*, August 9, p. 3.

1886q. [In Anon.] The Queensland Museum. *Brisbane Courier*, September 7, p. 3. Republished 1886, *Telegraph*, September 8, p. 5.

1886r. [In Anon.] Queensland Museum. *Brisbane Courier,* October 11, p. 6. Republished 1886, *Telegraph,* October 11, p. 5. Republished 1886, *Daily Observer,* October 11, p. 3.

1886s. On a probable new species of tree-kangaroo from north Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for October 27, 1886, p. v. Republished 1887, *Zoologischer Anzeiger* **10**(241): 22 (3 Jan.). (Abstract of de Vis, 1887a).

1886t. [In Anon.] The Queensland Museum. *Brisbane Courier,* November 8, p. 6. Republished 1886, *Daily Observer,* November 8, p. 6. Republished 1886, *Telegraph,* November 11, p. 5.

1886u. [In Anon.] Queensland Museum. *Brisbane Courier,* December 4, p. 3. Republished 1886, *Daily Observer,* December 4, p.6. Republished 1886, *Telegraph,* December 7, p. 3.

1887a. Notice of a probable new species of Dendrolagus. *Proceedings of the Royal Society of Queensland* **3**: 11-14.

1887b. Centriscus velitaris, Pall. *Proceedings of the Royal Society of Queensland* **3**: 31.

1887c. A post-Pliocene artiodactyle. *Proceedings of the Royal Society of Queensland* **3**: 42-47, pl. 1.

1887d. On a femur probably of Thylacoleo. *Proceedings of the Royal Society of Queensland* **3**: 122-128, pl. 3-4.

1887e. On new or rare vertebrates from the Herbert River, North Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for December 29, 1886, p. vi. Republished 1887, *Zoologischer Anzeiger* **10**(245): 127-128 (28 Feb.). (Abstract of de Vis, 1887h).

1887f. [In Anon.] Queensland Museum. *Brisbane Courier,* January 8, p. 5. Republished 1887, *Daily Observer,* January 8, p. 3. Republished 1887, *Telegraph,* January 10, p. 3.

1887g. [In Anon.] Queensland Museum. *Brisbane Courier,* February 7, p. 3. Republished 1887, *Telegraph,* February 7, p. 2. *Republished 1887, Daily Observer,* February 7, p. 3.

1887h. On new or rare vertebrates from the Herbert River, north Queensland. *Proceedings of the Linnean Society of New South Wales* (2)**1**(4): 1129-1137 (22Feb.).

1887i. [In Anon.] Queensland Museum. *Brisbane Courier,* March 5, p. 5. Republished 1887, *Daily Observer,* March 5, p. 3. Republished 1887, *Telegraph,* March 7, p. 2.

1887j. [In Anon.] Queensland Museum. *Brisbane Courier,* April 2, p. 3. Republished 1887, *Daily Observer,* April 2, p. 6. Republished 1887, *Telegraph,* April 4, p. 2.

1887k. [In Anon.] Queensland Museum. *Brisbane Courier,* May 7, p. 6. Republished 1887, *Daily Observer,* May 7, p. 6. Republished 1887, *Telegraph,* May 9, p. 3.

1887l. [In Anon.] Queensland Museum. *Brisbane Courier,* June 4, p. 6. Republished 1887, *Daily Observer,* June 4, p. 3. Republished 1887, *Telegraph,* June 6, p. 3.

1887m. [In Anon.] Queensland Museum. *Brisbane Courier,* July 2, p. 6. Republished 1887, *Telegraph,* July 2, p. 3. Republished 1887, *Daily Observer,* July 4, p. 3.

1887n. Annual report to the Trustees of the Queensland Museum. p. 1-2. *In* 'Queensland Museum (Annual report of the Trustees of)'. Queensland Parliamentary Paper C.A. 17-1889. (Government Printer: Brisbane). 11 pp.

1887o. [In Anon.] Queensland Museum. *Brisbane Courier,* August 8, p. 6. Republished 1887, *Telegraph,* August 8, p. 3.Republished 1887, *Evening Observer,* August 8, p. 6.

1887p. On an extinct mammal of a genus apparently new. [In Anon.] *Brisbane Courier,* August 8, p. 6. Republished 1887, *Evening Observer,* August 8, p. 6. Republished in Mahoney and Ride (1975: 187-188). (Abstract of de Vis, 1888aa).

1887q. [In Anon.] The Queensland Museum. *Telegraph,* September 9, p. 2.

1887r. [In Anon.] Queensland Museum. *Telegraph,* October 10, p. 2.

1887s. On a third species of the Australian tree kangaroos. [In Anon.] *Brisbane Courier,* October 17, p. 7. Republished 1887, *Evening Observer,* October 17, p. 3. (Abstract of de Vis, 1888ab).

1887t. [In Anon.] Queensland Museum. *Telegraph,* November 9, p. 2.

1887u. A contribution to the herpetology of Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for November 30, 1887, p.iii. Republished 1888, *Zoologischer Anzeiger* **11**(270): 51. (23 Jan.). (Abstract of de Vis, 1888ah).

1887v. [In Anon.] Queensland Museum. *Telegraph,* December 8, p. 2.

1888aa. On an extinct mammal of a genus apparently new. *Proceedings of the Royal Society of Queensland* **4**: 99-106, pl. 1-4.

1888ab. On a third species of the Australian tree kangaroo. *Proceedings of the Royal Society of Queensland* **4**: 132-134.

1888ac. On a supposed new species of *Nototherium.* [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for December 28, 1887, p. v. Republished 1888, *Zoologischer Anzeiger* **11**(273): 122. (5 Mar). (Abstract of de Vis, 1888ai).

1888ad. [In Anon.] Queensland Museum. *Telegraph,* January 9, p. 2.

1888ae. On an extinct genus of the marsupials allied to *Hypsiprymnodon.* [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for January 25, 1888, p. v. Republished 1888, *Zoologischer Anzeiger* **11**(274): 147-148 (19 Mar). (Abstract of de Vis, 1888am).

1888af. [In Anon.] Queensland Museum. *Telegraph,* February 7, p. 3.

1888ag. [In Anon.] Queensland Museum. *Telegraph,* March 9, p. 2.

1888ah. A contribution to the herpetology of Queensland. *Proceedings of the Linnean Society of New South Wales* (2)**2**(4): 811-826 (21 Mar.).

1888ai. On a supposed new species of *Nototherium*. *Proceedings of the Linnean Society of New South Wales* (2)2(4): 1065-1070, pl. 38 (21 Mar.).

1888aj. [In Anon.] Queensland Museum. *Telegraph*, April 9, p. 3.

1888ak. [In Anon.] [Queensland Museum]. This newspaper cutting is in the Minute Book for the meetings of the Board of Trustees, but I have been unable to locate it in the newspapers. It details the Curator's report, which would have been presented at the meeting of May 4th. There is the possibility that it was printed but not published.

1888al. [In Anon.] Queensland Museum. *Telegraph*, June 5, p. 3.

1888am. On an extinct genus of the marsupials allied to *Hypsiprymnodon*. *Proceedings of the Linnean Society of New South Wales* (2)3(1): 5-8, pl. 1 (5 Jun.).

1888an. [In Anon.] Queensland Museum. *Telegraph*, July 10, p. 2.

1888ao. Curator's annual report to the Trustees of the Queensland Museum. p. 1-2. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. Queensland Parliamentary Paper C.A. 54-1888. (Government Printer: Brisbane). 11 pp.

1888ap. [In Anon.] Queensland Museum. *Telegraph*, August 8, p. 10.

1888aq. Diprotodon minor. [In Anon.] *Brisbane Courier*, August 18, p. 8. Republished 1888, *Evening Observer*, August 18, p. 3. (Abstract of de Vis, 1888ar).

1888ar. On Diprotodon minor - Hux. *Proceedings of the Royal Society of Queensland* 5(2): 38-44, pl. 2.

1888as. [In Anon.] Queensland Museum. *Telegraph*, September 4, p. 10.

1888at. The genera Nototherium and Zygomaturus. [In Anon.] *Brisbane Courier*, September 15, p. 8. Republished 1888, *Evening Observer*, September 15, p. 3. (Abstract of de Vis, 1888au).

1888au. Note on the genera Zygomaturus and Nototherium. *Proceedings of the Royal Society of Queensland* 5(3): 111-116, pl. 4.

1888av. A glimpse of the post-Tertiary avifauna of Queensland. [In Anon.] *Sydney Morning Herald*, October 2, p. 3. Republished 1888, *Abstract of Proceedings of the Linnean Society of New South Wales* for September 26, 1888, p. iv. Republished 1888, *Zoologischer Anzeiger* 11(293): 65 (19 Nov.). (Abstract of de Vis, 1888ba).

1888aw. [In Anon.] The Queensland Museum. *Telegraph*, October 9, p. 6.

1888ax. The Australian ancestry of the crowned pigeon of New Guinea. [In Anon.] *Evening Observer*, November 17, p. 4. (Abstract of de Vis, 1888ay).

1888ay. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland* 5(4): 127-131, pl. 6

1888az. [In Anon.] [Queensland Museum]. This newspaper cutting is in the Minute Book for the meetings of the Board of Trustees, but I have been unable to locate it in the newspapers. It details the Curator's report, which would have been presented at the meeting of December 7th. There is the possibility that it was printed but not published.

1888ba. A glimpse of the post-Tertiary avifauna of Queensland. *Proceedings of the Linnean Society of New South Wales* (2)3(3): 1277-1292, pl. 33-36 (7 Dec.).

1888bb. On *Synaptodon aevorum*, a new genus of extinct mammals. [In Anon.] *Brisbane Courier*, December 17, p. 6. Republished 1888, *Evening Observer*, December 17, p. 2. Republished in Mahoney and Ride (1975: 189). (Abstract of de Vis, 1889aa).

1888bc. Characters of a scink, apparently new. [In Anon.] *Brisbane Courier*, December 17, p. 6. Republished 1888, *Evening Observer*, December 17, p. 2. (Abstract of de Vis, 1889ab).

1888bd. A new shrike-thrush. [In Anon.] *Brisbane Courier*, December 17, p. 6. Republished 1888, *Evening Observer*, December 17, p. 2. (Abstract of de Vis, 1889ac).

1889aa. On a new genus of extinct mammals. *Proceedings of the Royal Society of Queensland* 5(5): 158-160.

1889ab. Characters of a naked-eyed scink apparently new. *Proceedings of the Royal Society of Queensland* 5(5): 160-161.

1889ac. Colluricincla sibila sp. nov. *Proceedings of the Royal Society of Queensland* 5(5): 161-162.

1889ad. [In Anon.] The Queensland Museum. *Telegraph*, January 9, p. 2.

1889ae. [In Anon.] The Queensland Museum. *Telegraph*. February 6, p. 3.

1889af. Additions to the list of fossil birds. [In Anon.] *Brisbane Courier*, February 16, p. 3. Republished 1889, *Evening Observer*, February 16, p. 3. (Abstract of de Vis, 1889al).

1889ag. [In Anon.] The Queensland Museum. *Telegraph*, March 11, p. 2.

1889ah. Megalania and its allies. [In Anon.] *Brisbane Courier*, March 16, p. 6. Republished 1889, *Evening Observer*, March 16, p. 6. (Abstract of de Vis, 1889as).

1889ai. [In Anon.] A new bird. *Queenslander*, March 30, p. 600. Republished in Chisholm and Chaffer (1956: 9).

1889aj. [In Anon.] The Queensland Museum. *Telegraph*, April 12, p. 2.

1889ak. The Phalangistidae of the postertiary period. [In Anon.] *Evening Observer*, April 13, p. 4. Republished 1889, *Brisbane Courier*, April 15, p.6. Republished in Mahoney and Ride (1975: 189-190). (Abstract of de Vis, 1889at).

1889al. Additions to the list of fossil birds. *Proceedings of the Royal Society of Queensland* 6(1): 55-58 (before 11 May).

1889am. [In Anon.] The Queensland Museum. *Telegraph*, May 11, p. 5

1889an. On extinct animals formerly inhabiting Queensland. [In Anon.] *Brisbane Courier*, May 18, p. 3. Republished 1889, *Evening Observer*, May 18, p. 3. (Abstract of de Vis, 1889au).

1889ao. [In Anon.] The Queensland Museum. *Telegraph*, June 12, p. 3.

1889ap. Descriptions of Prionodura newtoniana (Meston's bower-bird) and Acanthiza squamata. [In Anon.] *Brisbane Courier*, June 17, p. 6. Republished 1889, *Evening Observer*, June 17, p. 6. (Abstract of de Vis, 1889bg, bi).

1889aq. Annual report of the Curator to the Trustees of the Queensland Museum. p.1-2. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. *Queensland Parliamentary Paper* C.A. 17-1889. (Government Printer: Brisbane), 11 pp.

1889ar. [In Anon.] The Queensland Museum. *Telegraph*, July 11, p. 2.

1889as. On Megalania and its allies. *Proceedings of the Royal Society of Queensland* 6(2&3): 93-99, pl. 4 (before 11 Jul.).

1889at. On the Phalangistidae of the post-Tertiary period in Queensland. *Proceedings of the Royal Society of Queensland* 6(2&3): 105-114, pl. 5 (before 11 Jul.).

1889au. On a bone of an extinct eagle. *Proceedings of the Royal Society of Queensland* 6(4): 161-162, pl. 10 (before 9 Aug.).

1889av. [In Anon.] The Queensland Museum. *Telegraph*, August 9, p. 3.

1889aw. [In Anon.] Queensland Museum. *Telegraph*, September 10, p. 2.

1889ax. On the genera *Nototherium* and *Zygomaturus*, in reply to Mr. Lydekker. *Annals and Magazine of Natural History* (6)4(22): 257-261 (Oct.).

1889ay. [In Anon.] Queensland Museum. *Telegraph*, October 11, p. 3.

1889az. Zoology of Bellenden-Ker, as ascertained by the late expedition under Mr. A. Meston. p. 30-35. *In* Meston, A., 'Report on the Government Scientific Expedition to the Bellenden-Ker Range (Wooroonooran), north Queensland'. *Queensland Parliamentary Paper* C.A. 95-1889, (Government Printer: Brisbane). 35 pp. Republished in Meston (1889: 81-92).

1889ba. Descriptions of two lizards, of genera new to Australian herpetology. [In Anon.] *Sydney Morning Herald*, October 31, p. 2. (Abstract of de Vis, 1890d).

1889bb. Description of two lizards of genera new to Australian herpetology. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for October 30, 1889, p. iv. Republished 1889, *Zoologischer Anzeiger* 12(324): 679. (30 Dec.). (Abstract of de Vis, 1890d).

1889bc. [In Anon.] The Queensland Museum. *Telegraph*, November 9, p. 2.

1889bd. List of birds, lizards, and snakes collected at Cambridge Gulf. *Proceedings of the Royal Society of Queensland* 6(5): 236-237 (before 9 Nov.).

1889be. Descriptions of two new vertebrates in Mr. Saville-Kent's collection. *Proceedings of the Royal Society of Queensland* 6(5): 237-239, pl. 14 (before 9 Nov.).

1889bf. Descriptions of new birds from Herberton. *Proceedings of the Royal Society of Queensland* 6(5): 242-244 (before 9 Nov.).

1889bg. A further account of *Prionodura newtoniana*. *Proceedings of the Royal Society of Queensland* 6(5): 245-248 (before 9 Nov.).

1889bh. Note on Colluricincla boweri Ram. *Proceedings of the Royal Society of Queensland* 6(5): 248 (before 9 Nov.).

1889bi. Description of an Acanthiza from Herberton. *Proceedings of the Royal Society of Queensland* 6(5): 248-249 (before 9 Nov.).

1889bj. [In Anon.] The Queensland Museum. *Telegraph*, December 13, p. 5.

1890a. [In Anon.] The Queensland Museum. *Telegraph*, January 10, p. 3.

1890b. [In Anon.] The Queensland Museum. *Telegraph*, February 10, p. 6.

1890c. [In Anon.] The Queensland Museum. *Telegraph*, March 12, p. 2.

1890d. Description of two lizards of genera new to Australian herpetology. *Proceedings of the Linnean Society of New South Wales* (2)4(4): 1034-1036 (15 Apr.).

1890e. [In Anon.] The Queensland Museum. *Telegraph*, April 16, p. 3.

1890f. [In Anon.] The Queensland Museum. *Telegraph*, May 14, p. 2.

1890g. Appendix G. Report on birds from British New Guinea. p. 58-61. *In* 'Annual Report on British New Guinea from 4th September, 1888, to 30th June, 1889; with map and appendices'. *Victorian Parliamentary Paper* No. 21-(2S)-3598. (Government Printer: Melbourne). 68 pp, map 1 (17 Jun.). Republished 1890, *Queensland Parliamentary Paper* C.A. 13-1890, p. 57-62 (24 Jun.) (offprint had pages numbered 1-5). Republished 1890, *Colonial Possessions Report* No. 103, p. 105-116 (12 Jul.). Also republished in de Vis (1891a, 1898d)

1890h. Appendix H. Report on reptiles from British New Guinea. p. 61-62. *In* 'Annual Report on British New Guinea from 4th September, 1888, to 30th June, 1889; with map and appendices'. *Victorian Parliamentary Paper* No. 21-(2S)-3598. (Government Printer: Melbourne). 68 pp, map 1 (17 Jun.). Republished 1890, *Queensland Parliamentary Paper* C.A. 13-1890, p. 62. (24 Jun.) (offprint had one page only). Republished 1890, *Colonial Possessions Report No.* 103, p. 116-117 (12 Jul.). Republished in de Vis (1898e).

1890i. Annual report of the Curator to the Trustees of the Queensland Museum. p.1-2. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. *Queensland Parliamentary Paper* C.A. 111-1890. (Government Printer: Brisbane). 19 pp.

1890j. Reptiles from New Guinea. [In Anon.] *Sydney Morning Herald*, August 28, p. 9. Republished 1890, *Abstract of Proceedings of the Linnean Society of New South Wales* for August 27, 1890, p. iii. Republished 1890, *Zoologischer Anzeiger* 13(346): 56 (13 Oct.). (Abstract of de Vis, 1890l).

1890k. Appendix U. New Guinea.- Report on zoology for the year 1889. p. 107-108. *In* 'Annual Report on British New Guinea from 1st July, 1889, to 30th June, 1890; with appendices'. *Queensland Parliamentary Paper* C.A. 105-1890. (Government Printer: Brisbane). 168 pp, maps 6, 4 pls (12 Nov.). Republished 1890, *New South Wales Votes and*

Proceedings (6s), p. 107-108 (3 Dec.). Republished 1891, *Colonial Reports. - Annual* No. 6, p. 64-69 (6 Apr.).

1890l. Reptiles from New Guinea. *Proceedings of the Linnean Society of New South Wales* (2)5(3): 497-500 (16 Dec.).

1891a. Report on birds from British New Guinea. *Ibis* (6)3(9): 25-41 (Jan.). Reprinted from de Vis (1890g).

1891b. [In Anon.] Accessions to the Museum. *Brisbane Courier*, February 14, p. 7. Republished 1891, *Queenslander*, February 14, p. 314.

1891c. Note on an extinct eagle. [In Anon.] *Sydney Morning Herald*, March 26, p. 9. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for March 25, 1891, p. iii. Republished 1891, *Zoologischer Anzeiger* 14(365): 20 (8 Jun.). (Abstract of de Vis, 1891l).

1891d. On the trail of an extinct bird. [In Anon.] *Sydney Morning Herald*, March 26, p. 9. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for March 25, 1891, p. iii. Republished 1891, *Zoologischer Anzeiger* 14(365): 20 (8 Jun.). (Abstract of de Vis, 1891k).

1891e. In confirmation of the genus *Owenia*, so-called. [In Anon.] *Sydney Morning Herald*, April 30, p. 6. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for April 29, 1891, p. v. Republished 1891, *Zoologischer Anzeiger* 14(366): 219, (22 Jun.). (Abstract of de Vis, 1891n).

1891f. The moa in Australia. *New Zealand Journal of Science* (2)1(3): 97-101 (May).

1891g. Remarks on post-Tertiary *Phascolomyidae*. [In Anon.] *Sydney Morning Herald*, May 28, p. 3. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for May 27, 1891, p. iii. Republished 1891, *Zoologischer Anzeiger* 14(368): 25 (20 Jul). (Abstract of de Vis, 1891o).

1891h. [In Anon.] Recent additions to the Queensland Museum. *Brisbane Courier*, June 9, p. 6. Republished 1891, *Queenslander*, June 13, p. 1131.

1891i. The incisors of *Sceparnodon*. [In Anon.] *Sydney Morning Herald*, June 25, p. 5. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for June 24, 1891, p. iii. (Abstract of de Vis, 1891p).

1891j. Annual report of the Curator to the Trustees of the Museum. p. 1-3. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. *Queensland Parliamentary Paper* C.A. 26-1891. (Government Printer: Brisbane). 12 pp.

1891k. On the trail of an extinct bird. *Proceedings of the Linnean Society of New South Wales* (2)6(1): 117-122 (9 Sep.).

1891l. Note on an extinct eagle. *Proceedings of the Linnean Society of New South Wales* (2)6(1): 123-125 (9 Sep.).

1891m. Residue of the extinct birds of Queensland as yet detected. [In Anon.] *Sydney Morning Herald*, October 1, p. 6. Republished 1891, *Abstract of Proceedings of the Linnean Society of New South Wales* for September 30, 1891, p. vi. Republished 1891, *Zoologischer Anzeiger* 14(377): 41 (16 Nov.). (Abstract of de Vis, 1892c).

1891n. In confirmation of the genus *Owenia* so-called. *Proceedings of the Linnean Society of New South Wales* (2)6(2): 159-165, pl. 13 (22 Dec.).

1891o. Remarks on post-Tertiary *Phascolomyidae*. *Proceedings of the Linnean Society of New South Wales* (2)6(2): 235-246 (22 Dec.).

1891p. The incisors of *Sceparnodon*. *Proceedings of the Linnean Society of New South Wales* (2)6(2): 258-262, pl. 22 (22 Dec.).

1892a. Appendix CC. Report on the zoological gleanings of the Administration during the year 1890-1891. p. 93-98, pl. 1. *In* 'Annual Report on British New Guinea from 1st July, 1890, to 30th June 1891; with appendices'. *Queensland Parliamentary Paper* C.A. 1-1892. (Government Printer: Brisbane). xxviii 149 pp., 1 pl., 13 maps (29 Mar.). Republished 1892, *Victorian Parliamentary Paper No.* 58-3865, p. 93-98, pl. 1 (12 May). Republished, in part, in de Vis (1892b).

1892b. Zoology of British New Guinea. Part I.- Vertebrata. *Annals of the Queensland Museum* 2: 3-12 (before 6 May). Reprinted, in part, from de Vis (1892a).

1892c. Residue of the extinct birds of Queensland as yet undetected. *Proceedings of the Linnean Society of New South Wales* (2)6(3): 437-456, pl. 23-24 (23 May).

1892d. Reptiles of New Guinea. p. 273-282. *In* Thomson, J.P., 'British New Guinea'. (Brisbane: Alexr. Muir & Morcom). xxviii 336 pp, plates, map (date of receipt written on reprint at Queensland Museum was 5 Aug.).

1892e. Curator's annual report to the Board of Trustees of the Queensland Museum. p. 1-3. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. *Queensland Parliamentary Paper* C.A. 81-1892. (Government Printer: Brisbane). 13 pp.

1892f. The ribbon fish. (A Regalecus in Queensland waters.) *Proceedings of the Royal Society of Queensland* 8(4): 109-113

1893a. Annual report of the Curator to the Trustees of the Museum. p. 1-2. *In* 'Queensland Museum. (Annual report of the Trustees of the)'. *Queensland Parliamentary Paper* C.A. 16-1893. (Government Printer: Brisbane). 11 pp.

1893b. Note on the upper incisor of *Phascolonus*. *Proceedings of the Linnean Society of New South Wales* (2)8(1): 11-12, pl. 1 (28 Jul.).

1893c. A thylacine of the earlier Nototherian period in Queensland. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for November 29, 1893, p. v. Republished in *Zoologischer Anzeiger* 17(439): 47 (5 Feb.). (Abstract of de Vis, 1894a).

1894a. A thylacine of the earlier Nototherian period in Queensland. *Proceedings of the Linnean Society of New South Wales* (2)8(4): 443-447 (5 Jun.).

1894b. A new Queensland locality for Zygomaturus. [In Anon.] *Evening Observer*, September 24, p. 2. (Abstract of de Vis, 1895b).

1894c. Appendix DD. Report on ethnological specimens collected in British New Guinea. p. 98-99. *In* 'Annual Report on British New Guinea from 1st July, 1893, to 30th June, 1894; with appendices'. *Queensland Parliamentary Paper* C.A. 93-1894. (Government Printer: Brisbane). xxxi 136 pp, 4 pls, 9 maps (1 Nov.) (offprint had one page only). Republished 1894, *Victorian Parliamentary Paper* S.- No.26-9601, p. 98-99 (1894).

1894d. Appendix EE. Report on ornithological specimens collected in British New Guinea. p. 99-105. *In* 'Annual Report on British New Guinea from 1 July, 1893 to 30 June, 1894; with appendices'. *Queensland Parliamentary Paper* C.A. 93-1894. (Government Printer: Brisbane). xxxi 136 pp, 4 pls, 9 maps (1 Nov.) (offprint had pages numbered 1-7). Republished 1894, *Victorian Parliamentary Paper* S.- No.26-9601, p. 99-105 (1894) (note that the citation of these references is wrong in Ingram, 1987). Republished 1894, *Blue Book* p. 1-7 , *vide* Sharpe (1895: 6); this publication has not been located and it is possible that Sharpe mis-cited the offprint.

1894e. Life. p. 104-118. *In* Tate, R., Rennie, E.H., and Bragg, W.H. (eds), 'Report of the fifth meeting of the Australasian Association for the Advancement of Science, held at Adelaide, South Australia, September 1893.' (A.A.A.S.: Sydney). xxx 691 pp, 18 pls.

1894f. Pelicanus validipes, De Vis, n. sp. p. 21, pl. 2, figs 5-6. *In* Ethridge, R. Official contributions to the palaeontology of South Australia. No. 6. Vertebrate remains from the Warburton or Diamantina River. pp. 19-22, pls 1-2. *In* Brown, H.Y.L., 'Annual report of the Government Geologist for year ended June 30th, 1894'. (Government Printer: Adelaide). 26 pp, 3 pls, 6 maps, 4 b.w. photographs.

1894g. A review of the fossil jaws of the *Macropodidae* in the Queensland Museum. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for November 28, 1894, p. i. Republished 1895, *Zoologischer Anzeiger* 18(466): 30 (21 Jan.). Republished 1895, *Proceedings of the Linnean Society of New South Wales* (2)9(4): 735 (28 Mar). (Abstract of de Vis, 1895c).

1894h. The lesser chelonians of the Nototherian drifts. *Proceedings of the Royal Society of Queensland* 10: 123-127, pl. 10.

1895a. Description of a fly-catcher, presumably new. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for April 24, 1895, p. i. Republished 1895, *Zoologischer Anzeiger* 18(480): 291 (22 Jul). (Abstract of de Vis, 1895d).

1895b. On the mandible of *Zygomaturus*. *Proceedings of the Royal Society of Queensland* 11(1): 5-11 (before 26 Jun.).

1895c. A review of the fossil jaws of the *Macropodidae* in the Queensland Museum. *Proceedings of the Linnean Society of New South Wales* (2)10(1): 75-133, pl. 14-18 (9 Sep.)

1895d. Description of a flycatcher, presumably new. *Proceedings of the Linnean Society of New South Wales (2)*10(1): 171 (9 Sep.).

1895e. Description of a tree creeper presumably new. [In Anon.] *Abstract of Proceedings of the Linnean Society of New South Wales* for September 25, 1895, p. i (26 Sep., *vide* Mathews, 1934). Republished 1895. *Zoologischer Anzeiger* 18(490): 468 (2 Dec.). (Abstract of de Vis, 1896).

1895f. Description of a tree creeper presumably new. [In Anon.] *Sydney Morning Herald*, September 27, p. 6. (Abstract of de Vis, 1896).

1895g. On the word "kangaroo" *Proceedings and Transactions of the Queensland Branch of the Royal Geographical Society of Australasia* 10: 35-45.

1896. Description of a tree creeper presumably new. *Proceedings of the Linnean Society of New South Wales (2)*10(4): 536 (29 Apr.).

1897a. Description of a new bird of paradise from British New Guinea. *Ibis* (7)3(10): 250-252, pl. 7 (Apr.).

1897b. Appendix X. Report on recent collections. p. 91. *In* 'Annual Report on British New Guinea from 1st July, 1895, to 30th June, 1896, with appendices'. *Queensland Parliamentary Paper* C.A. 8-1897. (Government Printer: Brisbane). xxxv 120 pp, 3 maps (15 Jun.) (offprint had one page only). Republished 1897, *Victorian Parliamentary Papers* 1897, p. 91 (29 Jun.).

1897c. Diagnoses of thirty-six new or little-known birds from British New Guinea. *Ibis* (7)3(11): 371-392 (Jul.).

1897d. The extinct freshwater turtles of Queensland. *Annals of the Queensland Museum* 3: 3-7, pl. 1-8 (before 19 Jul.).

1898a. Letter from Mr. C.W. de Vis. *Ibis* (7)3(13): 174-175 (Jan.).

1898b. On the marsupial bones of the Coimadai Limestone. *Proceedings of the Royal Society of Victoria* (2)10(2): 198-201 (May).

1898c. Appendix AA. Report on the birds for 1896-1897. p. 81-90. *In* 'Annual Report on British New Guinea from 1st July, 1896, to 30th June, 1897; with appendices'. *Victorian Parliamentary Paper No.* 23-5027. (Government Printer: Melbourne). xxvi 96 pp, 5 maps, 5 pls (5 Jul.). Republished 1898, *Queensland Parliamentary Paper* C.A. 6- 1898, p. 81-90 (26 Jul.) (offprint had pages numbered 1-10).

1898d. Appendix W. Report on birds from British New Guinea. pp. 58- 61. *In* 'Annual Report on British New Guinea from 4th September, 1888, to 30th June, 1889; with map and appendices'. Reprinted with additional appendices. (Government Printer: Brisbane). xxvii 72 pp, 1 map. Reprinted from de Vis (1890g).

1898e. Appendix X. Report on reptiles from British New Guinea. p. 62 *In* 'Annual Report on British New Guinea from 4th September, 1888, to 30th June, 1889; with map and appendices. Reprinted with additional appendices'. (Government Printer: Brisbane). xxvii 72 pp, 1 map. Reprinted from de Vis (1890h).

1899a. Remarks on a fossil implement and bones of an extinct kangaroo. *Proceedings of the Royal Society of Victoria* (2)12(1): 81-89, Pl. 7 (Jul.)

1899b. On some remains of marsupials from Lake Colongulac, Victoria. *Proceedings of the Royal Society of Victoria* (2)**12**(1): 107-111 (Jul.).

1901a. A Papuan kite. *Annals of the Queensland Museum* **5**: 3-5, pl. 1-2 (before 26 Jan.).

1901b. A further trace of an extinct lizard. *Annals of the Queensland Museum* **5**: 6, pl. 3 (before 26 Jan.).

1901c. Bones and diet of *Thylacoleo*. *Annals of the Queensland Museume*; **5**: 7-11, pl. 4-6 (before 26 Jan.).

1901d. Description of a *Charmosinopsis*. *Annals of the Queensland Museum* **5**: 12-13, pl. 8 (before 26 Jan.).

1901e. A new species of hairy-nosed wombat. *Annals of the Queensland Museum* **5**: 14-16, pl. 9-10 (before 26 Jan.).

1901f. Natural History. p. 98-116. *In* Hughes, J. (ed.), 'The Queensland Official Year Book, 1901'. (Brisbane: Government Printer). [viii] 425 pp, diagrams, plates, maps.

1905a. A contribution to the knowledge of the extinct avifauna of Australia. *Annals of the Queensland Museum* **6**: 3-25, pl. 1-9 (before 30 Sep.)

1905b. Fossil vertebrates from New Guinea. *Annals of the Queensland Museum* **6**: 26-31, pl. 10-13 (before 30 Sep.)

1905c. Papuan charms. *Annals of the Queensland Museum* **6**: 32-35, pl. 14 (before 30 Sep.)

1905d. Bats. *Annals of the Queensland Museum* **6**: 36-40 (before 30 Sep.)

1905e. Ornithological. *Annals of the Queensland Museum* **6**: 41-45 (before 30 Sep.)

1905f. Reptilia. *Annals of the Queensland Museum* **6**: 46-52, pl. 15 (before 30 Sep.)

1907a. Fossils from the gulf watershed. *Annals of the Queensland Museum* **7**: 3-7 (7 Jun.).

1907b. An eccentric rat. *Annals of the Queensland Museum* **7**: 8-9 (7 Jun.).

1907c. A New Guinea tree rat. *Annals of the Queensland Museum* **7**: 10-11 (7 Jun.).

1907d. A Papuan relic. *Annals of the Queensland Museum* **7**: 12-13, pl. 1 (7 Jun.).

1911a. On some Mesozoic fossils. *Annals of the Queensland Museum* **10**: 1-11, pl. 2 fig. 1-2, pl. 3 fig. 1, pl. 4 (1 Nov.).

1911b. Annelid trails. *Annals of the Queensland Museum* **10**: 12-14, pl. 3 fig. 2 (1 Nov.).

1911c. *Palaeolestes Gorei*, n.s. an extinct bird. *Annals of the Queensland Museum* **10**: 15-17, pl. 2 fig. 4-6 (1 Nov.).

1911d. Cestraciontidae. *Annals of the Queensland Museum* **10**: 18, pl. 2 fig. 3 (1 Nov.).

1911e. A wild dog from British New Guinea. *Annals of the Queensland Museum* **10**: 19-20, pl. 1 (1 Nov.).

1911f. Description of snakes apparently new. *Annals of the Queensland Museum* **10**: 21-25 (1 Nov.).

1911g. A second species of *Enoplosus* ("old wife" fish). *Annals of the Queensland Museum* **10**: 29 (1 Nov.).

1911h. A fisherman's spider. *Annals of the Queensland Museum* **10**: 167-168 (1 Nov.).

CAMPBELL, A.J., DE VIS, C.W., LEGGE, R.W. AND STIRLING, E.C. 1898. List of vernacular names for Australian birds. p. 128-154. *In* Liversidge, A. (ed.), 'Report of the seventh meeting of the Australasian Association for the Advancement of Science, held at Sydney, 1898.' (Australasian Association for the Advancement of Science: Sydney). lii 1161 pp, 36 pls (offprint had pages numbered 1-27).

NEW ANTIARCHS (DEVONIAN PLACODERM FISHES) FROM QUEENSLAND, WITH COMMENTS ON PLACODERM PHYLOGENY AND BIOGEOGRAPHY

G.C. YOUNG

Young, G.C. 1990 3 31: New antiarchs (Devonian placoderm fishes) from Queensland, with comments on placoderm phylogeny and biogeography. *Mem. Qd Mus.* 28(1): 35–50. Brisbane. ISSN 0079-8835.

Two new antiarchs are described from the Middle Devonian of the Broken River area of northern Queensland. *Wurungulepis denisoni* gen. et sp. nov. is an asterolepidoid represented by a single articulated trunk armour with associated pectoral fin bones and scales. It is referred to the family Pterichthyodidae, and most closely resembles the European genus *Gerdalepis*, but its trunk-armour proportions and scales are distinctive. The specimen is important in demonstrating the association of micro- and macrovertebrate remains in a single taxon of probable Eifelian age. *Nawagiaspis wadeae* gen. et sp. nov. came from a higher horizon in the Broken River Formation, of probable Givetian age. It combines various morphological characters previously regarded as typical of the asterolepidoids (e.g. tubercular ornament, no preorbital recess, short endocranial postorbital processes), or of the bothriolepidoids (prelateral plate, articular process on submarginal plate, anterior dorsolateral and posterior ventrolateral plates with common suture). It is referred to the latter group on the evidence of the cheek attachment. New information is provided on the structure of the jaws and cheek in antiarchs. ☐ *Devonian, placoderms, antiarchs, Pterichthyodidae, Bothriolepidoidei, phylogeny, biogeography, Queensland, Wurungulepis, Nawagiaspis, Broken River Formation.*

G.C. Young, Division of Continental Geology, Bureau of Mineral Resources, PO Box 378, Canberra, ACT, Australia 2601; 10 July 1988.

The antiarchs are a group of placoderm fishes well represented in Late Devonian strata throughout the world. They have been known from Australia since Hills (1929) described the species *Bothriolepis gippslandiensis* from the Upper Devonian rocks of eastern Victoria. From Queensland it was again Hills (1936) who first reported an antiarch from the Middle - Late Devonian near Gilberton, and recently other isolated occurrences have been listed by Turner (1982). Probably the oldest antiarch occurrence yet known from Australia is an asterolepid antiarch from the Cravens Peak Beds (Early-Middle Devonian) of the Georgina Basin in western Queensland (Young, 1984a).

In this paper two new antiarchs are described from the Broken River area of northern Queensland (Fig. 1). They are of interest in being of Middle rather than Late Devonian age, in their occurrence in marine limestones rather than fluviatile or lacustrine deposits in which antiarchs are most common, and in their excellent preservation. Although somewhat distorted, they are uncrushed, and their preservation in limestone has permitted preparation using the acetic acid technique to completely remove skeletal remains from the matrix. *Nawagiaspis wadeae* gen. et sp. nov., described below, provides morphological details on structures otherwise only known in a very few antiarchs. This specimen was collected by Dr Mary Wade from the Broken River Formation. The geology of this region has been summarised by Wyatt and Jell (1980), and the biostratigraphy of the Devonian sequence discussed by Mawson *et al.* (1985), and Mawson (1987). The second specimen came from the same region, but in slightly older Middle Devonian rocks.

Both specimens are housed in the Queensland Museum (prefix QMF). The prefix L signifies a University of Queensland locality number. Standard abbreviations for bones of the antiarch dermal skeleton as used in the text and figures are listed below.

ABBREVIATIONS

ADL	anterior dorsolateral plate
AMD	anterior median dorsal plate
AVL	anterior ventrolateral plate
ad1,2	anterior and posterior articular processes on SM

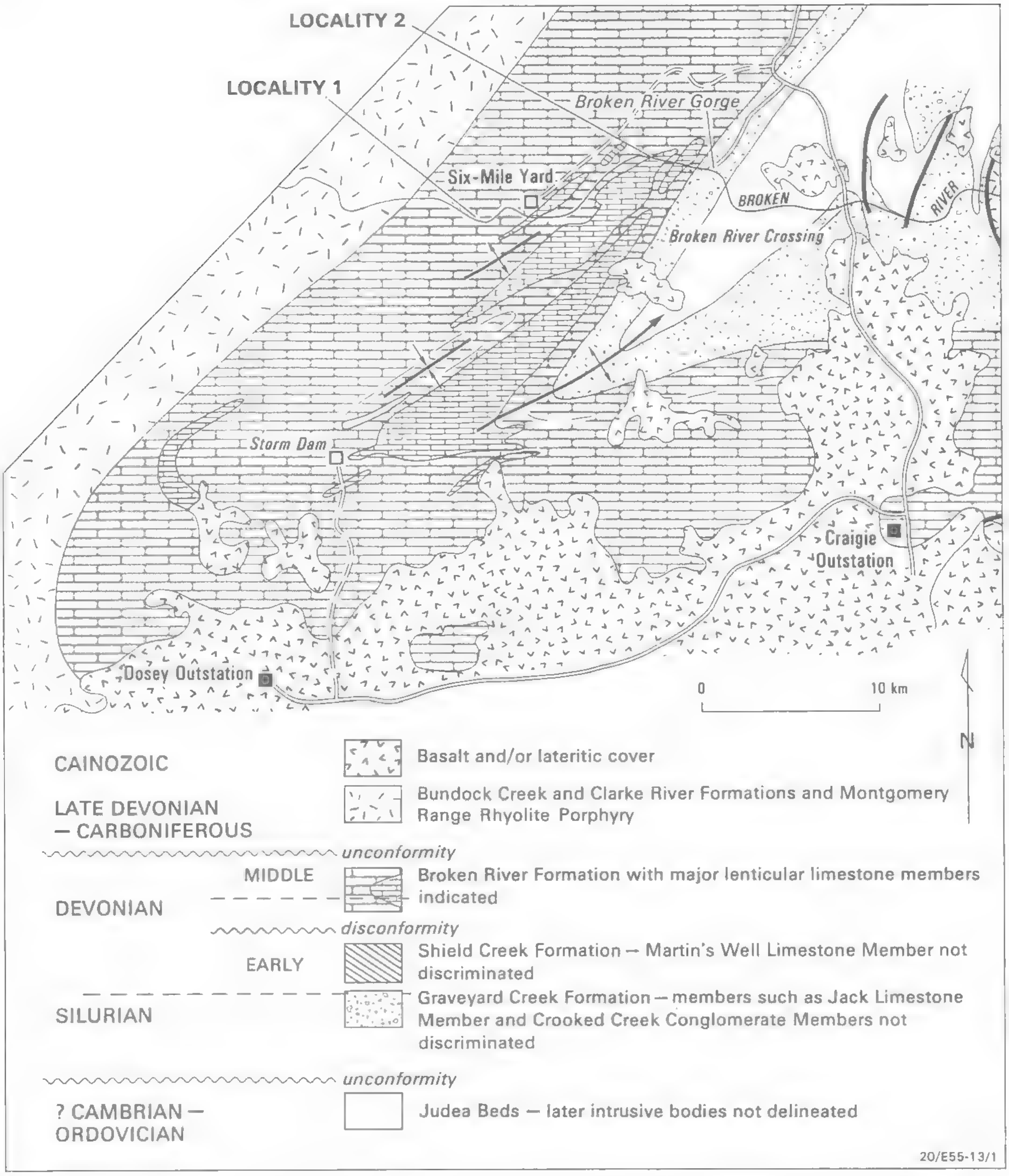

FIG. 1. Geology of the Broken River area, showing type localities for new taxa described in this paper (modified after Mawson *et al.*, 1985).

art	articular facet adjacent to axillary foramen
av	ventral articular area of SM plate
cit	crista transversalis interna anterior
cr	median ventral crest on AMD
cr.tp	crista transversalis interna posterior
dlr	dorsolateral ridge of trunk-armour
dma	tergal angle of trunk-armour
dmr	dorsal median ridge of trunk-armour
f.ap	fossa articularis pectoralis
f.ax	foramen axillare of AVL
fe.orb	orbital fenestra
gr. ul	groove for upper lip
ifc1	principal section of infraorbital sensory

	line on head-shield
ifc2	branch of infraorbital sensory line diverging on L
ifc3	section of infraorbital sensory line on suborbital plate
L	lateral plate
lcg	main lateral line groove
ln	lateral notch of head-shield
lpr	lateral process of head-shield
MxL	mixilateral plate
mvr	ventral median ridge of dorsal wall of trunk-armour
Nu	nuchal plate
nn	nasal notch on first sclerotic plate
oa.ADL	area overlapped by ADL
oa.MxL	area overlapped by MxL
ood	otico-occipital depression of head-shield
orb	orbital notch of L plate
PDL	posterior dorsolateral plate
PL	posterior lateral plate
PM	postmarginal plate
PMD	posterior median dorsal plate
PNu	paranuchal plate
PrL	prelateral plate
PrM	premedian plate
PVL	posterior ventrolateral plate
proc	preobstantic corner of head-shield
pr.po	depression on head-shield for dorsal face of endocranial postorbital process
prv2	posterior ventral process of dorsal wall of trunk-armour
psoc	postsuborbital sensory groove
pt1	anterior ventral pit of dorsal wall of trunk-armour
pt2	posterior ventral pit of dorsal wall of trunk-armour
SM	submarginal plate
SR	skull-roof
sal	subanal lamina of PVL plate
scl.1-3	sclerotic plates 1-3
soc	supraorbital sensory groove
vlr	ventrolateral ridge of trunk-armour

SYSTEMATIC DESCRIPTIONS

Class PLACODERMI
Order ANTIARCHI
Suborder BOTHRIOLEPIDOIDEI Miles (1968)

Nawagiaspis gen. nov.

ETYMOLOGY

After the Nawagi aboriginal tribe, one of the original tribes of the Broken River area.

DIAGNOSIS

A bothriolepid of moderate size, with tuberculate ornament on dermal bones sometimes arranged in radiating ridges. Skull probably with a short obstantic margin, preorbital recess absent or very shallow, and otico-occipital depression deep with endocranial postorbital processes terminating posterolateral to orbital fenestra. Suborbital plate short and high, with two notches and a small posteroventral process on its lateral margin. Biting margins of both jawbones lacking denticulation. Submarginal plate elongate, with a strong anterodorsal articular process. Prelateral plate triangular, with a pronounced anterior process and dorsal and posterior margins oriented normal to each other. Trunk armour short and high; posterior median dorsal with very strong ventral process and median ventral ridge. Anterior dorsolateral in sutural contact with posterior ventrolateral plate. Posterior dorsolateral and posterior lateral incompletely fused. Postbranchial lamina of anterior ventrolateral strongly developed, and axillary foramen small.

REMARKS

Nawagiaspis is distinguished from most other bothriolepidoids by its short endocranial postorbital processes, from *Bothriolepis* by its tuberculate ornament, from *Grossilepis* by the shape of the anterior median dorsal plate and various other features, from *Monarolepis* (= *B. verrucosa;* see Young, 1988) and probably *Dianolepis* by the strong posterior ventral process and ridge beneath the posterior median dorsal plate, and from *Microbrachius* and *Wudinolepis* by the absence of a preorbital depression. The species *Bothriolepis warreni* differs from other *Bothriolepis* species and resembles *Nawagiaspis* in its tuberculate ornament and short postorbital processes (Long & Werdelin, 1986, fig. 29), but other differences (e.g. skull shape, strong posterior ventral process) indicate that they are not closely related. The characters by which *Nawagiaspis* is placed in the suborder Bothriolepidoidei, and distinguished from non-bothriolepidoid antiarchs, are dealt with below.

Nawagiaspis wadeae sp. nov.
(Figs 2-7, 8A, 9-11)

ETYMOLOGY

After Dr Mary Wade, Queensland Museum, who collected the specimen.

Holotype
QMF16592, an articulated incomplete skull and trunk-armour with associated dermal bones of the cheek, jaws and sclerotic ring.

Locality
L4428, a small limestone outcrop on eastern side of gully 1 km upstream from Six Mile Yard, grid reference 596442, Burges 1:1,000,00 map (locality 1, Fig. 1).

Horizon
Broken River Formation, Middle Devonian, probably Givetian (J.S. Jell, pers. comm.).

Diagnosis
As for genus (only species).

Remarks
Some of the features included in the diagnosis above are no doubt specific features, which can be further analysed should additional specimens be discovered.

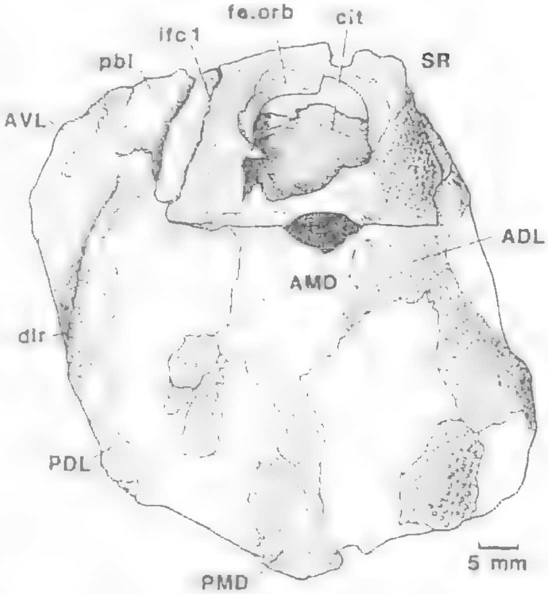

FIG. 3. *Nawagiaspis wadeae* gen. et sp. nov. Holotype in dorsal view (QMF16592).

Description
As collected, the dorsal, right lateral, and ventral surfaces had been exposed to weathering on the surface of a limestone nodule, and portions of the dermal bone were lost. Gaps were filled with plastic which in some cases preserved the visceral bone surface intact after acetic acid preparation. The cheek, jaw, and sclerotic bones fell away from the skull during preparation, but the rest of the specimen remained intact (Fig. 2).

FIG. 2. *Nawagiaspis wadeae* gen. et sp. nov. Holotype, QMF16592, incomplete skull roof and trunk-armour in dorsal view (x0.85).

The skull has incomplete margins except for the region of the neck-joint articulation. It is preserved with only slight displacement in its articulated position against the trunk-armour, so an outline restoration can be derived from surrounding structures. The left SM plate has a very close fit on the postbranchial part of the AVL (Fig. 10), and gives a reliable indication of the preorbital length of the skull, this being very incompletely preserved (Fig. 4A). In antiarchs generally a branch of the infraorbital sensory canal passes laterally off the skull-roof onto the prelateral plate of the cheek. The latter is preserved with its sensory groove (see below), and restored in its position in front of the SM plate (PrL, Fig. 4A) gives the approximate position of this branch on the skull roof. The main sensory groove on the skull is directed anteromesially from the neck-joint articulation (ifc1, Fig. 4), but at its anterior preserved end shows a lateral flexure which may be extended to the branching point of the lateral branch of this canal (ifc2). It is also evident from the configuration of the dorsal (mesial) ornamented edge on the SM plate (see below) that the skull had a lateral process (lpr) behind which was a lateral notch (ln) equivalent to the 'supraspiracular' notch of Stensiö (1948). However, the shape of the prelateral plate (see below) indicates that the prelateral notch of the skull was probably absent. The obstantic margin is obscured on the left side of the specimen by the AVL plate, and is broken away on the right (Fig. 3), but the general shape of the skull as restored suggests that it was relatively short. The close fit of the SM against the AVL, as noted above, suggests that there was no posterolateral extension of the PM plates of the skull. Finally, the smooth area along the anterior margins of the ADL and AMD plates of the trunk suggest a broad obtected nuchal area and convex posterior margin to the skull (Fig. 4B).

The visceral surface of the skull shows no sign of a preorbital recess. There is a strong paramarginal crista on both sides which fuses with the convexity surrounding the orbital fenestra such that the recess for the anterior postorbital process is a short notch posterolateral to the orbit (pr.po, Fig. 4B). A low

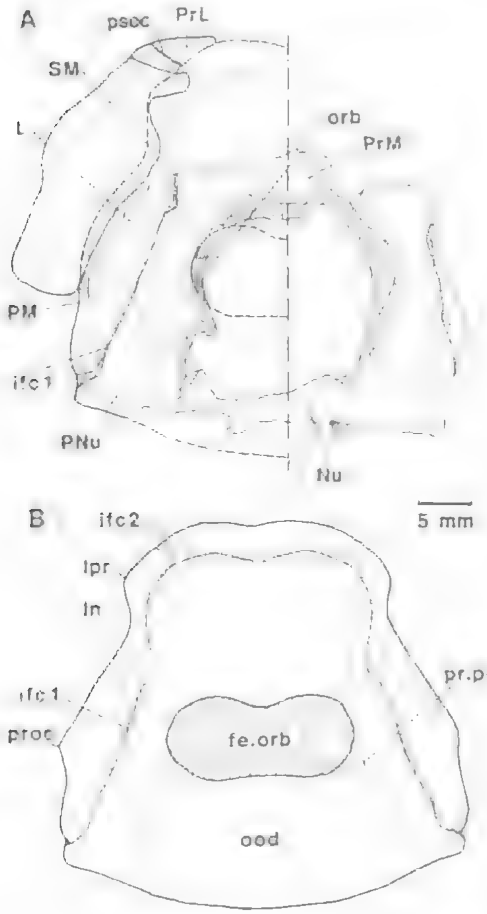

FIG. 4. *Nawagiaspis wadeae* gen. et sp. nov. A, incomplete skull, with left SM and PrL plates in position. B, skull roof restoration, based on A (after the holotype).

thickening on the bone extends anterolaterally from the postorbital process past the orbital fenestra (as far as preserved). The otico-occipital depression (ood) is delimited posteriorly by a strong transverse nuchal crista which, as far as preserved, has similar configuration to that of *Asterolepis ornata* (Stensiö, 1931, fig. 15). However, there is no sign of an extra ridge running laterally from the paramarginal crista, as occurs on the lateral plate of *Asterolepis* (e.g. Stensiö, 1931, fig. 8). This was interpreted by Young (1984b) as a remnant of the posterior postorbital process. The approximate limits of the endocranial impressions on the visceral skull surface are indicated in Fig. 4B.

Four sclerotic bones were retrieved from inside the skull cavity during preparation. Because of their small size and delicate nature the restoration presented here is not certain, but it appears that the three bones of the right sclerotic ring are represented, and the extra bone is the second sclerotic plate of the left eye. This is based on Stensiö's interpretation of *B. canadensis* (1948, figs 21, 30), which has been confirmed in the specimen of *Bothriolepis* from Gogo, Western Australia described by Young (1984b), in which the larger of the two posterior sclerotics is on the mesial side. Thus interpreted, both the sensory groove (soc) and the nasal notch (nn) have a mesial position in the restored sclerotic ring of *Nawagiaspis* (Fig. 5A). In this respect it resembles *Bothriolepis* in having the nasal openings notching the sclerotic ring of each side, the other side of the nasal opening presumably notching the lateral margin of the rostral plate (not known). This is in contrast to the condition in *Asterolepis* (e.g. Lyarskaya, 1981, fig. 24), or *Remigolepis* (e.g. Stensiö, 1948, fig. 16), where the nasal openings notch the anterior margin of the rostral plate, and have no connection with the sclerotic ring. However, as argued by Young (1984b), the condition in *Bothriolepis* is likely to be primitive for antiarchs generally.

Paired prelateral and submarginal plates of the cheek, and upper and lower jaw elements from the right side, are also preserved. The prelateral plate (Fig. 7) is of unusual shape, with a much longer anterior process than known in *Bothriolepis*. However, the sensory groove (psoc, Fig. 5C) crosses the plate in much the same position, and the prelateral abutts against the anterior edge of the submarginal in the same manner, as described for *Bothriolepis* by Young (1984b). The submarginal (Fig. 6) is again generally similar to that of *Bothriolepis* (Young, 1984b, pl. 57B, C), with a strong anterodorsal articular process (ad1, Fig.

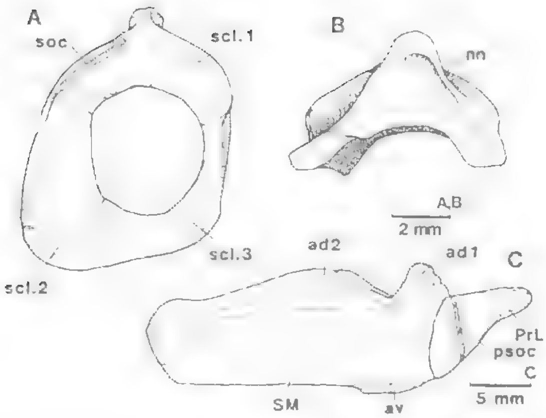

FIG. 5. *Nawagiaspis wadeae* gen. et sp. nov. A, restoration of right sclerotic ring in dorsal view. B, first sclerotic plate from the right side in ventral view. C, restoration of cheek plates from the right side, lateral view (after the holotype).

5C). It differs in being somewhat more elongate, with a straight ventral and convex dorsal margin. The dorsal margin carries a smooth bevelled area where the bone fitted against the lateral skull margin. The ventral margin is thickened at its anterior end to form a ventral articular surface (av), which is shown in the Gogo specimen of *Bothriolepis* to have been in contact with the lateral margin of the subcephalic division of the AVL plate of the trunk, to effect a seal to the branchial chamber when the operculum was closed (Young, 1984b, p. 640). In view of the close similarity in the arrangement of these bones in *Nawagiaspis* to those described by Young (1984b) it is highly probable that *Nawagiaspis* also had an infraprelateral plate, although it is missing from this specimen.

The SO plate differs from that of *Bothriolepis* in being relatively short, with an irregularly notched, near vertical posterior margin (Fig. 9A, B). The excellent preservation clearly shows that this irregular posterior margin is natural, lacking only

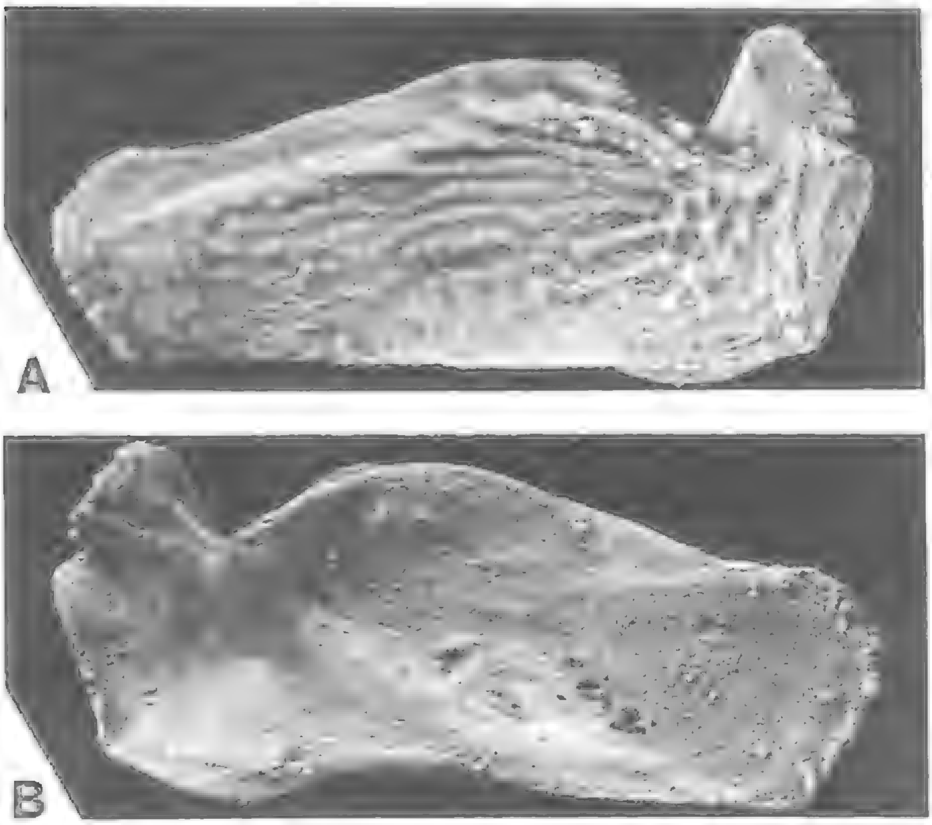

FIG. 6. *Nawagiaspis wadeae* gen. et sp. nov. Right submarginal plate from holotype in lateral (A) and mesial (B) views (x4).

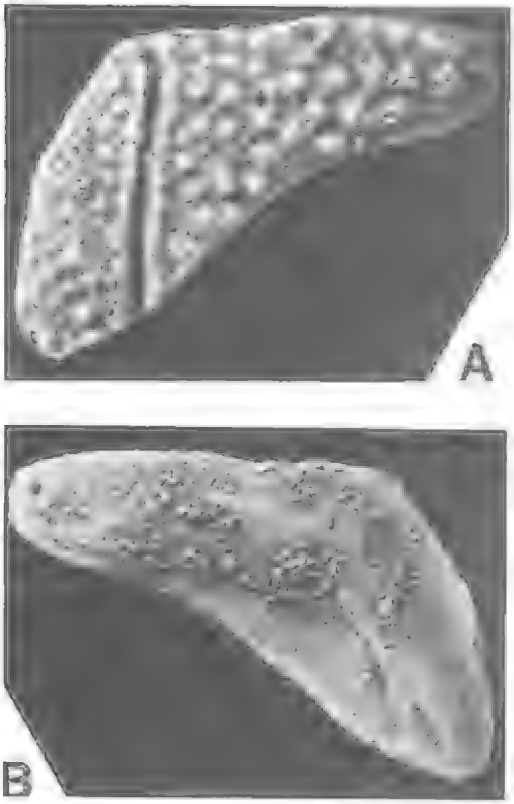

FIG. 7. *Nawagiaspis wadeae* gen. et sp. nov. Right prelateral plate from holotype in lateral (A) and mesial (B) views (x6).

a short posteroventral process (Fig. 8A). There is a smaller dorsal and a larger ventral notch on the lateral margin, a configuration not previously described for antiarchs. However, the bone resembles that of *Bothriolepis* in having a distinct posteroventral process, and a curved biting margin. As such there must have been a deep median notch between the left and right plates as in *Bothriolepis*, and in contrast to other genera where known (Fig. 8). The sensory groove (ifc3) terminates on the plate, in contrast to most other forms where it passes off the lateral margin (Fig. 8D, E). The visceral surface of the bone (Fig. 9B) shows a distinct ridge for supporting the palatoquadrate, as in *Bothriolepis* (Young, 1984b, fig. 3). Also as in that form there is a dorsomesial process forming a flattened area facing the symphysial plane, which may either have abutted against the SO of the opposite side, or else formed the attachment site for ligaments binding the two sides of the upper jaw together, as has been suggested for *Bothriolepis* (Stensiö 1948; Young, 1984b).

The infragnathal (Fig. 9C, D) resembles that of *Bothriolepis* in all its essential features, although the posterior non-biting portion is proportionately smaller (cf. Young 1984b, pl. 58). A final point is that the biting margins of both the upper and lower jaw elements of *Nawagiaspis* are smooth, in contrast to the serrations seen in *Bothriolepis*.

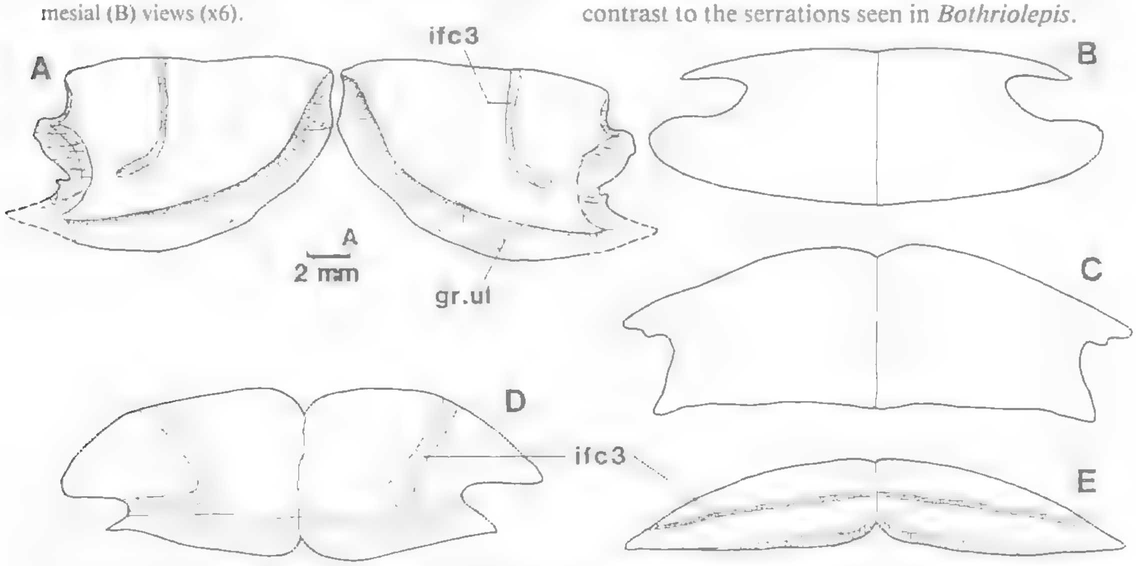

FIG. 8. Paired suborbital ('mental') plates forming the upper biting margin of the jaws in various antiarchs, external view (not to scale). A, *Nawagiaspis wadeae* gen. et sp. nov. (restored after the holotype); B, *Asterolepis scabra* (Woodward), after Nilsson (1941, fig. 5B); C, *Remigolepis* sp., after Nilsson (1941, fig. 6); D, *Pterichthyodes milleri* (Miller), after Hemmings (1978, fig. 6); E, *Asterolepis ornata* Eichwald, based on Lyarskaya (1981, figs 26, 73).

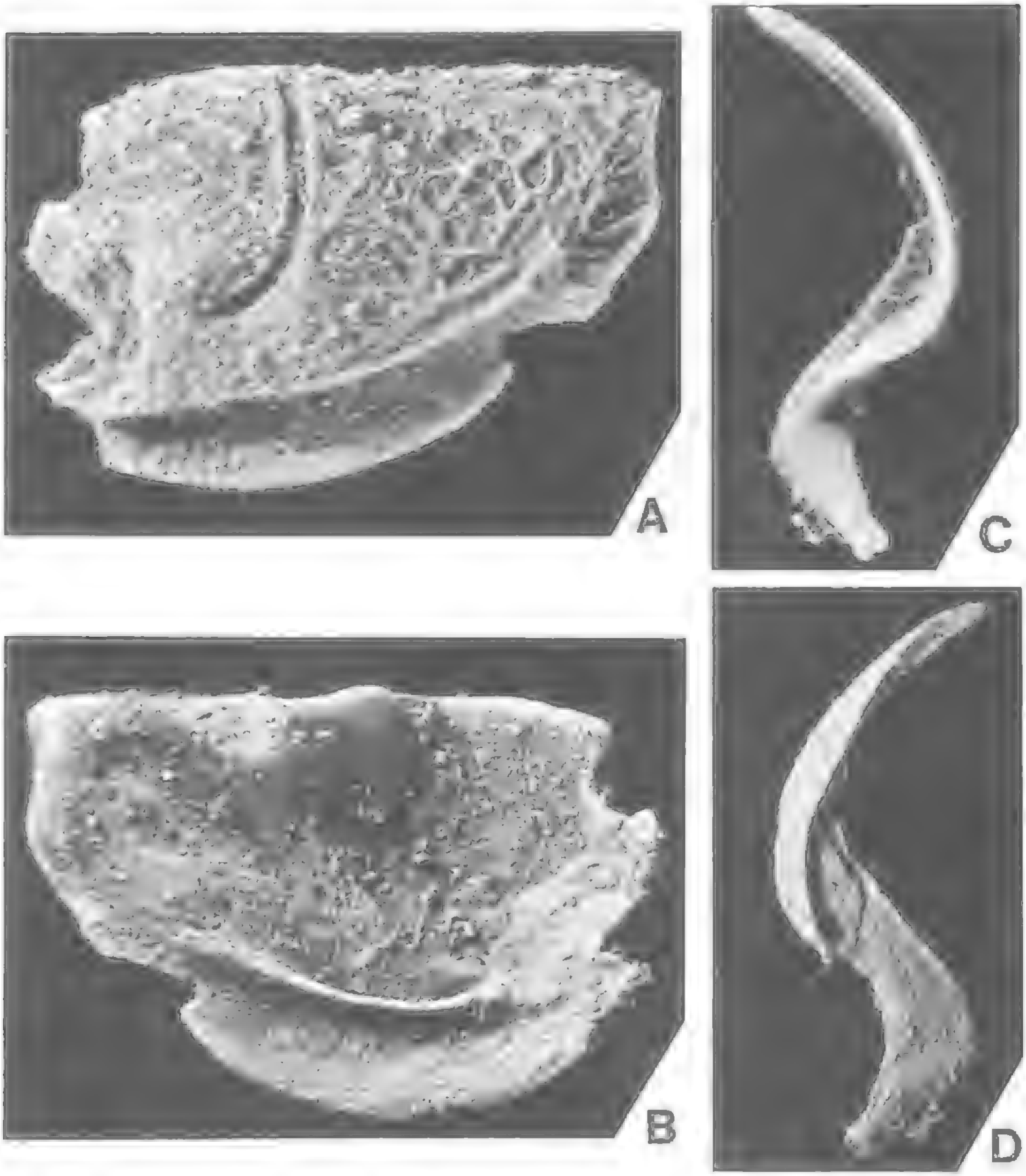

FIG. 9. *Nawagiaspis wadeae* gen. et sp. nov. Dermal bones of the upper and lower jaw as preserved in holotype. A, B, right suborbital ('mental') plate in external and internal views respectively; C, D, right infragnathal bone in dorsal and ventral views respectively (all x6).

The articulated trunk armour is relatively short and high. The distortion evident in anterior view (Fig. 10B) has been corrected graphically by restoring vertical and horizontal axes to rectangularity, to give angles of about 115° and 90° between dorsal and lateral and lateral and ventral walls respectively. The ventral wall is fairly flat, and the dorsal wall encloses an angle of about 130° at the midline (Fig. 11B). In dorsal view (Fig. 3) the dorsal wall is notable for its short broad proportions, with a restored midline length of about 47 mm, giving a L/B index of about 78. The dorsolateral ridge is distinctly curved, and in lateral view the midline is strongly arched rostrocaudally,

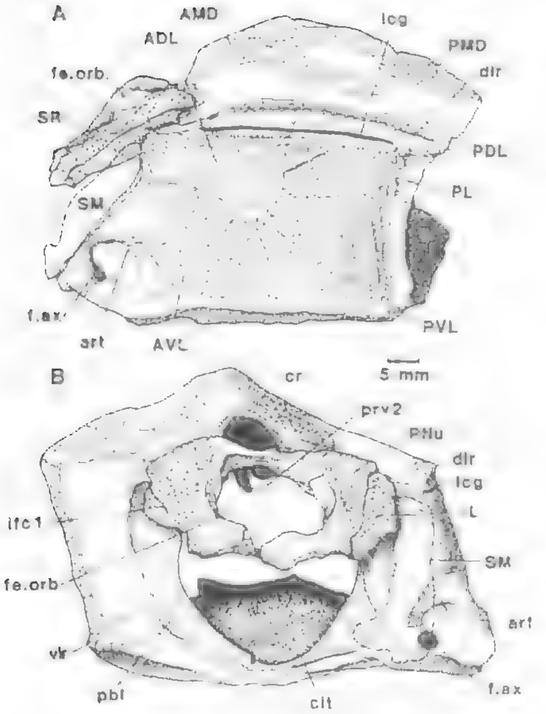

FIG. 10. *Nawagiaspis wadeae* gen. et sp. nov. Holotype in left lateral (A) and anterior (B) views, with position of the left submarginal plate against the trunk-armour indicated by a dashed line.

with the highest point at about the level of the AMD - PMD suture (Fig. 11A), in contrast to many other antiarchs where the highest point is the tergal angle of the AMD plate. The AMD shows only a faint external suture with the right ADL, but internal sutures on both sides are clear, and show that the plate had lateral corners, and was of similar length to, or slightly shorter than, the PMD. The anterior margin is missing but must have been about as wide as the weathered notch in the anterior margin of the trunk armour (Fig. 3), and it is clear that the AMD was not pointed anteriorly as it is in *Asterolepis* and *Remigolepis*. The posterior margin is poorly preserved and its shape is unclear. On its visceral surface the AMD shows a median ventral ridge, which at its anterior end is elevated as a crest (cr, Fig. 11A) behind the small oval pit (pt1) immediately inside the preserved margin. The levator fossa has been lost and is represented by the weathered anterior notch in the specimen.

The PMD shows the median section of the posterior transverse thickening just inside the preserved posterior margin (cr.tp, Fig. 11A), and it can be assumed that most of the length of the plate is preserved. Externally much of the plate is missing, and plate margins are obscure (Figs 2, 3). In front of the posterior transverse thickening on the visceral surface is a strongly-developed process projecting some 8mm beneath the surrounding bone surface, with the posterior pit facing anteriorly from its anterior surface (pt2, Fig. 11A). In front of this, another equally prominent median ventral ridge is developed (mvr), with a fairly flat ventral surface of cancellous bone which presumably abutted on the vertebral column.

The margins of the ADL are indistinct externally, but the dorsal margin is clear on the visceral surface. The dorsolateral ridge is strongly developed as a row of enlarged tubercles, and part of the obstantic process and main lateral line canal are visible in lateral view (Fig. 10A). Overall, the

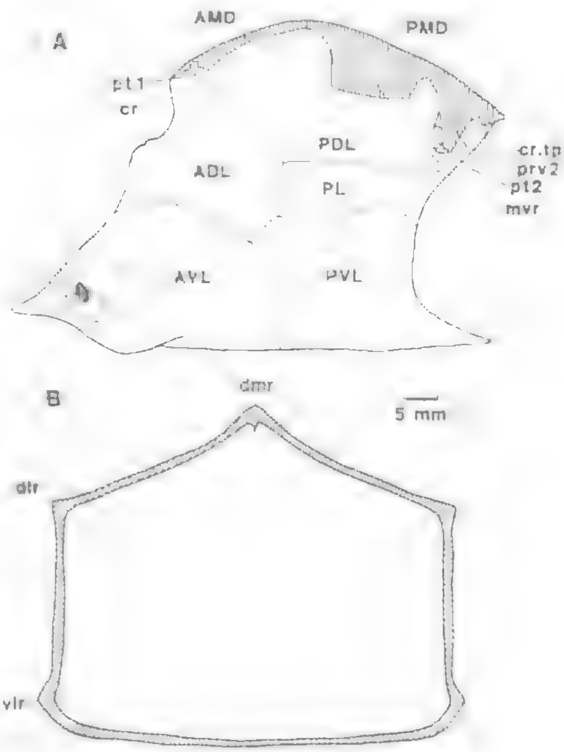

FIG. 11. *Nawagiaspis wadeae* gen. et sp. nov. A, trunk-armour in left lateral view, showing sagittal section through anterior and posterior median dorsal plates of the dorsal wall, and suture pattern for dermal bones of the lateral wall (based on the holotype). B, transverse section through trunk-armour at the level of the anterior dorsolateral plates (restored after the holotype).

lateral wall of the trunk is short and high, with a B/L index of about 66. Its surface is strongly ornamented, and bone sutures are indistinct externally. The tubercles may be aligned in radiating rows, and are fused into vertical ridges inside the posterior margins of the MxL and PVL plates. The suture pattern is clear on the internal surface of the left side, and the four major bones making up the lateral wall are relatively short and high. It is noteworthy that the ADL and PVL are in contact along a short suture, which separates the MxL from the AVL (Fig. 11A). This is the arrangement seen in bothriolepidoid antiarchs, in contrast to the situation in asterolepidoids, where the ADL and PVL are separated by intervening bones. However, the visceral surface also shows what appears to be an incipient suture between the posterior dorsolateral and posterior lateral components of the MxL plate, suggesting that these bones were incompletely fused. A similar situation has been reported in various asterolepidoids, including the Australian species *Sherbonaspis hillsi* as described by Young and Gorter (1981), but in this case the posterior lateral component is extensively overlapped by the AVL. Janvier and Pan (1982, fig. 11) suggested that the 'mixilateral' plate in bothriolepidoids and asterolepidoids was independently derived, in the former by fusion of the PL with the PVL, and in the latter by fusion of the PL with the PDL. As discussed below, the evidence of other characters still indicates independent derivation of the MxL in the two groups, but *Nawagiaspis* shows that in both cases the PL fused with the PDL, and not with the PVL as Janvier and Pan (1982) proposed.

The AVL is incomplete anteriorly, and most of the subcephalic lamina is missing. Noteworthy is the very strong postbranchial lamina (pbl, Figs 3, 10B), which is much better developed than in *Bothriolepis*. The region of the pectoral fin articulation is partly preserved only on the left side. Because of the curvature of the lateral wall this faced anterolaterally rather than laterally. There is a smooth depressed area above an elliptical projection which in lateral view partly obscures the axillary foramen immediately in front. In its position the projection (art, Fig. 10) corresponds to the articular facet posterodorsal to the axillary foramen previously described in an unnamed asterolepidoid from central Australia (Young, 1984b). The margins of the axillary foramen are poorly preserved, but it was evidently smaller than in *Asterolepis* or *Bothriolepis* (e.g. Stensiö, 1931, figs 40-42). The processus brachialis is completely missing from both sides of *Nawagiaspis*. The lateral lamina of the PVL is preserved on both sides, but the ventral wall of the trunk is badly fractured, and the shape of the MV plate and extent of the subanal lamina of the PVL are unknown. Anteriorly the margins are broken a short distance in front of the postbranchial laminae, so there is no information on whether the semilunar plate was a paired bone, the primitive condition, or a single plate as in *Bothriolepis*.

Suborder ASTEROLEPIDOIDEI Miles (1968)
Family PTERICHTHYODIDAE Stensiö (1948)
Wurungulepis gen. nov.

ETYMOLOGY

After the Wurungu aboriginal tribe, another of the original tribes of the Broken River area.

DIAGNOSIS

A pterichthyodid with a mid-dorsal length of the trunk-armour attaining at least 100 mm. Trunk-armour triangular in cross-section, with acute angles between lateral and ventral walls at the ventrolateral ridge. Maximum breadth at the level of the ventrolateral ridge, which slightly exceeds height of the trunk-armour.

REMARKS

Although poorly known, *Wurungulepis* may be distinguished from other pterichthyodid genera on the basis of trunk-armour shape and proportions as restored below. From *Sherbonaspis* it differs in the apparently higher and deeper AMD, which is probably of similar length to the PMD, the proportionately shorter and deeper ADL, MxL, AVL, and PVL plates, and the more tuberculate ornament. *Pterichthyodes* differs in having a proportionately longer AMD, and a lower and longer trunk-armour which is less triangular in cross-section, with a more narrow ventral surface. *Stegolepis*, *Byssacanthus*, and *Lepadolepis* have an obtuse rather than acute angle at the ventrolateral ridge, with the trunk-armour broader at the level of the dorsolateral ridge than the breadth of the ventral surface. *Byssacanthus* also differs in the proportionately longer AMD, and probably the median dorsal spine, and *Grossaspis* also has a high dorsal spine.

In the development of the trunk-armour *Wurungulepis* most closely resembles the genus *Gerdalepis* Gross. In both there is an acute angle between the lateral and ventral walls of the trunk-armour at the ventrolateral ridge, and the AMD is only slightly longer than the PMD. However, in cross-section the trunk-armour of *Gerdalepis* is higher and narrower, and in lateral view the PVL is noticeably lower and longer (Gross, 1941, fig. 2), whilst the ornament is of more densely packed tubercles. Whether the peculiar apical chamber of *Gerdalepis* is present in *Wurungulepis* is unknown.

Wurungulepis denisoni sp. nov.
(Figs 12, 13)

1981 'pterichthyodid-like form', Young & Gorter, p. 90.

ETYMOLOGY

After the late Dr R.H. Denison (1911-1985), who made a major contribution to the study of placoderm fishes (e.g. Denison, 1978).

HOLOTYPE

QMF16593, an articulated trunk-armour with associated pectoral fin bones and scales.

LOCALITY

L4339, north bank of Broken River, GR 640460, Burges 1:100000 sheet (locality 2, Fig. 1).

HORIZON

Broken River Formation, Middle Devonian, probably Eifelian (J.S. Jell, pers. comm.).

DIAGNOSIS

As for genus (only species).

DESCRIPTION

The holotype was collected as a single articulated trunk-armour from which most of the exposed bone was weathered off, although the ventral surface and part of the left lateral side are largely intact. The matrix has been partly dissolved in acetic acid but preparation was discontinued because the bone is badly fractured. Nevertheless a reasonable indication of overall trunk-armour shape can be obtained. The associated bones of the right pectoral fin are indeterminate. During preparation many scales and small bony fragments were released from the matrix.

The trunk-armour is short and broad, and triangular in cross-section (Fig. 12B). Estimated dimensions are: median height, 56 mm; breadth across the ventrolateral ridges, 62 mm; total length 108 mm. The AMD is preserved as a portion of tuberculated bone on the left side, and an impression of the visceral surface on the right. The dorsal-most preserved parts of left and right laminae of the AMD are about 5 mm apart, which suggests that this is close to the median dorsal ridge of the trunk-armour. It is assumed therefore that there was no median dorsal spine, although this is not certain.

The left lamina of the AMD is important in showing overlap areas for the ADL and MxL plates (oa.ADL, oa.MxL, Fig. 12A). The PMD and MxL plates are missing, but the overlap on the AMD and the level of the posterior margin (as indicated by the PVL plate) place some constraints on the restoration. The PMD must have been short and high, yet probably almost as long as the AMD (Fig. 12A), in contrast to the relative length of these bones in several other pterichthyodid genera (see above). The MxL (or PDL plus PL) must also have

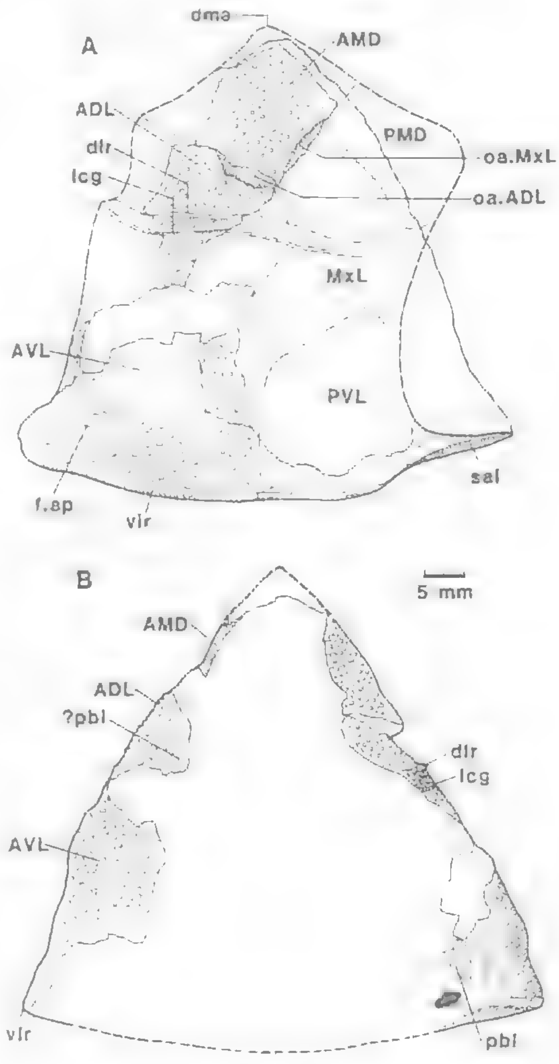

FIG. 12. *Wurungulepis denisoni* gen. et sp. nov. Holotype, QMF16593, an incomplete trunk-armour in left lateral (A) and anterior (B) views.

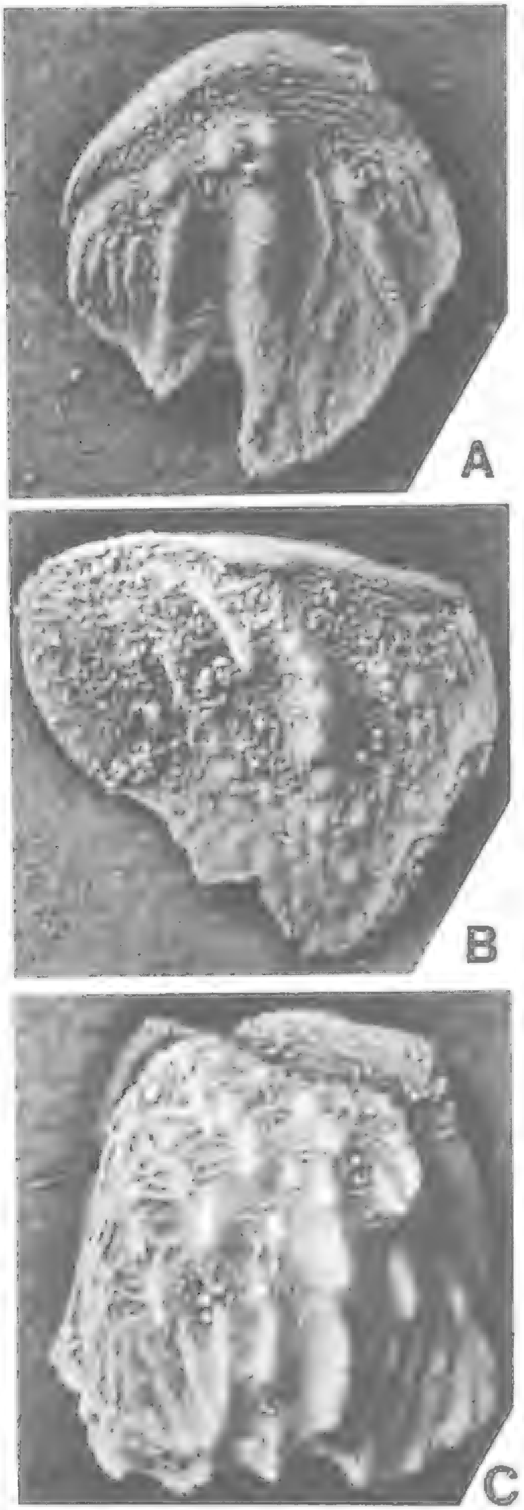

FIG. 13. *Wurungulepis denisoni* gen. et sp. nov. Examples of body scales from the holotype. (A, x18; B, C, x15)

been of short and deep proportions, judging by the shape of surrounding bones.

The ADL is partly preserved on both left and right sides, but only the left gives significant information, with short sections of the dorsolateral ridge and lateral line groove preserved (dlr, lcg). In anterior view the dorsal lamina of the plate is concave, and placed at a very obtuse angle to the lateral lamina. A small unornamented portion of the postbranchial lamina may be preserved on the right side (?pbl). The AVL has a large unornamented area on its lateral lamina (f.ap), which probably represents part of the articular fossa for the pectoral fin. However, the brachial process is missing, and there is no indication of the axillary fossa, which was presumably small as in other pterichthyodids. It is also possible that these structures were placed higher on the lateral wall, above the preserved part, as in *Lepadolepis* (Gross, 1933, pl. 3). The right AVL shows an area of tuberculate ornament, but no other features. Anteroventrally a poorly preserved portion of the postbranchial lamina is shown on the left side (pbl), but the anteroventral margin of the AVL is missing, so the form of the semilunar plate is unknown. Otherwise the ventral surface of the trunk-armour appears to be intact, but is mostly covered by matrix which cannot be readily removed without damage to the specimen. Part of the ventral lamina of the left AVL and PVL are visible in lateral view, the latter showing the full extent of the subanal lamina (sal). Most of the lateral lamina of the left PVL is missing above the ventrolateral ridge (vlr), but its length is indicated by the curvature of the free lateral margin of the subanal lamina. This in turn gives some idea of the length of the MxL and PMD plates, as noted above.

Although much of the bone has been lost from the holotype, it is evident that the component bones of the trunk-armour were short and high, and that the AMD and PMD plates were not greatly different in length. As noted above the triangular cross-section of the trunk-armour is otherwise seen only in *Gerdalepis,* whilst the great breadth of the ventral wall relative to median height is not encountered in any other described pterichthyodid. These features justify the erection of a new genus and species.

The preserved scales in the holotype show that *Wurungulepis* resembled *Pterichthyodes* in its heavy squamation. About a dozen relatively complete scales are available for study, showing a range of variation exemplified by the three illustrated scales (Fig. 13). Most scales have a rounded anterior margin and a pointed posterior margin. The latter may be irregular, or developed into several posterior processes. On the external surface of the scale is an unornamented anterior rim behind which is a shallow sulcus, corresponding to the overlap area for the preceeding scale described by Young (1984a, fig. 8). The ornamented part is covered with irregular tubercles or posteriorly directed ridges. The scale of Fig. 13A is a typical ridged scale, and that of Fig. 13B is an example where tubercles predominate. In both types there is generally an enlarged central ridge, tubercle, or tubercle row just behind the anterior sulcus. This is also a feature of the flank scales of *Pterichthyodes* (Hemmings, 1978, fig. 22C), and of the scales described by Young (1984a). Ventrally these flank scales have an ovate, shallowly-concave base which is generally between a half and two-thirds the length of the scale. In overall proportions these scales vary between slightly longer than broad (Fig. 13A) to up to one third broader than long. In the available sample there are no elongate scales like the ridge scales of *Pterichthyodes* described by Hemmings (1978).

The scale of Fig. 13C differs in its more quadrilateral shape. It has a distinctly depressed overlap area along the anterior and right lateral margin, and a contact face of similar width on the ventral surface inside the posterior margin. This scale presumably came from some restricted region of the body; a few other fragments in the acid residues may belong to similar scales but these may also be broken pieces of dermal bone from the fin exoskeleton.

DISCUSSION

Relationships of the New Taxa

The salient features of *Nawagiaspis* may be summarised in relation to the synapomorphies listed for the major groups of antiarchs by Young (1984c). The following features suggest asterolepid rather than bothriolepid affinity:

1. the tubercular ornament;
2. the general anteromesial direction of the infraorbital sensory canal groove across the paranuchal and lateral plates of the skull;
3. the absence of an extensive preorbital recess;
4. the short anterior postorbital process;
5. the absence of a central sensory canal;
6. (possibly) the short obstantic margin;
7. separate PL and L plates.

On the other hand the following suggest bothriolepid affinity:

8. the lateral position of the nasal openings;
9. the articular process on the SM plate;
10. the lack of a symphysis between the SO plates;
11. the broad anterior margin on the AMD;
12. the common suture between the ADL and PVL.

A decision regarding placement of *Nawagiaspis* depends on which of these similarities are symplesiomorphies, and which are valid synapomorphies. For features of the cheek and jaws this distinction is difficult to make because these aspects of morphology are poorly known in yunnanolepids, the obvious outgroup. In *Microbrachius* the cheek plates are poorly known and the prelateral plate was assumed to be absent by Hemmings (1978) because the concave skull margin resembled that of *Asterolepis*. This argument no longer applies since Lyarskaya (1981) has reported a prelateral in *Asterolepis*, although details of its structure are not available. The most interesting specimen of *Microbrachius* showing the cheek plates is DMSW P513, which as figured by Hemmings (1978, pl. 9, fig. 1) appears to show a space for the prelateral. Watson's earlier interpretation of this specimen (Watson, 1935, fig. 8), clearly shows this notch, and a mesial articular process on the SM plate. I therefore accept this as evidence that the articular process was present in this form, and with reference to the antiarch cladogram of Young (1988) this implies its presence also in *Dianolepis* and *Monarolepis*. The important character for placement of *Nawagiaspis* then becomes the shape of the nuchal plate, and whether it was excluded from the orbital fenestra by the postpineal plate as in *Dianolepis* (and the genus *Tenizolepis* Malinovskaya, 1977, if correctly referred to the bothriolepidoids), or whether it reached the orbital fenestra as in *Monarolepis*, *Grossilepis*, and *Bothriolepis*. Additional material is required to resolve this question.

Denison (1978) did not recognise a pterichthyodid grouping within his 'family Asterolepidae', and Janvier and Pan (1982) regarded *Stegolepis*, *Byssacanthus*, and *Pterichthyodes* as a paraphyletic group because of differences in the breadth of the lateral plate of the skull. Nevertheless, these and the other genera grouped by Young and Gorter (1981) and by Young (1984c, character 33, fig. 2) all conform in having a high short trunk-armour as described above for the new genus *Wurungulepis*. The short and high trunk-armour distinguishes the genera

Pterichthyodes, *Gerdalepis*, *Stegolepis*, *Byssacanthus*, *Grossaspis*, *Lepadolepis*, *Sherbonaspis*, and *Wurungulepis* from the low broad trunk-armour of other asterolepids. Outgroup comparison suggests that the short high trunk is the specialised condition, and for this reason a family Pterichthyodidae has been retained here, although clearly additional characters are needed to confirm the monophyly of the group (Janvier & Pan, 1982). The resemblance between *Wurungulepis* and *Pterichthyodes* in the ridged ornament on the scales could be a familial character, and, if so, the unnamed form from western Queensland (Young, 1984a) would also belong here. However, this character must remain provisional until the squamation in the other pterichthyodid genera listed above is better known. It should be noted, however, that in *Asterolepis* the scales have a predominantly tuberculate ornament (Lyarskaya, 1977, fig. 6), presumably the primitive condition.

BIOSTRATIGRAPHY

Middle Devonian antiarchs from Australia are still very poorly known, but the new forms described here are potentially important because they occur in marine limestones which may be subjected to conodont analysis. Assuming a close phyletic relationship to freshwater forms of similar age, they may provide another tool in correlating marine with non-marine Devonian strata. The new forms described here have little direct contribution to current understanding of Devonian vertebrate biostratigraphy in Australia, but they add to the taxonomic documentation of the faunas, which must proceed if the reliability of correlations and zonation using vertebrates is to be refined.

The Broken River Formation containing these new antiarchs has an age range of Lochkovian (*pesavis* conodont zone) to Givetian (Wyatt & Jell, 1980; Mawson *et al.*, 1985; Mawson, 1987). A detailed analysis of conodont faunas in the Middle Devonian part of the formation is not yet available, and in the Broken River area in the vicinity of the vertebrate localities (Fig. 1) the sequence is complicated by faulting and anticlinal folding, so that no reliable thickness can be ascertained (Wyatt & Jell, 1980). The lowermost Eifelian *partitus* conodont zone has been identified not far from the type locality of *Wurungulepis*, but conodont analysis of this section is again hampered by structural complication and possible debris-flow (allochthonous) contamination (Mawson *et al.*, 1985). It is to be hoped that new macro- or microvertebrate remains referable to *Nawagiaspis* or *Wurungulepis* will be found in other areas of the Broken River Formation more amenable to detailed conodont analysis (see Mawson *et al.*, 1985).

Young and Gorter (1981) perceived four distinct vertebrate faunas in the Australian Middle Devonian, of which the Broken River occurrences were included as the second youngest. The oldest was considered to be the *Wuttagoonaspis* fauna known from the lower part of the Mulga Downs Group in western NSW, and the Cravens Peak Beds and Lower Dulcie Sandstone in the Georgina Basin in central Australia. Young (1984a) described a small asterolepid antiarch from the Cravens Peak Beds, and suggested that it was the oldest representative of the group in Australia, based on an Emsian age for the *Wuttagoonaspis* fauna. Previously, the oldest asterolepid antiarch was reported to be *Gerdalepis* in the Eifelian Mühlenberg Formation of Germany (e.g. Andrews *et al.*, 1967), which belongs to the *Acinosporites macrospinosus* interval zone of the Eifel sequence, corresponding approximately to the upper *costatus* and *australis* conodont zones of the middle Eifelian (e.g. Streel *et al.*, 1987).

The possibility that asterolepid antiarchs occur earlier in Australia than elsewhere is of considerable interest, but this depends on the precise age of the *Wuttagoonaspis* fish fauna, which remains problematic. A maximum age for this fauna in western NSW is provided by the underlying marine Cobar Supergroup, which on the evidence of conodonts is largely or entirely of Lochkovian and Pragian age (Pickett, 1980, and pers. comm.). The existence or duration of a time break between the Cobar Supergroup and the overlying Mulga Downs Group containing the *Wuttagoonaspis* fish fauna is controversial, and some elements in the Cravens Peak Beds fish fauna might suggest a younger age within the Middle Devonian (Turner & Young, 1987). This would bring the asterolepid occurrence reported by Young (1984a) and that recorded here from probable Eifelian strata in the Broken River Formation into line with pterichthyodid occurrences elsewhere, which are Eifelian at the earliest (e.g. Denison, 1978). Determining a younger age limit for the *Wuttagoonaspis* fish fauna thus remains an important problem for resolution before the Middle Devonian vertebrate succession of Australia can be clarified.

ACKNOWLEDGEMENTS

I thank Dr Mary Wade and Dr John Talent for making the material available for study, and Dr John Jell for advice on localities and age. R.W. Brown and H.M. Doyle photographed the specimens, and Dr R.J. Ryburn provided assistance with the reference list through his 'Autoref' computer program. Drs J. Long and S. Turner kindly read and commented on the manuscript. Published with the permission of the Director, Bureau of Mineral Resources, Geology & Geophysics, Canberra.

LITERATURE CITED

ANDREWS, S.M., GARDINER, B.G., MILES, R.S. AND PATTERSON, C. 1967. Pisces. p. 637-83. *In* Harland, W.B., *et al.* (Eds), 'The Fossil Record'. (Geological Society of London: London).

DENISON, R.H. 1978. 'Placodermi. Handbook of Paleoichthyology, volume 2' (H-P. Schultze, Ed). (Gustav Fischer Verlag: Stuttgart). vi +128 pp.

GROSS, W. 1933. Die Wirbeltiere des rheinischen Devons. *Abh. Preuss. Geol. Landesanst.* **154**: 1–83.

1941. Neue Beobachtungen an *Gerdalepis rhenana* (Beyrich). *Palaeontographica* **93A**: 193–214.

HEMMINGS, S.K. 1978. The Old Red Sandstone antiarchs of Scotland: *Pterichthyodes* and *Microbrachius. Palaeontographical Society Monographs* **131**: 1–64.

HILLS, E.S. 1929. The geology and palaeontography of the Cathedral Range and Blue Hills in north western Gippsland. *Proceedings of the Royal Society of Victoria* **41**: 176–201.

1936. Records and descriptions of some Australian Devonian fishes. *Proceedings of the Royal Society of Victoria* **48**: 161–71.

JANVIER, P. AND PAN, J. 1982. *Hyrcanaspis bliecki* n.g. n.sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Eifelian of northeastern Iran, with a discussion on antiarch phylogeny. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **164**: 364–92.

LONG, J.A. AND WERDELIN, L. 1986. A new Late Devonian bothriolepid (Placodermi, Antiarcha) from Victoria, with descriptions of other species from the state. *Alcheringa* **10**: 355–399.

LYARSKAYA, L. 1977. New data on *Asterolepis ornata* from the early Frasnian deposits of the Baltic region. p. 36-45. *In* Menner, V.V. (Ed.), 'Essays on phylogeny and systematics of fossil agnathans and fishes'. (Dumkova Nauka: Moscow). (Russian).

1981. 'Baltic Devonian Placodermi. Asterolepididae'. (Zinatne: Riga). (Russian with English abstract). 152 pp.

MALIN OVSKAYA, S.P. 1977. The systematic position of the antiarchs from central Kazakhstan. p. 29-35. *In* Menner, V.V. (Ed.), 'Essays on phylogeny and systematics of fossil agnathans and fishes'. (Dumkova Nauka: Moscow). (Russian).

MAWSON, R. 1987. Documentation of conodont assemblages across the Early Devonian-Middle Devonian Boundary, Broken River Formation, north Queensland, Australia. *Courier Forschungs-Institut Senckenberg,* **92**: 251–73.

MAWSON, R., JELL, J.S. AND TALENT, J.A. 1985. Stage boundaries within the Devonian: implications for application to Australian sequences. *Courier Forschungs-Institut Senckenberg,* **75**: 1–16.

MILES, R.S. 1968. The Old Red Sandstone antiarchs of Scotland. Family Bothriolepididae. *Palaeontographical Society Monographs,* **122**: 1–130.

NILSSON, T. 1941. The Downtonian and Devonian vertebrates of Spitsbergen. 7. Order Antiarchi. *Skrifter om Svalbard og Ishavet* 82: 1–54.

PICKETT, J. 1980. Conodont assemblages from the Cobar Supergroup (Early Devonian), New South Wales. *Alcheringa* **4**: 67–88.

STENSIÖ, E.A. 1931. Upper Devonian vertebrates from East Greenland, collected by the Danish Greenland Expedition in 1929 and 1930. *Meddelelser om Grønland* **86**: 1-212.

1948. On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily bothriolepinae. With an attempt at a revision of the previous described species of that family. *Meddelelser om Grønland*, 139 (*Palaeozoological Groenlandica*, 2): 1–622.

STREEL, M., HIGGS, K., LOBOZIAK, S., RIEGEL, W. AND STEEMANS, P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Reviews in Palaeobotany and Palynology* **50**(1987): 211–29.

TURNER, S. 1982. A catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum,* **20**: 599–611.

TURNER, S. AND YOUNG, G.C. 1987. Shark teeth from the Early-Middle Devonian Cravens Peak Beds, Georgina Basin, Queensland. *Alcheringa* **11**: 233–44.

WATSON, D.M.S. 1935. Fossil fishes of the Orcadian Old Red Sandstone. p. 157-69, *In* Wilson, G.V., *et al.* (Eds), 'The Geology of the Orkneys'. *Memoirs of the Geological Survey of Scotland,* viii + 205 pp.

WYATT, D.H. AND JELL, J.S. 1980. Devonian and Carboniferous stratigraphy of the northern Tasman orogenic zone in the Townsville hinterland, North Queensland. p. 201-28, *In* Henderson, R.A. & Stephenson, P.J. (Eds), 'The Geology and Geophysics of northeastern Australia'. (Geological Society of Australia, Queensland Division: Brisbane).

YOUNG, G.C. 1984a. An asterolepidoid antiarch (placoderm fish) from the Early Devonian of the Georgina Basin, central Australia, *Alcheringa* **8**: 65–80.

1984b. Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis. Palaeontology* **27**: 625–61.

1984c. Comments on the phylogeny and biogeography of antiarchs (Devonian placoderm fishes), and the use of fossils in biogeography. *Proceedings of the Linnean Society of N.S.W.* **107**: 443–73.

1988. Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontographica* A202: 1–125.

YOUNG, G.C. AND GORTER, J.D. 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bureau of Mineral Resources, Australia, Bulletin* **209**: 83–147.

TWO NEW ARTHRODIRES (PLACODERM FISHES) FROM THE UPPER DEVONIAN GOGO FORMATION, WESTERN AUSTRALIA

JOHN A. LONG

Long, J.A. 1990 3 31: Two new arthrodires (placoderm fishes) from the Upper Devonian Gogo Formation, Western Australia. *Mem. Qd Mus.* 28(1): 51–63. Brisbane. ISSN 0079–8835.

Two new eubrachythoracid arthrodires are described from the Late Devonian (Frasnian) Gogo Formation, Canning Basin, Western Australia. *Fallacosteus turneri* gen et sp. nov., known from a complete individual, is an advanced camuropiscid with a snout similar to that of *Camuropiscis concinnus*. It differs in the arrangement of the cheek plates, and in the proportions of the headshield, the median dorsal plate and spinal plate, and has a characteristic suborbital plate indented posteriorly to meet the marginal plate. *Fallacosteus* is placed phyletically as the sister taxon to *Tubonasus*, implying that the tubular rostra of *Rolfosteus* and *Tubonansus* are convergent features. *Pinguosteus thulborni* gen. et sp. nov., known from an incomplete trunkshield, is believed to be a coccosteoid having unusually broad, short armour devoid of dermal ornament. Functional morphology of the camuropiscids is discussed.
☐ *Devonian, Frasnian, Gogo Formation, Placoderms, Arthrodire, Fallacosteus, Pinguosteus, Western Australia, Functional morphology.*

John A. Long, The Western Australian Museum, Francis St., Perth, W.A., 6001; 1 June 1988.

Two new fishes from the Late Devonian Gogo Formation are described here. Relationships o the more complete form, *Fallacosteus* gen. nov., are discussed along with the functional morphology of the camuropiscid group to which it belongs. As the Gogo fishes are three-dimensionally preserved, and placoderm morphology is well-known (Miles & Dennis, 1979; Dennis & Miles, 1979a, b, 1980, 1981, 1982, 1983; Miles, 1971; Miles & Young, 1977; Young, 1984; Forey & Gardiner, 1986; Dennis-Bryan, 1987), detailed plate-by-plate descriptions of the new forms are unnecessary. Following the approach of Miles and Dennis (1979), only the salient features of these new arthrodires are described, leaving the illustrations and tables of measurements to demonstrate their general morphology. The specimens are deposited in the Western Australian Museum (WAM). Throughout the paper the words "length, breadth and height" are abbreviated to L, B, and H respectively. Abbreviations used in the illustrations are listed below.

Field work carried out at Gogo over 1986/87 produced a large number of specimens including several new taxa and much new information on previously-described species (Long 1987a, b, 1988a, b, c). Although the two new genera described here are based on single individuals only, other Gogo arthrodire genera (*Harrytoombsia, Bruntonichthys, Bullerichthys, Camuropiscis laidlawi, Simosteus, Kimberleyichthys whybrowi, K. bispicatus*) were similarly defined on unique specimens. The range of intraspecific and intrageneric variation in arthrodires may be seen from new collections of Gogo coccosteids and *Eastmanosteus*. Observation of such variation permits determination of new genera founded upon single specimens. Because the acid-prepared Gogo material is undistorted, measurements and proportions of placoderm armour can be utilized accurately in distinguishing species, with narrow ranges for certain plate indices. Indices are here expressed as ratios of two linear dimensions multiplied by 100.

ABBREVIATIONS USED IN FIGURES

ADL	anterior dorsolateral plate
AL	anterior lateral plate
AMV	anterior median ventral plate
ASg	anterior superognathal
AVL	anterior ventrolateral plate
br.lam	branchial lamina of IL plate
CE	central plate
con	articular condyle of ADL plate
csl	central sensory-line canal groove
d.e	opening for the endolymphatic duct
Ifg	inferognathal bone
ifo	infraorbital sensory-line canal groove
IL	interolateral plate

lc	main lateral-line sensory canal groove
MD	median dorsal plate
MG	marginal plate
mll	main lateral-line canal groove
mpl	middle pit-line groove
mvr	median ventral ridge of MD plate
NU	nuchal plate
AVL	area on PMV plate overlapped by AVL plate
oa.MG	area on SO plate overlapped by MG plate
oa.PTO	area on SO plate overlapped by PTO plate
P	pineal plate
PDL	posterior dorsolateral plate
pec.f	pectoral fenestra
PL	posterior lateral plate
PMG	postmarginal plate
PMV	posterior median ventral plate
PN	postnasal plate
PNU	paranuchal plate
ppl	posterior pit-line groove
pp.lam	postpectoral lamina of PVL plate
PRO	preorbital plate
PSg	posterior superognathal bone
PSO	postsuborbital plate
PTO	postorbital plate
PVL	posterior ventrolateral plate
R	rostral plate
SM	submarginal plate
smd	submedian dorsal bone
SO	suborbital plate
soa	subobstantic margin of headshield
soc	supraorbital sensory-line canal groove
so.lam	suborbital lamina of SO plate
Sp	spinal plate
vpm	vertical section of subobstantic margin of headshield

SYSTEMATIC PALAEONTOLOGY

Order ARTHRODIRA
Suborder EUBRACHYTHORACI
Family CAMUROPISCIDAE
Dennis and Miles, 1979

Diagnosis

As in Long, 1988a.

Remarks

The new genus does not possess any unusual features to warrant amendment to the familial diagnosis, recently revised in the light of the discovery of a primitive new camuropiscid, *Latocamurus* (Long, 1988a).

Genus **Fallacosteus** gen. nov

Etymology

Latin *fallacio*, deceit; *os*, bone. Alluding to the rostral plate which resembles that of *Camuropiscis concinnus*. The gender is male.

Type Species

Fallacosteus turneri sp. nov.

Diagnosis

Camuropiscid arthrodire with flat, elongate rostral plate similar to that of *Camuropiscis concinnus*; headshield B/L index of 58; preorbital plates have zig-zag median suture; suborbital plate indented posteriorly to receive an anteroventral lobe from the marginal plate; marginal plate has an extensive anterodorsal lobe below main lateral-line canal groove which almost reaches the junction of infraorbital and main lateral line grooves; postsuborbital plate overlaps marginal plate and excludes submarginal from contact with suborbital plate; median dorsal plate has strongly-indented anterior margin with total B/L index close to 66; spinal plate very short; dermal ornament of small, densely-packed pointed tubercles.

Remarks

The new genus resembles *Camuropiscis concinnus* in the shape of the rostral plate. It differs from *C. concinnus* by the submarginal plate not contacting the suborbital, the broader headshield, shorter spinal, broader median dorsal, proportional size of the postorbital division of the cheek (Table 2), and morphology of the suborbital and marginal plates. It may be distinguished from the other camuropiscids by the shape of the rostral plate and proportions shown in Table 2. The total B/L index stated in the diagnosis and in Table 2 refers to the maximum breadth/maximum length of the median dorsal plate, not incorporating the paramedian length given in Table 1.

Fallacosteus turneri sp. nov.
(Figs 1-3, 4, 5B, 6, 7A)

1988c *Fallacosteus turneri*; Long, p. 439, 440, fig. 3 bottom, *nomen nudum*.

Etymology

For Dr Susan Turner, for her role in organising the de Vis Symposium and contributions to vertebrate palaeontology.

Diagnosis

As for genus.

TABLE 1. Measurements of (in millimetres) *Fallacosteus turneri* gen. et sp. nov., Holotype WAM 86.9.697, based on the scheme of Miles and Dennis (1979).

Length of skull	67.4	Length of Ifg	30
Breadth of skull across posterolateral angles	32	Length of biting division of Ifg	15
Breadth of skull across posteromedial angles	37.6	Length of trunk shield	85.5
Depth of skull	25	Breadth of trunk shield	39
Prepineal length	26.4	Depth of trunk shield	38.5
Length of orbit	16	Rostrocaudal length of flank armour	27
Length of NU	19.5	Length of pectoral fenestra	14
Length of lateral articular fossa	3.2	Length of MD	32.4
Depth of lateral articular fossa	ca.1.8	Breadth of MD	26
Angle between axis of articular fossa and dorsolateral surface of skull	250	Length of Sp	6
Length of cheek	36	Angle between Sp and rostrocaudal axis of armour	ca.11°
Length of postorbital division of cheek	21	Length of AVL	35
		Length of spinal division of AVL	17.5

Holotype

WAM 86.9.697, almost complete individual lacking only the parasphenoid, left submarginal and postmarginal plates.

Occurrence

From near Long's Well (close to locality no. 55 of Miles 1971, fig. 1). Gogo Station, near Fitzroy Crossing, Western Australia; Gogo Formation, Lower Frasnian.

Measurements

Table 1. Measurements follow points designated by Miles and Dennis (1979, figs 1-3). Proportional statements in the diagnosis along with other indices are shown with those of other camuropiscids in Table 2.

Description

The description of salient morphological features is given within a phylogenetic framework which assumes that because *Fallacosteus* is a camuropiscid then it is also a eubrachythoracid arthrodire possessing all the characters of this group (Dennis & Miles, 1983). The spindle-shaped armour of *Fallacosteus* is restored in lateral, dorsal, ventral and anterior views (Figs 1, 2). *Fallacosteus* is recognized as a camuropiscid by the following characters (from Long, 1988a):

(1). The rostral plate is broad posteriorly (Figs 4B, 7E), slightly broader than that in *C. concinnus* (Fig. 5A), having exactly the same outline in dorsal view as that of *Tubonasus* (Fig. 5C), and differing from the T-shape rostral plates of other coccosteoids (*sensu* Denison, 1984).

(2). The postnasal plate is deep and excludes contact between the suborbital and preorbital plates (Fig. 4A). Although the postnasal is only partly preserved, its full outline can be restored from its overlap areas on the preorbital and rostral plates (Fig. 1).

(3). The cheek unit is firmly attached to the lateral margin of the skull roof (Fig. 3; 4A). The suborbital is unique amongst camuropiscids in the shape of its dorsal margin and its indented posterior margin, and resembles *Camuropiscis* in the degree of interconnection between the cheek and skull roof (Fig. 6).

(4). The dentition is durophagous (Figs 4D-G). The toothplates closely resemble those of

TABLE 2. Comparative indices of certain morphological features in camuropiscid arthrodires. L, *Latocamurus*; C, *Camuropiscis concinnus*; R, *Rolfosteus*; F, *Fallacosteus* gen. nov., T, *Tubonasus*. (n) = number of specimens. Indices rounded to nearest whole number. Range stated where more than one specimen measured. HS = headshield, TS = trunkshield; plate names as in list of abbreviations.

	L (1)	C (1)	R (1)	F (1)	T (2)
Headshield B/L	ca.73	48	35	58	51-55
Orbit/prepineal L HS	ca.43	42	37	39	40
Descending lamina PRO/L PRO	33	28	45	28	36
L postorbital division cheek/skull L	41	27	19	31	25-28
MD plate B/L	58	61-66	68	80	68-74
Max. L MD B/L	54	60	60	67	67
TS B/L	ca.48	46	38	46	47
Sp.L/AVL L	34	23	ca.20	17	12-13
Pect.fenestra L/TS L	20	18	18	16	16

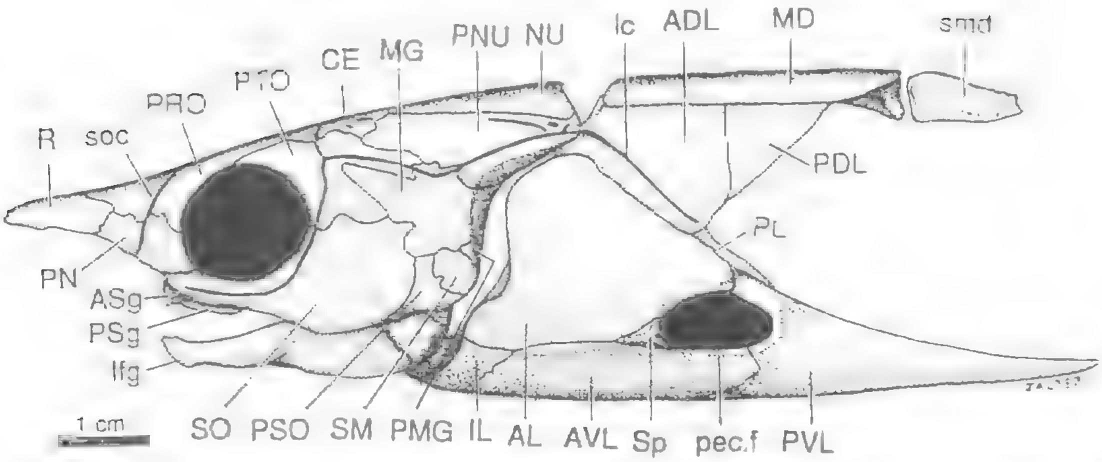

FIG. 1. *Fallacosteus turneri* gen. et sp. nov. Restoration of dermal skeleton in lateral view, after holotype WAM 86.9.697.

Camuropiscis, *Tubonasus*, and *Rolfosteus* in having broad, flat, crushing surfaces, differing from *Latocamurus* which has broad, rounded tubercles on the upper jaw toothplates.

(5). The postsuborbital and submarginal plates are reduced in size, relative to other coccosteiods, and form a tightly-connected unit (Figs 4A, 7A). The submarginal has an indented anterior margin where it meets the postsuborbital. A subcutaneous sensory pit, seen in *Tubonasus* (Dennis & Miles, 1979b, fig. 15A) is not present.

(6). Preorbital plates have medial contact (Fig. 4B). Unlike other camuropiscids the preorbital plates form a very jagged suture along their area of contact.

(7). The postmarginal sensory-line groove is not present (Fig. 4A).

(8). The main lateral-line groove always crosses the ventral part of the anterior dorsolateral plate (Fig. 4A). This character may occur in other arthrodires (e.g. *Harrytoombsia*), but in such cases a dorsal sensory-line groove is also developed. Camuropiscids display only the ventral branch of main lateral-line canal.

Although only characters 2 and 7 are unique to camuropiscids amongst arthrodires, all of the above characters are restricted to the family within the Coccosteoidei, and thus serve to define the monophyly of the group within this narrow frame of reference. It has been suggested that camuropiscids are derived from coccosteid stock and that *Incisoscutum* serves to bridge the gap with coccosteids (Denison, 1984; Long, 1988a).

Furthermore, *Fallacosteus* is identified as an advanced camuropiscid more derived than *Latocamurus* by virtue of:

(9). A pointed rostral plate (Figs 4A, B, 7E).

(10). The postsuborbital plate is smaller, being comparable in size with that of other camuropiscids (Fig. 6).

(11). The preorbital plates have more extensive median contact (Fig. 5), differing from *Latocamurus* which has only a very short area of contact between the preorbitals.

(12). The anterior lateral plate has extensive contact with the anterior ventrolateral plate (Figs 4A, C). This synapomorphy is one of the most distinctive features of advanced camuropiscids (Denison, 1984). The anterior ventrolateral plate lacks an upturned overlap lamina for the anterior lateral, seen also in *Tubonasus* (Dennis & Miles, 1979b, fig. 13H).

Fallacosteus is considered more derived than *Camuropiscis* or *Rolfosteus* because it shares the following synapomorphies with *Tubonasus:*

(13). The postsuborbital plate contacts the marginal plate and excludes the submarginal plate from contact with the suborbital plate (Fig. 6).

(14). The spinal plate is very short (Fig. 4A), shorter than in all camuropiscids except *Tubonasus* (Table 2).

(15). The pectoral fenestra is proportionately small (Table 2).

(16). The posterior margin of the cheek unit is almost vertically oriented and is more extensive than for other camuropiscids (vpm, Fig. 6).

DISCUSSION

This phylogenetic scheme leaves *Camuropiscis* and *Rolfosteus* as the stem group to *Fallacosteus*

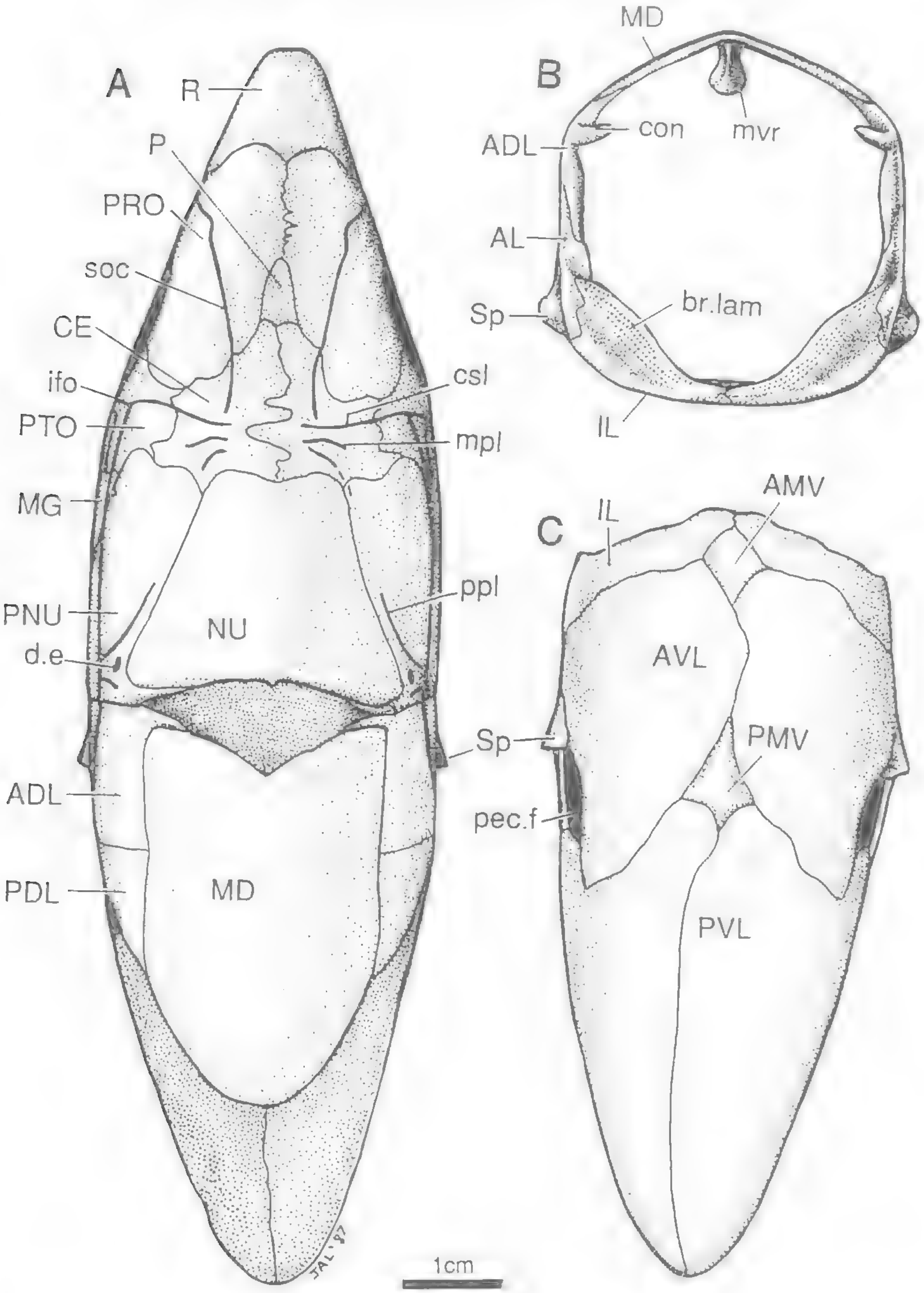

FIG. 2. *Fallacosteus turneri* gen. et sp. nov. Restoration of dermal skeleton in A, dorsal view, B, anterior view, and C, ventral view of trunkshield.

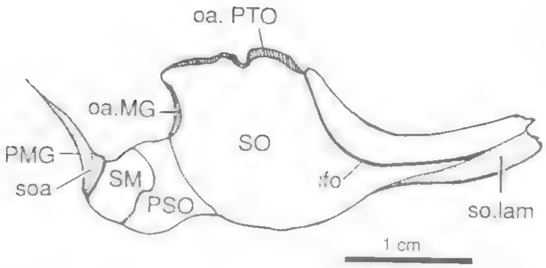

FIG. 3. *Fallacosteus turneri* gen. et sp. nov. Right cheek unit, with plates fitted together, after holotype WAM 86.9.697.

and *Tubonasus*, although there are no obvious characters uniting *Camuropiscis* and *Rolfosteus* as a distinct lineage.

In addition to these features, the following autapomorphies distinguish *Fallacosteus* from all other camuropiscids. The marginal plate has a very extensive anterodorsal lobe projecting far into the postorbital plate and almost reaching the junction of the infraorbital and main lateral-line grooves (Fig. 1). The ventral part of the marginal also projects into a concave margin on the suborbital plate (Figs 3, 4A). The holotype of *Tubonasus* shows a projection of the marginal plate into the postorbital plate, but this lobe includes the main lateral-line canal groove, whereas in *Fallacosteus* the sensory-line groove runs dorsal to the projecting lobe of the marginal plate. The dorsal margin of the suborbital plate is irregular but smooth, not sharply sutured to the skull roof as in *Camuropiscis*, but more firmly attached than for other camuropiscids (Fig. 6). The submarginal plate is indented anteriorly to receive a lobe from the postsuborbital plate (Figs 3, 4A). The preorbital plates meet in an irregular, sharply zig-zag suture. On the visceral surface of the rostral plate (Fig. 7E), a strong transverse ridge divides the anterior concave region from the flatter posterior region. The anterior region has a roughened surface, presumably for attachment of the rhinocapsular division of the endocranium.

Figs 7A-A' are a stereo pair of the visceral surface of the posterior half of the skull roof and cheek unit, showing typical features seen on other camuropiscids, such as the well-defined triangular depression on the postorbital plate (cf. Miles & Dennis, 1979, fig. 16, tri), the paired infranuchal pits, and the quadrate bone with its narrow detent process. The supraorbital vault has very weak postocular processes. The posterior face of the nuchal has only a single median process unlike the paired process of *Camuropiscis*.

The right pelvic girdle is well-preserved (Figs 4H, I), resembling closely that of *Camuropiscis* and *Incisoscutum* in approximately the same number and placement of neurovascular canals (Miles & Dennis, 1979, 1981). The girdle does differ in several points from that of *Camuropiscis*; the thickening of endochondral bone which rims the perichondral basal plate does not extend all the way around as in *Camuropiscis* but terminates at the level of the articular crest, as in *Incisoscutum*; the metapterygial articulation area is separated from the articular crest; the symphysial articulation area is posterolaterally-oriented in *Fallacosteus* instead of posteromedially-oriented as in *Camuropiscis*. If it can be assumed that the symphysial articulations had the same transverse orientation in the two genera, then the articular crest in *Fallacosteus* faced more posteriorly than in *Camuropiscis*. It appears that *Incisoscutum* had a similarly-directed pelvic girdle (Dennis & Miles, 1981, fig. 20).

The dermal ornament (Figs 4, 7A) consists of very closely-packed, high tubercles exactly as in *Camuropiscis*, being coarser than in *Latocamurus*, *Tubonasus* and *Rolfosteus*.

Suborder COCCOSTEOIDEI
Family indeterminate
Genus **Pinguosteus** gen. nov.

ETYMOLOGY

Latin *pinguis*, fat; *os*, bone. Alluding to the broad proportions of the armour. The gender is male.

TYPE SPECIES

Pinguosteus thulborni sp. nov.

DIAGNOSIS

A eubrachythoracid arthrodire having a very broad, short trunkshield with a posterior median ventral plate broader than long; a posterior ventrolateral plate with a short postpectoral lamina and a lateral lamina which meets the ventral lamina at 120°; anterior dorsolateral plate is twice as deep as long, with dorsal margin shorter than ventral margin; dermal bones lack ornament.

REMARKS

Despite the paucity of material, *Pinguosteus* is readily distinguished from all other known eubrachythoracids which possess a postpectoral lamina on the posterior ventrolateral plate (buchanosteids, coccosteids, pholidosteids, camuropiscids) by its unusually broad proportions. *Harrytoombsia* has the broadest trunkshield of the known Gogo arthrodires. It has a postpectoral

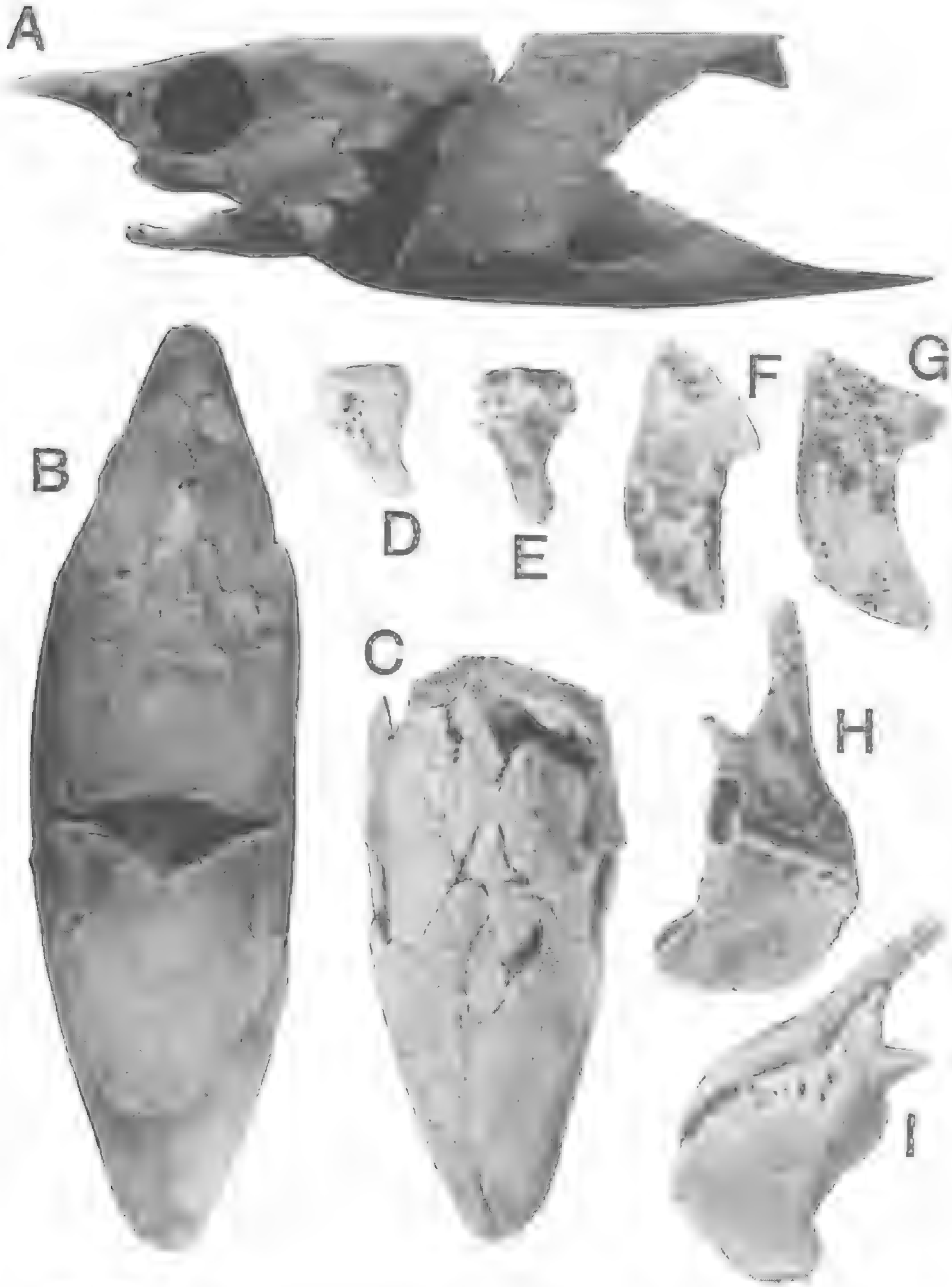

FIG. 4. *Fallacosteus turneri* gen. et sp. nov., holotype WAM 86.9.697.A, dermal skeleton in left lateral view; B, in dorsal view and C, in ventral view (trunkshield only), all natural size. D, left anterior superognathal in dorsal view. E, right anterior superognathal in ventral view. F, right posterior superognathal in ventral view. G, left posterior superognathal in ventral view (D-G, X 3). H, I, right pelvic girdle in (H) lateral view and (I) mesial view (X 3). Whitened with ammonium chloride.

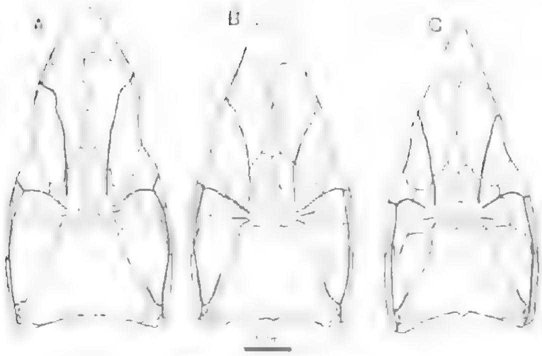

FIG. 5. Camuropiscid headshields in dorsal view. A, *Camuropiscis concinnus* (after Dennis and Miles 1979a, fig. 2); B, *Fallacosteus turneri* gen. et sp. nov.; C, *Tubonasus lennardensis* (after WAM 86.9.669).

lamina on the posterior ventrolateral plate (this excludes pachyosteomorph types such as *Eastmanosteus, Incisoscutum, Bruntonichthys* etc.), and the proportions of its trunk armour do not even closely approach that of *Pinguosteus* (Fig. 8). The absence of dermal ornament and shortness of the postpectoral lamina are further distinguishing features. I know of no other arthrodire likely to be confused with *Pinguosteus* since other broad-shielded forms either have dermal ornament or lack a postpectoral lamina (e.g. certain dinichthyids, homosteids, heterosteids; Denison, 1978).

Pinguosteus thulborni sp. nov.
(Figs 7B-D, F-I, 8A, 98)

1988c *Pinguosteus thulborni*; Long, p. 440, *nomen nudum*.

Etymology

For Dr Tony Thulborn, for his role in organising the de Vis Symposium and his contributions to vertebrate palaeontology.

Diagnosis

As for genus.

Holotype

WAM 86.9.698, only specimen, consisting of left anterior dorsolateral, posterior ventrolateral, posterior lateral and dorsolateral plates, posterior median ventral plate, imperfect right posterior ventrolateral plate, and a small pointed bone probably from the pelvic girdle.

Occurrence

Gogo Station, near Fitzroy Crossing, Western Australia; close to locality 79 of Miles (1971, fig. 1). Gogo Formation; Lower Frasnian.

Measurements

Posterior median ventral plate: L = 31 mm, B = 32.4 mm; anterior dorsolateral plate: H = 31.7 mm, L = 16 mm; posterior dorsolateral plate: H = 27 mm, L = 19.5 mm. Angle between ventral lamina and postpectoral lamina of posterior ventrolateral plate = 120°.

Description

As the plates are fully illustrated, the following comments deal with reconstruction of the trunk armour, an unusual, pointed bone probably from the pelvic girdle, and the dermal bone surfaces.

A small pointed bone (Figs 7B, C) referred to above, was found in association with the other remains in the same concretion. It is broad and flat at one end; the other end tapers sigmoidally to a sharp point. It lacks surface ornament or morphological features for attachment or overlap of other skeletal elements.

Discussion

The armour has been restored by fitting the posterior ventrolateral and posterior median ventral plates together with the medial margin of the first plate oriented approximately parallel with the rostrocaudal axis of the body (Figs 8A, 9). As in other arthrodires, the anterior ventrolaterals are restored as marginally shorter than the posterior ventrolaterals. The anterior dorsolateral and posterior dorsolateral plates overlap to give an idea of the lateral view of the armour (Fig. 9). An unusual feature of *Pinguosteus*, not seen in other Gogo arthrodires, is that the postpectoral lamina of the posterior ventrolateral plate is entirely visible in ventral view because the lateral lamina bends upwards at 120°, rather than at 90° as in most arthrodires. The specimens are not crushed or distorted, although some breakage occurred during preparation (Figs 7D, F). As reconstructed, the armour is unusually broad and short for an arthrodire with a deep profile. The broad posterior median ventral plate has a short transverse anterior margin for contact with the anterior median ventral plate.

From the asymmetry of the small pointed bone I assume it to be a paired element, not a singular intermyotomal bone, and most likely it comes from the pelvic girdle. In the pelvic girdle of *Fallacosteus* there is a stout ossification of endochondral bone around the perichondral basal plate, and it is likely that in *Pinguosteus tholborni* the endochondral rod became separated from the basal plate. It differs

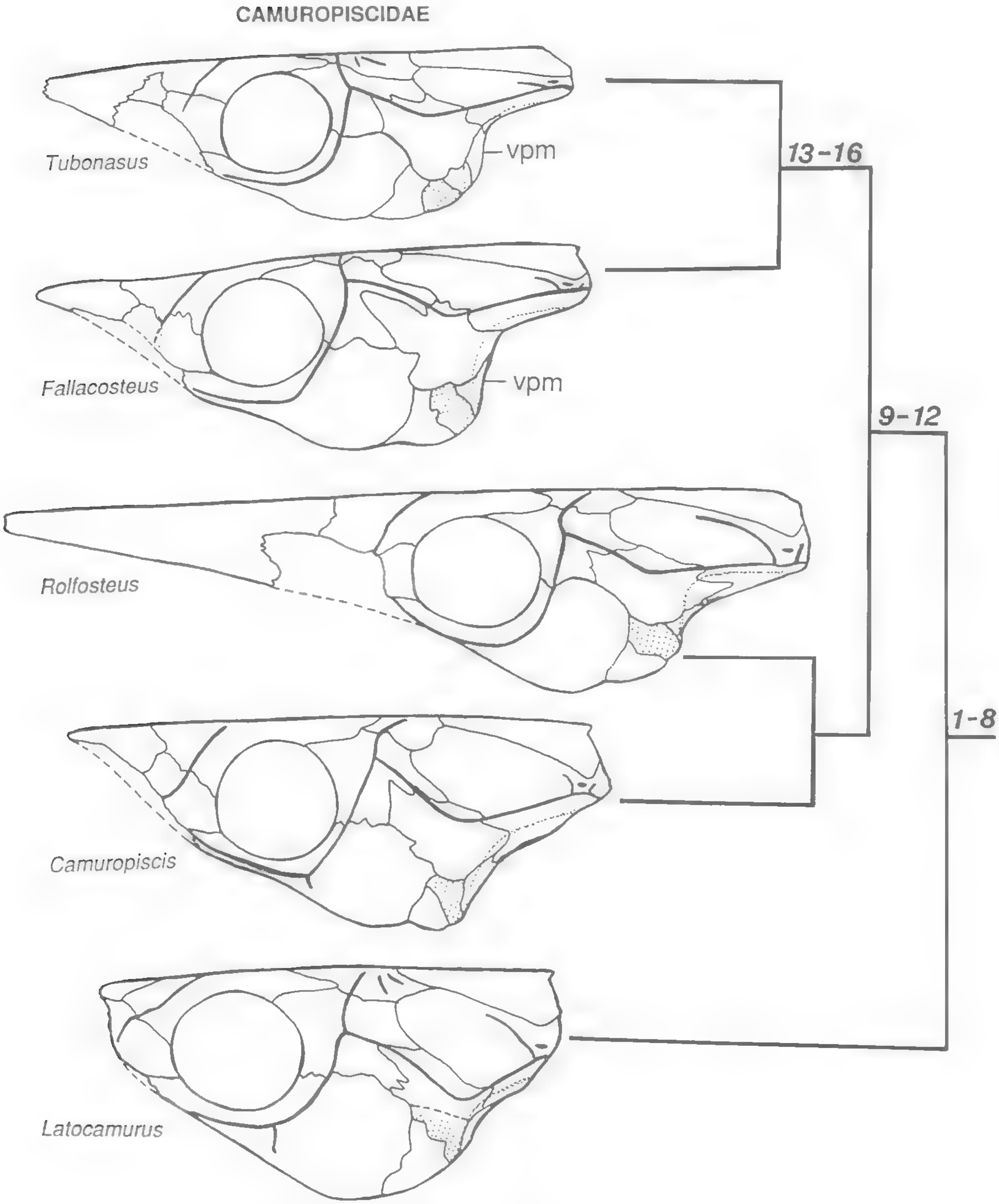

FIG. 6. Camuropiscid headshields in left lateral view arranged in scheme of interrelationships as discussed in text. Submarginal plates stippled. Synapomorphies listed in text.

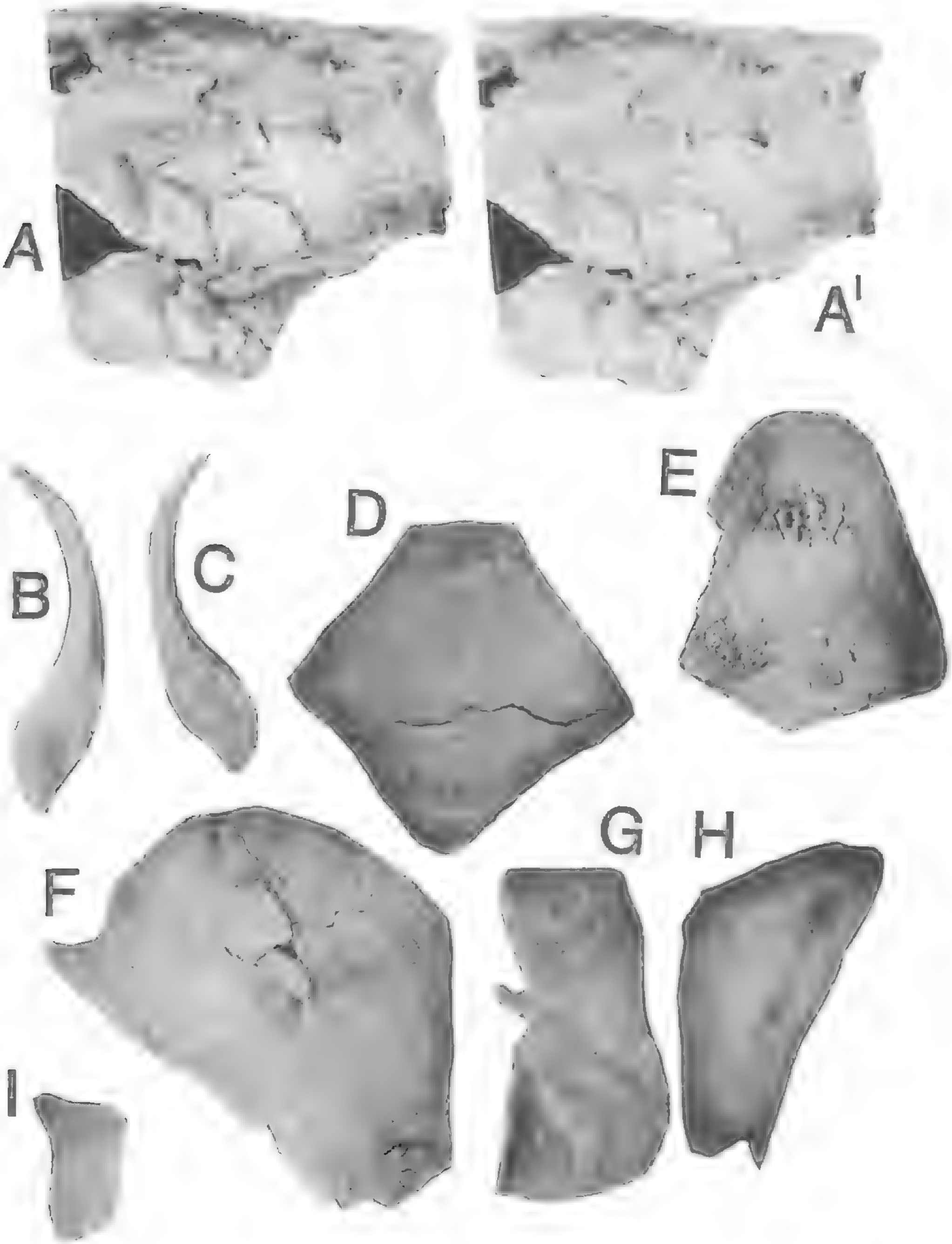

FIG. 7. A, E. *Fallacosteus turneri* gen. et sp. nov., holotype WAM 86.9.697. A, A' stereo pair showing visceral surface of right cheek and rear of skull roof (X 1.3); E, rostral plate in visceral view (X 2). B-D, F-I. *Pinguosteus thulborni* gen. et sp. nov., holotype WAM 86.9.698. B, C, possible endochondral rod from pelvic girdle in B, visceral? and C, lateral? views (X 5). D, posterior median ventral plate in ventral view; F, posterior ventrolateral plate in ventral view; G, left anterior dorsolateral plate in lateral view; H, left posterior dorsolateral plate in lateral view; I, right posterior lateral plate in lateral view (all X 1.5). Whitened with ammonium chloride.

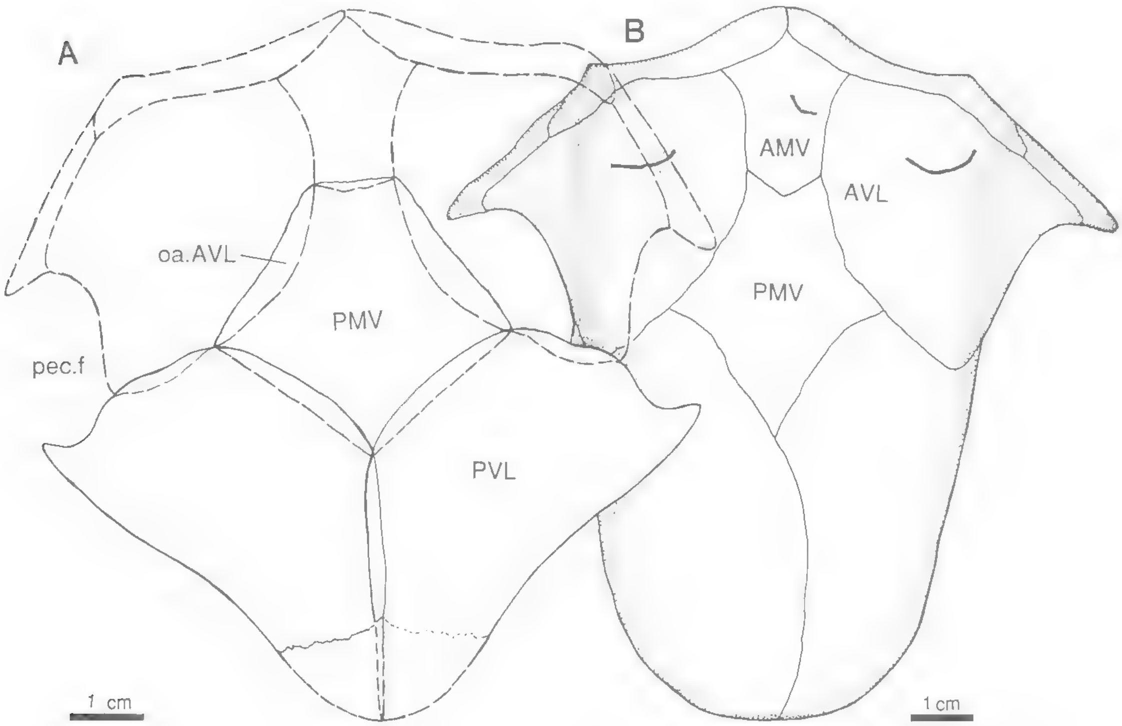

FIG. 8. Reconstructed trunkshield of (A) *Pinguosteus thulborni* gen. et sp. nov. in ventral view, compared with similar view of trunkshield of (B) *Harrytoombsia elegans* (after Miles & Dennis, 1979).

from that structure in *Fallacosteus* and *Camuropiscis* by having a broadened base. Alternatively, it could be a highly-reduced inferognathal (cf. *Homostius*), but if this were correct it resembles the inferognathal of an antiarch rather than that of an arthrodire (see

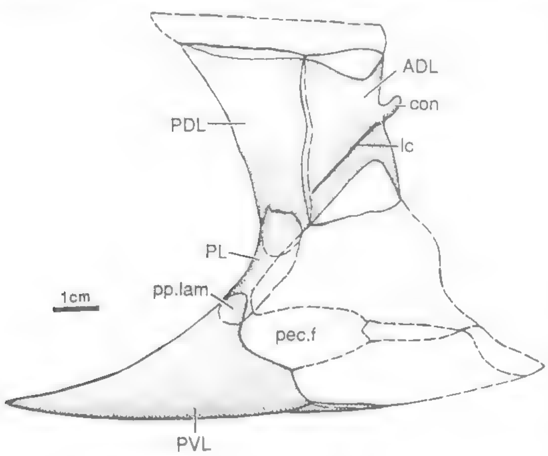

FIG. 9. *Pinguosteus thulborni* gen. et sp. nov., reconstructed trunkshield in lateral view, after holotype WAM 86.9.697.

Young, this volume). This interpretation is not supported by visible wear surfaces on the bone. As no bones from the head were found in the concretion it is likely that only the posterior part of the fish was preserved, and this favours the interpretation that this unusual element is a pelvic girdle bone. The pelvic girdle of *Holonema* contains a stout, rod-like bone with a thickened medially-directed base (pers. obs.), supporting the view that the curved, pointed bone in *Pinguosteus* is a pelvic bone.

The surfaces of the dermal bones lack tubercles or any other form of ornament. Some plates show areas of etched pitting, and it is possible that the few remains of *Pinguosteus* found in the same concretion came from the faeces of a large predator. Alternatively, the bones could have been attacked by algae or invertebrates whilst exposed on the muddy sea floor. If surface ornament was present on the plates originally there would certainly be some evidence of it after digestion, since older generations of tubercles are visible below the surface of bones (e.g. *Bullerichthys*, Dennis & Miles, 1980; *Eastmanosteus*, pers. obs.). Furthermore, the good preservation of the bone surface around the postpectoral lamina on the posterior ventrolateral plate shows the 'grain' of the dermal bone which has very fine depressions widely separated by perfectly smooth bone surface. I assume from these observations that *Pinguosteus* possessed dermal bones with smooth surfaces.

FUNCTIONAL MORPHOLOGY OF CAMUROPISCIDS

The relationships of the camuropiscids are shown in Fig. 6, based on synapomorphies listed above, and discussed by Long (1988a). From this scheme it is inferred that the tubular snouts of *Rolfosteus* and *Tubonasus* evolved independently, rather than by progression of rostral plate length from a common ancestor. This is supported by the complex arrangement of the posterior cheek regions shared by *Tubonasus* and *Fallacosteus* as well as other synapomorphies listed above. The major camuropiscid specializations (characters 1-8) have evolved in response to a durophagous diet. Thus modification of the jaw bones for crushing invertebrates or small fishes requires a firm junction between the cheek unit and the skull roof for increased pressure on the bite, and reduction in size of the postsuborbital plate which supports the quadrate and takes the most force during jaw adduction. At the anterior end of the skull the postnasal plate has been strengthened to sustain the increased pressure from the bite and brace the enlargened rostral plate. Further modifications for prey capture are seen in the very large eyes and elongation of the rostral plates and streamlining of body armour, presumably for reduction of drag when cutting through the water in pursuit of prey or escaping predators, possibly along the surface of the water as do modern sea gars (Alexander, 1967). This mode of surface-feeding would also favour the adaptation of a ventral course of the main lateral-line canal groove on the body.

Rolfosteus has the longest snout and most streamlined body armour yet retains a simple suborbital attachment to the skull roof, as does *Tubonasus*. The flat-snouted forms *Fallacosteus* and *Camuropiscis* have strongly attached cheek units, reflecting perhaps a different style of feeding which involved crushing prey of a harder nature than that eaten by *Rolfosteus* and *Tubonasus*. Possible food sources for camuropiscids could have been juvenile concavicarid crustaceans; these are commonly found as fossils in Gogo nodules and some species may have been nektonic (Briggs & Rolfe, 1983).

Placoderms similar to camuropiscids, such as *Oxyosteus* from the Frasnian Wildungen site, Germany, are believed to have evolved their long tubular rostral plates independently because of specializations shared in the trunkshield with other brachydeiroid arthrodires (Dennis & Miles, 1979b; Denison, 1984), and because of the absence of camuropiscid synapomorphies. Similar morphological features of camuropiscids and brachydeiroids, narrow elongated armour, durophagous dentition, for example, may have resulted from both groups preying on similar crustaceans. The close faunal affinity of crustacean faunas from Gogo and central Europe has been noted by Rolfe (1966).

ACKNOWLEDGEMENTS

Field work in the Kimberley over the 1986/87 seasons was funded by a grant from the National Geographic Society (#3364-86), and through a National Research Fellowship - Queen Elizabeth II Award. I sincerely thank my volunteer field assistants for their help collecting material at Gogo: Mr Chris Nelson, Ms Susan Creagh, Dr Richard Holst and Mr Terry Barnes, and thank Mr Jim Coulthard and Mr Len Hill for their permission to work on Gogo Station and Christmas Creek Station.

LITERATURE CITED

ALEXANDER, R. McN. 1967. 'Functional design in fishes'. (Hutchinson:London). 160 pp.

BRIGGS, D.E.G. AND ROLFE, W.D.I. 1983. New Concavicarida (New Order: ?Crustacea) from the Upper Devonian of Gogo, Western Australia, and the palaeoecology and affinities of the group. *Special Papers in Palaeontology* **30**: 249–76.

DENISON, R.H. 1978. Placodermi. 'Handbook of Paleoichthyology', vol. 2. (Gustav Fischer Verlag: Stuttgart, New York). 128 pp.

1984. Further consideration of the phylogeny and classification of the order Arthrodira (Pisces: Placodermi). *Journal of Vertebrate Paleontology* **4**: 396–412.

DENNIS-BRYAN, K. 1987. A new species of eastmanosteid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **90**: 1–64.

DENNIS, K.D. AND MILES, R.S. 1979a. A second eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **67**: 1–29.

1979b. Eubrachythoracid arthrodires with tubular rostral plates from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **67**: 297–328.

1980. New durophagous arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **69**: 43–85.

1981. A pachyosteomorph arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **73**: 213–58.

1982. A eubrachythoracid arthrodire with a snub-nose from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **75**: 153–66.

1983. Further eubrachythoracid arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **77**: 145–73.

FOREY, P.L. AND GARDINER, B.G. 1986. Observations on *Ctenurella* (Ptyctodontida) and the classification of placoderm fishes. *Zoological Journal of the Linnean Society* **86**: 43–74.

LONG, J.A. 1987a. A new dinichthyid fish (Placodermi; Arthrodira) from the Upper Devonian of Western Australia, with a discussion of dinichthyid interrelationships. *Records of the Western Australian Museum* **13**: 515–407

1987b. Late Devonian fishes from the Gogo Formation, Western Australia — new discoveries. *Search* **18**: 203–05.

1988a. A new camuropiscid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **94**: 233–58.

1988b. New information on the arthrodire *Tubonasus* from Gogo, Western Australia. *Memoirs of the Association of Australasian Palaeontologists* **5**: 81–5.

1988c. Late Devonian fishes from the Gogo Formation, Western Australia. *National Geographic Research* **4**: 436–50.

MILES, R.S. 1971. The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London*, **B263**: 101–232.

AND DENNIS, K.D. 1979. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* **66**: 31–62.

AND YOUNG, G.C. 1977. Placoderm interrelationships reconsidered in the light of new ptyctodonts from Gogo, Western Australia. *Linnean Society Symposium Series* **4**: 123–98.

ROLFE, W.D.I. 1966. Phyllocarid fauna of European aspect from the Devonian of Western Australia. *Nature, London* **209**: 192.

YOUNG, G.C. 1984. Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology* **27**: 635–61.

EARLY CARBONIFEROUS SHARK REMAINS FROM THE ROCKHAMPTON DISTRICT, QUEENSLAND

SUSAN TURNER

Turner, S. 1990 3 31: Early Carboniferous shark remains from the Rockhampton district, Queensland. *Mem. Qd Mus* 28(1): 65–73. Brisbane. ISSN 0079-8835.

Teeth of "bradyodont", cladodont and stethacanthid sharks have been found in the Tournaisian-Visean Rockhampton Group. The status of "*Deltodus australis*" Etheridge fil. 1892 is reviewed; this toothplate might be helodont or deltoptychiid. The new material includes petalodont, cochliodont, deltoptychiid, helodont, psammodont and psephodont toothplates which are compared with species from the Early Carboniferous of North America, Europe and the U.S.S.R.
☐ *Carboniferous, sharks, bradyodont, cladodont, stethacanthid, Rockhampton Group, Queensland.*

Susan Turner, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 30 July, 1988.

Records of Carboniferous shark teeth from Australia are sparse (Long & Turner, 1984). De Koninck (1878, 1898) identified a specimen from New South Wales sent to him by the Reverend W.B. Clarke as "*Tomodus convexus*"; this specimen was presumably lost when Clarke's collection was destroyed by fire in Sydney in the last century (Grainger, 1982). Hardman (1884) referred a tooth from presumed Lower Carboniferous rocks of Kimberley in Western Australia to the genus *Poecilodus*. The whereabouts of this specimen is unknown but shark remains including bradyodont and stethacanthid teeth are now known to be common in the Upper Devonian to Lower Carboniferous Fairfield Group of Western Australia (Thomas, 1957; Turner, 1982a, pers. obs.).

Until a few years ago there was only one Queensland record of a Palaeozoic shark tooth. Etheridge (in Jack & Etheridge, 1892) referred a shark tooth collected by Charles Walter de Vis, then Curator of the Queensland Museum, to a new species, *Deltodus australis*. The single specimen (Fig. 1A, 2A), collected by de Vis during a field trip to the "Agricultural Reserve" near Rockhampton was believed to be lost (Turner 1982b), but it was re-discovered during the move to the new Queensland Museum in 1986. This paper reviews the status of that species and introduces new material collected by Mr Greg Webb (then Department of Geology, University of Queensland; GW = his locality numbers) from the Rockhampton district since 1985; the de Vis specimen is discussed first, followed by short descriptions of the new material. No attempt is made here to review the status of the many bradyodont form and organ genera which are based primarily on teeth (see, Lund 1986). It should be understood that the generic names, and even higher taxa, are used by the author in the same way as multi-element taxonomy is used by conodont workers, or "scale species" used by thelodont workers. These are mostly names of convenience until such time as well-preserved complete fish are discovered. Bendix-Almgreen (1975) argued that the taxon 'Bradyodonti' was no longer acceptable; I follow his usage in this but retain the term 'bradyodont' for teeth which were presumably used for crushing and grinding and which cannot be assigned to a definite family. In recent years new material of fish bearing bradyodont and cladodont teeth has been found in the Carboniferous of Montana (e.g. Lund, 1985; Janvier & Lund, 1985); evaluation of these finds should allow better understanding of the nature and relationships of some of the isolated teeth.

NEW MATERIAL AND STRATIGRAPHY

Thirteen new shark teeth have been obtained from various limestones within the Rockhampton Group on the western limb of the Gracemere Anticline, west of Rockhampton (see Krotsch & Kay, 1977; Day *et al.*, 1983). The Rockhampton Group comprises three formations — the Gudman Oolite, the Malchi Formation and the Lion Creek

Formation (Fleming, 1967) — including extensive beds of sandy oolitic and pisolitic limestone, and calcareous sandstones and siltstones with abundant crinoid, shell and coral fragments. The vertebrate macrofossils are probably relatively common since the new material was found by a single geologist walking over sites without the intention of collecting such fossils. They are usually preserved as black apatite which stands out against the lighter-coloured limestone matrix. One of the shark teeth has been mineralised as pale turquoise-coloured or bluish-pink vivianite. The limestone samples were all treated with dilute acetic acid to remove the teeth and the remaining residues were searched for microfossils, though without success.

Only one of the new specimens was found in an isolated block near the main outcrop; the rest were found *in situ*. In some instances the limestone units containing the teeth are unnamed and the relationship within a measured section of one bed to another is not yet certain. In general, however, the Rockhampton sequence has been ordered and dated using evidence from conodonts (e.g. Druce, 1970; Mory & Crane, 1982). Webb (pers. comm.) is currently studying the coral faunas of the limestones containing vertebrate fossils.

Three teeth have been obtained from the Gudman Oolite, which is the basal, mid to late Tournaisian, formation of the Rockhampton Group (CuI and lower CuIIα of Druce, 1970; *Siphonodella sulcata* zone of Mory & Crane, 1982). These are identified as a helodont tooth, and two possible psephodont and/or cochliodont teeth.

From an unnamed limestone below the Cargoogie Oolite Member (outcrop 20-0 of Krotsch & Kay, 1977) within the Malchi Formation, thought to be low in the Visean (CuII — CuIIIα of Druce, 1970), have come cladodont (stethacanthid) teeth, a psephodont and another fragmentary bradyodont tooth.

From the Lion Creek Limestone Member and other limestones in the Lion Creek Formation (late Visean) come a helodont tooth, a possible psammodont tooth, a deltoptychiid tooth, a petalodont tooth as well as a cochliodont and possible psephodont teeth.

A small vertebrate microfauna which includes xenacanthid teeth, scales of neoselachian and hybodont sharks, as well as palaeoniscoid teeth, has been found in limestones at the top of the Rockhampton Group, which may be equivalent to the Late Visean Baywulla Formation (see Day *et al.*, 1983). This fauna will be examined in detail in another paper.

FOSSIL REMAINS

De Vis' Specimen

Deltoptychiid gen. et sp. indet.
Figs 1A, 2A, B

1892 *Deltodus? australis* Etheridge, in Jack & Etheridge p. 296, pl. 39, fig. 11.
1958 *Deltodus australis* Eth. fil., Hills, p. 93.
1982 *Deltodus*, Long, p. 68.
1982b *Deltodus? australis*, Turner, p. 602.
1984 *Deltodus australis*, Long & Turner, p. 237.

Specimen and Measurements

Queensland Museum (QM) F 809; 32 mm along the occlusal surface, 4 mm deep at broken end.

Locality and Age

The original locality is cited only as "Rockhampton district". In a note (Jack & Etheridge 1892, p. 199) Etheridge stated that in a letter, dated 25th July 1888, de Vis claimed that all the fossils he collected "are from the Agricultural Reserve: from the Fitzroy at Laurel Bank, about 10 miles from Rockhampton, westward to the Nine-mile Lagoon, thence to the Corporation Quarry, Athelstane Range, and to the northern outcrop (at the foot of Bersekers) of the synclinal beneath the township and bed of river". Etheridge gave the age as Permo-Carboniferous Gympie Beds. Hills (1958) then reported the bradyodont tooth as from the Permian "Gympie Series" of Queensland. Long (1982) followed Hills in this placement. De Vis, however, was in no doubt that his Rockhampton fossils were Lower Carboniferous in age, as all were labelled as such in his collection.

Remarks

Etheridge judged that the specimen should be placed in the genus *Deltodus* Agassiz 1859 ms. (see Newberry & Worthen, 1866) based on comparable specimens in the Enniskillen collection from the Early Carboniferous of Ireland. Newberry and Worthen (1866) gave the first formal description of the genus. Their description, however, would cover a wide range of different tooth morphotypes, not all of which would now be referred to *Deltodus*. For the Queensland specimen Etheridge noted only the character of the open and porous structure of the tooth — a clear indicator of the tubular dentine typical of many so-called bradyodont teeth. He also described the cross-section of the tooth as "semi-circular, abruptly so on the outer side". Etheridge remained in doubt, however, as he wrote "I do not feel at all certain that the reference to

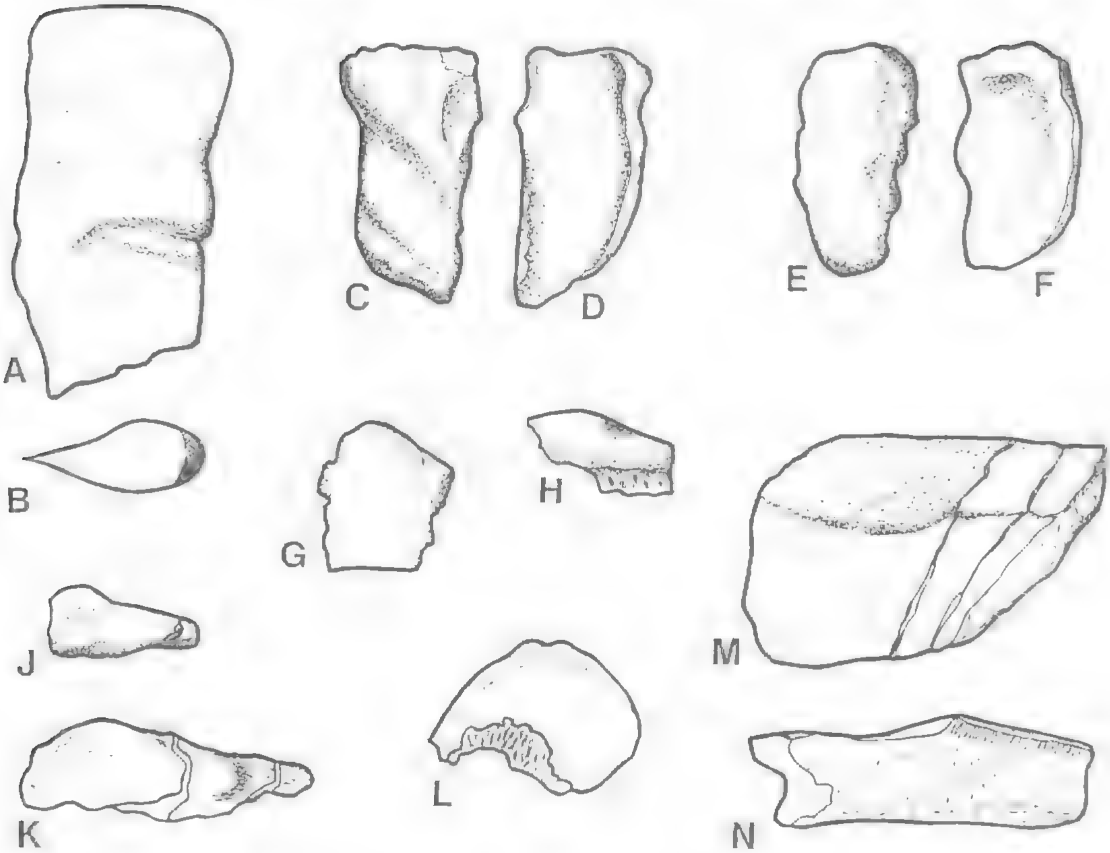

FIG. 2. Sketches of teeth from the Lower Carboniferous of Rockhampton. A. Deltoptychiid gen. et sp. indet. QM F809, crown view showing undulations, approximately X 3; B. Cross-section shape of tooth QM F809, approximately X 3; C. *Deltoptychius* sp. UQ F76061, crown view, approximately X 5.5; D. UQ F76061, ventral view, approximately X 5.5; E. Cochliodont gen. et sp. indet., UQ F6063, crown view, approximately X 5; F. UQ F76063, ventral view, approximately X 5; G. *Psephodus?* sp. indet., UQ F76054, crown view, approximately X 1.5; H. Helodont gen. et sp. indet., UQ F6055, lingual view, approximately X 3.5; J. Helodont?, UQ F76062a, crown view, approximately X 7; K. Helodont?, UQ F76062b, crown view, approximately X 14; L. Petalodont gen. et sp. indet., UQ F76060, lingual view, approximately X 6; M. *Psammodus* sp., UQ F76064, crown and lingual view, approximately X 1; N. UQ F76064, cross-section of tooth showing general histological structure, approximately X 1.

Deltodus is a correct one, but in the unsatisfactory state of our antiopodean scientific libraries, I am unable to make a more exact determination. If a species of this genus, it approaches *D. aliformis* McCoy, but is much more regular in outline, and lacks the contracted posterior end of that species'' (in Jack & Etheridge, 1892, p. 296). In fact the specimen exhibits no characteristics of the genus *Deltodus*, being too abraded to allow generic identification or even to be certain to which group of ''bradyodont'' teeth it might belong. From its overall size and rectangular shape it might be a helodont or deltoptychiid tooth. The presence of three indistinct diagonal undulations across the crown suggests that QM F809 belongs to the latter family.

NEW MATERIAL

TOURNAISIAN GUDMAN OOLITE

Psephodus? sp. indet.
Fig. 1G

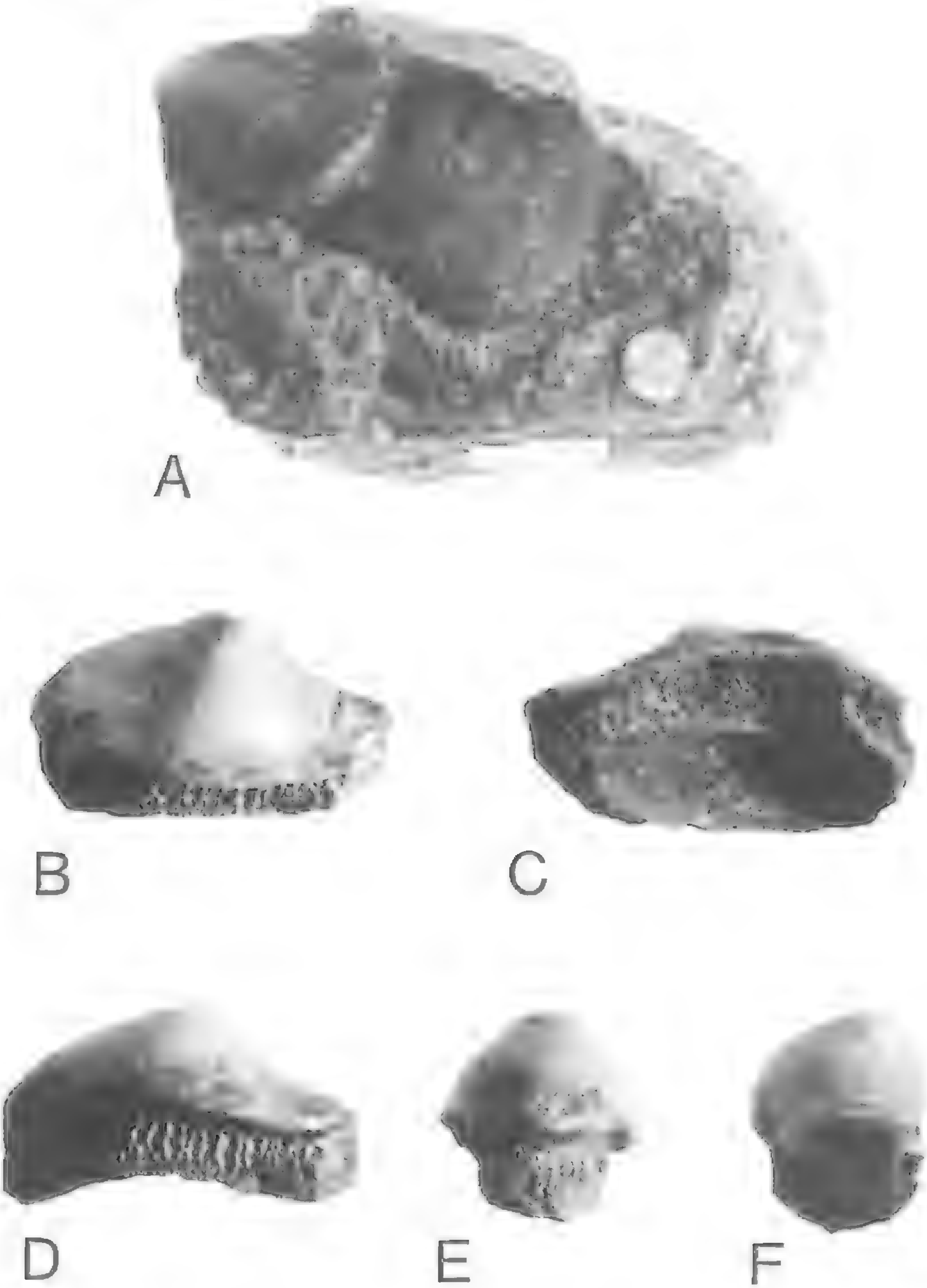

FIG. 1A. QM F809, deltoptychiid gen. et sp. indet. Lower Carboniferous, Rockhampton Group. Collected by Charles Walter de Vis. Dorsal view of crown; approximately X 2. B-D. UQ F76059, *Helodus* sp. Lower Carboniferous, Visean, Rockhampton Group, Lion Creek Limestone B. Dorsal (occlusal) view of tooth; C. Ventral view of base; D. Presumed lingual view showing foramina; E. Lateral view; F. Lateral view. All X 2.

MATERIAL

University of Queensland Geology Department (UQ) F 76053-54. UQ F 76053 is from L4890 (GW20) — on crest of second hill W of Malchi Nine-Mile Road, W of Lower Gracemere Lagoon — Ridgelands 1:100.000 (RI) 333.100; UQ F 76054 is from L4901 (GW23) — on eastern edge of crest of fourth hill W of Malchi Nine-Mile Road, W of Lower Gracemere Lagoon — RI 328.093.

MEASUREMENTS

Tooth UQ F 76053 has a crown measuring about 31 by 20 by 8.5 mm. Tooth UQ F 76054 is broken around the rim and slightly compressed, with shatter cracks across the crown. The tooth measures about 21.5 by 19 by 7 mm.

REMARKS

These teeth have gently rounded crowns which appear to be broader at one end. They are almost certainly cochliodont teeth and are tentatively referred to the genus *Psephodus* Agassiz (1859 ms.; St John & Worthen, 1883). This bradyodont genus is one of the earliest to occur in the Early Carboniferous of the U.S.A. (St John & Worthen, 1883). Teeth which might belong to this genus have been found in the Late Devonian of Western Australia (J.A. Long, pers. comm.), and Obruchev (1962) also recorded similar psephodont teeth in the Early Carboniferous of Kuzbas.

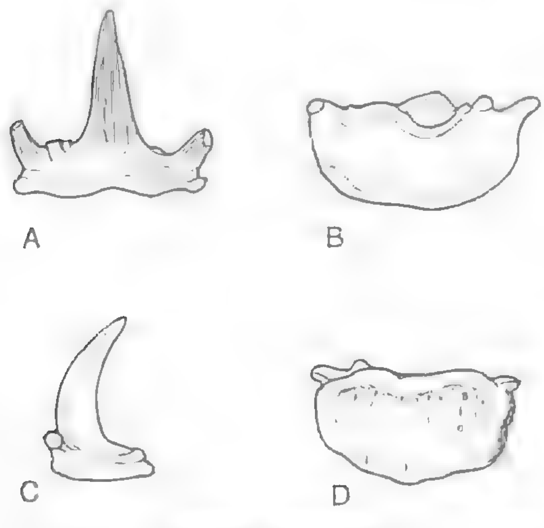

FIG. 3. UQ F76056, *Stethacanthus* sp. Lower Carboniferous, Visean, Rockhampton Group, Malchi Formation A. Labial view; B. Dorsal view; C. Lateral view; D. Basal view. Sketches all approximately X 4.

The Queensland teeth closely resemble the tooth forms called *Psephodus obliquus* and *P. placentus* St John and Worthen (1883) from the Tournaisian Kinderhook Formation (upper fish bed) of Iowa.

Helodont gen. et sp. indet.
Fig. 1H

MATERIAL

UQ F 76055 from L4899 (GW21) — on a crest of third hill W of Malchi Nine-Mile Road, W of Lower Gracemere Lagoon — RI 329095.

MEASUREMENTS

About 10 mm along the occlusal rim (broken at one end) and about 5 mm deep.

REMARKS

This tooth has an elongate rounded crown with a central raised area. There is a narrow neck groove, and the remains of the base show several large lingual foramina. This tooth could possibly be referred to the genus *Helodus* but until more material is available will be left indeterminate.

VISEAN MALCHI FORMATION

Stethacanthus sp. indet.
Figs 3A-D

MATERIAL

UQ F 76056 from L5014 (GW30 — limestone about 1.2 km SW of Granville Homestead, 80 m S of Limestone Creek, RI 242198; unnamed limestone, below Cargoogie Oolite Member.

DESCRIPTION AND MEASUREMENTS

The D-shaped basal surface of tooth UQ F 76056 is 15 mm by 7 mm. It has a marked labial lip behind which is a concave area with fine foramina arranged along the lee of the labial rim and set in shallow grooves within the concavity. The fine grooves and ridges cross the base to the lingual rim (Fig. 3D). The height of the main cusp above the labial base-cusp interface is 10 mm. There are about 10 strong striations on the labial surface of the cusp, and these curve proximally towards the midline of the cusp (Fig. 3A). There are strong lateral ribs on the main cusp, which curves gently backwards at an angle of about 20° (Fig. 3C). The two lateral cusps are directed outwards, with intermediate cusps represented by broken bases between these and the main cusp (Figs 3A, B). Two intermediate cusps are seen on the left labial side and three on the right (Fig. 3B).

REMARKS

This stethacanthid tooth is similar to that called '*Cladodus*' *thomasi* by Turner (1982a) found in the Early Carboniferous of Western Australia and north Queensland. The previously described specimens may now be referred to the genus *Stethacanthus* Newbery 1889 because of the configuration of the labial rim and lingual shelf on the base. The new tooth apparently has a small number of lateral cusps, four or less, and a deep D-shaped base. It resembles cladodont teeth including the form called *Cladodus ferox* Newberry and Worthen (1866) from the St Louis Limestone (Early Visean) of the U.S.A.

Cladodont fam., gen. et sp. indet.
Figs 4A-D

MATERIAL

UQ F 76057 from L4986 (GW36) — limestone outcrop RC2 E of Black Jin Creek, 500 m S of main Ridgelands-Rockhampton Road, R1270199; unnamed limestone, below Cargoogie Oolite Member.

DESCRIPTION AND MEASUREMENTS

Tooth UQ F 76057 has an elongate D-shaped base, 33 mm long by 10 mm across (Fig. 4B). There is a shallow D-shaped depression in the centre of the basal surface. Some fine foramina and thin grooves can be seen on the lingual basal surface. The lingual shelf on this specimen is quite narrow, with no prominent bosses, and the lingual border is gently undulated (Fig. 3D). There is a narrow labial basal shelf, 2 mm high. The central cusp is at least 20 mm high and the apex is missing. The surface is finely striated with distinct lateral ribs; there are 18-20 fine striations on the labial surface, some of which bifurcate towards the base of the cusp. The proximal striations curve away from the mid-line of the central cusp. Strong horizontal striations can be seen below the main cusp on the left labial side of the tooth (Fig. 4A). The main cusp curves back at an angle of about 60° (Fig. 4C). There are two lateral cusps at either end of the tooth directed outwards and backwards. There was probably at least one pair of smaller intermediate cusps, one of which is still represented by its base (Fig. 4d). The area between is too badly-preserved to provide the full cusp count.

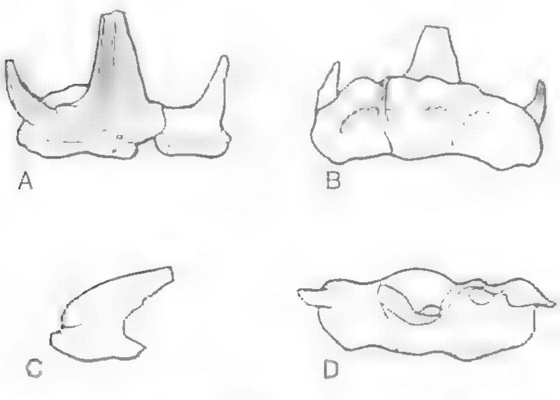

FIG. 4. UQ F76057 cladodont gen. et sp. indet. Lower Carboniferous, Visean, Rockhampton Group, Malchi Formation A. Labial view; B. Dorsal view; C. Lateral view; D. Basal view. Sketches all approximately X 3.

REMARKS

This tooth does not belong to *Stethacanthus* but might be from either a ctenacanth or perhaps the stethacanthid *Symmorium*.

Psephodus?

MATERIAL

UQ F 76065 from limestone RA1 (GWF-3M), WSW of Rockhampton, 18.1m above base of limestone at base of small ridge 100 m N of road, W of three-way junction near Deep Creek, approximately 1 km SE of Limestone Creek — L4988; unnamed limestone, Malchi Formation, Rockhampton Group; Visean.

DESCRIPTION AND MEASUREMENTS

Broken pieces of tooth about 10 mm square by 1 mm deep. Smooth crown surface with a slightly concave basal surface.

Bradyodont indet.

MATERIAL

UQ F 76058 from L5014 (GW30.2) — about 1.6 km SW of Granville Homestead, 80 m S of Limestone Creek (see above); unnamed limestone, Rockhampton Group.

REMARKS AND MEASUREMENTS

A small piece of crown, possibly psephodont, 7 mm by 10 mm.

LION CREEK LIMESTONE

Helodus sp.
Figs 1B-F

MATERIAL

UQ F 76059 from a crinoidal limestone (presumed to be from the Lion Creek Limestone), western end of outcrop 1 km NNE of Hillrose Homestead, 4-5 km ESE of Dalma township, near Rockhampton — L5421. The block was found in talus and not *in situ*.

DESCRIPTION AND MEASUREMENTS

The tooth is large, about 25 mm long by 10 mm labio-lingually and 15 mm deep. The crown of the tooth, the constricted neck and part of the labial base were exposed.

The crown (Figs 1B, D-F) is pitted evenly with fine pores, and is rounded in all directions with a strongly rounded and raised mid-portion, which is slightly skewed to one side. In cross-section, or in side view (Figs 1E, F), the crown is slightly concave on the labial surface and more strongly convex on the lingual surface. The crown-base interface is a narrow groove-like neck. The base itself is smaller than the crown, with an elongate D-shaped outline, and extends in the presumed lingual and downward direction. It has a maximum depth of about 5 mm (Fig. 1E). The presumed lingual surface on the base is perforated by a row of large foramina below which are smaller indentations and foramina (Fig. 1D). There are at least 22 coarse ribs separating the foramina (Fig. 1D). There are no clear foramina on the labial surface of the base, rather a concave trough passes down to the basal surface, which is itself slightly concave (Fig. 1C).

REMARKS

The tooth is nearest in form to those referred to *Helodus*. Most species referred to this genus are known only from teeth and teeth from a single dentition are so variable that if they were found separately they would be referred to different genera. Sadly, the teeth of one species known from articulated material, *Helodus simplex* Ag., are not well-known (e.g. Patterson 1965). There are many isolated teeth figured in the literature; Woodward in his 1889 Catalogue listed 48 species. Obruchev (1964) described a typical helodont dentition as comprising transversely elongated teeth in eight to nine series of four or five teeth in each half-jaw; the teeth in the middle (fourth and fifth series) are the largest and usually fuse into plates. As it is difficult, therefore, to orient an isolated tooth I have had to assume the lingual and labial directions.

Helodont teeth have been reported mainly from the Early Carboniferous of the U.S.A., Canada, Britain, France, Belgium and the U.S.S.R. as well as Australia (e.g. Turner 1982a). Teeth referred to the genus *Helodus* have been reported from the Late Devonian of the U.S.A.; the status of these teeth needs to be reviewed. *Helodus* teeth of different species have also been described from the Late Carboniferous and Early Permian of the U.S.A. (e.g. Woodward 1889) and from the Early Permian of Australia (Teichert 1943) and the Urals (e.g. Obruchev 1964). The Queensland tooth is very similar in size and shape to one figured by Obruchev (1962) and referred to the species *Helodus derjawini* of Tolmatchev 1924. This form occurs in the Tournaisian of the Kuznets Basin.

Petalodont gen. et sp. indet.
Fig. 2L

MATERIAL

UQ F 76060 from (GW6) WSW of Rockhampton, — first massive limestone near base of formation; Grid 8951 Ridgelands KV 194.120 — L4936.

DESCRIPTION AND MEASUREMENTS

The tooth is about 9 mm at widest by 6 mm at deepest with an intact occusal surface and rim and a broken basal rim. Crown with slightly convex labial and slightly concave lingual surface. Occlusal rim of crown strongly rounded with a medial pair of rounded denticulations rising a short way above the rim. Faint striations on the lingual occlusal rim. The basal roots apparently absent. The hard tissue of the crown is clearly shown on the broken basal surface; the structure is highly cancellous.

REMARKS

This presumed petalodont tooth, the first record for Australia, might be placed in the genus *Antliodus* or *Tanaodus*. Both genera were recently reviewed by Hansen (1985), and both are restricted to the Early Carboniferous.

Deltoptychius sp.
Figs 2C, D

MATERIAL

UQ F 76061 from GW6 WSW of Rockhampton, — first massive limestone near base of formation; Grid 8951 Ridgelands KV 194.120 — L4936.

DESCRIPTION AND MEASUREMENTS

The tooth measures 14 mm on the longest edge. The crown is subrectangular with a wider extension at one end. Three gentle undulations cross the crown surface at an angle of about 60° to the long axis. The basal surface is gently concave.

Helodont?
Figs 2J, K

MATERIAL

UQ F 76062 a,b from GWA-11, WSW of Rockhampton, limestone approximately 5 m above L4936 but further east; Grid 8951 Ridgelands KV 203.121 — L4968.

DESCRIPTION AND MEASUREMENTS

Both teeth are about 5 mm along broken occlusal length. One small elongate tooth with a central rounded dome (Fig. 2J); broken and worn with a central, slightly-raised dome and ridges of dentine separated by the bony tissue of the base (Fig. 2K).

REMARKS

These two small teeth were extracted together from the same small piece of rock. It is possible that both belonged to the same dentition and thus they have been considered together.

Cochliodont gen. et sp. indet.
Figs 2E, F

MATERIAL

UQ F 76063 from GW14 WSW of Rockhampton, — L4955 from near the top, limestone talus near large bioherm on southern flank of limestone ridge approximately 1 km NE of Hillrose Homestead; Grid — Ridgelands RI 198.177.

DESCRIPTION AND MEASUREMENTS

The toothplate measures 10 by 5 by 3 mm at greatest depth. The high crown is strongly arched with the highest point to the front of the crown (Fig. 2E). Some asymmetry with a steeper angle on the right side. Rim lightly inrolled on the right antero-lateral and opposite postero-lateral margins (Fig. 2F). The base is concave.

Psammodus sp.
Fig. 2M, N

MATERIAL

UQ F 76064 from GW16 the main limestone WSW of Rockhampton, in low-lying area immediately east and south of bend in road, 400 m N of Hillrose Homestead. Grid — Ridgelands RI 194.114 — L4981.

DESCRIPTION AND MEASUREMENTS

Crown surface about 80 by 25 mm. Depth of tooth about 20 mm. Lingual extension of base about 30 mm across. Large tooth with a well-worn flattened rectangular crown on a bony base with a lingual extension at an angle of about 45° (Fig. 2M). There is a marked step between the crown and lingual base. The broken cross-section shows the gross details of the histology (Fig. 2N); a thin upper layer of tubular dentine about 4 mm deep sits on a layer of more spongy tissue about 12-13 mm deep. The basal layer is a laminar bony tissue about 3 mm deep.

PALAEOECOLOGY

The oolitic and pisolitic limestones and the arenaceous limestones of the Rockhampton Group are thought to have been formed in high-energy environments along the shoreline bordering the eastern edge of the Connors-Auburn Volcanic Arc (Day *et al.*, 1983). They were laid down on shallow banks in the narrow, unstable continental Yarrol Shelf where the Calliope Island Arc might still have been emergent in places (Day *et al.*, 1983). Most of the vertebrate specimens have been found as isolated, and often well-worn or broken, teeth. The slow-growing tooth plates of the 'bradyodont' fish probably dropped to the seabed when the fish died, not necessarily near the life habitat, and might then have been rolled around in the swash forming the oolites. The cladodont teeth, however, are reasonably fresh and unbroken. These sharks probably lost their deciduous teeth by accidental breakage fairly near to the point of internment. No microfauna has been found in the high-energy limestones to date.

ACKNOWLEDGEMENTS

I wish to thank the Director, Dr Alan Bartholomai, and the Board of the Queensland Museum for continuing to support my work through an Honorary Research Fellowship of the Museum. I am most grateful to the Australian Research Grants Scheme which gave financial assistance through Grant E8115050. Greg Webb kindly allowed me to describe his specimens and gave me much advice on the geology of the area. Thanks also to Andrew Simpson (Geology Museum, University of Queensland) for curatorial assistance. Noel R. Kemp and Dr Anne Kemp offered valuable criticism of the manuscript.

LITERATURE CITED

BENDIX-ALMGREEN, S.E. 1975. Fossil fishes from the marine Late Palaeozoic of Holm Land-Andrup Land, North-east Greenland. *Meddelelser om Grønland* **195**(9): 1–38.

DAY, R., WHITAKER, W.G., MURRAY, C.G., WILSON, I.H. AND GRIMES, K.G. 1983. Queensland Geology. A companion volume to the 1:2 500 000 scale geological map (1975). *Geological Survey of Queensland, Publication* **383**: 1–194.

DE KONINCK, L.G. 1878. Faune de Calcaire Carbonifre de la Belgique. Première partie, poissons et genre nautile. *Musée royal d'histoire naturelle de Belgique, Annales* **2**: 1–152.

1898. Description of the Palaeozoic Fossils of New South Wales (Australia). *Memoirs of the Geological Survey of New South Wales, Palaeontology* **6**: 1–298.

DRUCE, E.C. 1970. Lower Carboniferous conodonts from the Northern Yarrol Basin, Queensland. *Bureau of Mineral Resources, Geology & Geophysics, Australia, Bulletin* **108**: 91–113.

FLEMING, P.J.G. 1967. Names for Carboniferous and Permian formations of the Yarrol Basin in the Stansell Area, Central Queensland. *Queensland Government Mining Journal* **68**(785): 113–6.

GRAINGER, E. 1982. 'The Remarkable Reverend Clarke. The life and times of the Father of Australian Geology'. 292 pp. (Oxford University Press: Melbourne).

HANSEN, M.C. 1985. Systematic relationships of Petalodontiform Chondrichthyans, p. 523–41 *In* Dutro, J.T. Jr and Pfefferkorn, H.W. (Eds), 'Compte Rendue vol. 5, Paleontology, Paleoecology, Paleogeography', Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère. (Southern Illinois University Press: Carbondale and Edwardsville).

HARDMAN, E.T. 1884. Report on the Geology of the Kimberley district, Western Australia. Government Parliamentary Paper no. 30, Government Printer, Perth: 1–22.

HILLS, E.S. 1958. A Brief Review of Australian Fossil Vertebrates, p. 86-107 *In* Westoll, T.S. (Ed.), 'Studies on Fossil Vertebrates'. (Athlone Press: University of London).

JACK, R.L. AND ETHERIDGE, R. fil. 1892. *The Geology and Palaeontology of Queensland and New Guinea.* Government Printer, Brisbane, xxxi + 768 pp.

JANVIER, P. AND LUND, R. 1985. Ces èstranges bêtes du Montana *La Rècherche 16*, **162**: 98–100.

KROTSCH, N.J. AND KAY, J.R. 1977. Limestone Resources of the Rockhampton Region. *Geological Survey of Queensland, Report* no. 98, 72 pp. + figs, separate.

LONG, J.A. 1982. The History of Fishes on the Australian continent, p. 54-85 *In* Rich, P.V. and Thompson, E.M. (Eds), 'The Fossil Vertebrate Record for Australasia'. (Monash University Offset: Clayton, Victoria).

AND TURNER, S. 1984. A checklist and bibliography of Australian fossil fish, p. 235-54 *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography & Evolution in Australasia. (Hesperian Press: Western Australia).

LUND, R. 1985. Stethacanthid Elasmobranch Remains from the Bear Gulch Limestone (Namurian E2b) of Montana. *American Museum Novitates* **2828**: 1–24.

1986. The Diversity and Relationships of the Holocephali. p. 97-106. *In* Uyeno, T., Arai, R., Taiuchi, T. and Matsuura, K. (Eds), 'Indo-Pacific Fish Biology'. (Ichthyological Society of Japan: Tokyo).

MORY, A.J. AND CRANE, D.T. 1982. Early Carboniferous *Siphonodella* (Conodonta) faunas from eastern Australia. *Alcheringa* **6**: 275–303.

NEWBERRY, J.S. 1889. The Palaeozoic Fishes of North America. *Monograph of the United States Geological Survey* 1889, **16**: 1–340.

AND WORTHEN, A.H. 1866. Descriptions of new species of vertebrates, mainly from the Subcarboniferous limestone and Coal Measures of Illinois. *Geological Survey of Illinois, Palaeontology* v. II, 9–134.

OBRUCHEV, D.V. 1962. Carboniferous Vertebrates, p. 212-20, *In* Chalfina, L.L. (Ed.), 'Biostratigrafiya palaeozoya sayano-altaiskoi hornoi oblasti', tom. III, Verchnii Paleozoi. *Trudy Sibirskogo nauchno-issledovatel'skogo instituta geologii i geofiziki i mineral'nogo syr'ya.*

1964. *Ribi i Byescheliustnie.* Vol. 11, 'Osnovy Paleontologii'. Moscow, 522 pp.

PATTERSON, C. 1965. The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London B* **249**: 101–219.

ST JOHN, O. AND WORTHEN, A.H., 1883. Descriptions of fossil fishes, a partial revision of the Cochliodonts and Psammodonts. *Geological Survey of Illinois, Palaeontology* **7**: 55–264.

TEICHERT, C. 1943. Bradyodont sharks in the Permian of Western Australia. *American Journal of Science* **241**: 543–52.

THOMAS, G.A. 1957. Lower Carboniferous deposits in the Fitzroy Basin, Western Australia. *Australian Journal of Science* **19**: 160–1.

TOLMATCHEV, I.P. 1924. Faune de calcaire carbonifère du bassin houiller de Kousnetssk. *Materialy po obschchei i prikladnoi geologii,* Leningrad no. **25**: 1–320 [In Russian; not seen].

TURNER, S. 1982a. Middle Palaeozoic elasmobranch remains from Australia. *Journal of Vertebrate Paleontology* **2**(2): 117–31.

1982b. A catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum* **20**: 599–611.

WOODWARD, A.S. 1889. 'Catalogue of the Fossil Fishes in the British Museum (Natural History). Pt 1. containing the Elasmobranchii.' (British Museum (Natural History): London). 474 pp.

A LACUSTRINE SHARK FROM THE LATE PERMIAN OF BLACKWATER, CENTRAL QUEENSLAND

EXTENDED ABSTRACT

MICHAEL R. LEU

Leu, M. 1990 3 31: A lacustrine shark from the Late Permian of Blackwater, central Queensland. *Mem. Qd Mus.* 28(1): 75–78. Brisbane. ISSN 0079-8835.

The Rangal Coal Measures in the Utah Development Company's open-cut coal mine, 20 km SSW of Blackwater, central Queensland, contain several mass-mortality horizons that have yielded a bobasatraniform (Campbell and Duy Phuoc 1983), at least twelve new genera of Palaeonisciformes, and two new genera of Elasmobranchii. One, a phoebodontiform, was an active cruising shark.

A new elasmobranch from the Late Permian of Queensland (Figs 1A, B), is characterised by a palatoquadrate with well-developed ethmoidal articulation, cladodont (phoebodontiform) dentition, absence of ribs, a non-lunate caudal fin, and dorsal finspines with an anterior keel and a flat to concave posterior wall whose postero-lateral margins bear three transverse rows of barb-like denticles (Fig. 2). The new form is known from three articulated specimens, the largest being 19.3 cm in length; a single finspine, 6-6.5 cm in length, indicates that these sharks may have attained lengths of between 50-75 cm.

The following interpretation of the functional morphology of the new form is based on studies of body shape and locomotion in sharks, (Thomson, 1976; Thomson & Simanek, 1977) specifically the mechanical action of the heterocercal tail.

The caudal fin of the new shark has a heterocercal angle between 17-25°, a dorsal thrust angle (Thomson & Simanek, 1977, p. 346) between 7.5-10°, a large epicaudal lobe, a sub-terminal lobe and a ventral hypochordal lobe. The moderate heterocercal angle of the tail indicates that the shark would have been capable of producing relatively powerful turning moments about the centre of balance, enabling it to change direction rapidly and efficiently. Thomson (1976) determined that sharks possessing a well-developed epicaudal lobe and low to intermediate dorsal thrust angles (intermediate angles range from 10-25°) are characterised by slow cruising speeds. At high speeds, such sharks would not be capable of maintaining in balance the various thrusts produced by the respective fin lobes. In summary, the new form, when active, would have been capable of high manoeuverability, slow cruising speeds and incapable of sustaining high speeds.

The non-lunate caudal fin is a character that Compagno (1977) and Young (1982, character 10) regard as synapomorphic for *Tristychius, Onychoselache, Hybodus, Palaeospinax* and Recent euselachians. Thomson and Simanek (1977) noted that the morphologies of neoselachian caudal fins, whether lunate or non-lunate, do not equate with current shark systematics. They concluded that the various tail patterns have been convergently derived and are related to different modes of life. Ctenacanthiform sharks probably possessed a variety of caudal fin architectures as functional adaptations for specific life habits. Due to the possibility of convergence, the non-lunate caudal fin of hybodonts, ctenacanths (*Bandringa*), and neoselachians cannot be construed as synapomorphic, regardless of whether the morphotypic condition was deeply forked and almost equilobate. Maisey's amendment to this character (Maisey, 1984, character 35, hypaxial endoskeleton of tail reduced) is consistent with the record. Further comparative study of the caudal endoskeleton of Recent sharks is required to ascertain if the primitive state can be convergently derived, as in the case of plesodic pectoral fins (Maisey, 1984, p. 366).

The following finspine characteristics of euselachians are widely shared amongst groups (Rieppel, 1982) such as xenacanths, ctenacanths, hybodonts and neoselachians: concave posterior wall, posterolaterally-situated denticles and posteriorly-placed central cavity. I concur with Dick (1978, p. 107) and Young (1982, p. 838) that the similarities between ctenacanth and neoselachian finspines are symplesiomorphies.

Maisey (1984, p. 365) considered that xenacanths were a specialised group of ctenacanthiform sharks because both possess dorsal finspines with a pectinate ornament (implying that the two groups, separated during, or prior to, the Middle Devonian) and a broad, expanded occipital segment (Maisey, 1984, characters 18, 19). Pectinate ornament of the ctenacanthiform variety may be a plesiomorphic euselachian character or convergently derived. The dimensions of the occipital segment of *Hybodus* resemble closely the xenacanth/Cleveland "*Ctenacanthus*" condition and differ significantly from those of most neoselachians (Leu, 1989). It is more parsimonious to regard a broad, expanded occipital segment as a primitive character shared by xenacanths, ctenacanths and hybodonts. In the absence of other shared characters, the evidence is too tenuous to demonstrate confidently that xenacanths are a specialised group of ctenacanthiform sharks. Even so, I intuitively agree, from a phenetic viewpoint, with Schaeffer's (1981, p. 61) conclusion that the Cleveland *"Ctenacanthus"* represents a sister group to *Xenacanthus, Tamiobatus* and *"Cladodus"*

Comparisons with placoderms and acanthodians suggest that a broad, expanded occipital region may be a primitive gnathostome character. Amongst the arthrodires, the phlyctaeniniids (*Kujdanowiaspis*) and the brachythoracids (*Pholidosteus* and *Tapineosteus*) possess extremely long and broad occipital segments. *Acanthodes* has a broad expanded occipital segment that extends beyond the otic region for 20.5%the total length of the neurocranium.

☐ *Permian, Rangal Coal Measures, Chondrichthyes, Blackwater, Queensland.*

Michael R. Leu, School of Earth Sciences, Macquarie University, NSW 2109; 25 May, 1988.

LITERATURE CITED

Campbell, K.S.W. and Duy Phuoc, L. 1983. A late Permain actinopterygian fish from Australia. *Palaeontology* **26**: 33–70.

Compagno, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* **17**: 303–22.

Dick, J.R.F. 1978. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Transactions of the Royal Society of Edinburgh* **70**: 63–109.

Leu, M.R. 1989. A Late Permian freshwater shark from eastern Australia. *Palaeontology* **32**: 000–000.

Maisey, J.G. 1984. Chondrichthyan phylogeny: a look at the evidence. *Journal of Vertebrate Paleontology* **4**: 359–71.

Rieppel, O. 1982. A new genus of shark from the Middle Triassic of Monte San Giorgio, Switzerland. *Palaeontology* **25**: 399–412.

Schaeffer, B. 1981. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bulletin of the American Museum of Natural History* **169**: 1–66.

Thomson, K.S. 1976. On the heterocercal tail in sharks. *Palaeobiology* 2: 19–38.

Thomson, K.S. and Simanek, D.E. 1977. Body form and locomotion in sharks. *American Zoologist* **17**: 343–54.

Young, G.C. 1982. Devonian sharks from south-eastern Australia and Antarctica. *Palaeontology* **25**: 817–43.

A B

FIG. 1A. An articulated specimen (QMF14470A) of the new genus preserved in lateral view, minus the distal portion of the caudal fin, X 1.5. B. An almost complete specimen (AMF72559A) of the new genus in lateral view, X 1. The circular feature is a plugged drill hole. Abbreviations: AMF, Australian Museum Fossil: QMF, Queensland Museum Fossil.

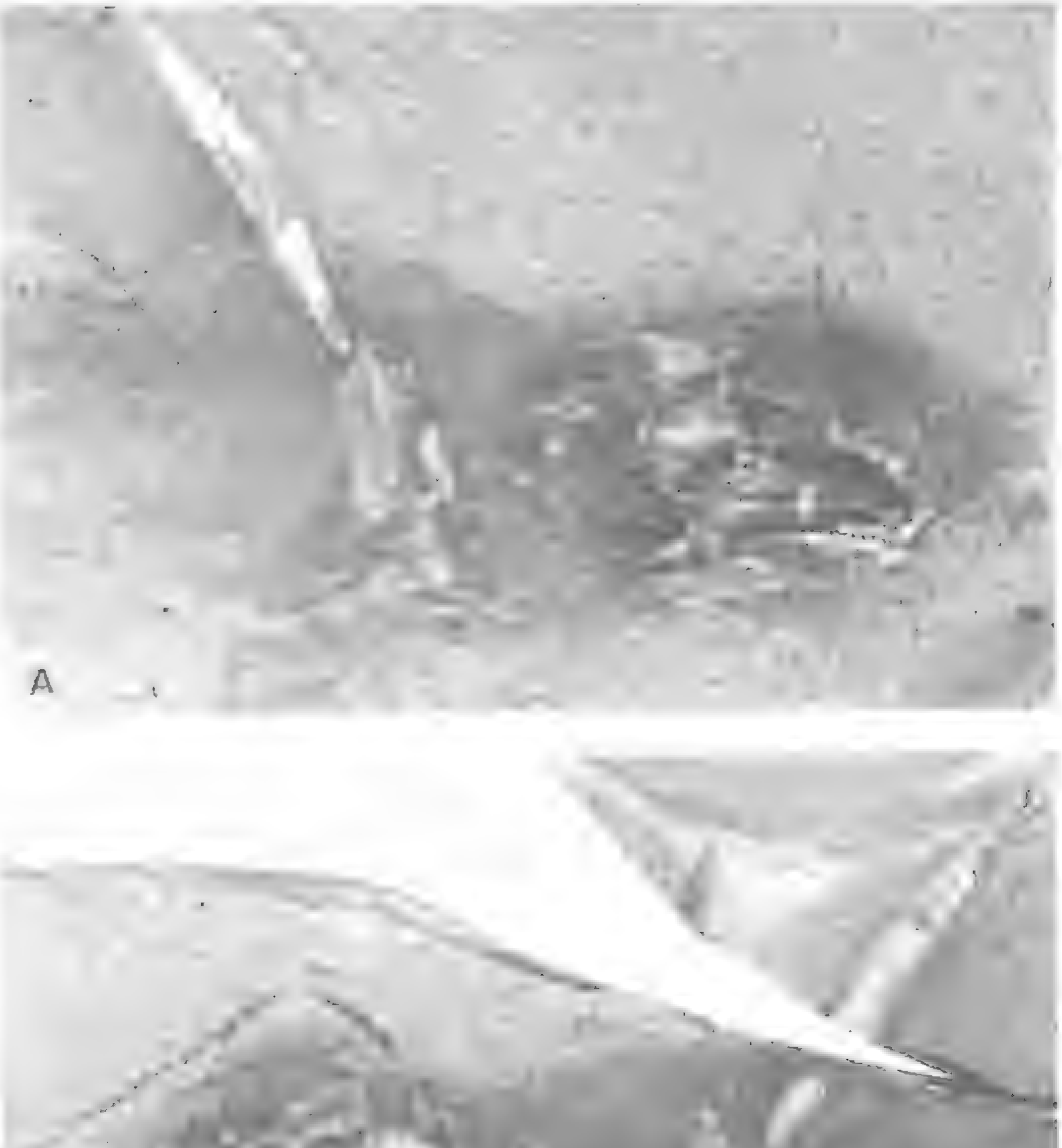

FIG. 2. Details of the head, pectoral girdle and anterior dorsal finspine of (A)QMF14470A (X 2.5) and (B)AMF72559A (X 2.3) respectively.

A PROBABLE NEOTELEOST, DUGALDIA EMMILTA GEN. ET SP. NOV., FROM THE LOWER CRETACEOUS OF QUEENSLAND, AUSTRALIA

TEMPE A. LEES

Lees, T.A. 1990 3 31: A probable neoteleost, *Dugaldia emmilta* gen. et sp. nov., from the Lower Cretaceous of Queensland, Australia. *Mem. Qd Mus.* **28**(10: 79-88. Brisbane. ISSN 0079-8835.

A new teleost, *Dugaldia emmilta* gen. et sp. nov., from the marine Toolebuc Formation (Lower Cretaceous, Albian) of Queensland has a tripartite occipital condyle (exoccipitals and basioccipital) indicating affinities with the Neoteleostei; there is insufficient evidence to allow its referral to a particular order. A number of characters common throughout teleosts are present in *Dugaldia:* a berciform foramen in the anterior ceratohyal, numerous branchiostegal rays, fusion of the parietals, the presence of a supraorbital and large intercalars and the absence of a basipterygoid process. This set of characters suggests that *Dugaldia emmilta* is a primitive neoteleost.

☐ *Osteichthyes, Neoteleostei, Cretaceous, Australia*

Tempe A. Lees, PO Box 84, Sussex Inlet, New South Wales 2540, Australia; 1 December, 1988.

To date only four Cretaceous actinopterygians have been described from Queensland: *Cooyoo australis* (Woodward, 1894); *Pachyrhizodus marathonensis* (Etheridge jr, 1905); *Flindersichthys denmeadi* Longman, 1932; and *Belonostomus sweeti* Etheridge jr & Woodward, 1892. *Pachyrhizodus marathonensis* and *C. australis* were redescribed by Bartholomai (1969) and by Lees and Bartholomai (1987) respectively.

A fifth actinopterygian, *Dugaldia emmilta,* is represented by a single specimen (GSQ9242) which is sufficiently well-preserved to show details of the neurocranium, palatoquadrate, opercular bones, hyoid apparatus and pectoral girdle. The specimen was collected from Early Cretaceous (Albian) sediments of the marine Toolebuc Formation, in the Cloncurry district of northwestern Queensland, and was prepared by etching in dilute acetic acid (technique modified from Toombs & Rixon, 1953).

SYSTEMATIC PALAEONTOLOGY

ACTINOPTERYGII
Subdivision: NEOTELEOSTEI

Order and Family uncertain
DUGALDIA gen. nov.
Type and only species *D. emmilta* sp. nov.

ETYMOLOGY

The specimen was collected from the Dugald River, Queensland.

Dugaldia emmilta gen. et sp. nov.
(Figs 1-6)

HOLOTYPE

GSQ 9242

ETYMOLOGY

Emmiltos Greek — tinged with red, referring to the colour of the limestone from which the specimen was collected.

HORIZON AND LOCALITY

Dugald River, Granada Station, north of Cloncurry, NW Queensland, Lat. 20° 12'S, Long. 140° 55'E. Marine limestones of the Toolebuc Formation, Lower Cretaceous, Albian.

DIAGNOSIS

Frontals broad and flat, forming about three-quarters of the neurocranial roof. Each is laterally rugose, with ridges extending anteriorly and posteriorly from a centre of ossification at posterior half of the lateral margin. Large intercalars located at postero-ventral corners of occiput, articulating with lateral margins of exoccipitals and postero-ventral corners of pterotics. Antero-lateral corner of sphenotic extended into ventral spur, with antero-ventral surface of this bone defining part of hyomandibular fossa. Dermethmoid meets frontals in semicircular interdigitating suture. Anterior surface exhibits large, median ridge extending downward onto vomer. Laterally the dermethmoid

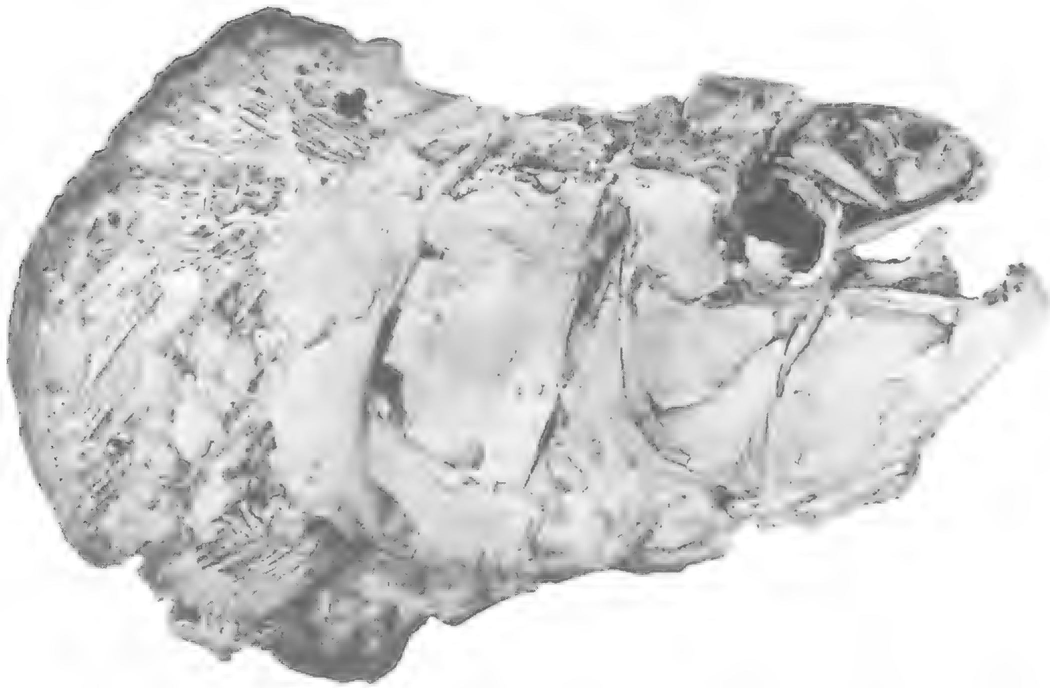

FIG. 1. *Dugaldia emmilta* gen. et sp. nov. Holotype (GSQ 9242), Albian Toolebuc Fm., Qld, right lateral view, showing external structure, approximately X 0.7.

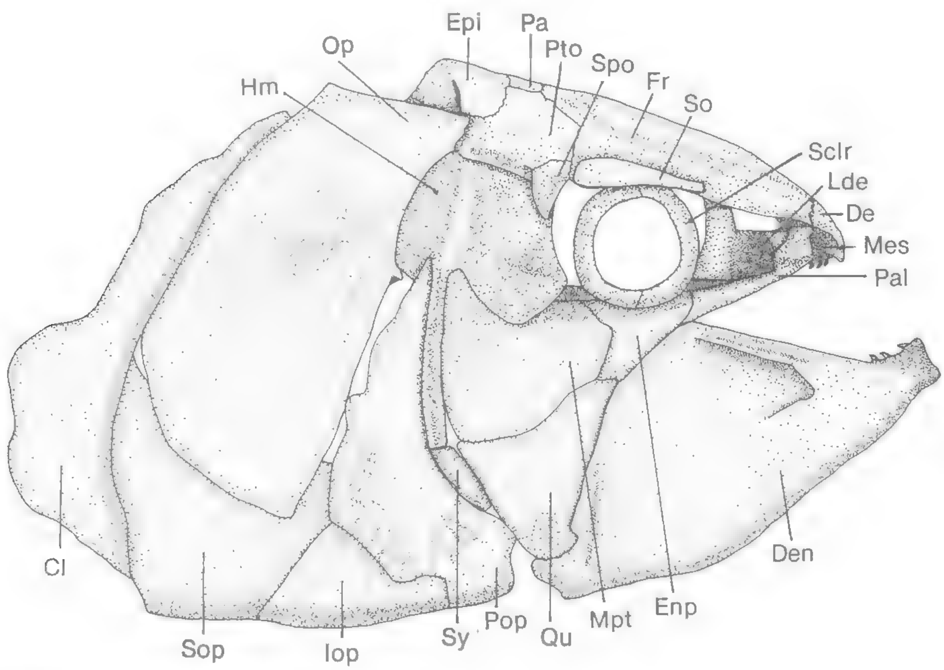

FIG. 2. *Dugaldia emmilta* gen. et. sp. nov. drawn from GSQ 9242. Restoration in right lateral view showing external structure, approximately X 0.75.

FIG. 3. *Dugaldia emmilta* gen. et sp. nov. GSQ 9242, left lateral view showing internal structures, X 0.75

overlies the mesethmoid. Mesethmoids developed into prominent curved wings that combine with lateral dermethmoid to form a facet for head of the palatine. The lateral dermethmoid is large and rectangular, a dorso-ventral depression dividing its lateral surface in two. A strut extends upwards from postero-dorsal surface of mesethmoid to articulate with ventral surface of frontals. Upper and lower hypohyals are joined by an interdigitating suture.

DESCRIPTION

NEUROCRANIUM

Viewed from the side the neurocranium (Figs 4, 6) is wedge-shaped. Its ventral margin is formed by the parasphenoid and its roof by the frontal and ethmoid bones. The posterior margin of the neurocranium is formed by the occipital bones. Dorsally the neurocranium is almost rectangular in shape.

Most of the dorsal surface is formed by the large flat frontals, which meet along a midline suture (obscured by damage posteriorly). Anteriorly the frontals join the dermethmoid by means of a posteriorly-curved semicircular denticulate suture (Fig. 5). Postero-laterally they are flanked by anterior extensions of the pterotics and posteriorly they meet the parietals. Centrally, the frontals are flat and unornamented (Figs 4, 5); laterally, ridges extend to the anterior and posterior margins of the bones. These ridges radiate from centres of ossification at the lateral margins of the frontals, approximately two-thirds of the way back from the anterior margin. The posterior margins of the frontals converge to meet at a point on the midline of the neurocranium, forming a U-shaped tongue of bone. This margin of the frontals is very weathered, making it difficult to interpret exactly the relationships of the bones in this region, particularly the form of the parietals. Thus it is not possible to determine positively whether or not the parietals join along the midline or are separated by the supraoccipital. However, the material that has been preserved indicates that the parietals were not separated by the supraoccipital but that they meet at the midline of the neurocranium. The parietals extend antero-laterally to enclose the V-shaped salient formed by the posterior parts of the frontals.

The pterotics (Figs 4, 5) are large bones, lying lateral to the parietals, which cover most of the postero-lateral surface of the neurocranium. They extend forwards to meet the frontals dorsally and the sphenotics ventrally, and they extend backwards to join the epiotics and exoccipital. The ventro-lateral surface of the pterotic forms the posterior half of the hyomandibular fossa, and the postero-ventral corner is extended into a pterotic spine. The lateral surface is vertically striated. On the antero-lateral corner is an elliptical depression which probably represents the lateral temporal fossa. This extends forwards onto the postero-ventral corner of the sphenotic.

The sphenotic (Fig. 4) forms the posterior margin of the orbit. Its antero-lateral corner is developed into a ventrally directed spur, while its postero-lateral corner defines the post-temporal fossa. Ventrally the sphenotic bears the anterior portion of the large hyomandibular fossa, which extends almost the entire length of the otic region of the neurocranium. It is a simple, horizontal, elongate depression of almost uniform width, though it is slightly expanded at its posterior and anterior ends. Ventro-medially the sphenotic meets the prootic.

The prootic (Fig. 4) is partly obscured by fractures and seems to have been pushed dorsally into the neurocranium. It appears to be a robust bone which articulates posteriorly with the basioccipital and the exoccipital, and ventrally with the parasphenoid. It shares an interdigitating suture with the ascending process of the parasphenoid.

The large exoccipitals (Figs 4, 6) cover most of the ventral half of the occiput. They form the dorsal

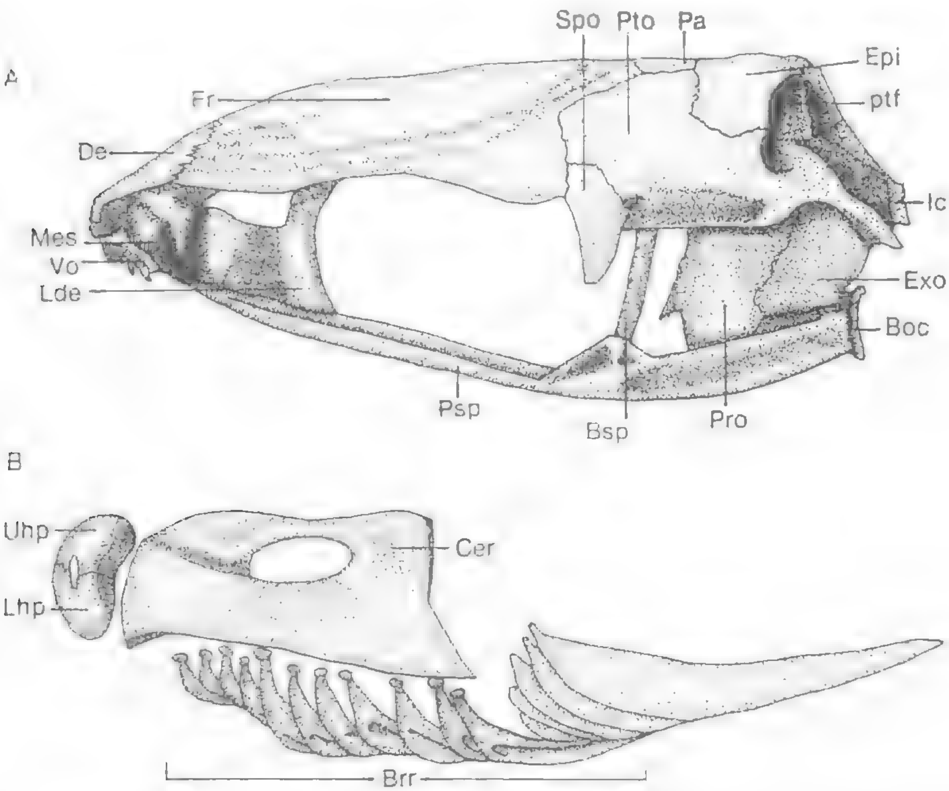

FIG. 4. *Dulgaldia emmilta* gen. et sp. nov. drawn from GSQ 9242, *A*. Neurocranium, left lateral view, X 1.35, B. Branchiostegal support and rays, left lateral view, X 1.1.

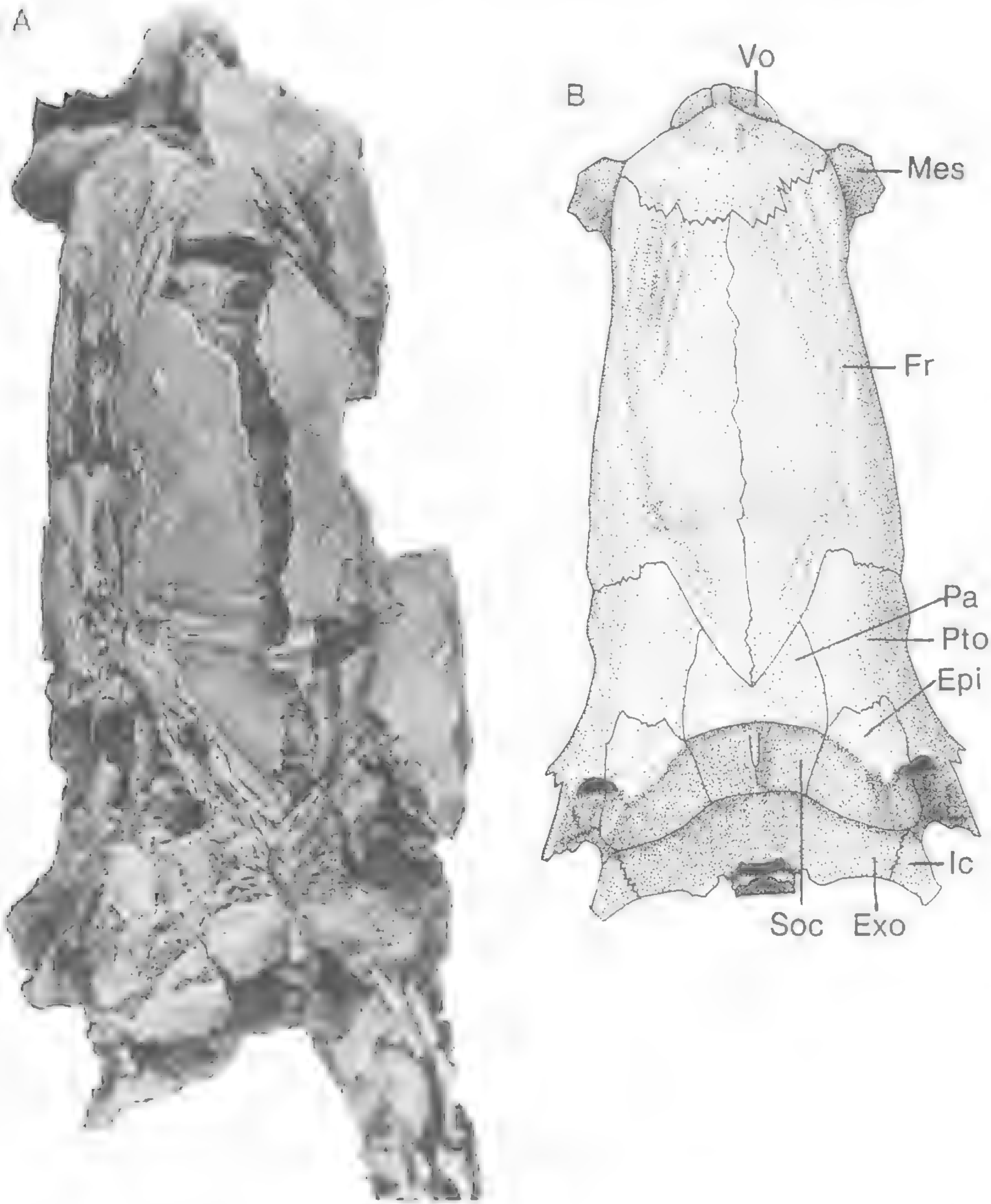

FIG. 5. *Dugaldia emmilta* gen. et sp. nov. A. Holotype (GSQ 9242) Dorsal view of neurocranium, X 1.7. B. Restoration of neurocranium in dorsal view, X 1.3.

portion of the occipital condyle and enclose the foramen magnum. The exoccipitals articulate dorsally with the supraoccipital and the epiotics and laterally with the intercalars. The median line of contact between the exoccipitals is marked by a prominent vertical ridge. Well-developed intercalars (Figs 4, 6) form the postero-ventral corners of the neurocranium. They join the lateral margins of the exoccipitals by an interdigitating suture and adjoin the postero-ventral corner of the pterotics. The subtemporal fossa is not evident.

The epiotics (Figs 4, 6) form the postero-dorsal corners of the neurocranium, lying dorsal to the exoccipitals and lateral to the supraoccipital. They combine with the pterotics to form the post-temporal fossa. This large fossa is roofed by the epiotics and appears to be oval, elongate dorso-ventrally with a central constriction at the suture between epiotic and pterotic.

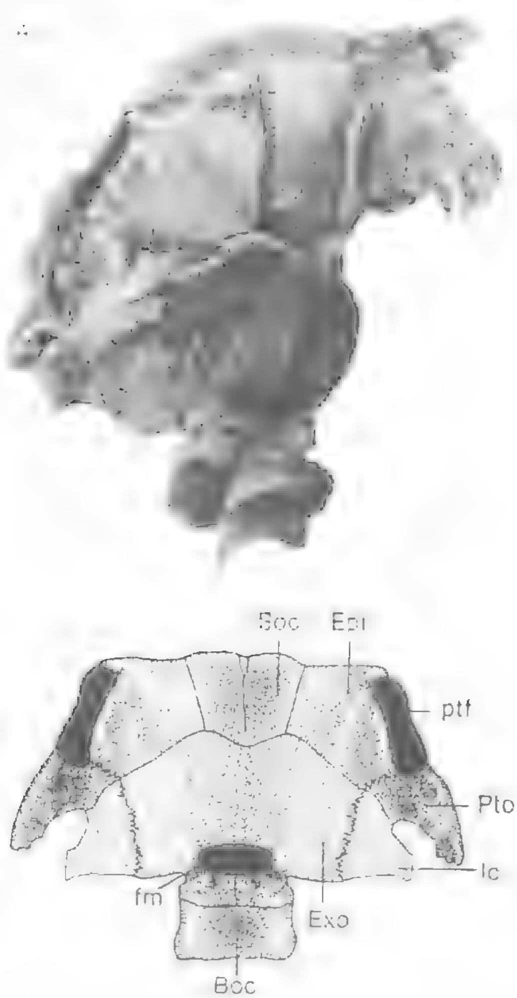

FIG. 6. *Dugaldia emmilta* gen. et sp. nov. A. Holotype (GSQ 9242), Qld, neurocranium, posterior view, X 4.1. B. Restoration of neurocranium in posterior view, X 2.1.

The supraoccipital (Figs 5, 6) lies medial to the epiotics and dorsal to the exoccipitals. Antero-dorsally it appears to join the parietals; however, this region of the skull is so badly weathered that it is impossible to ascertain the exact relationship between these two bones. Even so, the material preserved indicates that the supraoccipitals do not extend anteriorly to separate the parietals. The posterior face of the supraoccipital is markedly concave, with a small supraoccipital crest at the deepest point of the depression. When the neurocranium is viewed laterally the supraoccipital crest is not visible (Fig. 4).

The parasphenoid defines the ventral surface of the neurocranium. It is long, extending forwards from the posterior margin of the neurocranium to cover the dorsal surface of the vomer. The vomer is accommodated in the antero-ventral surface of the parasphenoid by means of a V-shaped depression. The remainder of the ventral surface of the parasphenoid is gently convex except beneath the otic region of the neurocranium. Here the (ventral) parasphenoid becomes gently concave and the lateral margins flare dorsally to form the ventral wall of the posterior myodome. The dorsal surface of the basisphenoid is sharply convex beneath the orbital region of the neurocranium and it then becomes concave beneath the otic region of the brain case forming the ventral compartment of the myodome. The parasphenoid is broadest anteriorly and posteriorly, constricting beneath the orbital section of the neurocranium. Longitudinally, the parasphenoid is gently convex ventrally beneath the orbital portion of the neurocranium. Behind its ascending process the parasphenoid is distinctly flexed through an angle of approximately 120 degrees. Its ascending process forms the postero-ventral margin of the orbital region of the brain case and shares an interdigitating suture with the prootic. At the base of the process a foramen for the internal carotid artery is evident. No teeth were found on the parasphenoid.

A basisphenoid (Fig. 4) extends from the alisphenoid (not visible) to the parasphenoid. It is a simple elongate shaft of bone with a flat lateral surface and a rounded ventral tip which articulates with the parasphenoid. The median vomer (Fig. 4) comprises a bulbous anterior head and a long tapering posterior process embedded in the parasphenoid. The antero-ventral surface of the head shows small hooked teeth on a tooth patch split by a mid-line groove. The antero-dorsal surface of the vomerine head is divided by a mid-line groove which receives a projection from the dorsal ethmoid.

The ethmoid region of the neurocranium (Figs 4-5) is composed of four bones: the dorsal dermethmoid, the median mesethmoid and the paired lateral dermethmoid bones.

The dermethmoid (Figs 2, 4, 6) forms the anterior end of the dorsal surface of the neurocranium. It joins the frontals anteriorly by means of a semicircular denticulate suture. The anterior margin shows a medially situated anteriorly directed "nose", the ventral surface of which is embedded in the head of the vomer and overlies the dorsal surface of the mesethmoids.

The mesethmoid (Figs 4, 5) articulates with the vomer antero-ventrally, the dermethmoid postero-ventrally and the frontals postero- dorsally. Its anterior surface exhibits a slightly concave facet which doubtless received the articulating heads of the maxilla and premaxilla. A pair of lateral wings is situated on the mesethmoid slightly in advance of its antero-lateral junction with the frontal bones. These wings combine with the lateral dermethmoids to form the articular facet for the palatine bone.

The lateral dermethmoids (Figs 2, 4) lie postero-ventral to the mesethmoid and articulate with the frontals dorsally and the parasphenoid ventrally. The ventro-lateral half of the lateral dermethmoid, the ventral margin of which articulates with the parasphenoid, is basically square, with a large vertical indentation along its midline. The anterior margin of this portion of the lateral dermethmoid joins with the mesethmoid to form a facet for the palatine head. Postero-dorsally the dermethmoid contracts to form a strut which articulates by means of an expanded head with the ventral surface of the frontals.

Hyomandibular Apparatus

The hyomandibular (Fig. 2) is composed of a large, dorsal head which contracts ventrally to join a strong ventrally directed shaft. The head, which is shaped like an irregular pentagon, is dominated medially by an extension of the ventral shaft. The dorsal margin of this polygon articulates with the hyomandibular fossa. Posteriorly the hyomandibular bone articulates with the opercular above and the preopercular below. There is no evidence that the hyomandibular has a preopercular process. Anteriorly the hyomandibular forms the rear margin of the orbit. Antero-ventrally it is covered by the metapterygoid.

The metapterygoid is sub-triangular in shape with a postero-ventrally directed apex. Its exterior surface is gently concave, as is the dorsal margin. Antero-dorsally it articulates with the entopterygoid and ventrally it abuts the quadrate.

The quadrate is also sub-triangular in shape. Its blunt apex abuts the articular portion of the mandible. Posteriorly it is joined by the symplectic bone.

The symplectic is wedge-shaped with its base joining the ventral edge of the hyomandibular shaft. From here it extends ventrally to a point, wedging between the quadrate and the antero-ventral margin of the preopercular.

The entopterygoid joins the antero-dorsal corner of the quadrate. It is almost entirely concealed by the metapterygoid and the quadrate. Only the anterior dorsal surface is visible; this is gently concave and extends anteriorly to meet the palatine bone. The ectopterygoid is concealed.

The palatine is a short stout bone. Dorsally it is markedly concave. Anterodorsally it bears a concave head, shaped like a clover-leaf, which articulates with the facet formed by the ventral surface of the mesethmoid and the lateral dermethmoid. Antero-laterally the palatine head exhibits another concave facet which must have received the head of the maxilla.

Hyoid Arch, Branchiostegals and Gill-Arches

The hyoid arch, branchiostegals and gill-arches (Fig. 4) are not well preserved. The posterior element of the ceratohyal is missing and none of the gill-arches has survived intact. The anterior ceratohyal is clearly visible. It is a strong, robust bone exhibiting a large oval 'berciform' foramen. A groove, for the efferent hyoidean artery, extends from the anterior margin of the foramen to the rounded antero-dorsal corner of the bone. The posterior margin of the anterior ceratohyal flexes anteriorly at an angle of approximately 120 degrees. The dorsal margin is slightly convex, and the ventral margin is gently sinuous. The ventral margin meets the posterior margin at an angle of approximately 45 degrees.

Both the dorsal and ventral hypohyals have been preserved, but are somewhat obscured by matrix and bone fragments. They are joined by means of a suture which is interdigitating anteriorly becoming simple posteriorly. At its mid-point this suture is dilated into a foramen. The lateral margins of these bones are difficult to discern, but it seems that they join together to produce a semicircular shape, curving anteriorly, with a slightly concave posterior margin.

Sixteen branchiostegal rays have been preserved, of which 11 meet the anterior ceratohyal. The other five presumably articulated with the missing posterior ceratohyal. Two types of branchiostegal ray are evident. Those adjoining the anterior ceratohyal are composed of a head which articulates with the ventral margin of the anterior ceratohyal. The head caps a cylindrical neck which expands into a posteriorly curved distal shaft. The lateral surface of the shaft exhibits a clearly defined, medially positioned, longitudinal groove which commences at the base of the cylindrical neck. The remaining branchiostegals are much simpler. The anterior, articulating portion of these rays is simply a short blunt projection from which the shaft expands distally to a broad, flat and gently curved ray.

Gill arches are not preserved. However, among the litter of bone fragments are abundant tooth plates, some bearing small, recurved teeth of uniform size. Evidently the apparatus was well toothed.

No gular plate is evident. It is not possible to determine if this is because it never existed or was not preserved.

Dermal Jaws

Only the dentary (Fig. 2) has been preserved and this can be observed only from its exterior surface. It is short and deep, with a high coronoid process located approximately midway along the dorsal margin. Just behind the antero-dorsal edge of the dentary the dorsal margin flattens and curves medially into the short mandibular symphysis. In its anterior half the dorsal margin of the mandible bears small teeth of uniform size. On the lateral surface of the mandible, immediately below the anterior portion of the oral margin, is a deep V-shaped depression (apex directed anteriorly). The angulo-articular, triangular in shape, constitutes the postero-ventral portion of the mandible and forms the articular facet. A groove along the ventro-lateral margin of the dentary marks the path taken by the mandibular sensory canal.

Circumorbital Bones

A single slender supraorbital and the incomplete remains of a sclerotic ring have been preserved (Fig. 2).

Opercular Bones

(Fig. 2) The four bones of the opercular series (preopercular, opercular, subopercular and interopercular) have all been preserved. These thin bones have all suffered some degree of damage along their margins.

The preopercular has a convex anterior margin which adjoins the hyomandibular, symplectic and quadrate. Posteriorly the preopercular meets the opercular, and ventrally it overlaps the interopercular. Sensory canals are indicated by ridges radiating from a point at approximately the mid-point of the anterior margin out to the posterior and ventral margins. The interopercular is mostly masked by the overlapping preopercular. It is oval in shape and the ventral quarter of the bone is curved medially.

The opercular has a rather badly damaged posterior margin. It appears to have been essentially semicircular in shape, with a convex posterior margin. The anterior margin shows a concave dorsal portion which articulates with the opercular process of the hyomandibular. The ventral two thirds of this margin are straight and join the preopercular ventrally. The opercular overlaps the subopercular and joins the cleithrum posteriorly. The subopercular is overlapped by the ventral margin of the opercular and the posterior portion of the interopercular. Consequently, something like a third of this bone is obscured from view. Like the interopercular it is curved medially. Most of the lateral surface of the subopercular is smooth and featureless, except where it abuts the anterior margin of the opercular bone. Here a narrow raised ridge is aligned parallel to the anterior margin of the opercular.

Pectoral Girdle and Fins

These bones are not well preserved and somewhat obscured by matrix and debris. The cleithrum is visible in lateral view, adjoining the posterior margins of both the opercular and subopercular bones. The anterior margin is gently curved both posteriorly and medially; the posterior margin bulges ventrally, giving the bone a 'd-shaped' appearance. The supracleithrum lies dorsal to the cleithrum, abutting the opercular bone, but is too poorly preserved to merit description. The post-temporal is not visible.

The partly-concealed scapular shows a fan-shaped dorsal head joined to a robust ventral stem which articulates with the coracoid. The coracoid, like the scapular, is only partly visible. The anterior portion is obscured from view and posteriorly it is only visible internally. A complex, posteriorly positioned head is evident articulating with the base of the scapular. From the head a long flat shaft of bone extends anteriorly, disappearing beneath the posterior branchiostegal rays. Eleven pterygials are visible behind the coracoid head.

There are indications of 11 pectoral fin rays, and although these are poorly preserved they appear to have branched distally. The first three fin rays are distinctly broader than the rest.

Vertebral Column

Eighteen vertebrae are preserved. Their centra are deeper than long and marked laterally by three deep longitudinal grooves which give the vertebrae a ribbed appearance. It is not possible to determine whether or not the vertebrae are autogenous. The tail has not been preserved.

Squamation

Some poorly preserved scales are visible. All appear to be identical and are large, thin and cycloid, showing concentric radii.

DISCUSSION

The many orders of neoteleosts have been distinguished on skeletal characters of the pharyngobranchial apparatus, upper jaw, rostrum and tail, along with characters of the soft tissues. Unfortunately the holotype of *Dugaldia emmilta* is not sufficiently well preserved to provide reliable information on these characters, so that it cannot be allocated to any particular order of neoteleosts.

A tripartite occipital condyle, comprising exoccipitals and basioccipital, has been regarded as a character defining the neoteleosts (Patterson, 1964; Rosen & Patterson, 1967; Fink & Weitzman, 1982; Lauder & Liem, 1983). Its occurrence in *Dugaldia emmilta* would seem to indicate affinities with this group. However, it should be noted that a tripartite occipital condyle has also been reported in some members of the Salmonidae (Fink & Weitzman, 1982; Lauder & Liem, 1983). On this basis Fink and Weitzman (1983) suggested that the Salmonidae should be regarded as the sister group of neoteleosts, a view which was adopted by Lauder and Liem (1983).

Rosen (1985) disagreed with this view, contending that the tripartite occipital condyle does not occur throughout the Salmonidae. He stated "…. this type of joint has a limited distribution only in recent salmonines and is therefore probably convergent." His conclusion was supported by Cavender and Miller (1972) who reviewed the occipital joints of modern and fossil salmonids.

It is difficult to assess the salmonid affinities of *Dugaldia* because the Salmonidae might not be a monophyletic group (Fink & Weitzman, 1982; Lauder & Liem, 1983; Rosen, 1985). Rosen (1974), in his study of salmoniform fishes, used both the form of the pharyngobranchial apparatus and the caudal skeleton to characterize salmoniforms. Unfortunately, the caudal skeleton has not been preserved in *Dugaldia emmilta* and the pharyngobranchial apparatus has been badly damaged. One feature on which Rosen placed particular emphasis was the arrangement of teeth on basihyal and basibranchial tooth plates. He considered that in their primitive arrangement these teeth "are small, uniform and close set. Among salmoniforms this basic pattern is modified in various ways" (Rosen 1974, p. 273). The incomplete basibranchial toothplate preserved in *Dugaldia* reveals a tooth pattern similar to the primitive pattern described by Rosen (1974). All the teeth appear to be small and uniform in size with the teeth on the margin of the plate showing no evidence of enlargement, which suggests that *Dugaldia* is not a salmonid.

However, more recent work (Fink & Weitzman, 1982) questioned the value of using the presence of a modified tooth pattern on the basihyal and basibranchial tooth plates to characterize salmonids. In contrast to Rosen (1974), Fink and Weitzman (1982) found some salmonids in which the teeth of the basihyal had not been modified from the small uniform tooth pattern described by Rosen (1974).

Overall, the skeletal evidence separating *Dugaldia emmilta* from the salmonids is equivocal. However, the modern natural distribution of the Salmonidae is confined to the Northern Hemisphere, and to date no salmonids have been recorded from the Early Cretaceous of the Southern Hemisphere. The family Galaxiidae does occur in Australia and has been grouped with the Salmonidae in the order Salmonoidei. However most workers (Fink & Weitzman, 1982; Lauder & Liem, 1983; Rosen, 1985) believe that the galaxiids should not be included in this group. *Dugaldia emmilta* shows little similarity with the galaxiids which lack a tripartite occipital condyle. Consequently it seems unlikely that *Dugaldia emmilta* is a member of the Salmonidae and that it is better placed with the neoteleosts.

ACKNOWLEDGEMENTS

I thank the staff of the Queensland Museum, particularly Dr A. Bartholomai and Dr P. Jell for help with the manuscript, Ms. L. Crevolla-Gillespie for assisting me with the plates and figures, and Mrs W. Wesener for all her patient typing.

ABBREVIATIONS

Boc-basioccipital; Bsp-basisphenoid; Brr-branchiostegal rays; Cer-ceratohyal; Cl-cleithrum; De-dermethmoid; Den-dentary; Enp- endopterygoid; Epi-epiotic; Exo-exoccipital; fm-foramen magnum; Fm-formation; Fr-frontal; GSQ-Geological Survey of Queensland; Hm-hyomandibular; Ic-intercalar; Iop-interopercular; Lde-lateral dermethmoid; Lhp-lower hypohyal; Mes-mesethmoid; Mpt-metapterygoid; Op-operculum; Pa-parietal; Pal-palatine; Pop-preoperculum; Pro-prootic; Psp-prasphenoid; ptf-post-temporal fossa; Pto-pterotic; Qld-Queensland; Qu-quadrate; Sclr-sclerotic; Spo-sphenotic; So-supraorbital; Soc-supraoccipital; Sop-subopercular; Sy-sym- plectic; Uhp-upper hypohyal; Vo-vomer.

LITERATURE CITED

Bartholomai, A. 1969. The Lower Cretaceous elopoid fish *Pachyrhizodus marathonensis* (Etheridge Jnr.) p.249-63. *In* Campbell, K.S.W. (Ed.) 'Stratigraphy and Palaeontology. Essays in honour of Dorothy Hill'. (A.N.U. Press: Canberra).

Cavender, T.M. and Miller, R.R. 1972. *Smilodonichthys rastrosus?* A new Pliocene salmonid fish from western United States. *Bulletin, Museum of Natural History, University of Oregon*, **18**: 1-44.

Etheridge, R. Jr. 1905. Description of the mutilated cranium of a large fish from the Lower Cretaceous of Queensland. *Records of the Australian Museum*, **6**: 5-8.

Etheridge, R. Jr. and Woodward, A.S. 1892. On the occurrence of the genus *Belonostomus* in the Rolling Downs Formation of Central Queensland. *Transactions of the Royal Society of Victoria*, **2**: 1-7.

Fink, W.L. and Weitzman, S.H. 1982. Relationships of the Stomiiform fishes (Teleostei), with a description of *Diplophos*. *Bulletin Museum of Comparative Zoology*, **150**(2): 31-93.

Forey, P.L. 1973. A revision of the Elopiform fishes, fossil and recent. *Bulletin of the British Museum (Natural History) Geology*, **10**: 1-222.

Lauder, G.V. and Liem, K.F. 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin Museum of Comparative Zoology*, **150**(3): 95-197.

Lees, T.A. and Bartholomai, A. 1987. Study of a Lower Cretaceous actinopterygian (fish) from Queensland. *Memoirs of the Queensland Museum*, **25**: 177-92.

Longman, H.A. 1932. A new Cretaceous fish. *Memoirs of the Queensland Museum*, **10**: 89-97.

McAllister, D.E. 1968. Evolution of branchiostegals and classification of teleostome fishes. *National Museum of Canada, Bulletin*, **221**: 1-239.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London*, **B247**: 213-482.

1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London*, **B269**: 275-579.

Rosen, D.E. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. *Bulletin of the American Museum of Natural History*, **153**: 265-326.

1985. An essay on enteleostean classification. *American Museum Novitates* no. **2827**: 1-57.

Rosen, D.E. and Patterson, C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History*, **141**(3): 357-494.

Toombs, H.A. and Rixon, A.E. 1959. The use of acids in the preparation of vertebrate fossils. *Curator*, **2**: 304-12.

Weitzman, S.H. 1967. The origin of the Stomiatoid fishes with comments on the classification of Salmoniform fishes. *Copeia*, 3: 507-40.

Woodward, A.S. 1894. On some fish-remains of the genera *Portheus* and *Cladocyclus* from the Rolling Downs Formation (Lower Cretaceous) of Queensland. *Annals and Magazine of Natural History*, (6) **14**: 444-7.

BIOGEOGRAPHY OF THE ENDEMIC FRESHWATER FISH *CRATEROCEPHALUS* (FAMILY ATHERINIDAE)

L.E.L.M. Crowley

Crowley, L.E.L.M. 1990 3 31: Biogeography of the endemic freshwater fish *Craterocephalus* (Family Atherinidae). *Mem. Qd Mus.* **28**(1): 89-98. Brisbane. ISSN 0079-8835.

Biogeography of the freshwater species of the atherinid genus *Craterocephalus* (hardyheads) is examined with reference to previous biogeographic studies of freshwater fish faunas in Australia and Papua New Guinea. A new hypothesis challenges the concept of recent speciation and suggests that there were two temporally separate invasions of ancestral types, giving rise to the two freshwater species groups of this genus. This hypothesis is supported by osteological work, which separates the freshwater hardyheads into two distinct lineages, and by the present distribution of hardyhead species in relation to the geologic history of Australia and Papua New Guinea.

☐ *Atherinidae, Craterocephalus, biogeography, Australia, Papua New Guinea.*

L.E.L.M. Crowley, School of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia; 29 June, 1988.

Australia is notably lacking in diversity of freshwater fishes, and it seems that Talent (1984) was perfectly justified in commenting that the endemic fish fauna was dull when compared with that of Africa and South America. McDowall (1981) was also correct when he suggested that the lack of taxonomic work precluded any realistic appraisal of Australian fish biogeography, whereas Whitley (1959) was probably incorrect when he suggested that the endemic fauna was too recent in origin to have allowed significant radiation of species. In contrast, I suggest that the paucity of freshwater species may be due to other factors:

i) the relative stability of much of the Australian continent throughout the Tertiary;
ii) the general aridity of much of the continent since mid-Miocene;
iii) the physiological adaptability of many of the smaller fish to changing habitats.

An additional factor, which does not account for the apparent paucity of freshwater fish but does contribute to statements such as those noted above, is the lack of taxonomic work.

TECTONIC STABILITY

The Australian mainland has been relatively stable since the Paleocene, apart from its continued northwards movement and Tertiary tectonism along the eastern and southern highland areas (Wellman, 1987). However, there have been marine transgressions (Lloyd, 1969; van de Graaff *et al.*, 1977; Veevers, 1984), the most recent of which separated Papua New Guinea from the Australian continent. During the Plio-Pleistocene there were also orogenies and epirogenies which resulted in river captures or changes in direction of river flow (Twidale, 1966; Heidecker, 1973; Maxwell, 1973; Hopley *et al.*, 1980), but these were restricted mainly to northern Queensland (Day *et al.*, 1983). During the last 60 million years, apart from Eastern Highland tectonics, there has been a lack of geological "vicariant events" in most of the continent, with concomitant lack of new habitats and, therefore, of speciation potential.

GENERAL ARIDITY

Australia is the second most arid continent in the world (Williams, 1984). Rainfall in Australia is seasonal and also very variable, with floods in some years and drought or near-drought in others. With such unpredictable rainfall, many freshwater habitats in central, northern and western regions of the continent are ephemeral and may have been so since the onset of aridity in the mid-Miocene (Bunting *et al.*, 1973; van de Graaff *et al.*, 1977; but see also Bowler *et al.*, 1976). Whilst such unpredictable conditions might be regarded as favouring speciation, ephemeral floodwaters allow dispersal of species and populations, both within and between river systems (Horn Scientific Expedition, 1896; Whitley, 1959; Glover & Sim, 1978a & b). During dry seasons populations retreat

C. s. fulvus
001000011011100101100101000100010100010101111111111
C. s. stercusmuscarum
001000011011100101110010000100010100011101111111111
C. dalhousiensis
001111110011100101010100000100010000001101111111001
C. randi
001000111111100101100100001000101001011100111111111
C. nouhuysi
001000011111100101100001000101010100011101001111001
C. lacustris
001000010111100111100000000100010100011011111111101
C. lentiginosus
000100111111100100001000100010001010000000011111111
C. eyresii
000000100100001101000000000001010100000110111111110000
C. cuneiceps
000000100100110000100101000110000010011010111100010
C. marjoriae
000000100000011010000000100110001000001101111110010
C. marianae
000000100000011010000001101111010100011001111110001
C. helenae
000100110000111010010101101111011110011100111110001
C. kailolae
000000100001011000000101000111010001111000000010111
C. honoriae
110101011010001010001011000000101000100011111111
C. pauciradiatus
001101110010000110101111000010111110000100111111110
C. capreoli
000111111110001111101011000111000100001100111111110
C. mugiloides
110101011010001011101001010010010100001100111111101

to refuge areas, some of which may be fed by natural springs. Other freshwaters may disappear completely during times of prolonged drought, so that their inhabitants perish. Dispersal with the onset of rain allows interbreeding between surviving, but previously isolated, populations (Glover, 1982). Floods occur frequently enough to ensure that the genetic integrity of species is maintained (see, for example, Russell, 1892; Simpson & Doutch, 1977; Allen *et al.*, 1986). So, present aridity and the vagaries of the climate cannot be considered as "vicariant events".

PHYSIOLOGICAL ADAPTABILITY

Habitats in Australia are frequently variable as a result of the climatic conditions. In dry seasons or drought, streams decrease in runoff and refuge areas may dry out, so that the water becomes warmer, more saline, anoxic, or more acidic (Glover, 1982). The evolution of the smaller fishes appears to have entailed selection in favour of maintaining broad physiological adaptability. The tolerance of freshwater fishes to adverse conditions

TABLE 1. Fifty-one characters (in order) used in the binary analysis based on an algorithm of Sneath and Sokal (1973). For each, positive statement = 1; negative = 0.

1. vomerine teeth, present/absent; 2. mesopterygoid teeth, present/absent; 3. 5th ceratobranchial, fused/unfused; 4. premaxillary teeth, restricted to front of jaw/not restricted; 5. dentary teeth, restricted/not restricted; 6. premaxillary teeth, visible externally/not visible; 7. anterior dentary, broad/narrow; 8. interdorsal pterygiophores, well developed/vestigial or absent; 9. mesopterygoid, large/small; 10. base premaxilla, broad/narrow; 11. urohyal ventral pocket, present/absent; 12. urohyal ventral wings, present/absent; 13. posterior notch of coracoid, large/small; 14. scapular foramen, large/small; 15. ventral flange of 5th ceratobranchial, large (high)/small (low); 16. ventral flange of 5th ceratobranchial, elongate/short; 17. lateral process terminal half centrum, long/short; 18. basal process parhypural, large/small; 19. posterior pterotic process, long/short; 20. posterior basibranchial toothplate, present/absent; 21. toothplates on 2 & 3 ceratohyals, present/absent; 22. toothplates on all hypobranchials, present/absent; 23. epibranchial toothplates on 2, 3 & 4, present/absent; 24. 1st ceratobranchial toothplates, present/absent; 25. mesethmoid, present/absent; 26. long teeth on anterior of 5th ceratobranchial; present/absent; 27. supraoccipital crest, large/small; 28. dermosphenotic, broad/narrow; 29. quadrate, very large/small; 30. metapterygoid, large/small; 31. 2ary process premaxilla large/small or absent; 32. anterior projection of coronoid, present/absent; 33. haemal arches of caudal vertebrae, curved/straight; 34. palatine, pointed/cylindrical; 35. palatine-nasal ligament, long/short; 36. antero-medial part of nasal deeply recurved/not deeply recurved; 37. ventral anterior process of nasal for attachment of palatine-nasal ligament, strongly hooked/not hooked; 38. neural plate of 2nd vertebra, large/small; 39. cleithrum anterior projection, present/absent; 40. supracleithrum, long, slender/short, broad; 41. infraorbital canal, open/enclosed; 42. post temporal canal, open/enclosed; 43. dorsal nasal canal, open/enclosed; 44. frontal and supraorbital canal, open/enclosed; 45. dorsal process of cleithrum, present/absent; 46. medial shelf of coracoid, large/small; 47. length medial pelvic wing, to tip/not; 48. width medial pelvic wing, broad/narrow; 49. post temporal canal, broad, shallow/narrow, deep; 50. infraorbitals, 3/less than 3; 51. epiotic crest, large/small.

has been discussed by Whitley (1945), Glover and Sim (1978a and b), Beumer (1979), and Glover (1979, 1982).

PREVIOUS TAXONOMIC WORK

The lack of taxonomic work, particularly for the smaller endemic fish, has attracted comment from McDowall (1981) and Keast (1981). In many cases it is not known how many species actually exist within a particular genus. This lack of knowledge is being remedied, with work in progress for a number of families and genera. The atherinids and related blue-eyes and rainbowfishes, for example, are possibly some of the best-known and best-studied of the small endemic fish.

HYPOTHESES

In 1978, both Ivantsoff and Patten, working on atherinid systematics, advanced independent hypotheses regarding the origins of three distinct groups within the predominantly freshwater atherinid genus *Craterocephalus*.

Patten (1978) stated: "There is no doubt divergence between the "*eyresii*" and "*stercusmuscarum*" groups occurred in the coastal seas of the Australian mainland. Western Australia

TABLE 2. Thirty-nine characters used in Felsenstein's (1985) Bootstrap analysis. The characters are designated as primitive (P), medium (M) and advanced (-) based on work by Rosen and Parenti (1981), White (1985) and B. Said (pers. comm.).

1, vomerine teeth, present, primitive; 2, mesopterygoid teeth, present, primitve; 3, basibranchial toothplate, present, primitive; 4, 5th ceratobranchials unfused, primitive; 5, mesopterygoid large, primitive; 6, fewer intraorbitals, advanced; 7, large 3rd intraorbital, primitive; 8, epiotic crest large, primitive; 9, basihyal bone long, primitive (3 states); 10, basihyal cartilage small, primitive (3 states); 11, unciate process of 1st epibranchial large, primitive (3 states); 12, urohyal ventral pocket present, primitive; 13, urohyal ventral wings present, primitive; 14, posterior process urohyal long, primitive; 15, coracoid posterior edge without notch, primitive; 16, scapular foramen small, primitive, 17, anterior medial process of pelvic long, primitive; 18, ventral flange of 5th ceratobranchial small (low), primitive; 19, ventral flange 5th ceratobranchial not elongated, primitive; 20, number of interdorsal pterygiophores reduced, advanced; 21, interdorsal pterygiophores well developed, primitive (3 states); 22, anal plate reduced, primitive (3 states); 23, reduced numbers of epipleural ribs on caudal vertebrae, advanced; 24, mesethmoid present, primitive; 25, enlarged teeth on anterior of 5th ceratobranchial, primitive; 26, supraoccipital crest large, primitive; 27, narrow dermosphenotic, advanced; 28, large quadrate, primitive; 29, narrow ectopterygoid, primitive; 30, anterior projection of coronoid small, primitive; 31, cleithrum with dorsal process, advanced; 32, cleithrum dorsal process large, advanced; 33, cleithrum with anterior process, primitive; 34, supracleithrum long and slender, primitive; 35, infraorbital canal enclosed, primitive (3 states); 36, post temporal canal enclosed, primitive; 37, nasal canal enclosed, primitive; 38, frontal and supraorbital canals enclosed, primitive; 39, dorsal process of cleithrum rounded, primitive.

C. s. fulvus	---PP-PPP-PPPPPPPPPPMP--P--PP—P—-P
C. s. stercusmuscarum	----PP-PPP-PPPPPPPPPP-P--P--PP---P----P
C. dalhousiensis	—-PPPPMM-PPPPPMPPPPP—P–PP—-P----P
C. randi	—-PPPPPP-PPPPPMPPPPMP--P--PP---P—-P
C. nouhuysi	—-PPPPPP-PPPPPPPPPP----P-PPP—-PM--P
C. lacustris	----PP-PMM-PPPPPPPPPP-- -P--PP-- ----P
C. lentiginosus	--PPPPPPPPPPPPP-PPPPM—-P--PP---P---P
C. eyresii	--P--- --P- ---P---MM--P-PPP --P - -P
C. cuneiceps	---P----MM----M-MPP--P---PP-PPPPPP----P
C. marjoriae	—P—-MM————PP--P--PP--PM---P
C. marianae	---P-P-PMM--------P-PP-PPPPPP-P-M-----
C. helenae	—P-P-PMM——M–PMPM-PPPP—P-PM----
C. kailolae	---P---P--P--P--M----P---PPP-P----PPPMP
C. honoriae	PPPPPPP—PPM–PM–PMM-----PP-P------
C. pauciradiatus	--P--PPP—-PM--P-PPPMM---P-PP--P-P----P
C. capreoli	--PPPPPP---PM--PP--PMM---PPPPP-P--M----
C. mugiloides	PPPPPPP----PM--PM--PMP-P–P-PP-P———

is the most likely dispersal centre since *Craterocephalus pauciradiatus* is found there and also *C. capreoli*, the most probable sister species of the combined "*eyresii*" and "*stercusmuscarum*" groups". However, he gave no indication of how or when these fish might have entered the freshwaters of Australia and Papua New Guinea.

Ivantsoff (1978) suggested: "It is possible that the marine ancestor of *Craterocephalus* had entered through Canning Basin and spread through epicontinental seas" (during the mid-Cretaceous). "As the seas withdrew it fragmented populations which eventually evolved into *C. cuneiceps* . . . *C. marjoriae* . . ., and *C. eyresii*" In addition he stated: "With the onset of Cainozoic the Great Artesian Basin and the Murray Basin became separated possibly providing a barrier which may have resulted in a new line leading to *Craterocephalus stercusmuscarum*, *C. lacustris* and *C. nouhuysi*."

My preliminary electrophoretic work suggests that members of the two freshwater species groups ("*eyresii*" and "*stercusmuscarum*") are so dissimilar genetically as to appear almost separate genera. As a result of this work, a third hypothesis may be presented as follows. Initial entry of the ancestral *Craterocephalus* species was from the N and NW, probably during the mid-Cretaceous (110-95 My) marine transgression when an epicontinental sea covered most of the mainland (Veevers, 1984). As the water regressed peripheral populations retreated with the marine/estuarine habitats. Other populations, isolated further inland, survived and gave rise to species in the "*eyresii*" group. Marine/estuarine populations reinvading during later marine transgressions (Oligocene/early Miocene), also from the N and NW, gave rise to the "*stercusmuscarum*" group.

MATERIALS AND METHODS

Wherever possible, osteological studies were made on at least two or three specimens of each species. Alizarin specimens were prepared using standard techniques developed by Taylor (1967). Results of observations were given binary values (1/0) for presence/absence, large/small (Table 1), or were coded as advanced/primitive (Table 2) following the works of Rosen and Parenti (1981), White (1985) and B. Said (pers. comm.). These values were used in two cluster analysis programmes. Analysis of binary values for 51 osteological characters used a procedure based on an algorithm from Sneath and Sokal (1973), modified by Dr G.M. McKay (Macquarie University). The primitive/advanced characters (39) were used in the "bootstrap" method of Felsenstein (1985) which includes an hypothetical ancestor with primitive characters.

The study used cleared and stained specimens from the following institutions: AMS — Australian Museum, Sydney; MU — Macquarie University, Sydney; WAM — West Australian Museum, Perth. Other specimens from the MU collection: KB Field number — collected by Mr Keith Bishop; JMP Field number — collected by Patten (1978); LC Field number — collected by the author; WI Field number — collected by Dr W. Ivantsoff.

List of Specimens

Craterocephalus honoriae JMP 75-5 (5) Smiths Lake, N.S.W.

Craterocephalus mugiloides KB 75-35 (4) Roeburne, W.A.; KB 75-46 (10) Perth, W.A.; KB 75-32 (5) Port Hedland, W.A.; JMP 77-15 (6) Exmouth Gulf, W.A.; AMS IA 6760 (1) Lindeman Island, Qld.

Craterocephalus capreoli WI 75-26 (1) Exmouth Gulf, W.A.; KB 75-32 (3) Port Hedland, W.A.

Craterocephalus pauciradiatus WI 309 (1) Cleaverville Creek, W.A.; WI 75-27 (3) Exmouth Gulf, W.A.

Craterocephalus eyresii WI 73-4 (3) Lake Bonney, S.A.; WI 70-52 (2) Peel River, N.S.W.; LC 84-1 (2) Warialda Creek, N.S.W.; LC 87-1 (2) Cockburn River, N.S.W.

Craterocephalus marjoriae JMP 77-5 (3) Tabulam, N.S.W.; MU 75-1 (1) Gayndah, Qld; JMP 75-76 (3) Gympie, Qld; LC 84-2 (2) Mary River, Imbil, Qld.

Craterocephalus marianae WI 78-1 (3) Magela Creek, N.T.

Craterocephalus helenae WAM P 25424-008 (2) Drysdale River, W.A.

Craterocephalus kailolae WAM P 17783-001 (3) Foasi Creek, Papua New Guinea.

Craterocephalus stercusmuscarum stercusmuscarum JMP 78-15 (1) Mackenzie River, Qld; JMP 75-70 (3) Mulgrave River, Qld; JMP 75-74 (2) Lotus Creek, Qld; WI 75-21 (2) Cairns, Qld.

Craterocephalus stercusmuscarum fulvus MU 70-22 (2), Manila, N.S.W.; JMP 75-39 (2) Lake Wabby, Fraser Island, Qld; JMP 75-60 (2) Goondiwindi, Qld; LC 84-3 (3) Mary River, Imbil, Qld.

Craterocephalus randi WI 70-41a (2); Fly River, Papua New Guinea.

Craterocephalus nouhuysi AMS 117319-001 (1) Lorenz River, West Irian; WAM P 27806-005 (2) Tabubil, PNG.
Craterocephalus lacustris WI 70-40c (7); WAM P 28159 002 (3), Lake Kutubu, PNG.
Craterocephalus lentiginosus WAM P 25029 003 (2) Prince Regent River, W.A.
Craterocephalus dalhousiensis WI 76-6 (7) Dalhousie Springs, S.A.

RESULTS

The three species groups identified by Ivantsoff (1978) and Patten (1978), namely "*eyresii*", "*stercusmuscarum*" and "*honoriae*", are now more clearly defined. Further species belonging to the first two groups have recently been described (Ivantsoff *et al.*, 1987a & b; Crowley & Ivantsoff, 1988).

The results of the cluster analyses (Figs 1 and 2) show that the "*stercusmuscarum*" group is more closely aligned with the "*honoriae*" group than it is with the "*eyresii*" group. Evidently the divergence between the first two groups was later than that between the two freshwater groups ("*eyresii*" and "*stercusmuscarum*").

In Figure 1 *C. s. stercusmuscarum* and *C. s. fulvus* cluster together and *C. randi* is close to this pair. The similarity between these fish suggests clinal variation rather than true specific differences, but there are minor morphological differences by which they may be recognized. *Craterocephalus marjoriae* and *C. marianae*, which previously were not recognized as separate species (see Ivantsoff *et al.*, 1987a), also cluster together, although there are major osteological differences between them. For example, *C. marianae* has well-developed interdorsal pterygiophores whereas *C. marjoriae* has none (or one or two vestiges at most). In this cluster analysis these two species are most closely aligned with *C. eyresii*.

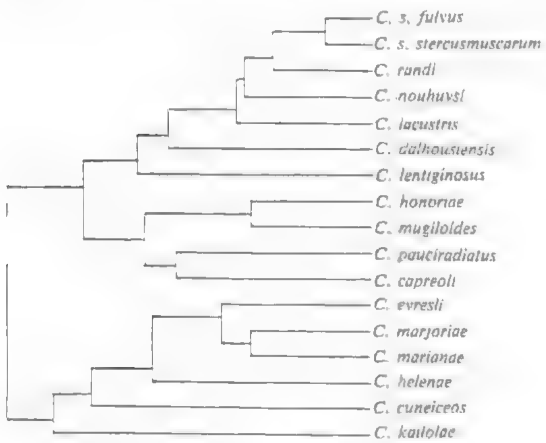

FIG. 1. Cluster analysis of *Craterocephalus* species using an algorithm based on Sneath and Sokal (1973).

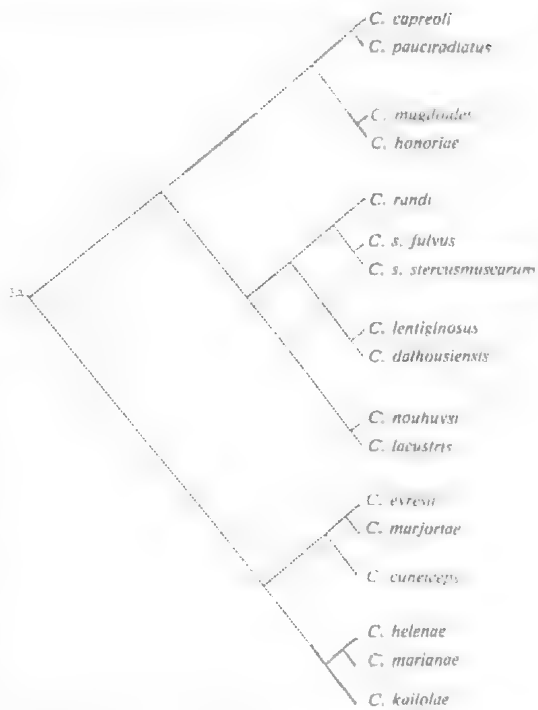

FIG. 2. Cluster analysis of *Craterocephalus* species based on the "bootstrap" method of Felsenstein (1985). Ha, hypothetical ancestor.

Although there are slight differences between the cluster analyses in Figures 1a and b, *C. dalhousiensis* and *C. lentiginosus* cluster together in both, as do *C. lacustris* and *C. nouhuysi*, the two species from the Highlands of Papua New Guinea and Irian Jaya. From the second analysis it is apparent that the "*honoriae*" and "*stercusmuscarum*" group are the same lineage whereas the branch leading to the "*eyresii*" group leads directly from the point of hypothetical ancestry. This is reflected in the cluster analysis (Fig. 1) where the "*honoriae*" and "*stercusmuscarum*" groups arise from the same branch even though no hypothetical ancestor is invoked.

DISCUSSION

The clustering of the (freshwater) "*stercusmuscarum*" group with the (marine)

FIG. 3. Distribution of *Craterocephalus* species. Areas of sympatry between "*eyresii*" and "*stercusmuscarum*" species are shown by cross hatching. Open circles, "*stercusmuscarum*" species; closed squares, "*eyresii*" species.

"*honoriae*" group in both analyses indicates that divergence between these two was probably later than the divergence of either from the "*eyresii*" group. These results support, but do not prove, the hypothesis of two separate invasions into freshwaters of Australia. Osteological differences are more apparent between some species of the "*eyresii*" group (e.g. *C. kailolae*, *C. marjoriae* and *C. marianae*; see Ivantsoff *et al.*, 1987b; Crowley & Ivantsoff, 1988) than between any species of the "*stercusmuscarum*" group. These differences imply more recent speciation in the latter group and a longer period of separation from the hypothetical ancestor for the "*eyresii*" species. The osteological differences are reflected in elecrophoretic work presently being carried out, and again the results suggest the possibility of two separate invasions of hardyheads into Australian freshwaters.

DISTRIBUTION, DISPERSAL AND BIOGEOGRAPHY

If the distribution of the two freshwater groups is examined (Fig. 3), sympatry is found between members of both groups throughout parts of the range in eastern and northern Australia. In the Murray/Darling drainage system *C. eyresii* and *C. s. fulvus* ("*stercusmuscarum*") may be sympatric whereas in the rivers of southeastern Queensland, *C. s. fulvus* is sympatric with *C. marjoriae* (a member of the "*eyresii*" group). In the Northern Territory, *C. marianae* ("*eyresii*" group) and *C. s. stercusmuscarum* are sympatric. Sympatry of *C. stercusmuscarum* with three species of the "*eyresii*" group in different areas (two of which are contiguous), again suggests a longer period of separation allowing for speciation in the latter ("*eyresii*") group.

Craterocephalus randi and *C. nouhuysi* may be sympatric in Papua New Guinea (Upper Fly River), where only members of the "*stercusmuscarum*" group are present in the southern drainages. Osteologically, *C. nouhuysi* is the most distinct of the "*stercusmuscarum*" group whilst *C. randi* is almost indistinguishable from *C. s. stercusmuscarum*. *Craterocephalus randi* may have been in contact with species of northern mainland Australia as recently as 7-10,000 years ago, during the last glacial period (which would account for the close similarity with *C. stercusmuscarum* both osteologically and morphologically); the two other species from the Highlands of Papua New Guinea, *C. lacustris*, and *C. nouhuysi*, have possibly been separated from the main "*stercusmuscarum*" population since the uplifting of the Highlands in the Oligocene/Miocene (Dow, 1977; Pigram & Davies, 1987). In the northern drainages of Papua New Guinea a single very distinctive species, most closely aligned with the "*eyresii*" group, is the only hardyhead known (Ivantsoff *et al.*, 1987b).

If the distribution of some members of both groups is examined in more detail, and with regard to the geologic history of Papua New Guinea and Australia, it becomes evident that Whitley's (1959) suggestion of recent origin cannot be valid. For example, *C. cuneiceps*, a member of the "*eyresii*" group, appears to have a disjunct distribution: it is found in the coastal rivers of Western Australia, and a morphologically similar fish (also similar in many respects to *C. eyresii*) is found in the Finke River of central Australia. While the region between these areas once had numerous rivers, some of which flowed eastward to the centre, there has been no continuous connection — either freshwater or brackish — since mid-Miocene times (van de Graaff *et al.*, 1977). Even during times of flood, when some of the prior lakes and streams of the region are again in evidence, there is still no evidence of connection. Although aligned with *C.*

cuneiceps, to which it appears morphologically and osteologically most similar, the identity of this central Australian fish is equivocal. Even though future studies may prove it to be a different species, the relationship between this fish and *C. cuneiceps* is very close, despite the possible 12-15 million years of separation.

Similarly, *C. eyresii* has a disjunct distribution: it is present in South Australia, and an osteologically-similar fish exists in the Murray/Darling drainages and the Goulburn/Hunter River system on the E coast of New South Wales. In the last case, river capture of the previously westward-flowing headwaters of the Goulburn River (in late Oligocene/ early Miocene times; Galloway, 1967; Wellman & McDougall, 1974) is suggested to account for the eastern population. Alternatively, this population, as well as other small species (e.g. retropinnids), might somehow have reached the Hunter River more recently. Complete disjunction between the South Australian and Murray/Darling populations has not been proven, as fish may possibly still move between the two drainages in times of exceptional floods. If such exchanges are not possible, then these populations of *C. eyresii* would have had no contact since the uplifting of the Flinders Ranges and diversion of the Murray River (see Veevers 1984, p. 143-9).

Excepting the possibility of *C. eyresii* and some other small species finding their way over the Liverpool Range, or between the Murray/Darling Drainage System and the Lake Eyre Drainage, the length of time indicated in these two cases (*C. cuneiceps*, *C. eyresii*) suggests that speciation in *Craterocephalus* has not been rapid.

In the "*stercusmuscarum*" group, *C. dalhousiensis* is found in a very restricted habitat which has only been in existence since Plio-Pleistocene times (5-2 My; (Krieg, 1984). Osteologically it is closest to *C. lentiginosus* (Figs 1 & 2) which is found in the Fitzroy and Prince Regent Rivers, southern Kimberleys, and, as mentioned previously, there has been no water connection between these areas since the mid-Miocene (van de Graaff *et al.*, 1977). However, the habitat of *C. dalhousiensis* is the very warm waters of the mound springs at Dalhousie (Ivantsoff & Glover, 1974) and it is possible that adaptation and speciation occurred fairly rapidly in such an unusual environment.

The distribution of *C. s. fulvus* in the Murray/Darling System, as well as in the southeastern coastal rivers of Queensland, suggests that this fish must have been present in these areas before the eruption of the Tweed volcanic shield, about 20-23 My (Wellman & McDougall, 1974). This, too, implies that the "*stercusmuscarum*" group also is not of "recent" origin.

Divergence between *C. eyresii* and *C. marjoriae*, with which *C. s. fulvus* is sympatric, probably occurred before the Miocene eruptions, and possibly during earlier tectonic instability of this region (Webb *et al.*, 1967). McCulloch (1914), in discussing the distribution of Murray Cod and Australian Perch in NE New South Wales and SE Queensland (similar to the distribution of *C. eyresii*, *C. marjoriae* and also *C. s. fulvus*), suggested that there could have been recent separation of the headwaters of the rivers in that area from those of the northern Darling River System. However, Stuart Rowland (pers. comm.) has found genetic differences between the eastern and western populations of Murray Cod. These differences suggest either that the Murray Cod is a recent but less genetically conservative species than *C. s. fulvus* (which has remained as a single species), or that it has been sympatric with the two "*eyresii*" group species for a longer period of time. In either case, speciation can hardly be of recent origin for any of these fish.

In northern Queensland *C. s. stercusmuscarum* is found in rivers on both sides of the Eastern Highlands. These highlands date from Miocene to late Pleistocene (Wyatt & Webb, 1970; Wellman, 1978, 1987; Coventry, 1980), and yet the hardyhead populations on either side are identical. This leads to the conclusion that either the hardyheads have recently entered these rivers from marine environments on both sides (Gulf of Carpentaria and Coral Sea) or there has been insufficient time for speciation to have occurred since the eastern and western flowing rivers were separated (Hopley *et al.*, 1980).

More unusual mechanisms have also been invoked to account for the present distribution of freshwater fishes in Australia. Rains of fishes have been documented (Whitley, 1959), and it is possible that some fish carried by water-spouts may be dropped in new and suitable habitats. The members of the Horn Scientific Expedition (1896) found fish in man-made bores at both Coward and Strangeways Springs in South Australia, and suggested that these may have been introduced as eggs on the feet or feathers of birds (see also Whitley, 1945). Presumably this latter mechanism would apply only to eggs which had adhesive filaments or could adhere to the birds in some other way. By comparison it seems more probable that much of the present distribution of freshwater fishes has resulted from dispersal in floodwaters coupled with the effects of past geologic events, as suggested by McDowall (1981).

The recent increase in taxonomic work has shown that there are many more species than were recognized when Whitley (1959), McDowall (1981), Keast (1981), and Talent (1984) wrote on the biogeography of Australian fishes. Much of the previous biogeographic work concerned the global affinities of the Australian ichthyofauna. McCulloch (1914) discussed the relationships of Australian galaxiids to those in other southern continents and islands, and also mentioned the "Antarctic Continent" theory (but unfortunately gave no reference for this quote). He also discussed the similarities of some marine fish to those of New Zealand, and to some extent South Africa, and the distribution of Australian marine fishes along the east coast. Haswell (1914) likewise discussed the affinities of galaxiids and also of the lungfish *Neoceratodus*.

The biogeography and affinities of Australian fish compared with those from other continents has been under review since late last century (see McDowall, 1981). However, the biogeography of freshwater fish within the continent has not previously been examined in detail, although the distribution has been discussed by some authors (e.g. McDowall, 1981; Merrick & Schmida, 1984).

Rosen (1964) proposed that atherinids could have originated in the brackish waters of Australia. If this were the case, then the family must be very old, since atherinids of Eocene age have been described from France (Chedhomme & Gaudant, 1984). Consequently Rosen's proposal would imply that atherinids dispersed from the Australian region before the Eocene. In its osteology the French Eocene atherinid, *Palaeoatherinia formosa*, is almost identical to the extant genus *Atherinomorus* (= *Pranesus*), although some of its characters appear more primitive (e.g. position of pectoral girdle). An alternative speculation is that atherinids may have originated in the Tethys Sea and come to the Australian region from there. Forman and Wales (1981) mentioned Tethyan influences in mid to Late Cretaceous fossil material from the Canning Basin and suggested that a warm current could have brought the Tethyan fauna to that region. Ancestral atherinids might also have come by this route and spread throughout the mid-Cretaceous Australian epicontinental sea.

As an alternative to mid-Cretaceous entry, initial invasion may have been via a southern route through the Eucla and Murray Basins during Late Cretaceous or Early Paleocene times, when separation of Australia and Antarctica may have occurred (Cande & Mutter, 1982). A second invasion may have taken place, as previously proposed, with speciation occurring between then and Late Miocene/Early Pleistocene. But if Forman and Wales (1981) are correct in recognising Tethyan influences in the Canning Basin, and, acknowledging the conservatism of the family through time from the meagre atherinid fossil record available, the earlier initial invasion does appear plausible.

Although Whitley (1959) and later authors (e.g. Allen & Cross 1982; Merrick & Schmida 1984) considered the freshwater fishes of Australia to be of recent origin, I suggest that despite the present lack of atherinid fossils in Australia (see, for instance, Turner, 1982), hardyheads at least (and most probably rainbowfishes with similar species distributions) are not the result of recent speciation. The existence of modern-looking fossil atherinids in the Eocene of France (Chedhomme & Gaudant, 1984) and the Pleistocene of Arizona, where fossils of an extant species have been found (Todd, 1974), indicate that atherinids are very conservative and that speciation is unlikely to have been rapid in this family.

It appears that the relative tectonic stability of Australia, combined with climatic conditions and the physiological adaptability of many of the small endemic fish, have been the major factors influencing speciation (or lack of it) in those fish families which have survived and are endemic to Australian freshwaters. Given these conditions, and the lack of large, permanent water bodies, it is not surprising that the Australian freshwater fish fauna appears depauperate when compared with that of South America or of Africa.

ACKNOWLEDGEMENTS

My thanks to Dr W. Ivantsoff (Biological Sciences, Macquarie University) for use of osteological specimens and for discussions and helpful criticism of the manuscript; to Dr G.M. McKay and Mr B. Said (Macquarie University) for their assistance with computing. I also thank the Australian Museum, Sydney, for a Grant for Post-Graduate Studies in Taxonomy, which enabled me to collect extensively in northern N.S.W. and southeastern Queensland.

LITERATURE CITED

Allen, G.R. and Cross, N.J. 1982. 'Rainbowfishes of Australia'. (Angus and Robertson: London, Sydney, Melbourne, Singapore, Manila). 141pp.

Allen, R.J., Bye, J.A.T. and Hutton, P. 1986. The 1984 Filling of Lake Eyre South. *Transactions of the Royal Society of South Australia* 110(2): 81–7.

Beumer, J.P. 1979. Temperature and salinity tolerance of the spangled perch *Therap on unicolor* Gunther, 1895 and the east Queensland rainbow fish *Nematocentris splendida* Peters 1866. *Proceedings of the Royal Society of Queensland* 90: 85–91.

Bowler, J.M., Hope, G.S., Jennings, J.N., Singh, G. and Walker, D. 1976. Late Quaternary climates of Australia and New Guinea. *Quaternary Research* 6: 359–94.

Bunting, J.A., Van De Graaff, W.J.E. and Jackson, M.J. 1973. Paleodrainages and Cainozoic paleogeography of the eastern goldfields, Gibson Desert and Great Victorian Desert. *Geological Survey Branch, Department of Mines, Western Australia Annual Report* 1973: 87–92.

Cande, S.C. and Mutter, J.C. 1982. A revised identification of the oldest sea-floor-spreading anomalies between Australia and Antarctica. *Earth and Planetary Science Letters* 58(1982): 151–60.

Chedhomme, J. and Gaudant, J. 1984. Sur une nouvelle espèce du genre *Palaeoatherina* Gaudant (Poissons Téléostéens, Atherinomorpha) découverte dans l'Eocène supérieur continental environs d'Organac-L'Aven (Ardèche). Géologie Méditerraniénne 11(4): 303–19.

Coventry, R.J. 1980. The Quaternary of Northeastern Australia: The inland regions, p. 387-82. *In* Henderson, R.A. and Stephenson, P.J. (Eds), 'The Geology and Geophysics of Northeastern Australia'. (Geological Society of Australia: Sydney).

Crowley, L.E.L.M. and Ivantsoff, W. 1988. A new species of *Craterocephalus* (Pisces: Atherinidae) and redescription of four other species. *Records of the Western Australia Museum* 14(2): 151–69.

Day, R.W., Whitaker, C.G., Wilson, I.H. and Grimes, K.G. 1983. Queensland Geology. A companion volume to the 1:2,500,000 scale geological map (1975). *Geological Survey of Queensland:* Publication 383, 194 pp.

Dow, D.B. 1977. A geological synthesis of Papua New Guinea. *Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 201.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39(4): 783-91.

Forman, D.J. and Wales, D.W. 1981. Geological evolution of the Canning Basin, Western Australia. *Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 210: 43–4.

Galloway, R.W. 1967. Pre-basalt, and post-basalt surfaces of the Hunter Valley, New South Wales, p. 293-314. *In* Jennings, J.A. and Mabbutt, J.A. (Eds). 'Landform Studies in Australia and New Guinea' (Australian National Press: Canberra).

Glover, C.J.M. 1979. Studies on Central Australian Fishes: Further observations and records, part 1. *South Australian Naturalist* 53(4): 58–62.

1982. Adaptations of fishes in arid Australia. p. 241-6. *In* 'Evolution of the Flora and Fauna of Arid Australia'. (Peacock Publications: South Australia).

and Sim, T.C. 1978a. Studies on Central Australian fishes: A progress report. *South Australian Naturalist* 52(3): 35–44.

and Sim, T.C. 1978b. A survey of Central Australian ichthyology. *Australian Zoologist* 19(3): 245–56.

Haswell, W.A. (1914). The animals of Australia. p. 228-229. *In* Knibbs, G.H. (Ed.) 'Federal Handbook. Prepared in connection with the eighty-fourth meeting of the British Association for the Advancement of Science'. (Government Printer: Melbourne).

Heidecker, E. 1973. Structural and tectonic factors influencing the development of recent coral reefs off northeastern Queensland. p. 273-98. *In* Jones, O.A. and Endean, R. (Eds) 'Biology and Geology of Coral Reefs'. (Academic Press: New York, London).

Hopley, D., Harvey, N. and Pye, K. 1980. The Quaternary of Northeastern Australia: the eastern coastal plains and continental shelf, p. 386-93. *In* Henderson, R.A. and Stephenson, P.J. (Eds) 'The Geology and Geophysics of Northeastern Australia'. (Geological Society of Australia: Sydney).

Horn Scientific Expedition to Central Australia. 1896. 'Part 1. Introduction, narrative, summary of results, supplement to zoological report, map'. Spencer Baldwin (Ed). p. 51-2. (Melville, Mullen & Slade: Melbourne).

Ivantsoff, W. 1978. Taxonomic and systematic review of the Australian fish species of the family Atherinidae with reference to related species of the Old World. Unpublished Ph.D. Thesis, Macquarie University, Sydney. 701pp.

Crowley, L.E.L.M., and Allen, G.R. 1987a. Descriptions of three new species and one subspecies of freshwater hardyhead (Pisces: Atherinidae: *Craterocephalus*) from Australia. *Records of the Western Australian Museum* 13(2): 171–88.

Crowley, L.E.L.M. and Allen, G.R. 1987b. Description of a new species of freshwater hardyhead *Craterocephalus kailolae* (Pisces: Atherinidae) from Safia, northeastern Papua New Guinea. *Proceedings of the Linnean Society of New South Wales* 109 (1986): 331–7.

and Glover, C.J.M. 1974. *Craterocephalus dalhousiensis* n.sp., a sexually dimorphic freshwater teleost (Atherinidae) from South Australia. *Australian Zoologist* 18(2): 88–98.

Keast, A. 1981. Distribution patterns, regional biotas, and adaptations in the Australian biota: a synthesis. p. 1895-998. *In* Keast, A. (Ed.) 'Ecological Biogeography of Australia'. Vol. 3. (W. Junk: The Hague).

Krieg, G.W. 1984. Dalhousie South Australia. 1:250,000 Geological Series — Explanatory Notes. *Department of Mines and Energy, South Australia.* 64pp.

LLOYD, A.R. 1969. Outline of the Tertiary geology of Northern Australia. *Australian Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **80**: 107-32.

MCCULLOCH, A.R. 1914. The Fishes of New South Wales. p.322-9. *In* 'British Association for the Advancement of Science. Handbook for New South Wales' (Edward Lee & Co: Sydney).

MCDOWALL, R.M. 1981. The relationships of Australian freshwater fishes. p. 1251-75. *In* Keast, A. (Ed.), 'Ecological Biogeography of Australia'. Vol. 3. (W. Junk: The Hague).

MAXWELL, W.G.H. 1973. Geomorphology of eastern Queensland in relation to the Great Barrier Reef. p. 233-72. *In* Jones, O.A. and Endean, R. (Eds.), 'Biology and Geology of Coral Reefs'. (Academic Press: New York, London).

MERRICK, J.R. AND SCHMIDA, G.E. 1984. 'Australian freshwater fishes. Biology and Management'. (Griffin Press Limited: South Australia). 409pp.

PATTEN, J.M. 1978. Osteology, relationships and classification of hardyheads of the subfamily Atherininae (Family Atherinidae). Unpublished M.Sc. Thesis, Macquarie University, Sydney, 169pp.

PIGRAM, C.J. AND DAVIES, H.L. 1987. Terranes and the accretion history of the New Guinea orogen. *Australian Bureau of Mineral Resources, Journal of Geology and Geophysics* **10**: 193-211.

ROSEN, D.E. 1964. The relationships and taxonomic position of halfbeaks, killifishes, silversides and their relatives. *Bulletin of the American Museum of Natural History* **127**: 217-68.

ROSEN, D.E. AND PARENTI, L.R. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. *American Museum Novitates* **2719**: 1-25.

RUSSELL, H.C. 1892. 'Results of Rain, river and evaporation observations made in New South Wales during 1890'. (Government Printer: Sydney).

SIMPSON, C.J. AND DOUTCH, H.F. 1977. The 1974 wet-season flooding of the southern Carpentaria Plains, northwest Queensland. *Australian Bureau of Mineral Resources, Journal of Geology and Geophysics* **2**: 43-54.

SNEATH, P.H.A. AND SOKAL, R.R. 1973. 'Numerical Taxonomy'. (W.H. Freeman: San Francisco). 573pp.

TALENT, J.A. 1984. Australian biogeography past and present: determinants and implications. p. 57-93. *In* Veevers, J.J. (Ed.), 'Phanerozoic Earth History of Australia'. (Clarendon Press: Oxford).

TAYLOR, W.R. 1967. Outline of a method of clearing tissues with pancreatic enzymes and staining bones of small vertebrates. *Turtox News* **45**(12): 308-9.

TODD, T.N. 1974. Pliocene occurrence of the recent atherinid fish *Colpichthys regis* in Arizona. *Journal of Paleontology* **50**: 462-66.

TURNER, S. 1982. A Catalogue of fossil fish in Queensland. *Memoirs of the Queensland Museum* **20**(3): 599-611.

TWIDALE, C.R. 1966. Late Cainozoic activity of the Selwyn Upwarp, Northeastern Queensland. *Journal of the Geological Society of Australia* **13**(2): 491-4.

VAN DE GRAAFF, W.J.E., CROWE, R.W.A., BUNTING, J.A. AND JACKSON, M.J. 1977. Relict early Cainozoic drainages in arid Western Australia. *Zeitschrift für Geomorphologie, neue folge*, **21**(4): 379-400.

VEEVERS, J.J. 1984. 'Phanerozoic Earth History of Australia'. (Clarendon Press: Oxford). 418pp.

WEBB, A.W., STEVENS, N.C. AND MCDOUGALL, I. 1967. Isotopic age determination on Tertiary volcanic rocks and intrusives of south-eastern Queensland. *Proceedings of the Royal Society of Queensland* **79**(7): 79-92.

WELLMAN, P. 1978. Potassium-argon ages of Cainozoic volcanic rocks from the Bundaberg, Rockhampton and Clermont areas of eastern Queensland. *Proceedings of the Royal Society of Queensland* **89**: 59-64.

1987. Eastern Highlands of Australia; their uplift and erosion. *Australian Bureau of Mineral Resources, Journal of Geology and Geophysics* **10**: 277-86.

AND MCDOUGALL, I. 1974. Potassium-argon ages of the Cainozoic volcanic rocks of New South Wales. *Journal of the Geological Society of Australia* **21**(3): 247-72.

WHITE, B.N. 1985. Evolutionary relationships of the Atherinopsinae (Pisces: Atherinidae). *Contributions in Science, Los Angeles County Museum of Natural History* **368**: 1-20.

WHITLEY, G.P. 1945. The Simpson Desert Expedition 1939. Scientific Reports No. 5. Biology - Fishes. *Transactions of the Royal Society of South Australia* **69**(1): 10-13.

1959. The freshwater fishes of Australia. p. 136-49. *In* Keast, A., Crocker, R.L. and Christian, C.S. (Eds), 'Biogeography and Ecology in Australia'. (W. Junk: The Hague).

WILLIAMS, M.A.J. 1984. Cenozoic evolution of arid Australia. p. 59-77. *In* Cogger, H.G. and Cameron, E.E. (Eds), 'Arid Australia', (Surrey Beatty and Sons: Sydney).

WYATT, D.H. AND WEBB, A.W. 1970. Potassium-argon ages of some northern Queensland basalts and an interpretation of late Cainozoic history. *Journal of the Geological Society of Australia* **17**: 39-51.

PROBLEMS ASSOCIATED WITH TOOTH PLATES AND TAXONOMY IN AUSTRALIAN CERATODONT LUNGFISH

EXTENDED ABSTRACT

A. KEMP

Kemp, A. 1990 3 31: Problems associated with tooth plates and taxonomy in Australian Ceratodont Lungfish. *Mem. Qd Mus.* 28(1): 99. Brisbane. ISSN 0079-8835.

Most Mesozoic and Cenozoic species of lungfish have been described on the basis of tooth plates, because jaw bones and other parts of the fish are rarely preserved. Tooth plates are not however, universally regarded as valuable for taxonomy (Peyer, 1917; Schultze, 1981), and they are definitely affected by environment, diet, and stage of growth (Kemp, 1977). Attempts have been made, to use features of the jaw bones as specific characters (Martin, 1982, 1984; Kemp & Molnar, 1981; Kirkland, 1987), but the jaw bones may also be susceptible to variation from similar sources.

Character analysis of a large number of jaw bones and tooth plates of the Recent Australian lungfish, *Neoceratodus forsteri* (Krefft, 1870), has been used to determine the effects of environment, diet, and stage of growth on the tooth plates and attached jaw bones of a single species, as well as the extent of inherent variation. The specimens were sorted into groups according to size and geographic origin, and characters of tooth plates and jaw bones were determined within each group. Results indicate that jaw bones were no more reliable than tooth plates for taxonomic purposes, since they were subject both to inherent variation and to the effects of diet. It is, however, possible to use both tooth plate and jaw bone characters as specific determinants, provided that differences due to inherent variation, growth, diet, and environment are recognized. Of these factors, differences due to environment and diet pose the greatest problem, and those due to growth the least.

The character analysis, divided into categories based on results obtained in the Recent species, can be used for determining species in the Mesozoic and Cenozoic lungfish of Australia, groups for which biometric analysis produces unreliable results (Kemp & Molnar, 1981). Tooth plates are of value in the taxonomy of Mesozoic and Cenozoic lungfish, and produce consistent results. A paper describing and discussing the character analysis in full has been submitted for publication elsewhere.

□ *Dipnoi, Taxonomy, Dentition, Australia.*

A. Kemp, Queensland Museum, PO Box 300, South Brisbane, Queensland, 4101, Australia;

LITERATURE CITED

KEMP, A., 1977. The pattern of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* (Krefft). *Zoological Journal of the Linnean Society* **60**: 223-58.

KEMP, A. AND MOLNAR, R.E. 1981. *Neoceratodus forsteri* from the Lower Cretaceous of New South Wales, Australia. *Journal of Paleontology* 55: 211-17.

KIRKLAND, J.I. 1987. Upper Jurassic and Cretaceous lungfish tooth plates from the Western Interior, the last Dipnoan faunas of North America. *Hunteria* **2**: 1-16.

KREFFT, G., 1870. Description of a gigantic amphibian allied to the genus *Lepidosiren*, from the Wide Bay District, Queensland. *Proceedings of the Zoological Society of London* **1870**: 221-4.

MARTIN, M. 1982. Nouvelles donnés sur la phylogénie et la systématique des Dipneustes postpaléozoiques, conséquences stratigraphiques et paléogéographiques. *Geobios, memoire special* **6**: 53-64.

MARTIN, M. 1984. Revision des Arganodontidés et des Neoceratodontidés (Dipnoi, Ceratdontiformes) du Crétacé Africain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **169**: 225-60.

PEYER, B. 1917. Über rezente und triassische Gebisse von Ceratodontidae II. Das Gebiss von *Ceratodus parvus* Ag. nebst Beitragen zur Kenntnis triassischer Ceratodontiden. *Zeitschrift der Deutschen geologischen Gesellschaft* **69**: 18-79.

SCHULTZE, H.-P. 1981. A dipnoan tooth plate from the Lower Cretaceous of Kansas, USA. *Transactions of the Kansas Academy of Sciences* **84**: 187-95.

INVOLVEMENT OF THE NEURAL CREST IN DEVELOPMENT OF THE AUSTRALIAN LUNGFISH *NEOCERATODUS FORSTERI* (KREFFT 1870)

Extended Abstract

A. Kemp

Kemp, A. 1990 3 31: Involvement of the neural crest in development of the Australian Lungfish, *Neoceratodus forsteri* (Krefft 1870). *Mem. Qd Mus.* **28**(1): 101–102. Brisbane. ISSN 0079-8835.

There is considerable evidence from amphibian, avian and mammalian embryos that migratory cells of the neural crest contribute to the formation of many organs and that these cells have far-reaching effects on the structure and function of the resulting adult (le Douarin, 1982). While some of this evidence may be 'misinterpretation and erroneous observations on unsuitable material' (Goodrich, 1930: 764), some is well founded, and there is little doubt that the neural crest is important in developing embryos of higher vertebrates.

Even though the migration of neural crest cells in elasmobranch embryos was recognized by Kastchenko as early as 1888, information on the role of neural crest cells in lower vertebrates is sparse because their embryos are less amenable to experimental manipulation than those of higher vertebrates. Using extirpation experiments, Newth (1951) found that cells of the neural crest in *Lampetra planeri* form part of the dorsal root ganglia, most of the melanophores, and some of the ectomesenchyme. Evidence from xenoplastic transplants indicates that neural crest cells are also involved in skeletal structures of the head in this species (Newth, 1956). Lopashov (1944) studied the role of neural crest cells in the origin of pigment cells and visceral cartilages in teleosts.

Serial sections of neurulae of *Neoceratodus forsteri* show that migrating neural crest cells begin to enter the embryo from the neural plate as the neural folds start to develop, and that migration continues as the folds form. The overall pattern of migration is reminiscent of that in amphibian embryos. However, experiments on *Neoceratodus forsteri* indicate that cells of the neural crest can be removed from both sides of the neural plate in the head region without affecting normal development or pigment patterns. A range of developmental stages was used, from early neural plate formation at stage 17 (when the folds are barely perceptible) to stage 22 (just prior to closure of the neural tube; stages defined by Kemp, 1982). This makes it unlikely that all the crest cells had already migrated before the extirpation experiments were performed. Either the embryos of *N. forsteri* are capable of a surprising degree of regulation, or cells of the neural crest are of limited importance in development of this animal. This result is in contrast to those of similar experiments performed on amphibian and bird embryos, where removal of neural crest cells produces marked abnormalities in development of the brain or visceral skeleton (le Douarin, 1982).

The possibility that the neural crest cells of at least one lower vertebrate are dispensable, and that other cells might fulfil their functions, is significant for embryological theory. The apparent difference in the importance of the neural crest in lungfish and higher vertebrates is also significant for phylogenetic theory. Some workers, basing their argument on the Recent lungfish, consider that lungfishes are the sister group of the tetrapods (Rosen *et al.*, 1981), but others have disagreed (Campbell & Barwick, 1986; Marshall, 1986; Panchen & Smithson, 1987; Schultze & Campbell, 1986). It is also possible that the 'target tissues' of lungfish neural crest cells (if any) differ from those of Amphibia. In the urodele *Ambystoma mexicanum* part of the tooth germ is of neural crest origin (Sellman, 1955) and the oral epithelium is ectodermal (Adams, 1924), at least in part (Chibon, 1970). Using orthotopic grafts with neural crest cells labelled with tritiated thymidine, Chibon (1966) found that the tooth papillae of the urodele *Pleurodeles waltii* contained labelled cells. In lungfish the mouth epithelium is of endodermal origin (Kemp, 1977a and pers. obs.) and determination of the tissue of origin of the mesenchyme component of the tooth germs is of considerable theoretical interest (Kemp, 1977b, 1979 and 1984; Smith, 1984).
☐ *Dipnoi, Neoceratodus, development, neural crest.*

A. Kemp, Queensland Museum, PO Box 300, South Brisbane, Queensland, 4101, Australia.

LITERATURE CITED

ADAMS, A.E. 1924. An experimental study of the development of the mouth in the amphibian embryo. *Journal of Experimental Zoology* **40**: 31–79.

CAMPBELL, K.S.W. AND BARWICK, R.E. 1986. Palaeozoic Lungfishes — A Review. *Journal of Morphology, Supplement* **1**: 93–131.

CHIBON, P. 1966. Analyse expérimentale de la régionalisation et des capacités morphogénétiques de la créte neurale chez l'Amphibien Urodele *Pleurodeles waltii. Memoires de la Société zoologique de France* **36**: 1–107.

CHIBON, P. 1970. L'origine de l'organe adamantin des dents. Étude au moyen du marquage nucléare de l'ectoderme stomodaéal. *Annales d'Embryologie et de Morphogenèse* **3**: 203–13.

Le DOUARIN, N. 1982. 'The Neural Crest'. Developmental Cell Biology. Series 12. (Cambridge University Press : Cambridge). 259 pp.

GOODRICH, E.S. 1930. 'Studies on the Structure and Development of Vertebrates'. (MacMillan: London). 837 pp.

KASTCHENKO, N. 1888. Zur Entwicklungsgeschichte der Selachierembryonen. *Anatomischer Anzeiger* **3**: 445–67.

KEMP, A.R. 1977a. Development of the Queensland Lungfish, *Ceratodus forsteri,* with special reference to the dentition. Unpublished Ph.D. thesis; University of Queensland.

1977b. The pattern of tooth plate formation in the Australian Lungfish, *Neoceratodus forsteri* (Krefft). *Zoological Journal of the Linnean Society* **60**: 223–58.

1979. The histology of tooth plate formation in the Australian Lungfish, *Neoceratodus forsteri* (Krefft). *Zoological Journal of the Linnean Society* **66**: 251–87.

1982. The embryological development of the Queensland Lungfish *Neoceratodus forsteri* (Krefft). *Memoirs of the Queensland Museum* 20(3): 553–97.

1984. A comparison of the dentition of *Neoceratodus forsteri* and *Callorhynchus milii. Journal and Proceedings of the Linnean Society of New South Wales* **107**: 245–62.

LOPASHOV, G.V. 1944. Origin of pigment cells and visceral cartilage in teleosts. *Compte rendu de l'Academie des sciences de l'U.R.S.S.* **44**: 169–72.

MARSHALL, C.R. 1986. Lungfish — Phylogeny and Parsimony. *Journal of Morphology Supplement* **1**: 151–62.

NEWTH, D.R. 1951. Experiments on the neural crest in the lamprey embryo. *Journal of Experimental Biology* **28**: 247–61.

1956. On the neural crest of the lamprey embryo. *Journal of Embryology and Experimental Morphology* **4**: 358–75.

PANCHEN, A.L. AND SMITHSON, T.R. 1987. Character diagnosis, fossils and the origin of tetrapods. *Biological Reviews of the Cambridge Philosophical Society* **62**: 341–438.

ROSEN, D.E., FOREY, P.L., GARDINER, B.G. AND PATTERSON, C. 1981. Lungfishes, Tetrapods, Palaeontology and Plesiomorphy. *Bulletin of* the *American Museum of Natural History* **167**: 163–264.

SCHULTZE, H.-P. AND CAMPBELL, K.S.W. 1986. Characterisation of the Dipnoi, a monophyletic group. *Journal of Morphology Supplement* **1**: 25–37.

SELLMAN, S. 1955. Some experiments on the determination of the larval teeth in *Ambystoma mexicanum. Odontologisk tidskrift* **54**: 1–128.

SMITH, M.M. 1984. Petrodentine in extant and fossil dipnoan dentitions: Microstructure, histogenesis and growth. *Journal and Proceedings of the Linnean Society of New South Wales* **107**: 367–408.

THE YOUNG ONES — SMALL TEMNOSPONDYLS FROM THE ARCADIA FORMATION

A.A. Warren and M.N. Hutchinson

Warren, A.A. and Hutchinson, M.N. 1990 3 31: The young ones — small temnospondyls from the Arcadia Formation. *Mem. Qd Mus.* 28(1): 103–106. Brisbane. ISSN 0079-8835.

An assemblage of small temnospondyl (Amphibia, Labyrinthodontia) skulls from the Arcadia Formation of Queensland is the only such collection from the Early Triassic. Using non-morphometric characters we have been able to identify, from among these specimens, juvenile capitosaurs and a rhytidosteid, whereas two skulls of similar size and superficially similar shape have been determined as mature dissorophoids. We caution against the use of skull proportions in labyrinthodont taxonomy and demonstrate that the trematosaurian group of labyrinthodonts can be considered to be neotenic in at least one character.

☐ *Amphibia, Labyrinthodontia, temnospondyls, Triassic, Arcadia Formation, capitosaurs, rhytidosteid, juveniles.*

A.A. Warren and M.N. Hutchinson, Department of Zoology, La Trobe University, Bundoora, Victoria 3083, Australia; 20 June, 1988.

One problem common to palaeontological and neontological studies of the Class Amphibia s the difficulty of determining to which known adult species a juvenile might belong. Small labyrinthodont amphibians of the order Temnospondyli are commonly found at several localities in the Permo-Carboniferous of Europe and the middle Pennsylvanian of Illinois. Originally assigned to the labyrinthodont Order Phyllospondyli, or branchiosaurs, these were recognised by Romer (1939) as having the characteristics of small or larval temnospondyls. While some of these Palaeozoic forms may now be assigned to various genera within the Eryopoidea and Trimerorachoidea, most remain sheltered beneath the enlarged umbrella of the Dissorophoidea.

The Early Triassic Arcadia Formation of Queensland has yielded a series of labyrinthodont fossils belonging to various families of temnospondyls. Most common components of the labyrinthodont fauna are members of the families Capitosauridae (Warren 1980; Warren & Hutchinson, 1988), Rhytidosteidae (Howie, 1972a; Warren & Black, 1985; Warren & Hutchinson, 1987), Brachyopidae (Howie, 1972b; Warren & Hutchinson, 1983) and Chigutisauridae (Warren, 1981). Rare and fragmentary specimens of the Trematosauridae (Warren, 1985b) and Plagiosauridae (Warren, 1985a) have also been found. In addition, the material collected from the Arcadia Formation includes a number of small skulls of rather uniform size and shape which initially proved difficult to place in a known family. These presumed juveniles are the smallest (youngest?) individuals to be recorded from the Triassic. Much larger juveniles of near-adult proportions have been described in the Triassic species *Benthosuchus sushkini* (Bystrow & Efremov, 1940) and *Parotosuchus peabodyi* (Welles & Cosgriff, 1965).

When considering the relationships of the Queensland juveniles we need to look at the families of Triassic temnospondyls known from Australia and must also consider the possibility that, as in the Palaeozoic, some specimens may be adults of small temnospondyl species such as those found within the Dissorophoidea.

CAPITOSAURIDAE

The first enlightenment came in 1984 when we discovered at the Duckworth Creek locality some one centimetre long skulls (QMF 12290, QMF 12291) in close proximity to remains of moderately-sized temnospondyls (QMF 12281, QMF 12282). Although the characteristic capitosaurid skull shape was not evident, so that the larger skull showed the proportions of a lydekkerinid while the smaller resembled a branchiosaur (Fig. 1), we soon realised that skulls of both sizes shared several characters of the Family Capitosauridae. In both we were able to recognise capitosaurid features such as the hamate process of the lower jaw, transverse ridges on the parasphenoid, inclusion of frontal bones in the

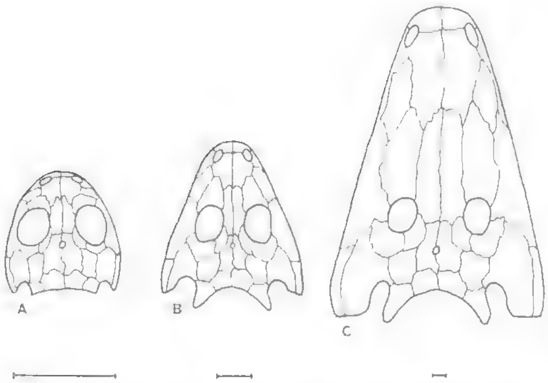

FIG. 1. Differences in proportions between the dorsal skull roofs of: A. *Parotosuchus aliciae* (QMF 12291), B. *Parotosuchus aliciae* (QMF 12281), C. *Parotosuchus gunganj*. All three specimens drawn to the same orbital length; scale bar = 1 cm.

orbits, well-developed falciform crest of the squamosal, and an oblique ridge on the pterygoid. Within the Capitosauridae the specimens could only belong to the genus *Parotosuchus,* with otic notches widely open posteriorly. It is also apparent that the two are conspecific, sharing an extremely hypertrophied oblique ridge on the pterygoid, the absence of a crista tabularis externa beneath the tabular horn, and the presence of ectopterygoid tusks. We have described them as *P. aliciae* (Warren & Hutchinson, 1988).

On criteria used by Boy (1974), the smallest *P. aliciae* skulls may be determined as immediately post-metamorphic individuals, since there is no trace of a branchial skeleton, whereas the larger are young adults. The apomorphies of *P. aliciae* are not found in either of the other species of *Parotosuchus* from the Arcadia Formation, *P. gunganj* and *P. rewanensis* (Warren, 1980). It appears that a mature adult of *P. aliciae* has not yet been found.

Enormous allometric changes accompany the growth of *P. aliciae* from the smallest individual to a mature capitosaur. Therefore, unless it can be demonstrated that a specimen is adult, morphometric features such as skull proportions, position and shape of orbits, length or width of individual skull bones, size of otic notch, depth of skull, and so on, should not be used to determine species, genera, or even families. For instance, if overall proportions were accepted as a valid criterion, the youngest *P. aliciae* skull could, be placed in the Dissorophoidea, the Chigutisauridae or the Rhytidosteidae, but certainly not in the Capitosauridae.

We have identified several other partial skulls as being juvenile capitosaurs, belonging to the genus *Parotosuchus* but not to *P. aliciae*. All are of juvenile size and shape, with large orbits, and all have one or more of the capitosaurian features mentioned above. Of these the most easily observed are the falciform crest of the squamosal and the inclusion of the frontal in the orbital margin. That this frontal inclusion is not itself a juvenile feature of temnospondyls, as might be inferred from Watson's implied growth series of *Onchiodon* (1963, fig. 1), is shown by some later studies of Palaeozoic dissorophoids and eryopoids; examples include *Amphibamus grandiceps*, a primitive larval dissorophid from Mazon Creek, Illinois (Milner, 1982), and *Sclerocephalus* sp. (Boy, 1974), an eryopoid, both of which have the frontals excluded from their orbits.

One unexpected feature of all the *P. aliciae* skulls is the presence on the occipital surface of a palatoquadrate fissure between the ascending ramus of the pterygoid and the squamosal. This was one character used by Warren and Black (1985) to divide most of the Triassic temnospondyls into two groups — a trematosaurian group (Trematosauridae, Rhytidosteidae, Brachyopidae, Chigutisauridae, Lydekkerinidae), in which the fissure is present, and a capitosaurian group (Rhinesuchidae, Uranocentrodontidae, Benthosuchidae, Capitosauridae, Mastodonsauridae, Almasauridae, Metoposauridae), in which it is absent. The presence of the palatoquadrate fissure in immature capitosaurids indicates that it may now be regarded as a juvenile character whose retention in the adult (or in larger specimens) is apomorphic for the trematosaurian group. Trematosaurians may thus be considered paedomorphic, and probably neotenic (*sensu* McNamara, 1986), in their expression of the palatoquadrate fissure. The fissure is apparently absent from Permian outgroups (Eryopoidea, Trimerorachoidea), although it does appear in the neotenic *Dvinosaurus* (Bystrow, 1938). By analogy with juvenile capitosaurs, trematosaurians are also neotenic in the absence, or weak development, of the tabular horns, and in some families, in the parabolic skull shape and large orbits.

RHYTIDOSTEIDAE

Another of the tiny skulls from Duckworth Creek, QMF 12293 (Fig. 2), appears not to have

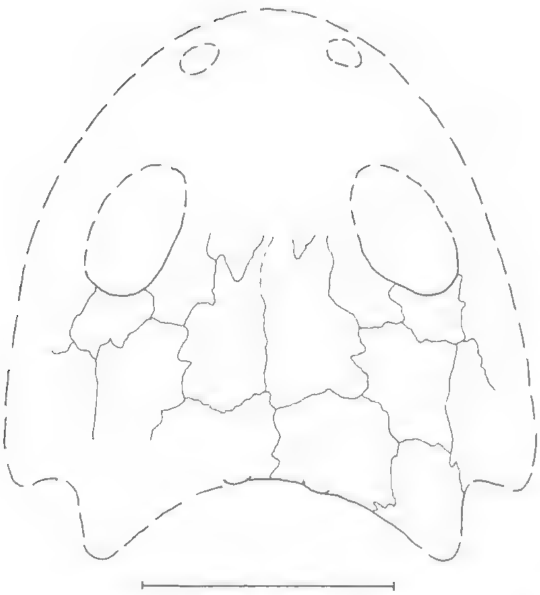

FIG. 2. Juvenile rhytidosteid skull (QMF 12293) in dorsal view. Provisionally referred to *Arcadia myriadens*. Scale bar = 1 cm.

had the frontal included in the orbital margin. It has pointed, widely-spaced tabular horns, a broad palate without the transverse ridges characteristic of capitosaurids, and its pterygoid and parasphenoid are highly denticulate. These are all characteristic features of the Family Rhytidosteidae. In addition, its ornament is finely textured, with many foramina entering the valleys between the ornament ridges. Similar foramina were noted by Cosgriff and Zawiskie (1979) as characteristic of some rhytidosteids, and were present also in *Arcadia myriadens* (Warren & Black, 1985). QMF 12293 is from the same locality as *A. myriadens*, and, although their ornament is differently textured, it is possible that this difference is ontogenetic. The skulls share two raised areas of ornament on the posterior skull margin, a feature not found elsewhere among rhytidosteids, and both apparently lack a parietal foramen. We refer QMF 12293 provisionally to *Arcadia myriadens* within the family Rhytidosteidae.

DISSOROPHOIDEA

Finally, two skulls (QMF 12284, 12285) with associated postcranial material from the Crater (field locality L78) have been identified as members of the superfamily Dissorophoidea (Warren & Hutchinson, in prep.; Fig. 3). This assignment is not without reservation as the skulls have features seen in no known dissorophoid and lack some which are characteristic for most members of the superfamily. Cranial characters which define dissorophoids, or have developed within the superfamily, and are present in QMF 12284 and QMF 12285 are: absence of lateral lines, large orbits and interpterygoid vacuities, basipterygoid joint fused but very narrow, parasphenoid plate without muscle crests or 'pockets', very large otic notch extending from tabular to quadrate, inclusion of frontals in the orbital margin, and an intervomerine depression. As well, various features of their postcranial skeleton, such as the reduced clavicle and gracile femur, indicate terrestriality, a way of life found in many dissorophoids. Of these various characters only the large interpterygoid vacuities and orbits have been identified as possible juvenile features (Boy, 1972). The two characters of our specimen which are particularly undissorophoid-like are the absence of a lachrymal and the (perhaps associated) lack of a lateral exposure of the palatine (LEP, Bolt, 1974). This lateral exposure was not universally present in dissorophoids but the absence of a lachrymal appears to be unique.

Within the Dissorophoidea our form is closest to *Micropholis stowi* (Boy, 1985), with which it shares an Early Triassic time-slot and Gondwanan distribution. In forthcoming work we propose to treat QMF 12284 and QMF 12285 as members of a new genus and species within the family Micropholidae (Warren and Hutchinson, in prep.).

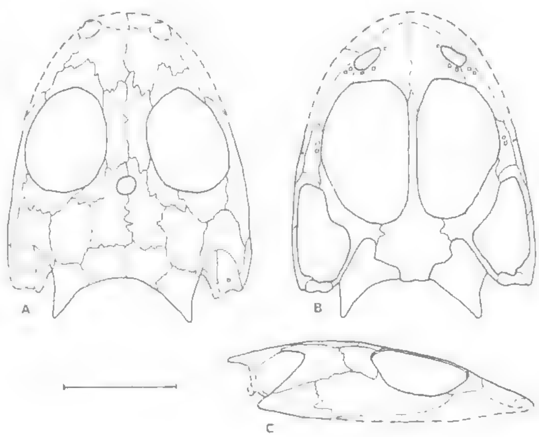

FIG. 3. Dissorophoid (QMF 12284) in A. dorsal, B. ventral, C. lateral views. Scale bar = 5 mm

CONCLUSIONS

Three results of this study are especially significant. First, it is often possible using apomorphic characters to identify, at least to family level, young juveniles of Triassic labyrinthodonts. Second, unless it can be determined that a specimen is adult, morphometric features such as skull proportions, position and shape of orbits, length or width of individual skull bones, size of otic notch, depth of skull etc., should not be used to determine species, genera, or even families. Third, the trematosaurian group of Triassic temnospondyls may be considered neotenic in the retention of a palatoquadrate fissure in the adult.

ACKNOWLEDGEMENTS

We thank Rob Jupp who found QMF 12281, Alice Hammerly who found QMF 12290 and QMF 12291, David Keen and David Walsh for drawing and photography and Rhonda McLauchlan for typing the manuscript. The project was supported by the Australian Research Grants Scheme.

LITERATURE CITED

BOLT, J.R. 1974. Evolution and functional interpretation of some suture patterns in Paleozoic labyrinthodont amphibians and other lower tetrapods. *Journal of Paleontology* 48: 434–58.

BOY, J.A. 1972. Die branchiosaurier (Amphibia) des saarpfalzischen Rotliegenden (Perm, SW-Deutschland). *Abhandlungen der Hessischen Landesamtes für Bodenforschung* 65: 1-37.

1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon-Trias). *Paläontologische Zeitschrift* 48: 235–68.

1985. Uber *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli, Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985: 29–45.

BYSTROW, A.P. 1938. *Dvinosaurus*, als neotenische Form der Stegocephalen. *Acta Zoologica* 19: 209–95.

AND EFREMOV, I.A. 1940. *Benthosuchus sushkini* Efr. - A labyrinthodont from the Eotriassic of Sharzhenga River: *Travaux de l'Institut palozoologiqe de l'Academie des Sciences de l'U.S.S.R.* 10:1–152.

COSGRIFF, J.W. AND ZAWISKIE, J.M. 1979. A new species of the Rhytidosteidae from the *Lystrosaurus* zone and a review of the Rhytidosteoidea. *Palaeontologica Africana* 22: 1-27.

HOWIE, A.A. 1972a. A brachyopid labyrinthodont from the Lower Trias of Queensland. *Proceedings of the Linnean Society of New South Wales* 96: 268–77.

1972b. On a Queensland labyrinthodont, p. 50-64 *In* Joysey, K.A. and Kemp, T.S. (Eds), 'Studies in Vertebrate Evolution'. (Oliver and Boyd: Edinburgh and London). 284 pp.

McNAMARA, K.J. 1986. A guide to the nomenclature of heterochrony. *Journal of Paleontology* 60: 4–13.

MILNER, A.R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology* 25: 635-64.

ROMER, A.S. 1939. Notes on branchiosaurs. *American Journal of Science* 237: 748–61.

WARREN, A.A. 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* 4: 25-36.

1981. A horned member of the labyrinthodont superfamily Brachyopoidea from the Early Triassic of Queensland. *Alcheringa* 5: 273–88.

1985a. An Australian plagiosauroid. *Journal of Paleontology* 59: 236-41.

1985b. Two long-snouted temnospondyls (Amphibia, Labyrinthodontia) from the Triassic of Queensland. *Alcheringa* 9: 293-5.

AND BLACK, T. 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia. *Journal of Vertebrate Paleontology* 5: 303-27.

AND HUTCHINSON, M.N. 1983. The last labyrinthodont? A new brachyopoid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transactions of the Royal Society of London* 303: 1–62.

AND HUTCHINSON, M.N. 1987. The skeleton of a new hornless rhytidosteid (Amphibia, Temnospondyli). *Alcheringa* 11: 291-302.

AND HUTCHINSON, M.N. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* 31: 857–76.

WATSON, D.M.S. 1963. On growth stages in Branchiosaurs. *Palaeontology* 6: 540–53.

WELLES, S.P. AND COSGRIFF, J.W. 1965. A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi* n.sp. from the Wupatki Member of the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences* 64: 1-61.

A MEIOLANIID TURTLE FROM THE PLEISTOCENE OF NORTHERN QUEENSLAND

EUGENE S. GAFFNEY AND GREG MCNAMARA

Gaffney, E.S. & McNamara, G. 1990 3 31: A meiolaniid turtle from the Pleistocene of northern Queensland. *Mem. Qd Mus.* 28(1): 107–113. Brisbane. ISSN 0079-8835.

Three horn cores and a caudal vertebra of a meiolaniid turtle were found in Unit A of the Late Pleistocene Wyandotte Formation (between 45,000 and approximately 200,000 ybp) of northern Queensland. The recurved horn cores are very similar to those of *Meiolania platyceps* of Lord Howe Island, except in size. The Wyandotte cores are more than twice as large as the Lord Howe cores and seem to indicate an animal about the same size as *Meiolania oweni* from the Late Pleistocene of southern Queensland. However, *Meiolania oweni* differs in having straight, flat horn cores, and the Wyandotte meiolaniid is tentatively identified as *Meiolania* cf. *M. platyceps* pending the discovery of better material.
☐ *Reptilia, Chelonia, Meiolaniidae, Pleistocene, Australia.*

Eugene S. Gaffney, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York 10024, USA; Greg McNamara, Department of Geology, James Cook University, Townsville, Queensland 4811, Australia; 1 June, 1988.

The extinct meiolaniid turtles of the Southern Hemisphere are probably the most fascinating and enigmatic of the chelonians. Their appearance is bizarre, with cranial horns and frills and a tail club, and their relationships have been the subject of controversy for a century (see Gaffney, 1983, for literature review and previous work). Although many specimens have been found on Lord Howe Island, mainland Australia has yielded only one partial skull and fragmentary elements. The discovery of meiolaniid remains in northern Queensland extends the range of the group considerably (Table 1) and provides further evidence that at least two meiolaniid taxa existed on the mainland during the Pleistocene.

Abbreviations: AM — Australian Museum, Sydney; BMNH — British Museum (Natural History), London; MM — Mining Museum, Sydney; NMV — Museum of Victoria, Melbourne; ybp — years before present.

MATERIAL

The four *Meiolania* bones described below were deposited within the basal gravels of Unit A of the Wyandotte Formation, a Late Pleistocene sequence that outcrops along the banks of Wyandotte Creek, N Queensland (McNamara, this volume). Unit A is lowermost within the sequence and consists of two distinct lithofacies — a fossil-bearing granule gravel with clay matrix, and a blue-grey clay from which fossils are unknown. On geomorphological grounds the base of Unit A cannot be older than a nearby basalt dated at 410,000 ybp, though here it is argued that the age is probably much less. Unit A basal sediments contain carbonised wood fragments beyond 14C range (45,000 ybp). The *Meiolania* specimens are therefore between 45,000 and 410,000 ybp. However, taking into account the time necessary to form an appropriate depocentre, it is more likely that the specimens are between 45,000 and (approximately) 200,000 ybp. All four bones were found in an area designated as site 1 (McNamara, fig. 1, this volume) and occurred at roughly the same horizon, about 50 cm above the base of the Wyandotte Formation. Two horn cores (NMV P183195 — left; NMV P183196 — right) were in close association, lying oblique to the horizontal, suggesting that they settled in a scour, perhaps after having been washed free from the same individual. A third horn core (NMV P183197) and a caudal vertebra (NMV P183198) were deposited about 50 cm downstream and within about 3 m of each other. Both were lying within the plane of the beds and both show abrasion. The clay-dominated sequence of Unit A represents a vertical accretion facies, typical of a meander cut-off. It implies high runoff, frequent flooding and permanent water — a situation which allows *Meiolania* to occupy the niche traditionally associated with the mythical bunyips!

BRIEF REVIEW OF THE MEIOLANIIDAE

Diagnosis

Eucryptodiran turtles with squamosal and supraoccipital produced into large posterior and postero-lateral processes that extend clear of the skull roof; medial plate of pterygoid separated ventrally from basisphenoid to form the interpterygoid slit; broad squamosal-quadratojugal contact ventral to quadrate (from Gaffney, 1983).

Included Taxa

TABLE 1. Distribution of Meiolaniidae.

	Locality	Age
1. *Niolamia argentina*	Argentina	pre-Oligocene post-Jurassic
2. *Crossochelys corniger*	Argentina	Eocene
3. Undetermined meiolaniid	South Australia	middle Miocene
4. Undetermined meiolaniid	New South Wales	?Miocene
5. Undetermined meiolaniid	Queensland	Miocene
6. *Meiolania platyceps*	Lord Howe Island	Late Pleistocene
7. *Meiolania mackayi*	Walpole Island	Pleistocene
8. Undetermined meiolaniid	New Caledonia	Pleistocene
9. *Meiolania oweni*	Queensland	Pleistocene
10. *Meiolania* cf. *M. platyceps*	Queensland	Pleistocene

Niolamia argentina

A skull and tail ring described by Woodward (1888, 1901) from 'Cretaceous or Eocene' deposits in Argentina, differs from other meiolaniids in having a relatively large occipital frill (A, B, and C scale areas) and a small anterior cranial region. The B scale/horn area is wider, flatter, and relatively smaller than in other meiolaniids for which the area is known. The surface morphology of the skull is more or less well-known from Woodward's description but no sutures were described. A re-examination of the specimen is badly needed.

Crossochelys corniger

Simpson (1938) named a partial skull from the Eocene of Argentina and compared it with *Meiolania* and *Niolamia*. Although Simpson regarded it as a distinct genus, Gaffney (1983) has suggested that it is a young individual of *Niolamia argentina*. The specimen is important in that it provides sutural and basicranial information. Even if it is distinct from *Niolamia*, these two taxa are closely related and may be compared as a unit with the Australasian meiolaniids.

Undetermined Tertiary meiolaniids from the Australian mainland

Fragmentary material from the Tertiary of South Australia and New South Wales has been identified by Gaffney (1981) as meiolaniid. The ages and localities of this material are documented in Gaffney's paper. Although the specimens reveal meiolaniids as important faunal elements in Australia to at least the middle Miocene, the absence (except as mentioned below) of skull material makes comparisons with the complete skulls of other meiolaniids difficult. One small B horn core (MM F13842) from the ?Miocene of Gulgong, NSW, shows close similarity to a small *Meiolania platyceps* B core figured by Gaffney (1983, fig. 25A; AM F18368). The Gulgong horn core is too small to show a marked degree of recurving but is more similar to *Meiolania platyceps* than to *Meiolania oweni*; it confirms the presence on the mainland of a taxon with recurved B horn.

Recent discovery by Dr Alex Ritchie (Australian Museum) of meiolaniid material from the Miocene Riversleigh deposits of western Queensland also extends the range of the group in the Tertiary.

Meiolania platyceps

The works of Anderson (1925, 1930) and Gaffney (1983, 1985) have made this taxon the best-known meiolaniid to date. Hundreds of specimens, including six skulls and three partial skeletons, are available for comparisons. The specimens were all found on Lord Howe Island, in calcarenites thought to be Late Pleistocene in age (see Gaffney, 1983, for review). The Lord Howe Island taxon exhibits a wide range of variation in many features of the skull and postcranium, but there is no evidence that more than one taxon is present, as the variation seems to be continuous (Gaffney, 1983).

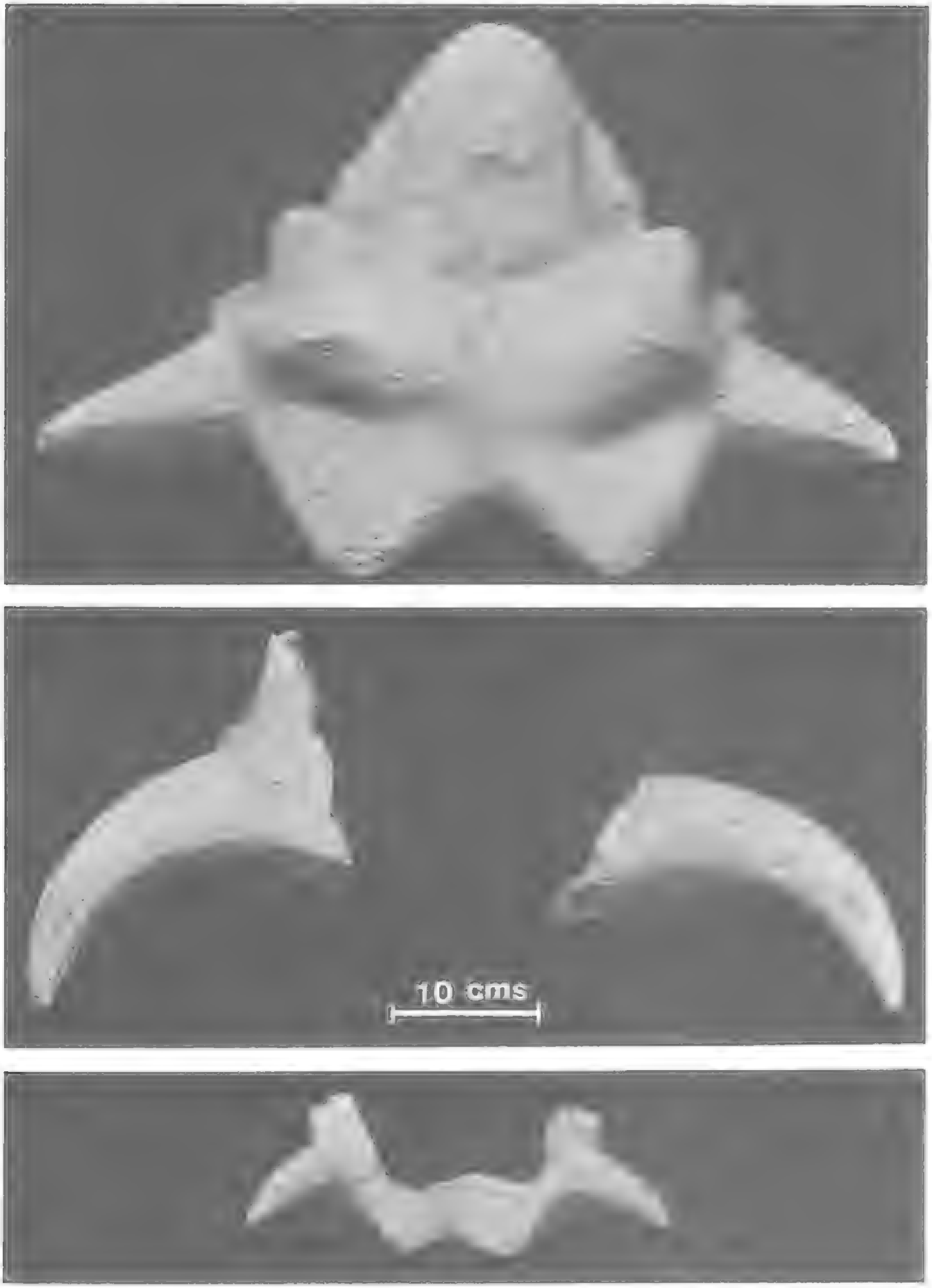

FIG. 1. Above — dorsal view of *Meiolania oweni*, BMNH R391, from Darling Downs, Queensland. Centre— dorsal view of NMV P183195 (left) and NMV P183196 (right) of *Meiolania* cf. *M. platyceps* from Wyandotte Station, Queensland. Below — dorsal view of AM F16866, *Meiolania platyceps* from Lord Howe Island, New South Wales. All photographs show casts at uniform scale

FIG. 2. *Meiolania* cf. *M. platyceps*, NMV P183197, Wyandotte Station, Queensland. Lateral view of left B horn core and fragments of skull roof. Anterior to left.

Meiolania mackayi and other New Caledonian occurrences

Anderson (1925) described some meiolaniid fragments from Walpole Island, including recurved horn cores similar to *Meiolania platyceps*, and assigned them to a new species, *M. mackayi*. The horn cores are consistently narrower than those of *M. platyceps* and seem to be from a smaller species (Gaffney, 1981). Subsequently Gaffney, Balouet and de Broin (1984) described meiolaniid cervicals from the main island of New Caledonia and a nearby island, extending the record of meiolaniids to three islands in the New Caledonian group (Walpole Island is about 100 miles SE of the main island).

Meiolania oweni

Owen (1881, 1882) described a large skull, tail club, and tail ring from the Pleistocene of King's Creek, on the Darling Downs of Queensland, and Woodward (1888) subsequently coined the name *Meiolania oweni* for this material. The skull (BMNH R391) differs conspicuously from *Meiolania platyceps* in having flat, laterally-directed B horns and a relatively large A horn scale area (see Gaffney, 1983, for more detailed cranial comparisons).

DESCRIPTION OF WYANDOTTE MEIOLANIID

Meiolania cf. **M. platyceps**

The Wyandotte meiolaniid material comprises three B horn cores and a caudal vertebra. Two of the horn cores, right and left, are very similar in size and shape and were found in close association. These cores, NMV P183195 (left) and NMV P183196 (right) are presumed to belong to a single animal and have been so restored in Fig. 1. The left core is more complete, consisting of a complete B horn area and much of the surrounding skull roof. The area of the C scale is preserved but the low boss of the C scale itself is broken off. Although sutures are not visible in any of the Wyandotte specimens, comparison with *Meiolania platyceps* from Lord Howe Island (figured in Gaffney, 1983) suggests that nearly all of the squamosal and some of the posterior part of the postorbital are present. Ventro-laterally the dorsal margin of the cavum tympani is preserved and gives another landmark for comparison (see Fig. 2). Posteromedially the lateral one-third or more of the flat A horn area is preserved. The internal surface of the core is very similar to that figured by Anderson (1925, pl. 32, fig. 4), showing the squamosal formation of the antrum postoticum. The antrum is the postero-lateral corner of the cavum tympani and again provides a useful landmark. The right horn core also has a complete B horn and agrees closely with the left horn, but lacks more of the bone around its base. Both cores have the surface texture well preserved and show a coarse pattern of grooves and foramina usually associated with nutrient vessels, presumably for the horny sheath surrounding the core.

The third Wyandotte horn core, NMV P183197, is a specimen from the left side, with much more of the skull roof than in the other two examples. However, the B horn core is so badly weathered and eroded that none of the original bone surface remains.

The most striking feature of the three Wyandotte cores is the large B horn, which is the size and shape of a cow's horn. The curvature is particularly noticeable and more pronounced than in most of the Lord Howe Island horn cores. Nonetheless, the Wyandotte cores are very similar to the Lord Howe Island material (Table 2) and are nearly identical, except in size, to specimen AM F1209, figured both by Anderson (1925, plate 34) and by Gaffney (1983, fig. 24). As documented in Gaffney (1983), the Lord Howe *Meiolania platyceps* has B horns that vary a great deal in size and shape, though nearly every example exhibits some degree of recurving and is oval, not flattened, in cross section. *Meiolania oweni* has a B horn that is triangular with straight sides and is perceptibly flattened. The Wyandotte cores agree with the Lord Howe Island *Meiolania platyceps* in these features.

By contrast the Wyandotte material is similar to *Meiolania oweni* only in its size. The cores indicate an animal with a skull at least as large as *Meiolania oweni* and probably 10-20% larger. However, it is clear that the Wyandotte specimens are more similar morphologically to *Meiolania platyceps* than to *Meiolania oweni*.

A specimen in the Queensland Museum, brought to our attention by Ms Anne Burke and R.E. Molnar, supplies another possible locality for a recurved type of horn core. QM F2344 is the middle third or so of a B horn core, possibly the left. The core is very close in size and shape to the Wyandotte horn cores. It is clearly recurved and oval, rather than being straight and flat, as in *Meiolania oweni*. Unfortunately the label indicates nothing beyond 'old collection, no data'. The specimen was lodged with Darling Downs material, which it resembles very closely in preservation and matrix. It is extremely unlikely to have originated from Lord Howe Island, where the preservation is quite different, and it may well indicate that the 'recurved' *Meiolania* was more widely distributed on the Australian mainland.

TABLE 2. Comparison of horn cores.

Meiolania platyceps (Lord Howe Island)			
	Width	Height	Width/Height
AM F1209 (left)	4.7	9.6	.48
AM F1209 (right)	4.9	9.3	.52
AM F47544 (right)	4.5	7.5	.60
AM F16866 (left)	4.5	8.3	.54
AM F16866 (right)	4.5	8.4	.53
Meiolania cf. *M. platyceps* (Wyandotte)			
NMV P183195 (left)	8.5	20.5	.41
NMV P183196 (right)	8.5	21.0	.40
NMV P183197 (left)	9.0	18.5	.49

A posterior caudal vertebra, NMV P183198, associated with the horn cores from Wyandotte, is nearly identical to caudals of *Meiolania platyceps* from Lord Howe Island, except in size. It bears particularly close resemblance to one example of the *M. platyceps* caudals illustrated by Gaffney (1985, fig. 15C; AM F18706). The haemal spine of NMV P183198, however, is more nearly vertical, as in AM F57984 (Gaffney, 1985, fig. 15B). In the restored tail of *Meiolania platyceps*, Gaffney (1985) suggested that AM F57984 was the fourth caudal while AM F18706 was the ninth or tenth; the total number of caudals in the restoration was conservatively estimated at ten. The caudal described here would appear to be placed posteriorly in the tail, judged on the centrum length and the low neural spine, but not at the end of the tail because the haemal arch is not sufficiently inclined.

The Wyandotte caudal lacks only a few areas: the distal portions of both transverse processes and the right prezygapophysis. There is nothing in the Australasian turtle fauna remotely similar to this caudal, but it appears morphologically primitive for Cryptodira (Gaffney, 1985) in retaining opisthocoelous centrum articulations and well-developed haemal spines. Similar caudals are found in generalized cryptodires such as baenids and chelydrids in the North American fauna.

The only significant morphological difference between the Wyandotte caudal and *Meiolania platyceps* caudals is size — the centrum of the Wyandotte caudal being 11.2 cm long whereas AM F18715 is less than half as big (4.8 cm long).

CONCLUSIONS

Following a careful re-examination of the type and only known specimen of *Meiolania oweni*, we can substantiate the reconstruction of Owen (1881) and confirm the differences between it and *Meiolania platyceps*. Two questions remain. 1) Is *M. oweni* a taxon distinct from *M. platyceps*, or should it be included in that variable species? And 2) if these two are distinct, which horn core morphology is derived for the Meiolaniidae? More extensive comparisons of *M. platyceps* and *M. oweni* may be found in Gaffney (1983), who concluded that these were distinct taxa and should be recognized as different genera. *Meiolania platyceps* is a very variable species as presently interpreted, and recurved horn cores are known in New Caledonia and, possibly, the Tertiary of New South Wales; both of these occurrences may also represent different species, suggesting that the morphology is not limited to Lord Howe Island *Meiolania platyceps*. However, it is clear that *Meiolania oweni* is distinct from *M. platyceps* in more features than the shape of the horn cores (see Gaffney, 1983) and that *M. oweni* and *M. platyceps* are not one taxon.

If this conclusion is accepted, which set of characters for horn cores are derived with respect to the other? And can those characters be used to define a monophyletic group? The wide geographic distribution of recurved horn cores in the Australasian region might suggest that such a feature is more primitive, but comparison with *Niolamia-Crossochelys* suggests otherwise. The comparison of basicranial features by Gaffney (1983) showed that *Meiolania platyceps* could be interpreted as advanced with respect to the basicranial features of *Niolamia-Crossochelys*. If this hypothesis were extended to associated characters, then a weaker but reasonable hypothesis would be that the large frill and flat horns of *Niolamia-Crossochelys* are primitive for Meiolaniidae and that smaller rounded horns are derived. *Meiolania oweni* would be interpreted as advanced over *Niolamia* in this feature, but not so advanced as *Meiolania platyceps*, which has nearly lost the frill. In this interpretation the recurved horns would also be regarded as derived in relation to the flatter, straight cores of *Niolamia* and *Meiolania oweni*. From this argument, it might be concluded that all those species with the recurved B horn constitute a monophyletic group.

The Wyandotte locality is about 1400 km from the Darling Downs habitat of *Meiolania oweni* — which is about twice as far as the 700 km separating the Darling Downs and Lord Howe Island. However, there is a lot of water in that 700 km, and so one might argue very reasonably that the Wyandotte meiolaniid should not be identified with the Lord Howe Island species. So, should the Wyandotte meiolaniid be named as a distinct species? At present it may be distinguished only on the basis of size and geographic provenance, and we do not consider that either criterion warrants the founding of a new taxon. Instead we prefer to express the existing uncertainty by identifying the Wyandotte meiolaniid as *Meiolania* cf. *M. platyceps*. The presence in the Pleistocene of Queensland of at least two species of gigantic meiolaniid is still interesting, whatever the nomenclature reflects.

ACKNOWLEDGEMENTS

We would like to express our gratitude to Mr Eddie Marsterson of Wyandotte Station, Queensland, for so wholeheartedly supporting research on his property. We are grateful for the hospitality and friendship of Peter and Sue Burger of Greenvale, Queensland. Without the fossil collecting ability of their offspring, Alexander, Benjamin, Michelle and Lara, this paper would not have been possible. We would also like to thank Mr Frank Ippolito for making the photographs and Ms Jeanne Kelly for making the casts used in the photographs. Work on meiolaniid and other extinct turtles was supported by NSF Grants DEB 8002885 and BSR 8314816 to E.S. Gaffney.

LITERATURE CITED

ANDERSON, C. 1925. Notes on the extinct chelonian *Meiolania*, with a record of a new occurrence. *Records of the Australian Museum* **14**: 223–42.

1930. Palaeontological notes no. II: *Meiolania platyceps* Owen and *Varanus (Megalania) priscus* (Owen). *Records of the Australian Museum* **17**: 309–16.

GAFFNEY, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates* **2720**: 1–38.

1983. Cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island. *Bulletin of the American Museum of Natural History* **175**: 361–480.

1985. The cervical and caudal vertebrae of the cryptodiran turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *American Museum Novitates* **2805**: 1–29.

BALOUET, J.C., AND DE BROIN, F. 1984. New occurrences of extinct meiolaniid turtles in New Caledonia. *American Museum Novitates* **2800**: 1–6.

OWEN, R. 1881. Description of some remains of the gigantic land-lizard *(Megalania prisca*, Owen) from Australia. Part II. *Philosophical Transactions of the Royal Society of London* (1880) **171**: 1037–50.

1882. Description of some remains of the gigantic land-lizard *(Megalania prisca*, Owen) from Australia. Part III. *Philosophical Transactions of the Royal Society of London* (1881) **172**: 547–56.

SIMPSON, G.G. 1938. *Crossochelys*, Eocene horned turtle from Patagonia. *Bulletin of the American Museum of Natural History* **74**: 221–54.

WOODWARD, A.S. 1888. Note on the extinct reptilian genera *Megalania*, Owen, and *Meiolania*, Owen. *Annals and Magazine of Natural History* (6) **1**: 85–9.

1901. On some extinct reptiles from Patagonia, of the genera *Miolania, Dinilysia,* and *Genyodectes*. *Proceedings of the Zoological Society of London* **1901**: 169–84.

A REVIEW OF THE AUSTRALIAN CRETACEOUS LONGIPINNATE ICHTHYOSAUR *PLATYPTERYGIUS*, (ICHTHYOSAURIA, ICHTHYOPTERYGIA)

MARY WADE

Wade, M. 1990 3 31: A review of the Australian Cretaceous Longipinnate Ichthyosaur *Platyptergius* (Ichthyosauria, Ichthyopterygia). *Mem. Qd Mus.* 28(1): 115-137. Brisbane. ISSN 0079-8835.

Platypterygius has hitherto been recognised by its pectoral fins, but it also possesses other unique features. Radiate-textured growth extends the maxilla to the nasal, dividing the area of the primitive elongate naris into a small, nearly oval, naris and an anteronarial *maxillary foramen*. The neural canal groove on the basioccipital tapered, to end less than half-way across the dorsal surface, so the neural cord turned upward at the occipital joint posterior to the exoccipitals. These latter bones were held together by a flexible sheet of connective tissue posteriorly, and the foramen magnum was mainly within the supraoccipital. Neural arches 1 to 32 were strongly reclined and neural spines 11 to 20(+?) had apical notches which presumably betray the existence of a large dorsal fin above the centre of gravity. Beginning about vertebrae 28-32 the zygapophysial facets were gradationally re-aligned from approximately 30° to vertical.

The new species *Platypterygius longmani* is erected on the basis of the best available material. This new taxon accommodates the species apparently represented by the indeterminate fragments *Ichthyosaurus australis* McCoy (1867), *I. marathonensis* Etheridge (1888) and many better specimens, all from the Albian of Queensland.

All known Australian ichthyosaurs were preserved in oxygenated environments and have floated and lost extremities during decomposition after death. Euxinic environments contain many individuals that never floated, consequently the extremities are much more likely to be preserved.

☐ *Reptilia, Ichthyosauria, Longipinnate, Platypterygius longmani, Cretaceous, Queensland.*

M. Wade, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 30 December, 1988.

De Vis, who we are honouring in this Symposium, came too late on the scene to describe the first Australian ichthyosaurs. These were collected near O'Connell Creek, a tributary of the braided Flinders River in North Queensland, by James Sutherland in 1865 and 1866, and were despatched promptly from Marathon Station to Professor M'Coy (or McCoy as he later spelt his name) for the collections at the Museum of Victoria (M'Coy, 1867, 1869).

The general area of these finds was in the upper Albian, part of a re-flooded Euroka Strait (Smart & Senior, 1980). This was the intake for ocean water into the Eromanga Basin Sea, across a broad sill between the Mt Isa and Georgetown Precambrian blocks. While the upper waters teemed with fish, cephalopods, and their predators, the sea floor had a restricted, almost monospecific, *Inoceramus* fauna. Perhaps this monotonous benthic fauna reflected a slightly hypersaline counter-current such as that which flows out of the Mediterranean just above the sill between Gibraltar and Africa. Further into the basin gypsiferous silts and shales interdigitate with fish-debris limestones or 'cannonball' concretions, as at 'Canary' Station near Boulia, NW Queensland. Together all these beds constitute the Toolebuc Formation. Charles and Andrew Robinson of 'Canary' have located five incomplete but identifiable ichthyosaurs to date, and a sixth example has just been collected there, with the skull and cervical vertebrae of a large embryo in the same nodule as part of the ribs of the adult. To the north the Allaru Mudstone overlies the Toolebuc Formation, and going east, it extends stratigraphically downward and replaces the upper Toolebuc. Ichthyosaurs are common in both formations. As they were usually encased in identical limestone nodules in both formations, and the formations themselves are subdivisions of older stratigraphic groups, provenance is not always clear from data associated with older finds.

The Eromanga Basin had a cool temperate climate in the Aptian and Albian (Day, 1969), and lacked warm-water fauna. It was practically an ichthyosaur feeding-lot, for the arcuate, basin-edge exposures of the Toolebuc Formation and Allaru Mudstone contain most of the world's known remains of Cretaceous ichthyosaurs.

Specimens registered with the prefix QMF are those of Queensland Museum fossil collection, those with prefix MVP belong to the Museum of Victoria, Palaeontology collection. Registered material considered in this paper is listed below.

Holotype QMF2453, Telemon lease, Dunluce Station, via Hughenden. Found in limestone nodules in the shale (Toolebuc Fmn) of the hill halfway between the abandoned Telemon homestead and its abandoned woolshed. Collected, prepared and donated to Queenland Museum by J. Edgar Young. In translating 'one mile from homestead' into 1.6 km from either building, a spuriously exact location is achieved. The spot is not yet relocated.

Paratypes figured or mentioned here, or as *Platypterygius australis* by Wade 1984:

QMF551, Galah Creek, near Hughenden.
QMF3348 (and QMF3389, left wrist and arm only) Stewart Park, Nelia; Toolebuc Fmn.
QMF10686, Boree Park; Toolebuc Fmn.
QMF12314, Kilterry; Allaru Mudstone.
QMF16811, Canary, SE of Boulia, NW Queensland; Toolebuc Fmn.
QMF16812, juvenile within F16811.
QMF13261, Canary, SE of Boulia; Toolebuc Fmn.
QMF12317, near 'Big Hole', Flinders River, near Julia Creek; Toolebuc Fmn.
QMF2299, Brixton, W of Barcaldine, Central Queensland; Allaru Mudstone.
QMF2573, Lydia Downs, Nelia; limestone of either formation.
MVP12989, and associated material numbered P12992, P22653-4, P22656-61. All were numbered 48 by Sutherland; limestone nodule in gypseous shale, Flinders River near O'Connell Creek; Allaru Mudstone.
MVP12991, forefin collected by Sutherland, in 1866, near Flinders River; Allaru Mudstone.
MVP12990, skull fragment collected by Sutherland, in 1866, and numbered 60. Flinders River near O'Connell Creek; Allaru Mudstone.

All specimens but one are from North Queensland; the exception, QMF2299, is the most southeasterly specimen.

We have enough material to establish the intraspecific variability of many bones besides the humeri (Wade, 1984). Acid preparation on the most promising portions of several specimens is still under way, and will probably continue intermittently for years because the longipinnates are not nearly as well known as the latipinnates *Ichthyosaurus* (Sollas, 1916; McGowan, 1973a) and *Ophthalmosaurus* (Appleby, 1956, 1958, 1961). '*Ichthyosaurus* cf. *latifrons*' Watson and Townend (*in* Romer, 1968) is a species of *Temnodontosaurus* (Appleby, pers. comm.).

Longman (1922) described the Galah Creek skull, QMF551, and had made a restoration sketch of the head in side view. His photographs (his plates 1 and 2) substantiate his complaint that the matrix, which was harder than the bone, could not be removed satisfactorily. His restoration is a classic example of his X-ray vision. He suspected even then that there was no suture dividing the large quadratojugal into lower quadratojugal and higher supratemporal, for he wrote of it with doubt and indicated it only with a faint, dashed straight line. In other respects there is little difference between his restoration and that which Romer (1968) subsequently based upon "*Myopterygius*" *americanus* (Nace), *recte* also *Platypterygius* (McGowan, 1972b). Romer dispensed with the hypothetical suture and the name supratemporal, and showed less curvature in the rear of the lower jaw. In general, Longman's specimen was less damaged than Romer's and he is therefore the more accurate of the two in restoring the jugal, maxilla, pre-narial maxillary foramen, naris and narial crest, even though his artist was less artistic than Romer's. Evidently Longman's work was unknown to Romer in 1968, since Romer was scrupulous about crediting other workers.

The Galah Creek skull has undergone acid preparation (Wade, 1984, fig. 1c; Figs 1, 2), which has been halted lest original articulation be lost. Description of individual bones will depend more on the well-preserved but badly disrupted MVP12989 and other specimens. Essential background to ichthyosaur description is the preservational history.

Preservation

The taphonomic history of ichthyosaurs differs strongly in oxygenated and euxinic environments, and food remains are preserved chiefly or only in the latter. All Australian material to date has been retrieved from oxygenated environments, but when the oil shales near Julia Creek become economically viable there is hope of well-preserved ichthyosaurs.

Schaeffer (1962) made a prolonged study including taphonomic history of dolphin carcasses in the North Sea and some of its inlets, and suggested (Schaeffer, 1972) that it would be applicable to ichthyosaurs. In part, it is. The North Sea is only slightly less land-locked than was the Albian Australian Eromanga Basin Sea. Both seas were (or are) oxygenated and (at least before netting of the North Sea) teemed with the fish, cephalopods and marine tetrapods of their day. Live marine tetrapods are just negatively buoyant (with turtles as heavy exceptions, and temporary, deep-breathing light exceptions). Relatively few of those that contributed skeletons to the fossil record would have died so rapidly that they escaped death by drowning. Both compression at depth and the weight of water replacing air would have caused the bodies to lie on the sea floor until decomposition had generated enough gas to buoy them up to the surface. Schaeffer recorded the movement of certain carcasses to and fro for weeks or even months; sometimes stranding intervened. Ultimately even connective tissue disintegrated, and the carcasses were reduced to skin-wrapped agglomerations of bones by the time they sank.

The geologist receives skeletons from the fossil record at a stage after they left Schaeffer's jurisdiction. The skin-wrapped bones have lost their binding and are either encased in early-formed calcareous deposits or deformed in more compressible sediments. So far as ichthyosaurs are concerned, two differences stand out from dolphins. First, in ichthyosaurs the jaws had snapped together and had stayed together — unless the connective tissues of the skull had disintegrated — implying that they had a decay-resistant, possibly ligamentous, mechanism for maintaining closure. This observation should be regarded as an extension of the description of musculature by McGowan (1973), not as an alternative. Second, partly- articulated specimens are relatively common in comparison with disarticulated assemblies. Evidently these sank at a somewhat earlier stage of disintegration than many dolphins. Perhaps they were less fatty. The extremities, fin edges and tips, hind limbs and tail fins had usually suffered greatly, and it is normal for little of them to remain. Small-toothed forms, with correspondingly short tooth roots, are gaining a reputation for toothlessness that may be quite undeserved, and may relate to the floating or not floating (below) of the corpses (contrast Appleby, 1956, p. 444, pl. 2, fig. 1, or 1958, pl. IV, with Martill, 1987a). The teeth, or at least their enamelled portions, were approximately vertical to the jaw (Figs 3A, C) but some sets of jaws show a relative antero-posterior movement which has displaced the interlocked teeth in the tooth grooves of premaxilla/maxilla and dentary as a mass. Alternatively, crushing of the less resistant parts of the skull may displace the more rearward teeth, laterally in QMF551, the Galah Creek skull (Longman, 1922; Wade, 1984). Since tooth loss from the grooves tends to be wholesale when it occurs, toothless ichthyosaurs should not be casually accepted as fact unless atrophied tooth grooves, or an alternative method of feeding, have been demonstrated. The latter possibility has been partly substantiated by McGowan (1979) for one species of *Stenopterygius*, *S. quadriscissus*, and denied for other species of the genus.

Preservation in euxinic basins is also the preserve of the ichthyosaur and the geologist. Hofmann (1958) traced the effects of taphonomy on the Holzmaden specimens of *Stenopterygius* (Toarcian). These may show current transport or *in situ* breakage, crushing and other deterioration, but many skeletons are essentially complete. Tails terminate in reduced, down-turned tail-fin vertebrae such as are rarely found in oxygenated environments. Fingers and toes taper to tiny phalanges, lateral digits are complete, and fossils of connective tissue surrounds are known. Even some newly born or half-born juveniles lie with their mothers. These are not skeletons of carcasses that have floated for weeks, and many have not floated at all from the place they touched down after death. The Middle Triassic Tessin *Mixosaurus* (Kuhn-Schnyder, 1964) are similarly well-preserved in black shales. Bone-scatter due to flattening is their most common deformation, and stomach contents are commonly represented by fish scales.

Rotting and mineralization are accelerated in euxinic conditions (Allison, 1988). In some iron-rich sediments sulphide decomposition is a problem. The holotype of *Platypterygius platydactylus* Broili (1907) had been excavated and mounted before Broili was able to describe it. The specimen was in part magnificently preserved and in part destroyed by iron sulphide decomposition. The coracoid and parts of some other bones were compressed. Little is known of the upper and inner parts of the skull, but the axial vertebrae are intact except for the proximal 18 or so down-turned vertebrae of the tail fin (Broili, 1907; Wade, 1984) and the tail tip. The pelvic girdle, rear fins, and much of the pectoral fin had deteriorated completely. In all, it seems to have been a fairly typical case of preservation in an euxinic environment.

NOMENCLATURE

All the specimens here appear to be *Platypterygius 'australis'* (McCoy). The species is caught up in nomenclatural problems because McCoy described it from the first material that came to hand — a few centra, which were not figured and are still at least temporarily lost (Wade, 1984). According to the collector, James Sutherland, the holotype was 'numbered 48 (five vertebral joints)', but McCoy (1867) did not state whether the rib condyles were single (from tail) or double (from body or neck). The measurements he gave do not allow the assumption that the holotype was a close fit to any of the 1866 material (McCoy, 1869) that Sutherland found at the same locality and also numbered 48. This material comprised a poorly articulated skull, with atlas/axis and the next 32 vertebrae in articulation, accompanied by two pairs of larger tail centra (Wade, 1984). These latter might perhaps articulate with the holotype, if it were assumed that McCoy confused height (his 'depth') and width, and if the original piece were found. Unfortunately there is no objective means of relating the holotype to identifiable material, even if it were found and fitted to these tail centra.

Although Etheridge (1888) described a snout fragment (QMF1448) as *Ichthyosaurus marathonensis,* he was inclined to recant and accept it as possibly *I. australis* by the time of Jack and Etheridge (1892, pp. 505-8). The custom of accepting all the material McCoy had handled as the composite holotype of *'I. australis'* arose in Etheridge's day, and Chapman (1914) remarked that *Ichthyosaurus australis* McCoy was 'typically represented by a nearly complete specimen'. This was a strange remark from a worker who had illustrated the smaller remnant of two partial skulls. He figured MVP12990, skull no. 60 of Sutherland's collecting, together with an incomplete forefin MVP12991 which has been separated from its collecting number. From registered data forefin MVP12991 belonged either with skull 48 or skull 60, but the holotype is the five centra nominally described in 1867, and is neither of the two skulls, each with associated material, vaguely discussed en bloc by McCoy in 1869.

McCoy's type description is brief (McCoy, 1867): 'The remains are of the two well-marked genera *Ichthyosaurus* and *Plesiosaurus*. Of the former there are numerous vertebrae, deeply biconcave with conical articular surfaces, the centrum 4 inches wide, 3 inches deep and 1½ inch (sic) long. The species I name *Ichthyosaurus australis* (M'Coy).'

The collector and donor, James Sutherland, also mentioned the dimensions 3'' x 4'' in his letter of conveyance to McCoy, though unfortunately he did not specify which was height or width. No (other ?) specimen of Eromanga Basin ichthyosaurs is known to have undamaged vertebrae that are decidedly wider than high (='deep'), but it is debatable whether McCoy would have mentioned mild distortion.

If a neotype for *Ichthyosaurus australis* McCoy were to be chosen, partial skull MVP12989 with 34 vertebrae attached, and 4 more associated, would deserve serious consideration. This was found at the type locality only one year after the holotype, and by the same collector. McCoy (1869) made joint mention of this and another specimen under the name *Ichthyosaurus australis,* so the individual has impeccable paper credentials. It lacks fins and humeri and so cannot be distinguished from *Platypterygius hercynicus* (Kuhn) or *P. americanus* (Nace) at a specific level, although the basioccipital is sufficiently close to that of *P. hercynicus* to establish the generic affinity. The skull has a teratologic internasal suture consisting of a row of holes, as its nasal bones were small and met only intermittently in the mid-line. Its bones are well-preserved, though many of them are badly displaced and some are broken. A lower jaw intervenes along the head's median suture, and the two halves of the cranium and rear of the snout are at right angles to each other, the left side being rotated inward. Perhaps because of the aberrant nasals, the nares are small and not easily comparable with other specimens. The base of the basisphenoid is much less flat than the two others known. The latter character may prove to be of doubtful value because Appleby (1961) has emphasized the variability of many of the bones. However, MVP12989 is the most peculiar ichthyosaur skull yet collected in Australia. The probability that it is conspecific as well as congeneric with the remainder of the Australian Cretaceous ichthyosaurs is high, but it is morphologically unsuitable as a neotype for the majority. All the same, any other specimen will always seem a less authentic representative of McCoy's species and of the type locality. In this quandary the future stability of the nomenclature will probably be better served by a new name for the Australian ichthyosaur species most common in the Eromanga Basin; it should be based on the most characteristic material to hand so that it can

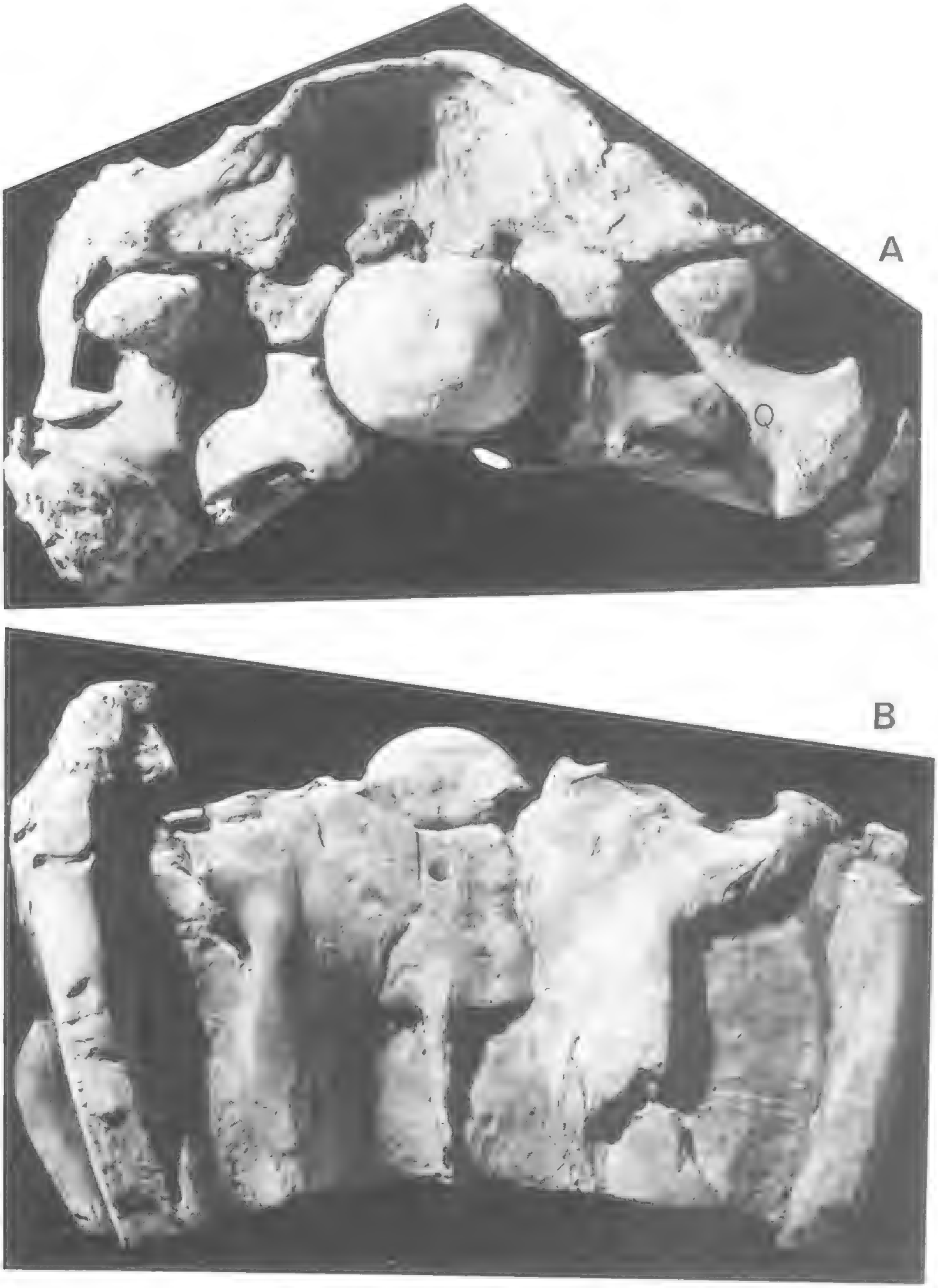

FIG. 1. *Platypterygius longmani* n.sp., paratype F551. A, posterior view of skull. Both exoccipitals have rotated to expose their bases, but have remained side by side; cartilage extended the stapes shaft into the adjacent quadrate socket. Compare Fig. 2B, posterior part of skull in ventral view; right pterygoid and stapes are displaced from basisphenoid and basioccipital respectively. Scale bar = 10 cm.

be specifically determined without reference to other specimens.

SYSTEMATICS

Platypterygius longmani sp. nov.
(Figs 1-6)

? *Ichthyosaurus australis* M'Coy 1867 (indet.).
Ichthyosaurus australis M'Coy 1869.
? *Ichthyosaurus marathonensis* Etheridge 1888 (indet.)
Ichthyosaurus australis McCoy (Jack and Etheridge, 1892).
Ichthyosaurus australis McCoy (Chapman 1914).
Ichthyosaurus australis McCoy (Longman 1922, 1935, 1943).
? *Myopterygius australis* (McCoy) Teichert and Matheson (1944).
Platypterygius australis (McCoy), McGowan, 1972b,c.
Platypterygius australis (McCoy), Wade (1984).
? *Platypterygius australis* (McCoy), Murray (1985).

PROVENANCE

Albian of Eromanga Basin in Queensland: Toolebuc Formation and Allaru Mudstone. The basin also contains ichthyosaur remains in South Australia. *P. longmani* may also be the form known from several specimens, mainly vertebrae, near Darwin, Northern Territory of Australia. These last originate from inner shelf deposits (Murray, 1985) and may indicate the spread of *P. longmani* around the continental shelf.

The foremost worker on Australian ichthyosaurs has been Longman (1922, 1935, 1943), a relative newcomer in comparison to Sutherland, McCoy and Etheridge, but a most percipient worker in many fields. The species is therefore dedicated to him as *Platypterygius longmani* n. sp.

The Galah Creek skull (QMF551, Figs 1, 2) which Longman described in 1922, has no known body so it is necessary to choose the Telemon ichthyosaur, QMF2453 (Longman, 1935, 1943; Wade, 1984) as holotype. This is the nearest to complete Cretaceous specimen on record. It has a good, though obliquely flattened skull (Figs 3A, C), an almost complete axis, many adaxial rib-ends, a damaged pectoral girdle, both humeri (one with wrist articulated) and sundry displaced phalanges (Wade, 1984, figs 1a, b, 2b). Two of several photographs taken during collection by J. Edgar Young, who donated the specimen and photographs to Queensland Museum, attest to the original arrangement of bones in the proximal end of its front fin. McGowan (1972b) accidentally referred his comments on fin structure, not to his copy of a J. Edgar Young photo, but to an arbitrary phalange arrangement that was put together simply for the photograph of the whole specimen. As the arrangement was based roughly on Young's photo, it did correctly have seven digits. It differs in many details from the arrangement now on display, but I regard even this as unauthentic. Another photograph taken by J. Edgar Young, and loaned by Mrs Hazel Young, shows that the snout was 16 cm longer when collected than it is now (compare Figs 3C, 4). The skeletal length, in its discovered state, was given as 18 feet, 5.4 m without the tail fin. The somewhat shorter measure of today, 4.92 m, is probably also due to loss of matrix and obliquity between numbers of tail vertebrae, now individually separate, and aligned vertically. However, it is 11 vertebrae shorter than *P. platydactylus* (Broili) (see p. 128).

DIAGNOSIS

A moderately large, long-snouted ichthyosaur with many strong teeth on premaxilla and maxilla. A pre-narial maxillary foramen which checked the growth of the premaxilla is present, exposing the maxilla, with locally radiating growth, reaching the nasal bone anterior to the naris. Parts of the maxilla may be overlain by superficial flanges of prefrontal, lacrimal and jugal, and premaxilla,

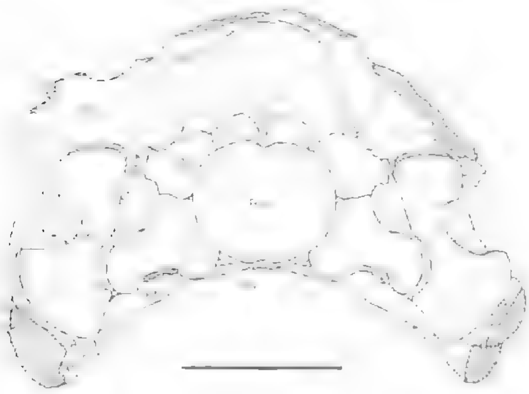

FIG. 2. *Platypterygius longmani* n.sp., paratype QMF551. Sketch of occiput; based on Fig. 1A, but with major displacements corrected. Abbreviations: An, angular; Ar, articular; Bo, basioccipital; Bs, basisphenoid; E, exoccipital; O, opisthotic; Pa, parietal; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; S, stapes; Sa, surangular; Sq, squamosal (dr, descending ramus). Scale bar = 10 cm.

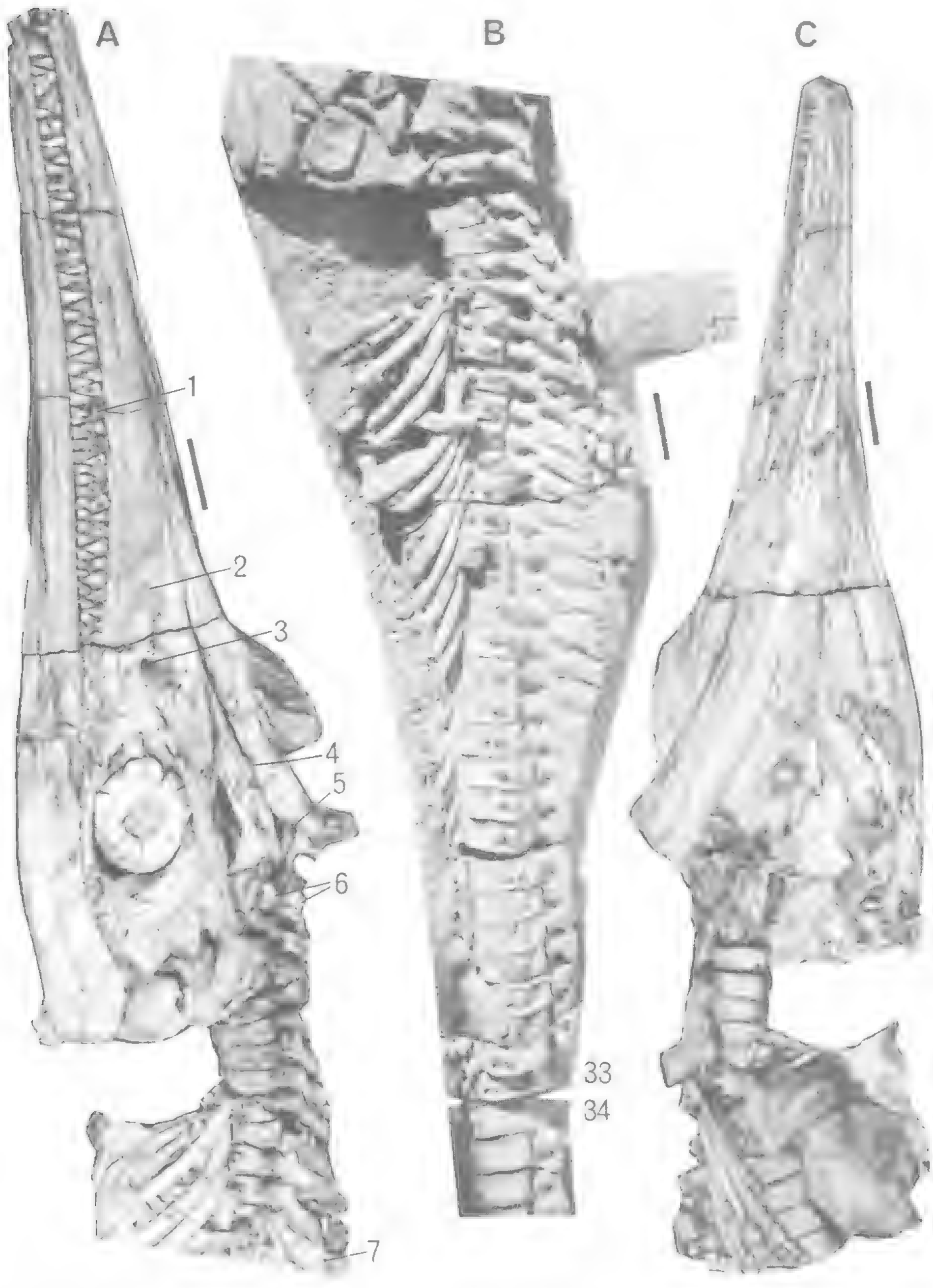

FIG. 3. *Platypterygius longmani* n.sp., holotype, QMF2453. A, skull in left lateral view. Showing 1, anteriormost maxillary tooth; 2, anteronarial maxillary foramen in fork of premaxilla; 3, naris (accidentally enlarged at nasal-maxilla suture during acid preparation; see Longman, 1943); 4, pineal foramen; 5, supraoccipital arch projecting at rear of interparietal suture; 6, exoccipitals (displaced, but have remained together in all three examples where known); 7, V-shaped notch at tip of neural spine in vertebra 11. B, anterior part of vertebral column in left lateral view. Vertebrae 2-32 show reclined articulated neural spines; V-shaped apical notches are evident on neural spines from vertebra 11 to at least vertebra 20 (more posterior spines eroded). Displacement between vertebrae 25 and 26 is an artefact; up to 8 vertebrae may be lacking between vertebrae numbered 33 and (arbitrarily) 34. C, skull in ventral view; left humerus is visible (in slightly skewed dorsal and distal view) between coracoid and scapula fragments. Each scale bar = 10 cm.

FIG. 4. *Platypterygius longmani* n.sp. The holotype (QMF2453) during excavation at Telemon Station, April-May 1935. Skull is exposed in ventral view; three small fragments at tip of snout add approximately 16 cm to measurement of total skull length. Photograph by J. Edgar Young.

around the lower three sides of the nares. The nares are oval to bean-shaped, with a foramen, sometimes accompanied by a crescent of varied fine to coarse perforations, through the nasals above each; the perforations, especially when multiple, help to delineate a narial crest or ridge between them and the dorsal ends of the nares. The orbit is oval in all specimens, and the sclerotic plates form a paraboloid ring thickened at the outer edges; adjacent plates are locked together by a tongue-and-groove structure (like floor-boards). The internasal suture is variable from fully closed to a row of holes (P12989) in different animals (see Wade, 1984, for discussion). The supraoccipital is a high arch of bone enclosing most of the foramen magnum. The paired supraoccipital foramina are anteriorly-opening slots below which the bone expands in antero-lateral wings. The exoccipital facets of the supraoccipital face postero-ventrally, while the impressions of semicircular canals and sacculus face antero-ventrally. Exoccipital/basioccipital facets approach each other to as little as 7 mm apart, the exoccipital shafts draw apart, and their exoccipital/supraoccipital facets draw together again leaving a rear opening to the skull which is more strongly figure-8-shaped than in *Ophthalmosaurus*. The exoccipitals tend to turn back-to-back and stay together, the same way up, when they are displaced. The basioccipital condyle faces almost directly backward. Opisthotic has a large, blocky head and small shaft. Stapes inserted into quadrate laterally and is mesially braced against the basioccipital in a ventro-lateral position (Figs 1, 2). Atlas/axis is heart-shaped in end view, with atlas end appreciably larger in diameter; antero-ventral angle forms a hypapophysis which is roughened for cartilage articulation. From axis to 32nd vertebra the neural arches are strongly reclined, and the zygapophysial faces meet at approximately 30° to horizontal in an antero-dorsal position (Fig. 5). From the holotype, the 11th to 20th neural arches (at least) have the crest of the neural spine divided into anterior and posterior peaks by an asymmetric V-shaped apical notch which is quite broad and slightly rough (as if to attach cartilage). Preservation failures blur the diagnosis toward the posterior. The 21st and subsequent neural arches are progressively more eroded apically, with loss of the notch. From 28th the zygapophysial faces began to approach vertical but were lost as preservation deteriorated. The 46th vertebra present is the first with single rib articulation, but the 33rd and 34th are badly eroded and between them a sudden step in the gradually lowering height of the rib apophyses records loss of centra. Over 45 vertebrae with twin rib-

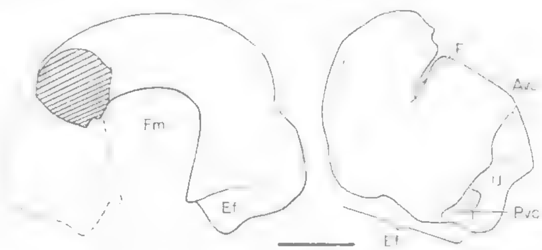

FIG. 5. *Platypterygius longmani* n.sp., paratype MVP12989. Supraoccipital in anterior view (left) and lateral view (right). Abbreviations: Avc, impression of anterior vertical canal; Ef, facet for attachment of exoccipital; F, foraminal slot; Fm, foramen magnum; Pvc, impression of posterior vertical canal; U, impression of utriculus. Scale bar = 2 cm.

articulations, and more than 36 vertebrae with single articulations; tailfin vertebrae are small, but their number is unknown (two collected). Postero-dorsal vertebrae had vertical zygapophyses (caudal arches unknown). Unweathered small tailfin vertebrae have dorso-lateral ridges on either side of the neural groove (QMF12314).

Clavicle adjacent to, but not enclosed by, scapula at any point. Glenoid facet faces laterally when coracoids are undistorted. Femur 0.7 of the length of humerus (QMF10686). Humerus with prominent dorsal and ventral trochanters. Size and shape of pisiform socket and presence or absence of lageniform socket depend on width of distal humeral face compared to total proximal width of radius, ulna, and pisiform; if sufficient space is available, the lageniform (defined p. 129) articulates with humerus.

The three primary fingers lie one below each of radiale, intermedium and ulnare. They are supported by three anterior (radiale) accessory fingers and three posterior (ulnare) accessory fingers. The primary fingers and adjacent first radiale or ulnare accessory fingers form a close-fitted pavement of rectangular phalanges. Phalanges of the more marginal accessory fingers have less regular shapes. The digits increase in length from the anteriormost 3rd radiale accessory (the shortest) to an irregularly-paved tip distal to the most posterior digit (the 3rd ulnare accessory digit). All finblade bones are tightly appressed. The ulnare digit may bifurcate about midlength, to prevent excessive narrowing of the finblade.

Description

Skull

Anterior. The tip of the beak has been preserved in F13261 (paratype from Canary Station, collected and donated by Mr Andrew Robinson). The lower jaw is slightly shorter and shallower than the upper, and its anterior pair of teeth are locked into the 2-3 sockets of the upper jaw. These teeth had been expected to lock into the 1-2 sockets, since the broken snouts of the Galah Creek, Telemon and Stewart Park ichthyosaurs were all a little slighter in the lower jaw than the upper. This occurrence suggests a certain amount of plasticity in the fit of the jaw. Evidently the upper lip would have closed around the edge of the lower, providing a watertight seal when the mouth was closed. The animals still would have needed some sort of throat-valve, equivalent in function to that of a crocodile, to enable the mouth to be opened under water.

Lateral view. Figure 3A has been oriented to give the best possible lateral view of the holotype skull and anterior vertebrae. This skull has been discussed previously (Longman, 1943; Wade, 1984). The maxilla carried 25 teeth and one gap, and the premaxilla 19 plus four gaps and a missing tip previously estimated at 10 cm (Wade, 1984), but now considered 16 cm on photographic evidence (Fig. 4). Sixty teeth per jaw ramus is a conservative estimate.

Although *P. longmani* is quite a large ichthyosaur the naris is small, with an antero-lateral projection of the maxilla rendering it asymmetric, though broadly oval. It is always accompanied by a distinct antero-narial maxillary foramen which caused the premaxilla to fork proximally, preventing it from covering the maxilla anterior to the naris. The forms with horizontally elongate nares (McGowan, 1976) have openings which end anteriorly in a narrow embayment reminiscent of the size and position of the maxillary foramen. It seems possible that as the snout elongated, the elongate naris of primitive form was divided in two by an outgrowth of the maxilla, for its growth pattern radiates in an arc here. This outgrowth isolated the foramen and the surround of the nostrils from one another. The nares are a point of weakness, even at their reduced size, and skulls are usually broken through or close to them.

The strongly ossified sclerotic ring was well described by Longman (1943). At the edge of the inner opening the sclerotic ring is only slightly convex. Outward, the surface describes a short paraboloid. A thick outer margin appears to have offered ample space and surface roughening for muscle attachment. Two areas of great thickening are spaced in the third of a ring which is now free in MVP12989. They suggest four chief adjustor muscle attachment areas within the whole muscle ring. Similar thickening is seen through a chip at the anterior longitudinal diameter in the right eye of QMF3348, the Stewart Park skeleton. The sclerotic plates interlock, with the edge of one plate fitting into a longitudinal groove in the adjacent edge. This tongue-and-groove structure would prevent any movement to change the shape or size, but would have allowed growth and strengthened the paraboloid at the same time. The simple overlap described by McGowan (1973a) for *Ichthyosaurus* would have been less prohibitive of movement than the structure of *Platypterygius*. The latter is closely similar to the structure Watson and Townend (*in* Romer, 1968) figure for '*Ichthyosaurus* cf. *latifrons*', a *Temnodontosaurus*. Claims of mobility in other ichthyosaurs (e.g. *Mixosaurus;*

Dechaseaux, 1955), should be re-examined because mobility would weaken resistance to pressure and seems inherently unlikely. The plates presumably protected the whole ball of the eye from deformation during rapid under-water movements — after all, their possessors usually lived by catching fish and cephalopods, and none of these is likely to have moved slowly. There is no modern sclerotic structure which impinges on the visual operations of an eye, so a very contractile iris, to cope with vast changes in light intensity, should be restored inside the sclerotic ring opening. Human eyes are peculiar in their need to swivel the stereoscopic area, and are a most unsuitable model for the amount of 'white' to be seen around a normal, non-stereoscopic, eye. It is probably correct to fit the ichthyosaur eye with lids and a transparent nictitating membrane, like crocodiles, as the span is unduly large for a thin transparent scale like that of snakes. The skin should cover at least the greater part of the sclerotic ring area (contrast Frey in Reiss, 1986; and Chapman in Taylor, 1987b). The orbit is elliptical, and the proportions of 19.5 cm long to 12.7 cm high, exhibited by the right side of the Stewart Park skull, seem undistorted. Internal diameter of its sclerotic ring is 4.2 cm. Externally the plates curve steeply into the matrix at 12 cm diameter, so that external diameter of the ring must have been close to minimum diameter of the orbit. Anterior-posterior movement of the visual area was likely to be less than its diameter, judging from these ring and socket sizes; it was possibly much less, for the anterior angle of the socket is shallow. The unborn F16812 had an orbital length of 8.5 cm, and skull postnarial length of 16 cm. The snout is broken off at a lower jaw length of 45 cm. Total skull length was probably just over half a metre.

The rear of the skull. This is best preserved in the Galah Creek specimen QMF551 (Longman, 1922; Wade, 1984). Figure 1 shows the occiput as preserved, and Figure 2 shows it reconstructed by correcting for major displacements.

Noteworthy differences from *Ichthyosaurus* and *Ophthalmosaurus* are: first, that the occipital condyle is a greater proportion of the width of the basioccipital (7.3/9.0 cm in QMF551; Figs 1, 2); and, second, its attachment area is not tilted upward posteriorly. The large hammer-shaped adaxial heads of the stapes are braced against the basioccipital antero-laterally and, to a lesser extent, against the basisphenoid postero-laterally. The stapes are separated ventrally by 3-4 cm in different specimens (see Fig. 1B). The cartilaginous lateral end of the stapes was inserted into a postero-lateral sharp-edged hole (stapes insertion) in the quadrate. Posteriorly the pterygoids (Fig. 1B) have a mesial overlapping contact with the lateral two-fifths of the basisphenoid; they overlap the whole ventral side of the stapes shaft, and the quadrate shaft external to the stapes insertion. This massive line-up of bones appears, from size and orientation, likely to have taken as much of the stress of quadrate-articular joint movements as the upper quadrate shaft leading to the squamosal, and braced by the quadratojugal. The opisthotic-stapes contact is at the horizontal diameter of the basioccipital (Figs 1, 2), so that the stapes facet is ventro-lateral and the opisthotic facet dorso-lateral on the basioccipital. The opisthotic-basioccipital contact is flat and, like all the basioccipital contacts, apparently had cartilaginous surfaces on both sides. Laterally, the opisthotic contacts the squamosal close to the head of the quadrate, but is separated from the quadrate by a descending ramus of the squamosal. The quadrate is very similar to that of *Ophthalmosaurus* (Appleby, 1956, fig. 7). The quadrate can be described as approximately harp-shaped, if the articular facet and neighbouring thick portion of the quadrate shaft is compared to the foot and resonating box, from which both "posts" arise, with a thinner fan-shaped area between them. The stronger, longer "post" terminates in the quadrate-squamosal facets, its main facet being terminal and its minor facets at the outer edge (Figs 1, 2). The shape of the main head is a large sector of a circle; in MVP12989, the only quadrate freed of matrix, it is a 90° sector, while in QMF551 it is broader, but not fully exposed. From the centre, and extending out from the more mesial radial face, the thinner, fan-shaped portion of the quadrate describes an arc forward and downward to the top of the shorter, anterior "post". This tapers as it curves up from the articular facet, until it terminates as only a slight broadening of the anterior side of the fan. The whole arcuate fan is topped by a groove, roughened for cartilage attachment, and depressed between sharp edges, as described for *Ophthalmosaurus* by Appleby (1956). The curve of the anterior 'post' delineates Appleby's 'anterior notch of the quadrate', and the postero-lateral curve of the posterior 'post', his 'posterior notch of the quadrate'.

The dorso-lateral quadrate head is set into a stout socket of the squamosal bone, which makes up the rear outer corner of the temporal fossa and, indeed, the whole thickness of its rear wall. The rear wall extends further ventrally on the inside of the socket than the outside. The grain of the bone radiates in every possible direction from the centre of the socket, and this grain carries through to the extreme tip of a strong ramus of bone directed downward and anteriorly between the quadrate head and the opisthotic head. Figures 1 and 2 show more of its rear edge on the left side than right. The parietal adjoins the squamosal on the rear of the skull, superficial or mesial to the opisthotic socket, and either bone may lie against the short opisthotic shaft laterally. The parietal forks into a short branch which forms the base of the posterior arch of the skull roof, and a longer antero-mesial branch with its mesial surface directed against the blocky opisthotic head, while its opposite face is applied to the descending ramus of the squamosal, wrapping around its mesial and anterior sides. The descending ramus is the longer, and also lies against the opisthotic head. The squamosal and parietal thus make a contact parallel to the opisthotic/basioccipital facet, and complete the stabilization of the basioccipital.

The descending ramus of the squamosal (in VMP12989) thickens anteriorly and passes down from the body of the squamosal to form much of the posterior and lateral walls of the temporal fossa. It extends through the embrace of the anteromesial flange of the parietal, and more ventrally forms a long, wide, tapered plate joint with an ascending ramus which is welded to the pterygoid. This ascending ramus probably originated from a separate centre of ossification. The descending ramus shows the striations of the main squamosal ossification pattern on its face, which is also slightly fluted. These minor and major elevated structures meet complementary depressed and raised structures on the tapering ascending ramus, so that the joint must have been immovable in life. The ascending ramus articulation naturally faces mesially to complement the outer face of the squamosal's descending ramus.

Antero-ventrally, the mesial angle between the ascending ramus and the pterygoid proper accommodated the basipterygoid process of the basisphenoid in a sharp-edged socket. Thus the ascending and descending rami make a solid shaft extending from basipterygoid process to the rear of the temporal fossa. Watson and Townend (1968, fig. 9A left) very clearly figure a connection between the quadrate wing of the pterygoid and the descending lamella (ramus) of the squamosal in *Temnodontosaurus* sp. (= "*Ichthyosaurus* cf. *latifrons*") as well as an epipterygoid. McGowan (1973) more lately described two structures arising from the pterygoid. He did not join the 'quadrate wing' to the descending ramus of the squamosal but discussed its fit against the side of the quadrate — although he figured the ramus (1973, fig. 46) partly between the quadrate and the 'quadrate wing'. *Platypterygius* is relatively short in comparison to height and width in its basisphenoid length. It is not possible by looking at *Platypterygius* to judge the accuracy of the several reconstructions of this area in forms with a greater proportionate basisphenoid length. What is clear is that here one structure is occupying the place and function which historically have been assigned to two. The cartilage edge of the quadrate fan, here, seems to have been practically median in the temporal fossa rear base, and to have been directed upward and anteriorly.

The matrix-free bones used here are those of MVP12989, but they receive abundant confirmation from QMF2453 and QMF551; only the ascending and descending rami and basisphenoid/basioccipital contact depend wholly on VMP12989. This was used for etching because the bones were in very good condition, though displaced sufficiently to require refitting. Laterally the inwardly flaring quadratojugal foot rests on the dorsal edge of the outwardly flaring part of the quadrate foot, and the laterally flat quadratojugal shaft rises to meet the squamosal, just outside the head of the quadrate (Figs 1, 2).

The parietal arch is higher than a semicircle, and encloses the high arch of the supraoccipital (*vide* QMF2453 and MVP12989) which rests on the exoccipitals and encircles at least three-quarters of the foramen magnum. The foramen magnum and the space between the exoccipitals are combined in the fossil as a single figure-8-shaped space. The parietal may overlap on the squamosal in the rear suture, (*vide* QMF551) although the opposite overlap occurs here in the parietal-squamosal crest: as a result flanges of the parietal lie over the squamosal above and behind the upper half of the opisthotic-squamosal contact. They interdigitate in MVP12989. Inside the temporal fossa of QMF551, the squamosal-parietal suture picks its way down the middle of the rear wall of the temporal fossa, squamosal overlying parietal. This suture can also appear in the usual position in which it is recorded, in the inner posterior corner of the temporal fossa. The ventrolateral-anterior wings of the supraoccipital (Fig. 5), the opisthotics and the prootics all carry the impressions of two semicircular canals and the adjacent parts of the utriculus or sacculus, but except for the supraoccipital, these bones are not yet clear of matrix, and the arrangements of the ear must await later description. Every word which McGowan (1973a) said about the lack of directional hearing

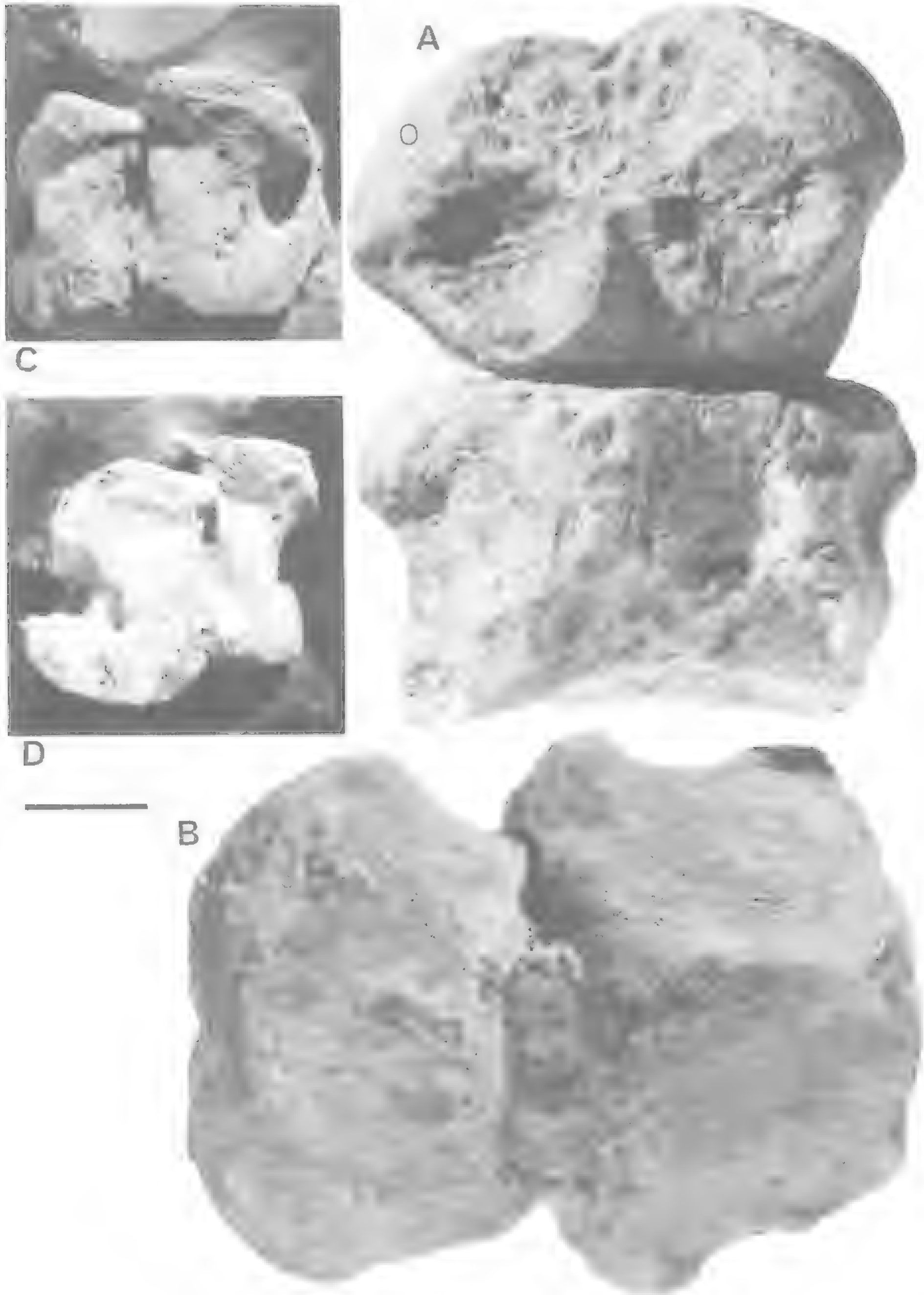

FIG. 6. *Platypterygius longmani* n.sp., paratype MVP12989. A, basioccipital and atlas/axis in dorsal view; showing neural canal furrow terminating as a small tapered depression less than half-way across the basioccipital. The furrow is flanked by large scars for attachment of exoccipitals; anterior to tip of the furrow is a pair of larger medially-contiguous depressions for the hind brain. Facet for opisthotic (O) is situated antero-medially. Floor of neural canal is damaged on axis. B, basioccipital and atlas/axis in ventral view; showing hypapophyseal facet on atlas, and stapes facet (S). C, D, two views of the paired exoccipitals; despite major displacement the two bones have remained in close association. Scale bar = 2 cm.

of ichthyosaur ears receives support from these bones. The huge semicircular canals bespeak specialization for balance, which was needed, for they were rapid, agile movers in a uniform milieu, and could not rely on their eyes and feet to relate them to a substrate, like land-dwelling reptiles. Directional vibrations may have been detected in the skin, rather than the ear.

The supraoccipital (Fig. 5) resembles that in *Ophthalmosaurus* (Appleby, 1956, 1958) but curves in more at its feet, as the exoccipital facets are close together. The foramen terminates at the height of the dorsal corner of the lymphatic foramina which are such a distinctive feature of the latipinnate supraoccipitals (Appleby, 1956, 1958; McGowan, 1973a). *Temnodontosaurus* sp., a Liassic longipinnate, had fully enclosed foramina (Watson & Townend, *in* Romer, 1968). Appleby (letter dated 3rd October, 1988) tells me that he has a Lower Hauterivian *Platypterygius* to describe, with these foramina encircled by bone. Here a pair of foraminal slots, open anteriorly, represent these foramina, and tend to separate antero-lateral wings from the main arch enclosing most of the foramen magnum (Fig. 5). This arch rises from postero-ventral sockets holding the upper exoccipital facets. Exoccipitals are easily displaced *as pairs* (three examples) but tend to turn back to back (two of the three). No single exoccipitals have been found. From this it is assumed that the exoccipitals were both joined posteriorly to the same sheet of connective tissue, and only the supraoccipital enclosed the functional foramen for the nerve cord. The exoccipitals closed to 8 mm apart at their bases in VMP12989 and 1 cm in QMF551, unlike *Ichthyosaurus* exoccipitals; basally they walled only an inwardly and upwardly tapering relic of the wide channel for the axial nerve cord which is found on the atlas/axis (Fig. 6A) and other vertebrae. The nerve cord had thus begun to turn from horizontal toward dorsal as it crossed the junction of atlas and occipital condyle, thus avoiding potential stress at the mobile joint. It also results in a steeply-dipping hind brain to bring the 12th nerve to its exoccipital foramina. This contortion is apparently a better solution to the relative shortening of the cranium than to telescope the hind brain. The basisphenoid-basioccipital contact sloped at 50° to 60° to the horizontal, but if the basioccipital condyle is excluded, the basioccipital is about twice as long dorsally as ventrally. The result is very little up-slope on the occipital condyle. That the occipital condyle of *Platypterygius* is correctly oriented to take an almost horizontal vertebral column is confirmed by Figure 1B, because any attempt to tilt upward the basioccipital and basisphenoid would bring the long parasphenoid down against the tongue. The exposed length of the parasphenoid projects 24 cm beyond the basisphenoid. It takes origin from below a wide, shallow pit floored by the antero-ventral edge of the basisphenoid, but over-grew it adposteriorly, almost to the posterior carotid foramen. Anteriorly, the carotid foramen is dumbell-shaped in P12989, and lies just above this pituitary pit (Watson & Townend *in* Romer, 1968).

Axis

In numbering vertebrae the fused atlas/axis is counted as two, here, and by most authors. Length, width and height are measured parallel to these dimensions of the animal

The atlas/axis is almost heart-shaped in end view. In the Kilterry specimen (QMF12314) and MVP12989 its ventral angle is just under 90°. As usual there is one high-set rib condyle, vertically elongate, on the atlas and two equidimensional condyles on the axis. The greater diameter of the atlas end produces a ventro-anterior ridge, almost a keel, on the front half of the fused vertebrae. This (Fig. 5) is sculptured anteriorly for cartilage, and is a hypapophysial facet.

Interestingly, the straight Telemon axial skeleton is very similar to the '(a) type with straight tail without elongated neural spines in the tail' of Riess (1986, p. 102). The chief exemplar of this '(a) type' is *Shonisaurus* with a concave basioccipital condyle, convex atlas, and paired condyles on the zygapophyses. His second (convergent) example is *Eurhinosaurus*. In *Platypterygius* the zygapophysial condyles are single; the prezygapophysis is set on a slight, anteriorly concave pedestal, and the postzygapophysis in neural arches 2-30, is part of a backward slope from the top of a similar, less concave rear to the arch. It is sloped 30° in antero-dorsal vertebrae, steepening from 28-32 onward. In QMF2453 the neural spines, posterior to the neck, have increased in length and height until spine 20, at which point they become progressively more eroded dorsally but still increase in length for another 10-12 vertebrae, until indications of height and finally shape are lost (Fig. 3B). However, the complete to almost-complete spines 11-20 each have a broad V-shaped re-entrant in their apices, rising to short peaks anteriorly and posteriorly. The posterior peak is the longer, though height seems constant. These re-entrants are wholly in quite thick bone, sometimes with a slight border (Fig. 3A, vertebra

11; Fig. 3B, vertebrae 11-20). They provided adhesive surfaces presumably for cartilage, rather than connective tissue, as the articulating surface was quite broad. Ligaments are less likely, as the facet does not thin in the V. It is impossible to observe the posterior extent of these structures, but after vertebra 32 (and several missing vertebrae after the eroded 33) the neural spines probably cease to be raked backward, and the zygapophyses are re-aligned toward vertical. It is tempting to assume that the rearward slope and successive overlap of neural spines 11 to 20+, and their notched apices, indicate the position of a dorsal fin, strengthened by a median row of cartilages. If so, it is more anterior than that attributed to *Stenopterygius*, in the position of the dorsal fin of *Orca*. Though probably the upslope would have been raked backward as steeply as the neural spines, the posterior edge is an utter unknown which may have overhung at 50-60^0 (vertebrae 28-31) or been filled in. There is a hint of similar apical notches to be seen in the figure of the most oblique spines on antero-dorsal vertebrae of *Ichthyosaurus conybearei* Lydekker (McGowan, 1974b, fig. 9, holotype, BMNH 38423). But the structure should have been described already if it is common.

The axis, like the following vertebrae, has two rib apophyses, the higher touching the base of the neural arch. The succeeding conditions are: vertebrae 3-13 cervical and front antero-dorsal vertebrae with the upper condyle touching the base of the neural arches; 10-30, rib condyles gradationally eased away from neural arch and descended slowly from 'touching neural arch' to lateral; 34-45, postero-dorsal vertebrae with both rib condyles positioned ventro-laterally. (Severe weathering of the right sides of 33/34 suggests that these were exposed at discovery. The loss of vertebrae here is indicated by greater subsequent distance between neural arch and upper rib condyle, and the fact that the change-over to single rib condyles occurred at at vertebra 54 in Broili's *P. platydactylus* — eight vertebrae more than holotype *P. longmani*). Vertebra 46 has a long, vertical single rib apophysis, and thereafter the apophyses are single and rounded. Other examples of the change-over to single apophyses show that they may be single and long on one side of the vertebra while still double on the other; this is the case in one of a sequence of the three largest vertebrae in our collections, found loose and without identifiable material, from Yam Bore Creek, QMF16791a-c). These specimens were scattered and lay flat, and have been greatly compressed longitudinally to about 4 cm long. Height at centre dorsal to base 13.4 cm (two specimens). Shape oblate, widest below centre, 13 and 14 cm, rather distorted (same two vertebrae). In this position the height of the edges of the neural groove is lost, but this measurement can be used on abraded material. In fact, the vertebrae are all higher than wide, by inclusive measurement.

Lateral displacement of the rear of the Telemon skeleton by 1-2 m, is shown in a collecting photograph by J. Edgar Young. The quality of preservation has deteriorated posteriorly, and since collection the original sequence of vertebrae has been disordered. A few poorly preserved vertebrae may be wrongly positioned still. Vertebrae may be missing after 78, where there is a sudden diminution in size in 79-81, but *P. platydactylus* (Broili, 1907, pl. 12) shows a similar diminution in 91, 92; it may indicate enclosure in the base of the tail fin. *P. longmani* 82 and 83 are diminutive from the tail down-turn. The Telemon specimen thus has 11 fewer vertebrae preserved in the horizontal axis than the holotype *P. platydactylus*, but its axis was broken in two. Restoring the eight vertebrae less than *P. platydactylus* to the eroded mid-dorsal region would add 36 cm to the length between the rear of the dorsal fin and the pelvic fins; restoration of the remaining three vertebrae less, close before the tail bend, would add 6 cm or a little more there, so that the probable dimensions of *P. longmani* holotype become: head, 1.49 m (see Fig. 4); atlas/axis to last double-headed ribs 2.52 m; single-headed ribs 1.43 m. Axial length, 5.44 m plus tail fin; total length under or over 6 m, depending on the adjustment of the tail bend.

The distal tail vertebrae of QMF2453 rarely show rib apophyses because of largely chemical erosion (they were outside the calcareous nodules), but it is possible to trace the bases of rib condyles in a low lateral position, instead of ventro-lateral, at and just after 66. The redistribution of muscle mass in the rear tail that Appleby (1979) described, presumably took place here too. The very high position of the cervical rib attachments (and adjacent anterodorsals) bespeaks the powerful neck musculature used in diving.

The two tail fin vertebrae 82 and 83 resemble those of Broili (1907, figs 2, 3) except in their poor preservation; more were scattered among the Kilterry skeleton, QMF12314. These last are very well-preserved, and have the dorso-lateral portions drawn up into smooth longitudinal ridges on either side of the neural canal; they are distinctly higher than wide, with anterior rim larger than the posterior rim, and a narrower waist. The general shape is thus not the cotton-reel shape made known by Broili (1907), though many of his may have been stuck down by the dorsal side. His mentioned faint trace of the neural cord is not figured.

The fore fins and coracoids were described by Wade (1984).

In terms of most ratios and characters tabled by Mazin (1981) for *Grippia*, 'Mixosaures', Liassic latipinnates and Liassic longipinnates, the holotype *P. longmani* (or, where marked *, QMF10686) yield: 2, premaxillary segment/mandible = 0.44; 3, prenarial length/mandible = 0.65; 4, longitudinal diameter orbit/skull postnarial (same plane) = 0.58; 5, longitudinal diameter orbit/mandible = 0.15; 6, internal diameter sclerotic ring/longitudinal diameter orbit = 0.26; 7, length naris/longitudinal diameter orbit = 0.14; 9*, max. width pectoral fin/length pectoral fin = 0.48; 11*, length femur/length humerus (both crushed) 0.7; 12, distal breadth humerus/length humerus = 0.73 (to 0.85 in broad humeri); 14, number maxillary teeth = 26; 15, number primary fingers in pectoral fin = 3; 16*, total fingers = 9; 17*, phalanges in longest finger = 37 (including fin-tip phalanges which are not really aligned in fingers, though the pavement tip recurves to terminate below the last digit, ulnare accessory digit 3).

Comparisons

Skeletons of other Cretaceous ichthyosaurs are rare, and not adequately described except for *Platypterygius platydactylus* (type species) and *P. hercynicus* Kuhn, 1946. McGowan (1972b) has mentioned considerable skeletal material with *P. americanus* (Nace) but only added description of proximal portions of pectoral fins to the redescription of the skull by Romer (1968). Kiprijanoff (1881) described scattered bones of various sizes in his brilliant monograph. His material is now known as *Platypterygius kiprijanoffi* (Romer), or by the older species name bestowed by Kiprijanoff, *P. campylodon* (Nesov *et al.*, 1988).

Wade (1984) indicated that the particular four-bone-wide forearm of *Platypterygius* was a generic character, and the attachment or lack of attachment of the sesamoid bones to the humerus was presumably of specific value, as it was localized in geographic distribution and/or time. After discussion with Appleby on the fact that the sesamoid bones on the ulnar side were the best attached in *P. 'australis'* while the flask-shaped bones of the radial sides were best attached in *P. americanus* (McGowan, 1972b, pl. 1), Appleby suggested the employment of the term lageniform for the radial accessory bone. The use of pisiform and lageniform appeals to me as a better solution than trying to dispense with the established name pisiform for the ulnar accessory. It also recalls the constancy of the general shape McGowan (1972b) described. The pisiform of *P. longmani* always, and the lageniform sometimes, was articulated to the humerus. In *P. hercynicus* Kuhn (1946, pl. 1, figs 4, 5; pl. 3, figs 5, 6) the left-fin pisiform and lageniform appear to be in small sockets, while in the right fin they appear merely to lip against the distal corners of the humerus. The left humerus is shortened by compression and, as far as the figure shows, pressure could have achieved the result. However there is no need to rely on sockets to differentiate the humerus of *P. hercynicus*, since this is done by the immense dorsal trochanter. *P. kiprijanoffi* (Romer) lacks both pisiform and lageniform socket, but its radial humeral edge is squarer than its ulnar edge (Kiprijanoff, 1881, pl. 14, figs 1, 2), so presumably it is closer to *P. americanus* and even *P. hercynicus* than to *P. longmani* and *P. platydactylus*. It remains to be seen whether whole fins will bear out the hints obtained from the humeri.

Kiprijanoff (1881, pl. 9, fig. 1) and Romer (1968, figs. 2, 3) restored their ichthyosaur skulls with elongate nostrils against which the premaxilla forks. Both were damaged in this region, and the restorations may owe much to restorations of other ichthyosaurs. *P. platydactylus* and *P. hercynicus* figured material can add no data comparable with the *P. longmani* naris.

P. longmani and, as Krapf (in Broili, 1907, pl. 12) figured serially diminishing phalanges on the leading finger, possibly *P. platydactylus*, have a short leading-edge finger to their fins, but only *P. longmani* has a near-complete fin blade. In this the remaining accessory and primary fingers are serially terminated so that the front edge of the fin-blade skeleton is reclined all the way to its tip. *Eurhinosaurus huenei* has a similar digit arrangement but it is not described from *Excalibosaurus costini* McGowan (1986, fig. 1a), the apparent ancestor of *Eurhinosaurus*, and convergence is likely. *P. americanus* has no complete fin blades described, but has no larger proportion of dorsal trochanter to humeral shaft than *P. longmani* and *P. platydactylus*. *P. hercynicus* Kuhn has coupled its immense dorsal trochanter with full-length primary and secondary fingers (Kuhn, 1946, pl. 3, figs 5, 6). Both pisiform and lageniform lip against the edges of the humerus, but have little or no room to socket there.

The broad expanse of bone near the outer tip of the fin seems reason enough for the exceptional dorsal trochanter, as the animal cannot have avoided the necessity to control much more leverage than the tapered fins exerted. The array of occipital bones is practically identical in Kuhn's figures and *P. longmani*, though less complete in *P. hercynicus*.

From these comparisons and observations it is possible to conclude that the rear of the skull is important for major differentiation, even when there is a degree of convergence (*Ophthalmosaurus* is more like *Platypterygius* in rear-end proportions than the earlier *Ichthyosaurus* is), but the total pectoral fin is the more sensitive structure at specific level.

CLASSIFICATION IN RELATION TO *PLATYPTERYGIUS*

The descent of ichthyosaurs is very incompletely known. Either the fossils or the descriptions of earlier ichthyosaurs and ichthyosaur-like animals are lacking. Their described history begins in the Middle Triassic, with two forms that are at least ordinally distinct: Mixosauria Appleby, 1979, and Ichthyosauria Jaeger, 1824. Appleby (1979) divided the Ichthyopterygia into four 'orders' — Mixosauroidea, Longipinnatoidea, Heteropinnatoidea and Latipinnatoidea. Mixosauroidea were distinguished from the other three taxa by many characters of the axial column including tail fin, girdles and limbs, as well as teeth and proportions of the head; in the other three 'orders' the differences were of proportion, paired fin structure and degree of reduction of the pelvic girdle. A major two-fold division of these ichthyosaurs is thus implied by the data, and was used by Mazin (1983) in the form Mixosauria and Ichthyosauria and is followed here. Longipinnates, heteropinnates and latipinnates are subordinate to Ichthyosauria.

The classification of ichthyosaurs is going through a period of disarray. On the one hand Appleby is working on a morphologic/stratigraphic basis designed to uncover evolutionary trends, and on the other Mazin (1983) has started, and Riess (1986) has 'simplified', a cladistic analysis in which the plesiomorphy or apomorphy of a number of basic characters is very suspect. For example: Mixosauria and Ichthyosauria had most of their skull joints formed by overlapping bones bound by connective tissue in life; the median longitudinal suture of the snout is smooth and vertical. The snout was thus capable of passive displacement, in response for example to biting on a belemnite guard or a stout bone with only left or right jaws. McGowan (1973) has carefully considered and rejected the idea of a fully kinetic skull. The pineal organ penetrates the skull posterior to the snout as in other Ichthyosauria, usually through the fronto-parietal suture and above the orbits. In *Grippia* (Mazin, 1981) it is wholly parietal and above the rear of the orbits. The nasals were not elongated, so the nostrils were relatively and absolutely close together, more dorsal than lateral, enclosed between nasals and maxilla, and superficially, the premaxilla. *Grippia* thus has a more primitive narial position than any other described ichthyosaur, and Mazin was probably correct in assigning it to a sister-group of the immediate ichthyosaur ancestor. It seems unlikely that the ancestral dentition was specialized for shell-crushing as that would have inhibited the development of passively displacable snouts, a constant character of all other ichthyosaurs, and probably of the mutual ancestor, as the premaxillae to nasals of *Grippia* tended to split along a straight median suture (Mazin, 1981, fig. 3). In *Grippia* the maxillary teeth were not just short expanded cones, but had started to form a pavement, an irregular double line (Mazin, 1981, fig. 7a). Mazin (1981, figs 3, 4) shows two specimens in which, despite flattening, the frontal to parietal portion of the median suture does not open like the premaxilla-nasal portion or the rear of the parietals. Dechaseaux (1955) has figured slightly modified rear maxillary teeth on *Mixosaurus* and Mazin discusses them; these are probably more like the ancestral condition than the double line in *Grippia*. The order Ichthyosauria had isodont teeth.

A tooth-density index that depended on teeth counted in the central 10% of the snout was utilized by McGowan (1976). His objective care in counting teeth present in a fossil, and excluding any gaps from consideration, brings this ratio under doubt. McGowan (1976) found 14 teeth on the maxilla of *Platypterygius americanus*, where, in the same individual (University of Wyoming 2421) Romer (1968) found teeth and gaps enough to restore 22. The Telemon *P. longmani* (Fig. 3A) has 25 teeth + 1 gap on the maxilla, about 60 teeth in each of its four jaw rami. In confining himself to measureable or countable skull characters, McGowan (1976) related, at 'logical' familial level '*Leptopterygius*' *acutirostris* and *Mixosaurus cornalianus* among others. The generic placement of *acutirostris* is fluid: McGowan (1976) changed the assignment to *Temnodontosaurus* in a footnote and back to *Leptopterygius* in 1979 (in a paper in which he referred to his 1976 paper). Mazin (1983) uses a placement in *Stenopterygius* in the table quoted by

Riess (1985), and Appleby recommended placement in *Temnodontosaurus*. The measurements used by McGowan (1976) for multivariate characters are repeatably defined, but that is not enough to make them taxonomically significant; it is necessary to know what is being measured — the feeding guild to which an animal belongs (Massare, 1987) or its relationships? Tooth-size is normally correlated with the height of the jaw (a fair measure of the jaw's strength) and both are related to diet and the feeding method. Appleby's (1979) use of a post-narial length to form a ratio with orbital length is a distinct improvement on a ratio of orbital length and jaw length, since it eliminates snout length — the most variable quantity in closely-related ichthyosaurs, and one most likely to be responsive to hunting technique and prey. For other proportions Appleby used ratios of single bone measurements, which eliminate the compounding or minimization of variation that can arise sporadically when measurements are spread over several bones. Although it is necessary to be conscious of gaps in our knowledge of occurrences, Appleby's technique of plotting comparative measurements in morphologically related groups against time is very informative of trends.

Appleby (1979) showed that a distinctive style of fin-broadening with the introduction of a mid-fin digit distal to the wrist gave rise to animals with heteropinnate fins, as distinct from those with longipinnate fins. Further acceleration brought the digit head into the distal carpal row, as *Protoichthyosaurus prostaxlis* gave way to *Ichthyosaurus intermedius*, and so animals with heteropinnate fins gave rise to those with latipinnate fins. The single-bone proportions he gave substantiate his fin-sketches, and it is possible by means of them to recognize the Rhaetic *Temnodontosaurus tenuirostris*, which can be described as the first longipinnate at present known to have broadened its fins, as a forerunner in the heteropinnate lineage.

This style of fin-broadening was characterized chiefly by the introduction and acceleration of the mid-fin accessory digit, either single or subsequently forked, to a longipinnate plan. The mid-fin accessory digit terminated proximally either in the metacarpal row or often in the distal carpal row (as a twin bone to the centrale). This second centrale has been widely accepted as a primary wrist bone *because of its contacts* but its derivation becomes glaringly obvious if the midfin accessory digit is picked out in a number of illustrations of the earliest Jurassic heteropinnate and latipinnate fins; those corresponding to the names *Protoichthyosaurus prostaxalis* (Appleby 1979), *Ichthyosaurus intermedius* Conybeare and *Ichthyosauts communis* Conybeare (Appleby, 1979; and, for example, McGowan, 1974b). Accessory digits were often added laterally, but the lineage retained acceleration in the midfin as a tendency, and occasionally the intermedium was fitted into the forearm between the radius and ulna.

The problem of inadequate preparation bedevils ichthyosaur taxonomy even when workers know what to look for, and have access to appropriate material. For example, McGowan (1979) was able to see the basioccipital of *Stenopterygius* in full three dimensions in only one example of an isolated bone, 'possibly' of *Stenopterygius*, in his all-embracing investigation of German Lower Jurassic ichthyosaurs. Parts of the two lineages are clear: the extended heteropinnate to latipinnate lineage which Appleby (1979) established — starting with '*Leptopterygius*' *tenuirostris* (which he later informed me was a *Temnodontosaurus*) — and the very short *Excalibosaurus-Eurhinosaurus* lineage which McGowan (1986) suggested could have arisen from '*Ichthyosaurus tenuirostris*'. After all the work on *Stenopterygius*, our most common ichthyosaur, the intractable beast still has no obvious close relatives. Its fused ischiopubis is a barrier to an ancestral position in relation to *Platypterygius* unless and until ischiopubes are discovered there. Its forefin is marginally longipinnate but shows considerable irregularity, including interdigit rows of small sesamoid bones (Johnson, 1979). What is known of the basioccipital is shared by primitive and latipinnate ichthyosaurs, and is unlike *Platypterygius*. The dorsal fin of *Platypterygius* was probably well forward of that in *Stenopterygius*. It would be interesting to know whether *Stenopterygius* had the same pterygoid-squamosal rami as *Platypterygius*. The isolated skull *Grendelius* is a potential platypterygiid, as McGowan suspected from the first, but its basioccipital is still "on the way" to that of *Platypterygius*. While Appleby has informed me that Watson and Townend (1968) were studying a *Temnodontosaurus* sp., their specimen has the elongate basisphenoid-basioccipital with basioccipital peg seen also in *Ichthyosaurus* (Appleby, 1961), and McGowan (1979) states that *Temnodontosaurus platyodon* has no such peg. In short, two to four lineages are being attributed to temnodontosaurid ancestry, which is possible, since species do not interbreed, but messy for taxonomy. More probably, differentiation of the Ichthyosauria had not proceeded beyond about family level when the group died out.

The style of fin broadening that led to *Platypterygius* was free of advanced midfin accessory digits, although the only near-complete fin has doubling of one primary finger halfway down. This is possibly unusual in the species because two attempts to re-fuse it, once to each of the neighbouring fingers, through a wide phalange, also occur (Wade, 1984). The genus can be traced back from Cenomanian (USSR and USA) to Hauterivian (R.M. Appleby, pers. comm.), and it seems probable that the poorly-known *Grendelius* belongs to this lineage because the basioccipital has no 'peg' overhanging the basisphenoid, like *Platypterygius*, and the much older *Temnodontosaurus platyodon* (Lower Liassic). It also has no very large, ventro-lateral 'apron' of smooth material in posterior view, though not so little as *Platypterygius*. The state of this basioccipital dorsal side is unknown or, at least, unfigured and undescribed. The nature of the pterygoid-squamosal rami is probably unknown because the skull of *Grendelius* was much shattered.

Intraspecific variability includes quite common discrepancies between left and right finblades. Discrepancies arise for example if a digit is rather wide, when a single phalange may be replaced by two, or a single digit by two. The presence or absence of small lateral digits may be taphonomic or natural to the animal (Johnson, 1979). Appleby (1979) recorded one fin pair in which one blade was 4 mm wider than the other, but that is not necessarily as lopsided as it sounds, because the bony blades were surrounded by wide marginal zones of connective tissue, muscle and skin (Andrews, 1924), and could have contained a great deal of internal variation in functionally similar outer coverings. Because of the spontaneous variability about the number of bones in any fin area (McGowan, 1974b, fig. 5; Appleby, 1979, text-figs 1b(i), (ii); Johnson, 1979, many examples), samples as large as possible should be employed in trying to establish a trend. But it is tempting to suggest of *Protoichthyosaurus prostostealis* Appleby (1979, text-figs 2b(i), (ii)), that acceleration has carried the head of a forked mid-fin accessory digit through the distal carpal row into a position where it competed for space with the intermedium. While a wrist-bone could be eliminated by crowding, there was no gap there for a bone to develop spontaneously, without predecessor, in both fins. The addition of partial midfin ulnare digits by longipinnates, which has been shown in *Eurhinosaurus* and *Platypterygius*, has not resulted in anything like the heteropinnate to latipinnate development. Nor does the addition of posterior and anterior sesamoid digits make latipinnates unrecognizable (*Ophthalmosaurus, Brachypterygius*) since, with the establishment of a second centrale, a median suture was placed below the centre of the latipinnate intermedium, as the two centrales pushed each other into axial positions between radiale and intermedium and intermedium and ulnare. An interdigit suture thus lies below the centre of the intermedium in latipinnates. Now that Appleby has detected the supplementary mid-fin digit in *Protoichthyosaurus*, it should be possible to 'decelerate' and recognize it at earlier stages of development in Upper Triassic material.

More than strict adherence to geometry is required to establish homeomorphy in a morphologic sequence with major time-gaps. Mazin (1983, *vide* Riess, 1985) in establishing a cladistic diagram, and Riess (1986) in simplifying it, have ignored alike the lack of Triassic latipinnates and the presence of earliest Jurassic heteropinnates without a second centrale but with a well-developed digit lying alongside the centrale digit, although often ending a little less proximally. The proximal phalange of this digit having been accepted as a primary distal carpal (once acceleration had carried it into position in the distal carpal row; e.g. McGowan, 1972a, fig. 1c), the latipinnates were classed as having five primary digits. One character by which lateral sesamoid (or auxiliary) phalanges are commonly recognized is that they appear first in axillary positions lateral to two adjoining phalanges of a neighbouring digit (see McGowan, 1972a, fig. 2; 1974a, fig. 1). By this means, and by examining the bones at the proximal end of digits, one or two accessory distal carpals each side of three primary distal carpals have been recognized (Kuhn, 1946, pl. 3, figs 5, 6; Wade, 1984, fig. 2A). Mazin (1983) placed Cretaceous *Platypterygius* with two sesamoid distal carpals anteriorly and two or three posteriorly in an assembly of left-overs with Middle Triassic to Lower Jurassic longipinnates, some without any accessory carpals, the borderline heteropinnate *Leptopterygius*, and *Eurhinosaurus*, each with one accessory distal carpal, and unknown *Grendelius*. *Stenopterygius*, also with one axillary posterior distal carpal and one corresponding posterior proximal carpal, alongside three aligned proximal and distal carpals in each row, is considered to have four primary distal carpals (McGowan, 1976) and a homeomorph of the captorhinomorph pisiform (Johnson, 1979, illustrates this classic Continental view adhered to by Mazin, 1983, and Riess, 1986). None of the above workers considers that *Stenopterygius* shared with *Eurhinosaurus* a fin-broadening achieved with retention of longipinnate characters. McGowan (1979) decided that the terms latipinnate and longipinnate were not valid as major taxonomic subdivisions, and they have been used almost to the neglect of other characters. They do seem to reflect valid lineages but too much value has been placed on them.

In the Triassic the niche for rather small, broad-finned ichthyosaurs was filled by *Mixosaurus*, but all Mixosauria died out at the end of the Middle Triassic. In the Rhaetic and earliest Liassic the longipinnates commenced to enter this niche. Fin-broadening accompanied changes which extensively altered the proportions of the whole skeleton (McGowan, 1972a, 1974b; Appleby, 1979), and presumably took the heteropinnate to latipinnate stock into eating habits or habitats in which they did not compete extensively with their forebears, as the broad-fin experiment was repeated in late or mid-Liassic. This time the narrow-finned longipinnates themselves died out at the end of the Liassic.

RESTORATION

Chapman (*in* Taylor, 1987b) has produced a very business-like restoration of an ichthyosaur, non-Martill (1987b). Taylor (1987b), by a careless use of quotation marks, attributed to Wade (1984) use of the terms 'low gear' and 'high gear' for ichthyosaur fin and tail propulsion respectively. Wade used neither, although 'high gear' is very apt, because 'holding station', a term she did use, involves many non-progressive motions like rising to breathe in sleep, or just keeping level in the water when not swimming. Of course, fins may also be used for slow movement where remaining in a certain vicinity is the aim, not progress. For all of these, 'low gear', with its implications of utilizing greater power, and making slow progress, is unsuitable, even though less speed eventuates from fin swimming than tail drive in all normal shapes of fish and, presumably, ichthyosaurs. Massare (1988) points out that fins are energy-efficient at low speeds and tails at higher speeds.

In discussions on locomotion models for ichthyosaurs, most workers seem to have assumed only one style of locomotion per major taxon. Marine animals of normal fish-like adaptations are not so limited (Wade, 1984). They use fin movements for holding station, and sinuous tail movements to progress from place to place, either fast or slowly. Dean (1906) described the rather restricted movements of a *Neoceratodus fosteri* that had travelled half-way around the world by ship, and was still confined in an aquarium. *N. fosteri*, either free or in a spacious enclosure, make most of their locomotory movements by slow or fast sinuous tail movements like other fish, using their paired fins to hold station, or to brace against the substrate, or to rest there for long periods (A. Kemp, pers. comm., 1988). *Inia*, the Amazon dolphin, lives in waters not famous for pellucid visibility that would make its movements easy to follow. It is usually discussed as seen in its encounters with man. Even in a primitive state, man is a notorious example of sacrificing speed in any one milieu to a wide range of abilities, such as the terrestrial locomotion of an upright observation tower, climbing, and swimming. To associate with man, sociable *Inia* use their idling locomotion, fin propulsion (McGowan, 1974), but that does not mean that they have no means of fast propulsion although McGowan's words 'frequently used for skulling' seem to have been read that way. Riess (1985, 1986) identifies three possible structures of ichthyopterygian tail fin, which he couples to four described forms of locomotion: the *Neoceratodus* type (*vide* Dean, 1906), the *Inia* type (*vide* McGowan, 1972b), the *Leptopterygius* type (Bauer, 1898), and the *Mixosaurus* type (Kuhn-Schnyder, 1964; Appleby, 1979). The first two, from the nature of the models employed, are potentially useful as descriptions of ichthyosaur idling movements, but they are not descriptions of normal progressive locomotion. In view of the decidedly specialized tailfin vertebrae of *Eurhinosaurus* and *Platypterygius*, Riess and Frey's spirited restorations (Riess, 1986) of the *Eurhinosaurus* tail will have to await evaluation by further illustration and documentation of the tail to tailfin vertebrae. The ecologic clash involved in placing *Eurhinosaurus* in a swordfish feeding-type and a '*Neoceratodus*' swimming-type is considerable.

Riess (1985, 1986) redescribed ichthyosaur paired fins, making good use of material recorded by Andrews (1924) and by Owen (1840, 1881). These soft part data he fitted to well-preserved bony finblades, to produce relatively large fins with supple tips and edges. He generalised his description to most types of fin, particularly those with spaces between phalanges, omitting only the *Platypterygius* type of long and wide fins, with a tight bony pavement, already described by Wade (1984) with much the same conclusions, as they were both based on the same soft part literature, and an early study of potential movements by

Oemichen (1938). As Riess' thesis must have been well-advanced when Wade published, similar ideas must have occurred to both. Riess favours a very upright position for the scapula and clavicle, like Johnson (1979). The distal end of the Stewart Park *Platypterygius longmani* specimen, with clavicle and scapula associated with ribs and vertebral column, has the clavicle and scapula almost parallel to those vertebrae still in natural position, but the ribs are distorted, straightened by flattening (Wade, 1984, fig. 2c). The left scapula and clavicle of QMF2453 were found in a closely similar position but became detached during acid preparation. They are not conclusive evidence against Riess' interpretation, for the coracoids of one were displaced and those of the other were lost. In *Platypterygius* the scapula is widened enough distally that even in Riess' reconstruction, it could have rested on two ribs. This might have sufficed for an aquatic animal, though not for the girdle of a weight-bearing limb. Preservation is not adequate to indicate the shape of the probable cartilage termination of the scapula.

Taylor (1987a) has offered a new interpretation of the direction of thrust generated by ichthyosaur tails, demonstrating that thrust could have operated at the 'centre of balance' (*sic*) rather than at the downward angle at the centre of gravity previously used in calculations (e.g. see McGowan, 1973b). Taylor's stress on neutral depth as the hunting or cruising depth is perhaps a little precise for nature; hunting depth is generally the depth that best suits the prey of the season, not necessarily the hunter. The ability to adjust 'neutral depth' quickly would be the best adaptation for a hunter to acquire. Restorations sometimes show ichthyosaurs letting out air under water, but they are unlikely to have opened their nostrils while in action under water. Broadly attached fins, such as *Platypterygius* seems to have had, are rather stiffly attached to the body, as in sharks of comparable size, but sufficiently flexible outwardly (Wade, 1984; Taylor, 1987a) to allow any direction of steering. Wade's suggestion of a slight upward set on the main part of the fins of *Platypterygius*, even when diving, was stress on a safety factor. Airplane wings similarly tilt up to the front for stability. Most of the potential problems that would have arisen from allowing the huge front fins to be pressured from above would have been due to forward movement. The effects of negative pitch (hopefully not present for Taylor, 1987a) and slightly *greater* (not lesser) density than water would have been comparatively minor. Taylor's attempt to summarize McGowan's work and Wade's (which were not in full agreement) in the same sentences rendered him incomprehensible at that point, but he presented his own thoughts more successfully. He described a pitching action which was presumably used, though commonly not as vigorously as figured (Taylor, 1987a, text-fig. 2) in normal breathing. The most economical way to breathe was to break water with as little of the head as possible. Cruising cetaceans normally reach the surface in an asymptotic curve that just breaks the surface as the animal finishes breathing out. Using an adjustable plasticene model, it is possible to see that if the *Platypterygius* snout was straight, most of it would emerge at the top of an asymptotic curve swum high enough to bring the nostrils above water. But long ichthyosaur snouts, as seen in *Platypterygius longmani*, *P. americanus*,

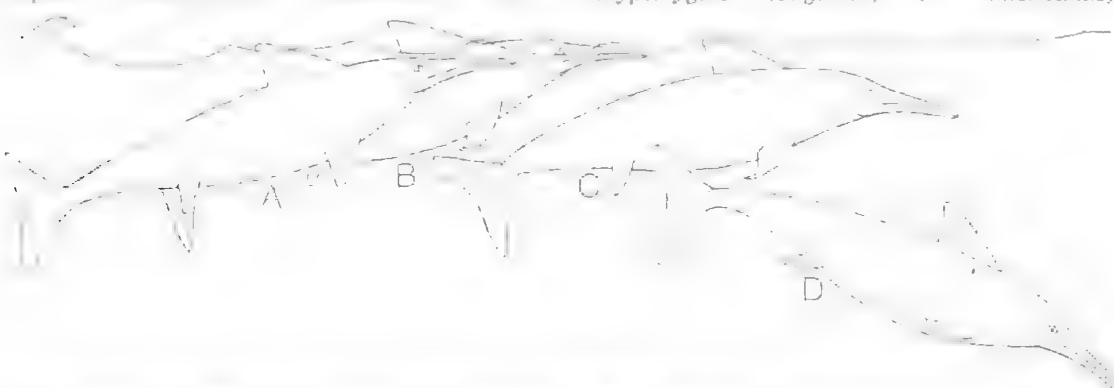

FIG. 7 Sequence of diagrams to demonstrate *Platypterygius longmani* surfacing to breathe at cruising speed. Diagrams C and D may be interpreted as alternatives or as a sequence. Fineness ratio (length from front of orbit/maximum depth of body) varies between 4.6 and 4.8 because of the animal's ability to modify flexure of the tail. As restored the tailfin comprises 80 cm of vertebrae plus terminal cartilage. Approximate ratios of head : body + neck : whole tail are 3:5:4.

Temnodontosaurus tenuirostris and *Leptopterygius acutirostris*, and even some medium and short snouts e.g. (*Ichthyosaurus breviceps*), dip down toward the tip. Their snouts probably broke water only with part of the upper surface (Fig. 7). The pineal organ presumably informed the animal about waves or other surface conditions of the water-cover, by pressure or light intensity, or both, prior to air exposure.

The top of the head would have had to be exposed in breathing, but whether much of the dorsal side of the neck or shoulders were usually exposed would have depended on the relative effort required to bend the neck or lift that part of the body above the water. It is quite likely to have been individually variable. Since fins are designed for use in water, it is certain that lateral fins were not flourished in the air save in desperation or display. The head is a long or short inflexible front segment to the axis, but maximum possible movement on the occipital joint of *Platypterygius* was probably 10° in a vertical plane (direct measurement from VMP12989) and the same laterally. Half of that suppleness would have sufficed for diving during breathing, to judge by films of cruising whales. The antero-dorsal neural spines each overlapped the succeeding centrum, but the postero-dorsal and following caudal vertebrae were confined only by the zygapophyses and the massive longitudinal muscles attached to neural spines situated above their own centra; 1° freedom per average vertebral joint would have supplied more than enough suppleness laterally, and the total of 30° or more bend in the dorso-ventral plane was adequate for diving, if the variable tail bend was not enough. Massare (1988) evaluated the likelihood of suboscillatory or oscillatory caudal fin action for progressive movement and preferred oscillatory, as the proportions of the tail resemble dolphins, which use oscillatory action. The tail-base vertebrae of *Platypterygius* were commonly largest, but some specimens had a very gradual slow increase in size and were almost stable from early postero-dorsal into the tail, before diminishing. Thus the tail base was one of the least flexible parts of the axial column, and this would not only have made it relatively strong, but would have tended to minimize the yaw incipient in tail-swing. If Martill (1987b) was correct that there was no dolphin-like or shark-like dorsal fin to stabilize the body against yaw and roll, then an alternative structure was needed, and an alternative explanation for the V-shaped articulation surfaces on *Platypterygius* neural spines 11 to 20+. Although cartilage extensions dorsally could support varied shapes of mid-dorsal ridges, all are effectively dorsal fins. Martill pointed out that a great difference between dolphin shape and ichthyosaur shape was the retention of the rear fins throughout ichthyosaur history. These he suggested controlled 'roll'. Rather than working in tandem with the fore fins, the rear fins, situated immmediately below and to the sides of the largest diameter of the axial column, may well have had the task of helping to compensate for yaw by exerting a counter-drag on the centre of gravity. This new-old idea has also been mentioned recently by Taylor, who did not comment that hindfin compensation for yaw would be applied virtually in the same plane as the tail thrust if the old model for thrust were correct. It is time someone competent in marine architecture had a say!

Wade (1984, pp. 108-11) discussed the functioning of *Platypterygius* in general terms, concluding like Taylor that the tail provided the main driving force and the pectoral fins did most of the steering. Massare (1988) came to the same conclusion in her much more significant study. After comparing potential ichthyosaur densities with what is known of crocodiles and sea-snakes, Wade (1984, pp. 108-11) concluded: 'Whatever the density of extreme juveniles, older ichthyosaurs were probably as dense as sea-water' [at the same depth is implied] 'or a little denser. Comparison favours slight negative density'. The propensity to float, crocodile-like, at the surface she also attributed to ichthyosaurs. The mechanism by which a floating crocodile changes to a sinking crocodile has now been described as exhaling slightly before closing the naris (Green, 1988, p. 20) and Molnar (pers. comm.) tells me it is easily observed in small specimens (these would have to exhale relatively more air). It is a mistake to simplify the activities we attribute to animals known as fossils from the not-far-distant past to something much more elemental than is seen today.

THE LAST ICHTHYOSAURS

Platypterygius longmani lived through to the end of the Albian, at least, but *P. americanus* and *P. kiprijanoffi* lasted well into the Cenomanian. Nesov *et al.* (1988) have listed the ichthyosaur fauna of USSR as background to the apparent extinction of ichthyosaurs linked with the 'great turnover of ecosystems in the period from Cenomanian to late Turonian'. Taylor (1987b) did not give a reason for his recent assertion that ichthyosaurs lived to the end of the Cretaceous, which is unlikely. Baird (1984) has removed a number of scattered bones from contention, and the putative 'last' record is by Teichert and Matheson (1944) from the Lower Santonian of Dandaragan, Western Australia. Their collection consisted of eight ichthyosaur (and eight plesiosaur) centra and other bones. They were recovered by the seiving of an exploratory sample for a commercial phosphate open-cut mine, so their original disposition is unknown. The deposit was a fossiliferous nodule bed. Fresh breakage aside, the ichthyosaur postero-dorsal centrum figured is relatively undamaged; natural features such as the ventro-lateral rib apophyses, neural arch facets and margins of the centrum are figured as unworn. The three views given do not suggest derivation from older rocks, though that is possible. This and the other ichthyosaur bones are within the range of variation of *Platypterygius* and a number of other ichthyosaurs, and Teichert (*in* Teichert & Matheson, 1944) correctly did not identify them. Teichert suggested that the species here named *Platypterygius longmani* might be a *Myopterygius*, (*Platypterygius americanus* (Nace) was known as *Myopterygius americanus* at the time), and this name is found in collections and semipopular literature from time to time.

ACKNOWLEDGEMENTS

From the first my studies were aided by a generous supply of reprints from Dr C. McGowan of Royal Ontario Museum, and later by discussion and correspondence with Dr R.M. Appleby, University of Hull, and by his permission to cite the correspondence. Dr R. Wild of Paläontologische Abteilung des Staatlichen Museums für Naturkunde in Stuttgart very kindly demonstrated the beautiful Holzmaden ichthyosaurs in his care, and Professor Kuhn-Schnyder facilitated my viewing the Tessin mixosaurs at the Paläontologisches Institute und Museum der Universität, Zurich. The British Museum ichthyosaur display was also viewed, and C. Walker showed me some of the material in storage. Dr T.H. Rich of the Museum of Victoria facilitated the loan of material studied by McCoy (1869), and gave permission to prepare it, while Dr T. Darragh produced Sutherland's letters of conveyance for scrutiny. Dr R. Molnar of Queensland Museum has provided a helpful sounding-board for ideas and further access to literature. Readers will benefit from the editorial review Dr R.A. Thulborn provided.

I am grateful to all these helpful people, and also to those who have donated original material, from James Sutherland and J. Edgar Young to Charles and Andrew Robinson and Mrs Hazel Young.

REFERENCES

Allison, P.A. 1988. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Palaeobiology* 14(2): 139-54.

Andrews, C.W. 1924. Note on an ichthyosaur paddle showing traces of soft tissue. *Proceedings of the Zoological Society of London* 2:532-37.

Appleby, R.M. 1956. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proceedings of the Zoological Society of London* 126: 403-47.

1958. 'A catalogue of the Ophthalmosauridae in the collections of the Leicester and Peterborough Museums'. (Leicester Museums and Art Gallery: Leicester).

1961. On the cranial morphology of ichthyosaurs. *Proceedings of the Zoological Society of London* 137: 333-70.

1979. The affinities of Liassic and later ichthyosaurs. *Palaeontology* 22(4): 921-46.

Baird, D. 1984. No ichthyosaurs in the Upper Cretaceous of New Jersey . . . or Saskatchewan. *The Mosasaur* 2: 129-33.

Broili, F. 1907. Ein neuer *Ichthyosaurus* aus der norddeutschen Kreide. *Palaeontographica* 54: 139-62.

Chapman, F. 1914. 'Australasian fossils'. (George Robertson: Melbourne). 341 pp.

Day, R.W. 1969. The Lower Cretaceous of the Great Artesian Basin. p. 140-73 *in* Campbell, K.S.W. (ed.), Stratigraphy and Palaeontology Essays in honour of 'Dorothy Hill' (Australian University Press, Canberra).

Dean, B. 1906. Notes on the living specimen of the Australian lung fish, *Neoceratodus fosteri*, in the Zoological Society's collection. *Proceedings of the Zoological Society of London* 1: 168-78.

Dechaseaux, C. 1955. Ichthyopterygia. p. 376-408 *in* Piveteau, J. (ed.). 'Traité de Paléontologie'. 5. (Masson et Cie: Paris).

Etheridge, R. Jnr. 1888. On additional evidence of the genus *Ichthyosaurus* in the Mesozoic rocks (Rolling Downs Formation) of northeastern Australia. *Proceedings of the Linnean Society of New South Wales* 2(3): 405-9.

Green, J. 1987. Crocodile I: Go ahead make his day! *Geo, Australia's Geographical Magazine* 9(4): 16-29.

Hofmann, J. 1958. Einbettung und Zerfall der Ichthyosaurier im Lias von Holzmaden. *Meyniana* 6: 10-55.

Jack, R.L. and Etheridge, R., Jnr. 1892. 'Geology and palaeontology of Australia and New Guinea'. (Government Printer: Brisbane). 2 vols.

Johnson, R. 1979. The osteology of the pectoral complex of *Stenopterygius* Jaekel (Reptilia, Ichthyosauria). *Neues jahrbuch für Geologie und Palaeontologie, Abhandlungen* 159: 41-86.

KIPRIJANOFF, W. 1881. Studien über die fossilen Reptilien Russlands. Th. 1. Gattung *Ichthyosaurus* Konig aus dem Sewerischen Sandstein oder Osteolith der Kreidegruppe. *Memoires de l'Academie Imperiale des Sciences de St Petersbourg, VII Serie,* 28(8), 103 pp.

KUHN, O. 1946. Ein Skelett von *Ichthyosaurus (Platypterygius) hercynicus* n. sp. aus dem Aptium von Gitter. *Bericht der Naturforschung Gesellschaft Bamberg* 29: 69–82.

LONGMAN, H. 1922. An ichthyosaurian skull from Queensland. *Memoirs of the Queensland Museum* 7: 246–56.

1935. Palaeontological notes. *Ichthyosaurus australis. Memoirs of the Queensland Museum* 10: 236.

1943. Further notes on Australian ichthyosaurs. *Memoirs of the Queensland Museum* 12: 101–4.

MASSARE, J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7(2): 121–37.

1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. *Palaobiology* (14)2: 187–205.

MAZIN, J.-M. 1981. *Grippia longirostris* Wiman, 1929, un Ichthyopterygia primitif du Triassique inférieur du Spitzberg. *Bulletin du Museum National d'Histoire naturelle, Paris,* ser. 4, 3, section C, no. 4: 317-40.

MARTILL, D.M. 1987a. A taphonomic and diagenetic case study of a partially articulated ichthyosaur. *Palaeontology* 30(3): 543–55.

1987b. Prokaryote mats replacing soft tissues in Mesozoic marine reptiles. *Modern Geology* 11: 265–9.

M'COY, F. 1867. On the occurrence of *Ichthyosaurus* and *Plesiosaurus* in Australia. *Annals and Magazine of Natural History* (3)19: 355–6.

1869. On the fossil eye and teeth of the *Ichthyosaurus australis,* M'Coy, from the Cretaceous formations of the source of the Flinders River. *Transactions and Proceedings of the Royal Society of Victoria,* 9: 77–8.

MCGOWAN, C. 1972a. The distinction between latipinnate and longipinnate ichthyosaurs. *Life Sciences Occasional Papers, Royal Ontario Museum* 20: 1–8.

1972b. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. *Contributions to Geology, University of Wyoming* 11(1): 9–29.

1972c. Evolutionary trends in longipinnate ichthyosaurs with particular reference to the skull and fore fin. *Life Sciences Contributions, Royal Ontario Museum* 83: 1–38.

1973a. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. *Bulletin of the British Museum (Natural History) Geology* 24(1): 1–110.

1973b. Differential growth in three ichthyosaurs: *Ichthyosaurus communis, I. breviceps,* and *Stenopterygius quadriscissus* (Reptilia, Ichthyosauria). *Life Sciences Contributions, Royal Ontario Museum* 93: 1–21.

1974a. A revision of the longipinnate ichthyosaurs of the Lower Jurassic of England, with descriptions of two new species (Reptilia: Ichthyosauria). *Life Sciences Contributions, Royal Ontario Museum* 97: 1–37.

1974b. A revision of the latipinnate ichthyosaurs of the Lower Jurassic of England (Reptilia: Ichthyosauria). *Life Sciences Contributions, Royal Ontario Museum* 100: 1–30.

1976. The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Canadian Journal of Earth Sciences* 13(5): 668–83.

1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontographica, A,* 166: 93–135.

MURRAY, P.F. 1985. Ichthyosaurs from Cretaceous Mullman Beds near Darwin, Northern Territory. *The Beagle, Occasional Papers of the Northern Territory Museum, Arts and Sciences* 2(1): 39–55.

NESOV, L.A., IVANOV, A.O. and KHOZATSKIY, L.I., 1988. On the discovery of the remains of ichthyosaurs in the U.S.S.R. and the problem of faunal change in mid Cretaceous. *Vestnik Leningrad University,* Ser.7, no. 1(7): 15-25. [In Russian, English summary.]

OEMICHEN, E. 1938. Essai sur la dynamique des ichthyosauriens longipinnati et particulierement d'*Ichthyosaurus burgundiae (Goud.). Annales de Paleontologie* 27: 91–114.

OWEN, R. 1881. Monograph of the fossil Reptilia of the Liassic formations Part III, Ichthyopterygia. *Palaeontographical Society Monographs,* 35: 83–134.

RIESS, J. 1985. 'Fortbewegungsweise, Schwimmbiophysik und Phylogenie der Ichthyosaurier'. Dissertation, University of Tübingen.

1986. Fortbewegungsweise, Schwimmbiophysik und Phylogenie der Ichthyosaurier. *Palaeontographica,* A, 192: 93–155.

ROMER, A.S. 1968. An ichthyosaur skull from the Cretaceous of Wyoming. *Contributions to Geology, University of Wyoming* 7(1): 27–41

SCHAEFER, W. 1962. 'Aktuo-Paläontologie nach Studien in der Nordsee'. (Kramer: Frankfurt am Main).

1972. 'Ecology and palaeecology of marine environments'. (University of Chicago Press: Chicago).

SMART, J. AND SENIOR, B.R. 1980. Jurassic-Cretaceous basins of northeastern Australia. p. 315-18. *In* Henderson, R.A. and Stephenson, P.J., 'The geology and geophysics of northeastern Australia'. (Geological Society of Australia, Queensland Division: Brisbane).

SOLLAS, W.J. 1916. The skull of *Ichthyosaurus* studied in serial sections. *Philosophical Transactions of the Royal Society of London* (B) 208: 63–126.

TAYLOR, M.A. 1987a. A reinterpretation of ichthyosaur swimming and buoyancy. *Palaeontology* 30(3): 531–5.

1987b. Reptiles that took on the sea. *New Scientist,* 26 Nov. 1987: 46–51.

TEICHERT, C. AND MATHESON, R.S. 1944. Upper Cretaceous ichthyosaurian and plesiosaurian remains from Western Australia. *Australian Journal of Science* 6: 167–70

WADE, M. 1984. *Platypterygius australis,* an Australian Cretaceous ichthyosaur. *Lethaia* 17: 99–113.

SKULL ELEMENTS AND ADDITIONAL REMAINS OF THE PLEISTOCENE BOID SNAKE *WONAMBI NARACOORTENSIS*

JOHN BARRIE

Barrie, D. John. 1990 3 31: Skull elements and additional remains of the Pleistocene boid snake *Wonambi naracoortensis*. *Mem. Qd Mus.* **28**(1): 139–151. Brisbane. ISSN 0079-8835.

Skeletal remains representing most elements of the large extinct snake *Wonambi naracoortensis* are reported from Pleistocene sediments at Henschke's Quarry Fossil Cave, Naracoorte, South Australia. These specimens include a large number of previously undescribed cranial and post-cranial elements, allowing a fuller description of this poorly known animal. No extant Australasian species compares closely with *Wonambi naracoortensis*, which seems to have been a Gondwanan relic resembling most closely the fossil genus *Madtsoia*, known from South America, Africa and Madagascar. *Wonambi's* skeletal architecture suggests it was adapted for climbing, possibly inhabiting the caves wherein its remains have been found.
☐ *Reptilia, Serpentes, Boidae, Wonambi, Pleistocene, South Australia.*

D. John Barrie, P.O. Box 227, Coonalpyn, South Australia 5265, Australia; 1 June 1988.

Henschke's Quarry Fossil Cave consists of a series of small caverns and fissure fills in the Oligocene-Miocene limestones of the Murray Basin (Wells *et al.*, 1984) at Naracoorte, southeastern South Australia (Fig. 1). Several fissures in the area have produced a large quantity and variety of Pleistocene vertebrate remains. One fissure of Henschke's Quarry Fossil Cave, excavated under the direction of the South Australian Museum, contained sediment and fossils accumulated from a natural pit-fall trap (Pledge, 1981).

Subsequent excavations by the author in adjacent fissures yielded some excellently preserved additional material, including associated skeletal elements of the large snake *Wonambi naracoortensis*. The original description (Smith, 1976) was based on eight vertebrae and a jaw fragment. This paper provides the first adequate description of the skull and supplements existing knowledge of the post-cranial elements.

MATERIAL

The remains collected were from two snakes, the more complete being 17% larger than the other. Remains of the larger snake (Fig. 2) were used for the descriptions as they best represented the undescribed elements.

The larger snake (specimen HJD2:84Wi) comprises: left maxilla, anterior part of right maxilla, incomplete left palatine, basioccipital, basisphenoid, left opisthotic-exoccipital, left prootic, fragment of right parietal, left and right dentaries, left surangular, 27 upper thoracic vertebrae, 53 lower thoracic vertebrae, two caudal

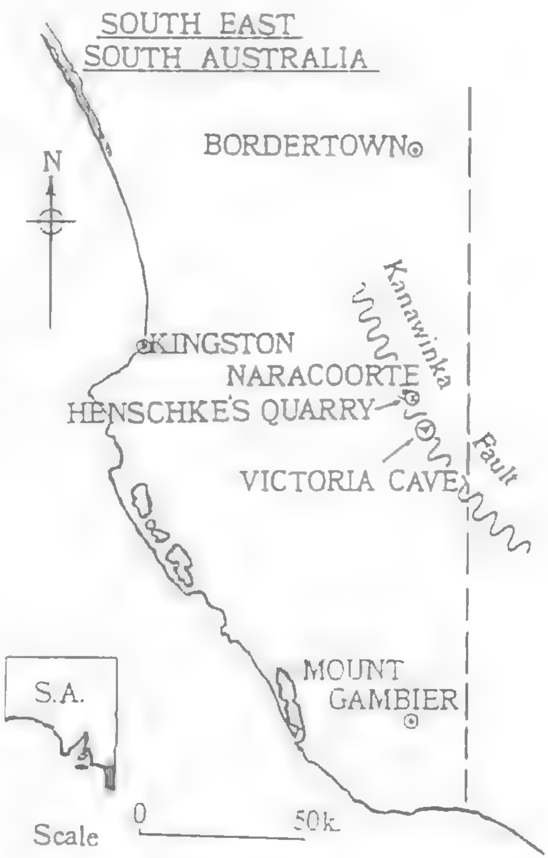

FIG. 1. Locality map, southeastern South Australia.

FIG. 2. The assembled remains of *Wonambi naracoortensis*, specimen number HJD2:84Wi. Length of display 1.5 m.

vertebrae with bifid fixed ribs, seven caudal vertebrae with single fixed ribs (one a fused pair). 152 ribs with rib heads (80 left, 72 right), numerous fragments of rib shafts. Remains of the smaller snake (specimen HJD1:83Wi) comprise: right maxilla, posterior part of parietal, possible pterygoid fragment with seven tooth-sockets, 24 upper thoracic vertebrae, 38 lower thoracic vertebrae, four caudal vertebrae (one with bifid fixed ribs, three with single fixed ribs), 50 ribs with rib heads (30 left, 20 right — including one with fused shaft), numerous fragments of rib shafts. Both specimens are currently in the author's private collection, but arrangements are being made to lodge the larger example (HJD2:84Wi) with the South Australian Museum, Adelaide.

Specimens used in comparisons: SAM R26137, *Python sebae;* SAM unnumbered, *Python* cf. *P. molurus;* SAM R27307 and VM R5850, *P. reticulatus;* SAM R29579, *Boa constrictor;* SAM R26955, *Morelia spilota variegata;* SAM R16053b, *Candoia (Enygrus) australis;* SAM R26966, *Acrochordus arafurae;* BM(NH) 1901-3-29-77, *Trachyboa boulengeri;* AMNH 3154 and BM(NH) R2976, *Madtsoia bai;* SAM R3906, *Liasis olivaceus;* SAM P27777, *Wonambi naracoortensis*. Institutional abbreviations: AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); SAM, South Australian Museum; VM, Victorian Museum.

Abbreviations (Figs 5-9, 11, 12): a.opht., arteria ophthalmica; ao.vc., anterior opening of vidian canal; ap.l., lateral aperture for recessus scala tympani; ar., articular; ar.co., coronoid articulation; bpt.p., basipterygoid process; bo., basioccipital; bs., basisphenoid; cen., centrum; cf, costal foramina; c.fr., cerebral foramen; ch.p., choanal process; cid., cid-nerve; de., dentary; e.o., exoccipital; epg?, ectopterygoid?; f?, frontal?; f.jug., foramen jugularis; f.o., fenestra ovalis; lat.w., lateral wing of parietal; lhp., lymphapophysis; l.sf., lingual shelf of dentary; m., maxilla; m.f., mandibular foramen; m.gve., Meckel's groove; n.s., neural spine; oc.c., occipital condyle; op., opisthotic (fused to exoccipital); op.f., optic fenestra; pa., parietal; pg?, pterygoid?; pl., palatine; pm?, premaxilla?; po.vc., posterior opening of vidian canal; poz., postzygapophysis; pro., prootic; prz., prezygapophysis; q?, quadrate?; r.a.p., retroarticular process; s.f.r., single fixed rib; sg.c., sagittal crest; soc., supraoccipital; s.tur., sella turcica; V2, maxillary branch of trigeminal nerve; V3, mandibular branch of trigeminal nerve; VI, abducens nerve; VII, facial nerve; zsp., zygosphene; zyg., zygantrum.

DETAILS OF EXCAVATION

Commercial quarrying exposed the Henschke's Quarry Cave System in the late 1960's. Subsequently the owner discovered a sloping silt bed littered with bones. The South Australian Museum commenced excavations in 1969 and

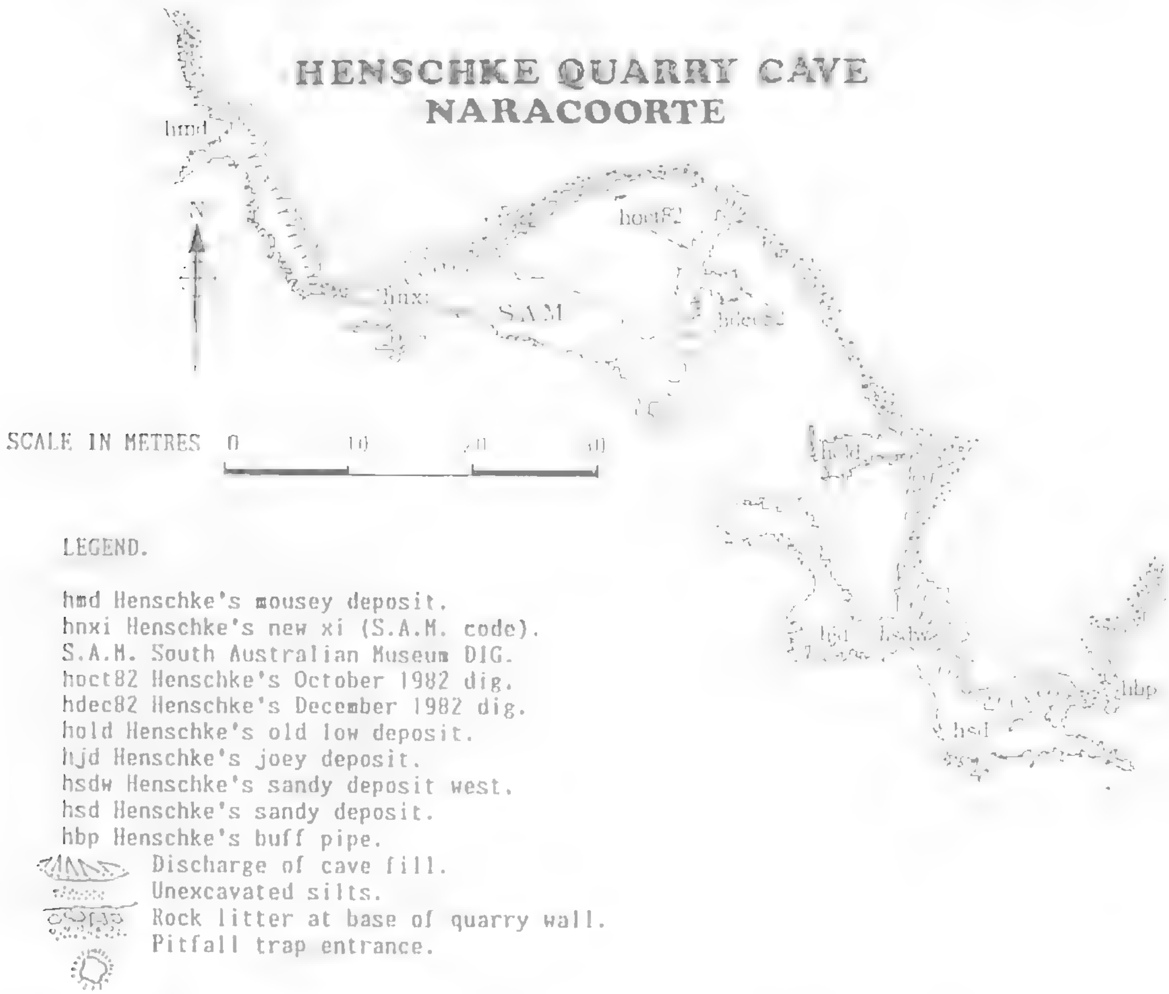

FIG. 3. Plan of fissure excavations at Henschke's Quarry.

periodically conducted 'digs' up to 1981. After the known fossil-bearing silt had been exhausted, I approached the quarry owner and received permission to continue searching. An exposure of pale sands produced some well-preserved bones, and this was followed along the quarry face to some red silty sediments that yielded the remains of *Wonambi*. Between 1982 and 1986 the fissure coded HJD (Figs 3, 4) was excavated and surveyed. Material removed was recorded in 'dig' lots, and the locations of larger skulls and material from rarer species were plotted onto charts as the dig progressed. Specimens were cleaned, usually washed and dried, then strengthened by immersion in a 10% solution of PVA and water. The venture has been funded by the author, and has occupied more than 8,600 man hours to date.

DESCRIPTION

Cranial and dental features of *Wonambi naracoortensis* are compared to those of other snakes in Table 1.

Maxilla: The maxilla (Figs 5, 6) is 81 mm long, anteriorly robust but considerably reduced in depth and thickness in its posterior two-thirds. A trough passes transversely across the dorsal surface from below the orbit to the lingual side two-thirds from the anterior extremity. The dorsal surface rises to a crest at a point one-third from the anterior, forming an articular surface for the prefrontal. The posterior end shows a small area for articulation with the ectopterygoid. Five small foramina of roughly equal size penetrate the maxilla between the anterior tip and the orbit.

There are 22 tooth sites in the maxilla, with

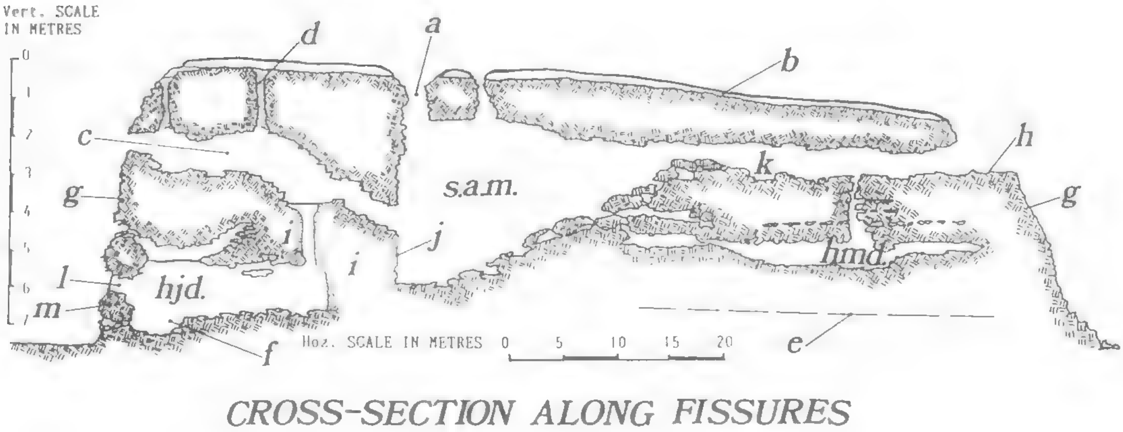

FIG. 4. Cross-section along cave system at Henschke's Quarry.
Abbreviations: a. entrance to pit-fall trap over main cavern; b. Terra rossa soil profile; c. cavern investigated by SAM (no evidence of bones); d. solution tube filled with Pliocene Parilla Sands; e. interface between harder Naracoorte Limestone Member and the softer underlying bryozoal sequences of the Gambier Limestone; f. lowest extent of deposit, produced remains of *Wonambi;* g. quarry faces; h. bench level at quarry exposing entrance to k; hjd. deposit excavated by the author 1982-1986; hmd. deposit excavated by the author 1982-1986 (contained only extant species in upper levels); i. material unexcavated due to hazardous conditions; j. hard calcified clay plugging lower deposit; k. shallow cavern leading to the bone bed in s.a.m.; l. entrance to hjd exposed by digging away quarry debris; m. fallen boulders; s.a.m. cavern excavated by SAM 1969-1981.

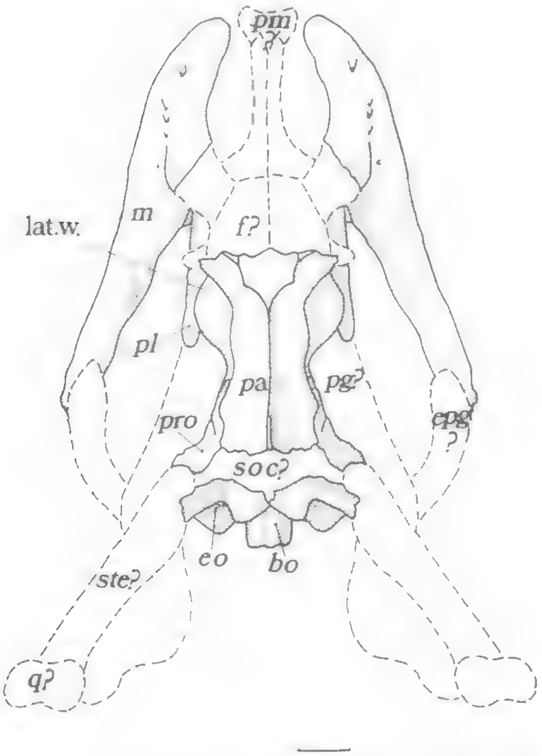

FIG. 5. *Wonambi naracoortensis,* skull in dorsal view; scale bar 1 cm.

functional teeth approximately alternating with developing replacement teeth (lost from this specimen). The conical teeth are of typical boid-like form and are directed posteriorly at approximately 45° to horizontal. The anterior teeth show a slight reverse curvature and cutting edge (Frazetta, 1966); the posterior teeth are smaller and point lingually at approximately 45°, as well as posteriorly. The teeth are smaller and more numerous than in any other species examined in this study (Table 1).

Palatine: The body of the palatine (Fig. 6) is broad and rather flat. The lateral maxillary process is damaged, but the primitive choanal process (Underwood, 1976) is well developed and forms a sub-circular perforation as it approaches the anterior end of the tooth row. The anterior articular surface of the choanal process is thickened and contains a hollow with a foramen at its base. A small foramen is also present in the antero-dorsal surface of the choanal process, just behind its widest point. A ridge crosses the ventral surface of the lateral process, commencing against the anterior end of the tooth row and curving away from it posteriorly. The anterior part of this ridge defines the lingual side of the sub-circular perforation. Posteriorly the ridge diminishes at the widest extent of the palatine. The articulation with the pterygoid is indicated by a notch between the posterior end of the tooth row and the rear part of

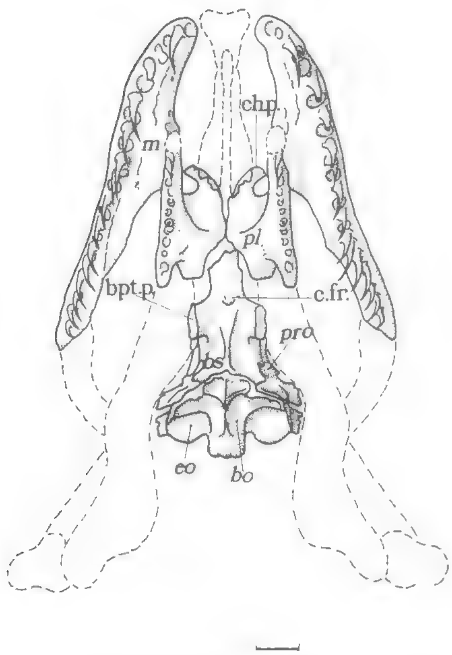

FIG. 6. *Wonambi naracoortensis,* skull in ventral view;

the lateral process. The extreme anterior end of the tooth row is missing; there was possibly one more tooth site in addition to the 12 preserved. The small and close-set teeth are directed posteriorly and curve back sharply to lie at about 30° to the horizontal. The proportional width of the palatine is exceeded only in *Acrochordus arafurae* (SAM R26966). In its general form the palatine is matched most closely in the tropidophids *Tropidophis taczanowski* (Underwood, 1976) and *Trachyboa boulengeri,* while the number of teeth is approached most closely in *Acrochordus arafurae* (9 teeth).

Dentary: The dentary (Fig. 7) is dorso-ventrally compressed and broad. It achieves its greatest depth at the facet for articulation with the complex of other bones forming the lower jaw. The facet extends for approximately 44% of the length of the dentary. Meckel's groove is deep and broad, tapering anteriorly, and is open to the tip of the dentary. The missing splenial would fit along its inswept postero-ventral surface. One small foramen is situated beneath tooth sites 6 and 7. There are 25 sites for teeth, including vacant sites for developing replacement teeth (not preserved).

TABLE 1. Comparisons of cranial elements. All linear dimensions are scaled to uniform maxilla length (84 mm) in *Python reticulatus* (SAM R27307). The few measurements available for *Madtsoia* are: no. of tooth sockets, dentary, 9+; dentary foramina, adjacent to teeth, 3.8; number of foramina (dentary), 3 (all of these measurements for *M. bai*, British Museum (Nat. Hist.) R2976); and angle of zygapophyses, 22° (*M. bai*, AMNH 3154), and 20° (*M. madagascariensis*, after Hoffstetter, 1959). Paracotylar foramina are present in both species.

	Wonambi naracoortensis	*Trachyboa boulengeri*	*Candoia australis*	*Acrochordus arafurae*	*Constrictor constrictor*	*Python sebae*	*Python molurus*	*Python reticulatus*	*Python reticulatus*	*Morelia spilota*	*Liasis olivaceus*
Scaling Factor	1.04	11.66	6.46	5.49	2.79	3.56	2.22	1.00	0.91	3.23	2.13
Maxilla length	84	84	84	84	84	84	84	84	84	84	84
Dentary length	78.3	112	87.88	91.1	82.3	79	85.3	83.4	81.5	80.4	74
Mid-Dentary width	14.9	18.7	6.46	8.8	8.4	10.7	16.2	13.3	13.1	7.4	8.5
Basioccipital width	27.4	37.3	30.37	35.7	26	28.1	27.8	27.8	25	23.14	30.7
Basioccipital length	24	31.5	26.49	23.1	21.8	23.1	25.1	25.1	15.3	13.7	23.9
Basipterygoid width	17.8	26.8	27.1	23.1	27.9	23.1	24.4	24.4	17.5	14.9	24.2
Distance Basipterygoid to Condyle	40.4	61.9	64	42.8	43.5	48	48.9	36.1	32.1	46.8	43.7
Width of Palatine	17.3	14.0	9.69	19.8	10.3	9.3	8.7	—	6.3	6.8	7.0
Surangular width	12.1	17.5	9.1	8.2	19.5	9.6	12	8.4	8.6	8.1	6.6
Surangular length	88.3	154	102.7	128.5	91.2	87.2	98.4	94.8	94	97.9	85.5
Surangular height	6.5	31.5	19.4	8.8	20.1	18.2	28.4	22.2	25.2	25.8	21.3
Articular width	9.6	19.8	10.34	20.9	10.3	7.8	14	13.4	13.5	12.3	9.4
Articular height	10.1	10.5	7.75	19.2	10.9	8.9	14	15	15.4	12.9	8.3
Length Mandibular Fenestra	17.8	22.2	31	15.4	9.8	24.9	31.1	4.2	5.7	11.3	5.8
Width Mandibular Fenestra	2.1	3.5	6.5	5.4	2.2	3.9	6.2	3	3.2	5.5	2.1
TEETH SIZE											
Maximum length Dentary	9	14	21.9	17	17.9	12.5	16.7	16	16.5	16.8	15.1
Minimum length Dentary	4.2	3.5	4.5	9.9	4.2	4.3	5.6	6.3	6.2	4.2	4.7
Maximum length Maxilla	9.4	14	20	18.1	16.5	13.9	15.6	18	16.3	16.2	15.8
Minimum length Maxilla	4.4	8.2	5.2	8.8	4.2	4.3	7.1	6.3	6.4	3.2	4.3
NO. OF TOOTH SOCKETS											
Maxilla	22	16	18	20	19	17	19	17	17	17	19
Palatine	12+	7	6	9	5	7	6	7	7	5	6
Dentary	25	21	18	17	18	18	20	16	16	19	19
Pterygoid	—	16	10	13	12	8	10	9	11	9	11
FORAMINA											
Dentary adjacent teeth	6-7	5-6	5-6	5-6	6-7	5	4-5	4-5	4	4	4-5
Number of Foramina	1	1	1	2	1	1	1	1	1	1	1
Maxilla adjacent teeth	5-9	—	4-5	9-12	5-6	4-6	4-9	4-5	3-6	4-5	3-4
Number of Foramina	5	0	2	2	2	3	3	3	3	1	2
Angle of Zygapophyses	22°	—	3°	0°	0°	3°	9°	3°	3°	10°	3°
Presence of Paracotylar Foramina	Y	Y	Y	Y	Y	N	N	N	N	N	N

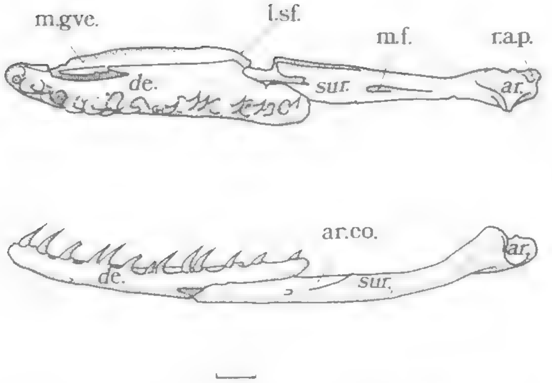

FIG. 7. *Wonambi naracoortensis*, left mandible in dorsal view (above) and lateral view (below); scale bar 1 cm.

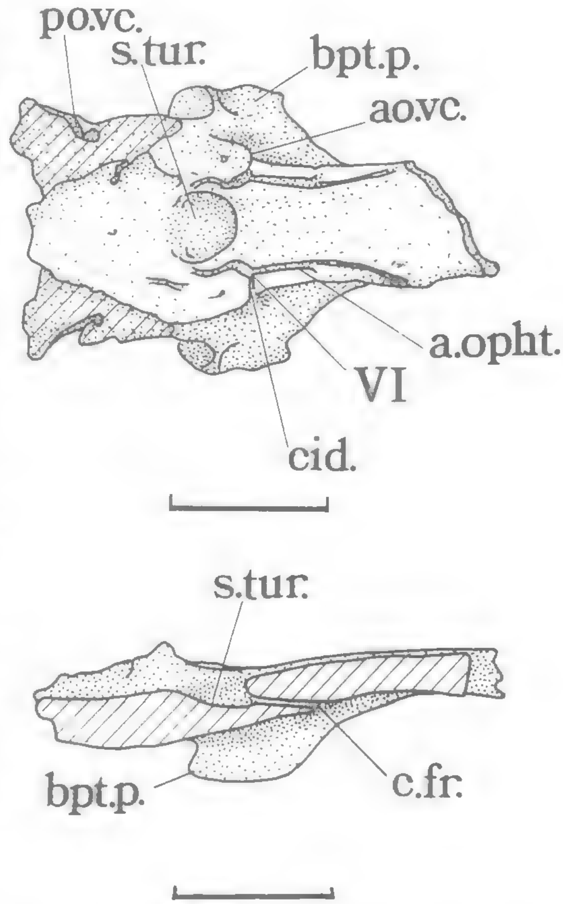

FIG. 9. *Wonambi naracoortensis*, basisphenoid in dorsal view (above) and sagittal view (below); hatching indicates articular surface for prootic; scale bar 1 cm.

The conical teeth are directed posteriorly along the dentary at approximately 45° to horizontal; the hindmost ones are directed lingually at almost 60° to the axis of the dentary.

Wonambi naracoortensis has numerous (25) tooth sites, and of the species examined only *Trachyboa boulengeri* (21 tooth sites) approaches *Wonambi* in this respect. The dentary resembles that of *Madtsoia*, as described Hoffstetter (1959), in the form of the lingual shelf along the ventral surface, although it is even more pronounced in *Wonambi*. However, *Madtsoia* has three prominent fossae on the external surface of the dentary, compared to *Wonambi's* single small one, and *Madtsoia* has only nine tooth sites anterior to the articulation for the surangular whereas *Wonambi* has 15 tooth sites.

Surangular: The surangular (Fig. 7) is wider than high and lacks a coronoid process. The mandibular foramen is a small channel in the otherwise rather flat dorsal surface, and it extends forwards approximately half-way from the articular. The articulation with the dentary doubtless allowed some flexion, since the broad, flat antero-ventral surface fitted loosely into the cleft at the posterior end of the dentary. An ascending ridge articulates with a corresponding groove in the dentary. This ridge-and-groove articulation would serve to keep the two elements aligned during flexion. Anteriorly the lingual surface has a groove that aligns with Meckel's groove in the dentary. Just forward of the articular surface for the quadrate, the surangular is almost circular in cross-section. The surface of the articular is saddle-shaped and extends obliquely across the surangular (lingual side forward) at almost 60% to the axis of the jaw.

By comparison with the other species examined, *W. naracoortensis* has a surangular that is shorter

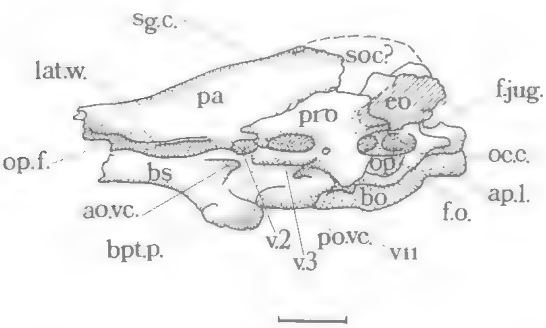

FIG. 8. *Wonambi naracoortensis*, brain-case in left lateral view; hatching indicates articular surface for supratemporal; scale bar 1 cm.

than average, though its maximum width is unexceptional. The lack of a coronoid process is shared with *Acrochordus arafurae;* all other specimens examined possessed a prominent coronoid process.

Basioccipital: The basioccipital (Figs 5, 6, 8) forms the ventral and major part of the occipital condyle. The ventral surface is strongly keeled. A slight transverse ridge extends from the keel's most ventral point to a process along the junction with the prootic. The basioccipital is widest at the spheno-occipital process for the insertion of hypaxial neck muscles. This is at the junction with the prootic/opisthotic, beneath the vestibular fenestra (Rieppel, 1979) into which the stapes would penetrate. The proportions of the basioccipital are matched in the other species examined.

Basisphenoid: Immediately anterior to the basioccipital, the basisphenoid (Figs 6, 8, 9) forms a continuation of the underside of the brain-case. Its upper surface has a prominent sella turcica, between the anterior openings of the vidian canals which are exposed on the outer surface of the basisphenoid above the prominent basipterygoid processes. From the sella turcica a small oval cerebral foramen is directed antero-ventrally. This foramen exits on the ventral surface just anterior to the basipterygoid processes. The keel below the basioccipital continues forwards on to the underside of the basisphenoid. This keel flattens between the basipterygoid processes and bifurcates to enclose the cerebral foramen. On the mid-dorsal margin of the basisphenoid, foramina occur at the junction with the prootic, possibly for nerve V_2. The highly-developed basipterygoid processes point outwards, downwards and posteriorly. The articulation with the pterygoid is sub-triangular, with the apex of the triangle rising as a ridge to meet the brain-case at the anterior extremity of the prootic. Just in front of this rising ridge is the anterior opening of the vidian canal (Underwood, 1976). The posterior opening of the vidian canal exits at the back of the basipterygoid processes, at the junction with the prootic. The anterior end of the basisphenoid, the basi-parasphenoid (Underwood, 1976), is missing from this specimen. The basisphenoid ends in a rather solid, flat rectangular section, representing the broad base of the cultriform process. The ventral surface exhibits a slight ridge anterior to the cerebral foramen.

A distinctive and undoubtedly primitive feature is the cerebral foramen, which is shared only with *Trachyboa boulengeri* among the specimens examined. The basipterygoid processes are as highly developed as in any of those specimens. Both left and right vidian canals are of similar size in *Wonambi.*

Opisthotic-Exoccipital: The opisthotics and exoccipitals (Figs 5, 6, 8) are fused. The exoccipitals form the upper and smaller portions of the occipital condyle and are hollowed posteriorly to allow flexion of the atlas vertebra at the condyle. In this hollow is the jugular foramen for nerves IX, X, XI and three smaller hypoglossal foramina for nerve XII. The anterior margin forms the rear wall of the fenestra ovalis. Inside the vestibular fenestra, which should be encased by the crista circumfenestralis, is the lateral aperture of the recessus scala tympani. The posterior margins of the exoccipitals form almost the entire foramen magnum. Their contact above the foramen is at best minimal, but minor damage may have reduced this slightly. This contact appears to be even less than in *Dinilysia patagonica* (Rieppel, 1979, after Estes *et al.,* 1970), which is the most ancient snake skull described to date. The apparent lack of a crista circumfenestralis and the minimal contact between the exoccipitals above the foramen magnum are both primitive features matched in *Dinilysia* and close to the conditions in lizards (Rieppel, 1979).

Prootic: The prootic (Figs 5, 6, 8) is an irregular element partially encasing the side of the brain cavity. It articulates with the dorsal edges of the basioccipital and basisphenoid, and lies anterior to the opisthotic- exoccipital and posterior to the lower margin of the parietal. Anteriorly it contributes to the margin of the foramen for nerve V_2. Behind this are the larger foramen for nerve V_3 and a smaller one for VII. Other tiny foramina are present, one of which would be for V_4. The posterior edge of the prootic forms the margin of the fenestra ovalis in the vestibular fenestra. This should be enclosed by the crista circumfenestralis, which is illustrated by Rieppel (1979) as a bubble-like structure penetrated by the stapes. However, there is no evidence of this structure on any of the associated elements. It is also noteworthy that the genus *Acrochordus* is recorded as lacking a crista circumfenestralis (McDowell, 1975) or, at best, as having it highly modified (Rieppel, 1979).

Parietal: An anterior fragment of the right parietal of specimen HJD2:84Wi (Figs 5, 8) contacts the basisphenoid and encases the anterior dorsal surface of the brain. A near-complete parietal (SAM P27777), identified from the Victoria Fossil Cave, also near Naracoorte (Fig. 1), is used to supplement the description. This

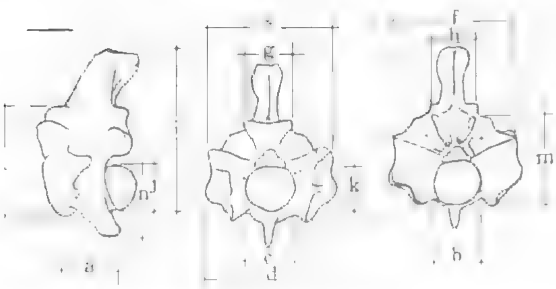

FIG. 10. Measurements of vertebrae. Example shown is an upper mid-thoracic vertebra with prominent hypapophysis and three paracotylar foramina; scale bar 1 cm. Measurements: a, length, condyle to cotyle, measured ventrally; b, condyle width; c, cotyle width; d, width across diapophyses; e, width across prezygapophyses; f, width across postzygapophyses; g, zygosphene width; h, zygantrum width; i, height, from ventral margin of condyle to crest of neural spine; j, condyle height; k, cotyle height; l, height, from zygosphene to base of cotyle; m, height, from dorsal margin of condyle to tip of hypapophysis.

near-complete parietal was from a smaller individual and has been enlarged proportionally in reconstructing the skull.

Anteriorly the parietal has a well-formed sagittal crest and is rather slender overall, having only a slight swelling centrally. Its overlapping articulation with the supraoccipital has the form of an inverted 'V'. The front part of the parietal is nearly flat on the dorsal surface, and the articulation with the frontals is irregular. The parietal overlaps the frontals for most of its width and is overlapped, possibly by the post-frontals, at the outer surfaces. An indication of the optic foramen is present on the lower anterior sides, enclosed within the parietal, frontal and (possibly) basi-parasphenoid. Above this a rounded, slightly downturned wing extends posteriorly past mid-length of the parietal. This feature has not been observed on any other specimen examined. A small projection pointing posteriorly contacts the prootic at the foramen for the nerve V_2. The ventral edge of this foramen appears to be formed by contact with the basisphenoid, though slight damage to the prootic may have removed an extension that completed the foramen.

Pterygoid: A thin, flat and quite broad fragment containing seven tooth sites appears to be part of the pterygoid. While its margins are damaged, so that its orientation is in doubt, the remains of an articular surface probably represents the articulation with the basipterygoid process. The presumed anterior part of the tooth row is curved, unlike all other specimens examined. The tooth sockets are smaller than those in the palatine and very close-set, which suggests the pterygoid may have contained numerous teeth. Such an arrangement would be consistent with the other tooth-bearing elements of *W. naracoortensis*.

Vertebrae: Comparisons with the eight thoracic vertebrae described by Smith (1976), and additional vertebrae since obtained from the Victoria Fossil Cave, confirm that the material collected does represent *Wonambi naracoortensis*.

The vertebrae have broad paradiapophyses, high neural spines that slope posteriorly, and possess variable numbers of small paracotylar foramina (none to three per vertebra). The vertebrae were initially sorted into body regions following Simpson (1933). The anterior thoracic vertebrae are identified by the presence of hypapophyses. Posterior thoracic vertebrae are similar in form, but lack hypapophyses. Anterior caudal vertebrae

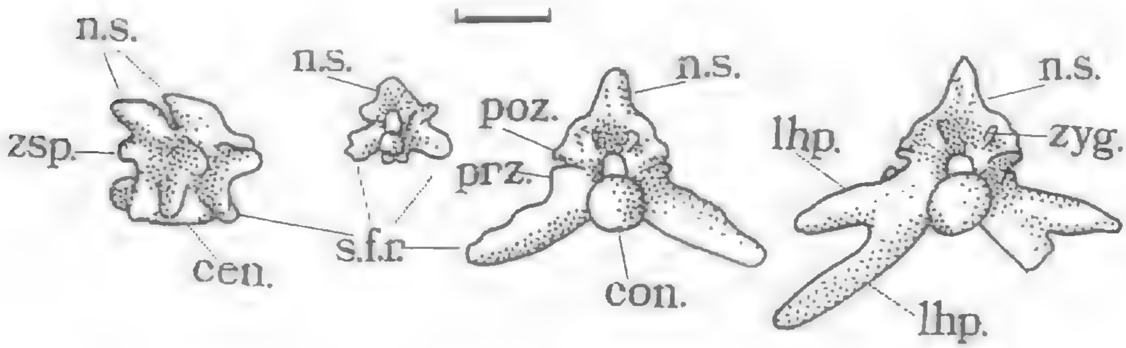

FIG. 11. *Wonambi naracoortensis*, variations in caudal vertebrae; scale bar 1 cm.

(Fig. 11) have bifid diapophyses (or fused ribs) which were termed lymphapophyses by Romer (1956) since they house the lymph hearts. These vertebrae are of limited number, never more than ten (Simpson, 1933). Finally there are the posterior caudal vertebrae (Fig. 11), with single fixed ribs. One of these is a fused pair, a feature seen in other snakes examined. The posterior caudal vertebrae are much more numerous than the anterior caudals, varying from 15 to 92 in species tabulated by Simpson (1933).

The newly-collected vertebrae were derived from two individual snakes — 89 from a large individual and 66 from a smaller one. Where possible, 14 measurements were taken of each vertebra, using dial calipers (Fig. 10). Many vertebrae were damaged by the mechanics of excavation, as well as from the apparent activities of termites. Nevertheless, damaged vertebrae could often be measured from the sagittal plane, thus giving a half-value which could then be doubled to provide measurements such as maximum width across paradiapophyses. These numerous measurements allowed even small fragments to be plotted in sequence; thus it proved possible to estimate the maximum number of vertebrae and, hence, *Wonambi's* body length.

The 14 measurements were plotted on slips of paper in distinctive colour codes; by aligning these slips adjacent to each other it was possible to establish the correct sequence of vertebrae in the snake. All the resulting data are lodged with the South Australian Museum.

On examining the resulting sequence of anterior thoracic vertebrae, it was noticed that some had hypapophyses and others did not. All those vertebrae without hypapophyses transpired to be from a location one to two metres away from the major accumulation. The colour-coded slips representing vertebrae from that second locality were removed. Both sets of slips when placed in sequence, presented a neat progression of dimensions, revealing that the material comprised the remains of two snakes. The conspecificity of the two individuals was illustrated simply by graphing the dimensions of the smaller animal's vertebrae on to an elastic strip and stretching it to the same size as the larger specimen. All dimensions matched when the elastic was stretched uniformly.

The slips were also spaced to conform with a graph which approximated the contours of the

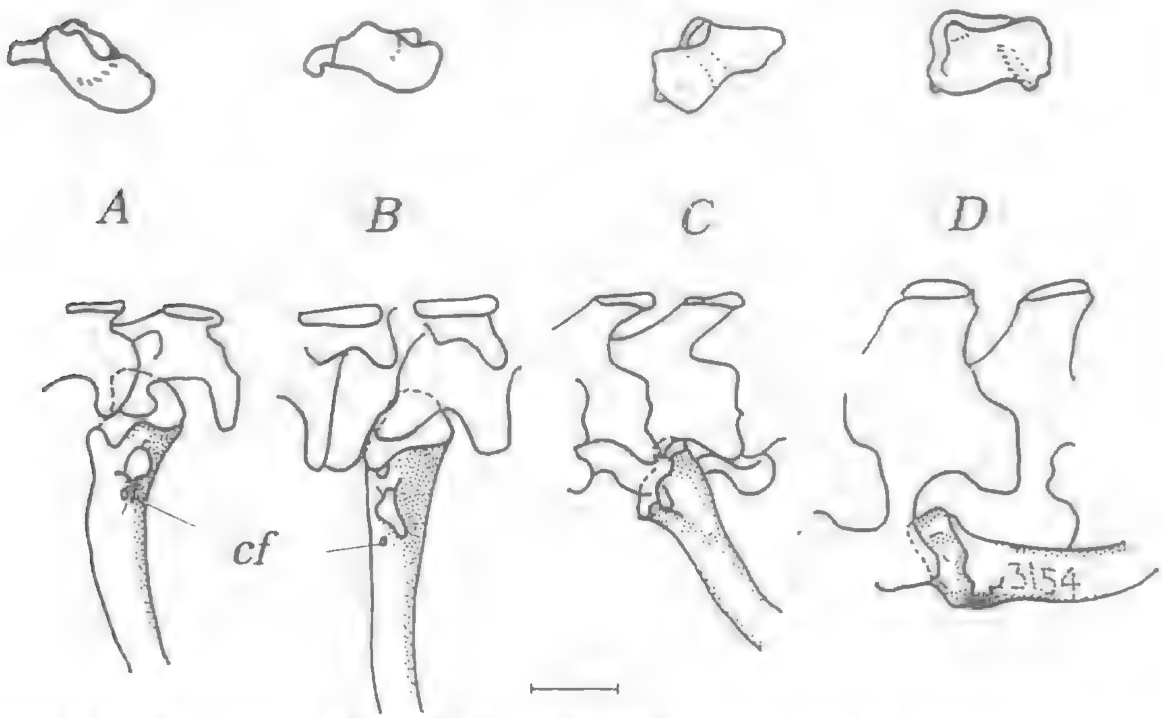

FIG. 12. Rib heads, in proximal view (above), and their articulations in postero-dorsal view (below); scale bar 1 cm. A, *Python molurus;* B, *P. reticulatus;* C, *Wonambi naracoortensis;* D, *Madtsoia bai.*

modern boid — *Morelia spilota variegata* (SAM R26955). On this extant specimen the width of every fifth vertebra was measured. The data were graphed to compare with the graphs of *Wonambi*. This exercise revealed remarkable similarity in general form, although some significant gaps were evident in the *Wonambi* sequence. The slips of specimens showing termite damage were noted. This form of damage was limited to the larger sequence of vertebrae and coincided mainly with the margins of missing sections.

From these comparisons it was concluded that *W. naracoortensis* probably had between 350 and 400 vertebrae. This certainly lies within boid limits tabled by Rochebrune (cited by Simpson, 1933).

The average length for a vertebra is 14.2 mm. Adding a nominal 0.5 mm to each vertebra for cartilage, 140 mm for cranium and cervicals and an estimated 100 mm for extreme posterior caudals, it was calculated that *Wonambi* was between 5.39 metres and 6.13 metres in total length.

Ribs: Most of the ribs were damaged in the same way as the vertebrae. An attempt to arrange the ribs in sequence, using measurements from the head and shaft, proved fruitless because there was too little variation from one rib to the next.

The free ribs are holocephalous, although the rib head is partly divided, (a slightly concave portion, a ridge then the adjacent cupped dorsal area). The articulation is with the large, prominent paradiapophysis (Smith, 1976) anteriorly placed at each side of the centrum. The shaft is steadily curved, the distal extremity ending in a cylindrical shaft with a cup-shaped termination for attachment of the cartilaginous connection of the ventral scutes. The proximal end of the shaft is more ovoid in cross-section. The anterior ribs exhibit an expanded costal process for the attachment of muscles (Fig. 12). *Python reticulatus* and *P. molurus* present a well-developed costal process, extending from the dorsal cupped area. In *Wonambi* the costal process is not as conspicuous because the rib head sweeps gently to its tip. The process would, in fact, be much more robust than in the pythons examined, but less so than *Madtsoia bai*. Both *P. reticulatus* and *P. molurus* exhibit a large foramen at the base of the costal process whereas *P. molurus* exhibits several smaller foramina posterior to it. None of these is evident in *Wonambi*.

In *Wonambi* the lymphapophyses of the caudal vertebrae are very solid, the upper ramus extending almost horizontally and the lower slanting at approximately 30° below the horizontal. They contrast with the fine, flattened and down-turned lymphapophyses of *P. molurus*. The bifid ribs of *M. spilota variegata* are much more like those of *Wonambi* but are unproportionally smaller in size.

Discussion

Wonambi was a large, heavy-bodied snake, though its skull, teeth and anterior vertebrae are relatively small and delicate. A 6 metre individual with a diameter of about 250 mm and a girth of about 800 mm could have weighed 250 kg. The skull is dorso-ventrally compressed and the orbits are set well forward. The lower jaw is very lightly constructed, the nearest comparison being with *Acrochordus*, an aquatic species. On the lower thoracic vertebrae the angled zygapophyses of *Wonambi* resemble those of *Madtsoia*. The longest extant snake, *Python reticulatus*, has almost horizontal zygapophyses inclined at only 3°; those of *Python molurus* (Indian Rock Python) are inclined at about 10°, compared to *Wonambi* and *Madtsoia* inclined at about 20-22°. The inclination of zygapophyses is discussed by Romer (1956), and in general terms the greater the inclination the greater is the constraint on lateral flexion. In snakes this restricts one major means of locomotion, lateral undulation, but it increases the ability for vertical flexion. The tall neural spines provide anchorage for muscles having greater mechanical advantage than those in snakes having low neural spines. Similarly the prominent paradiapophyses provided a good anchorage for the ribs and their associated muscles; narrower attachment to the vertebrae would lessen the mechanical advantage of the associated muscles. The advantage achieved with broad paradiapophyses may have outweighed the limitation resulting from steeply-inclined zygapophyses.

Wonambi was too bulky to have been an arboreal snake, although its climbing ability may have been reasonably good — a necessary requirement if it occupied caves. It is possible that *Wonambi* had feeding habits similar to those of *Acrochordus*, fish being available in the lagoons of its habitat. Large prey capable of struggling vigorously are unlikely to have been taken, since *Wonambi's* jaws were rather weak. The reduction in lateral flexion would limit its ability to constrict animals, thus implying that it subsisted mainly on small prey.

Wonambi's remains were found in the lowest portion of the deposit, an area of horizontally-banded sediments, gritty sands alternating with red silts. The bedding inclined steeply along the side furthest from the entrance through which it must have accumulated. This bedding pattern was consistent with the formation of a miniature delta, with sediment washing into a cave-pond and forming an inclined bank in deeper water. Evidently the cave contained water that would have been attractive to snakes. If the water was permanent, the age of the deposit is likely to coincide with a higher water-table and a closer coastline, possibly over 100,000 years ago (Schwebel, 1983). This is consistent with recent dating of the Victoria Fossil Cave (Veeh, unpublished) and also with similarities in the faunas of the two deposits. Snakes, particularly large ones, are very dependent on water, so it is likely that increasing aridity across the continent placed considerable pressure on the population of large snakes, possibly leading to their extinction. How such large snakes survived so long in temperate conditions remains a mystery.

In her original description Smith (1976) compared the vertebrae of *Wonambi* to those of the genus *Madtsoia*. Both share the back-sloping neural spine, broad paradiapophyses, paracotylar foramina and the lack of accessory processes. *Madtsoia* (Hoffstetter, 1959) also shares the inswept lingual shelf on the underside of the dentary and Meckel's groove being open to the tip.

Wonambi's primitive nature is also evident when it is compared to other species known to possess plesiomorphic character states. Paracotylar foramina (Underwood, 1976) are shared with the extant Tropidophinae, *Bolyeria*, *Casarea*, *Candoia*, *Boa*, *Acrochordus*, and the fossil genera *Madtsoia* and *Gigantophis*. A well-developed choanal process (Underwood, 1976) is shared with some members of the same group. The small contact between the exoccipitals is shared with the fossil *Dinilysia patagonica* (Rieppel, 1979). The apparent lack of a crista circumfenestralis is shared with *Dinilysia* and, less certainly, with the Acrochordidae (McDowell, 1975). The *Acrochordus* specimen I examined (*Acrochordus arafurae*, SAM R26966) certainly appears to have a crista of some form.

Wonambi's ribs, hitherto undescribed, appear intermediate between those of *Madtsoia* and those of the pythons. They are generally heavier in structure than the ribs of pythons and show no evidence of the costal foramina seen in some extant species (e.g. *Python molurus* and *P. reticulatus)*. Underwood's (1976) phyletic analysis indicates that the Pythoninae examined (*Python*, *Liasis* and *Morelia)* are similarly separated from the Boini. Pythons are a more homogeneous group in almost all features examined. Since *Wonambi* does not seem to be closely related to pythons I have concentrated on comparisons with those of the Boini possessing paracotylar foramina. Underwood's first group includes *Casarea*, *Bolyeria* and the Tropidophinae. These are differentiated from other boids by the hyoid cornua being parallel, the absence of pelvic spurs from females, the left lung being reduced, and a terminal entry of the trachea into the lungs. These features cannot be determined in *Wonambi's* fossil remains, but *Wonambi* shares the primitive choanal process and cerebral foramina with some members of the Tropidophinae. The second group includes *Candoia (Enygrus)*, *Boa* and the fossil snakes *Madtsoia* and *Gigantophis*.

Underwood's (1976) phenetic analysis also clusters the pythons, species possessing paracotylar foramina are grouped, *Bolyeria*, *Casarea*, and the Tropidophinae. The one exception is *Boa*, and that does not appear to have close affinities with *Wonambi*.

Rage (1982) illustrates the phylogenetic relationship of snakes, clustering *Dinilysia*, *Xenopeltis*, *Boa*, *Paleophis*, *Nigerophoides* and *Acrochordus*. He suggests that the elapids, colubrids and vipers evolved from ancestral stock among the Acrochordidae, subsequently dispersing in the Eocene and Oligocene. He illustrates the possible migration routes from Laurasia to Australia, Africa and South America in the Miocene. Rage also considered the earlier radiation of snakes from Gondwanaland during the Cretaceous, which may have entailed migrations by the descendants of *Madtsoia*. *Wonambi*, only recently extinct, represents a diverse group of Gondwanan survivors, several of which (*Candoia*, *Casarea*, *Bolyeria* and *Tropidophis*) have remained isolated from suspected migration routes (Fig. 13).

The absence of extant Australasian species sharing plesiomorphic character states with *Wonambi*, excepting perhaps *Candoia* and *Acrochordus*, has been established. Immunodiffusion studies of plasma transferins in extant Australasian elapids (Schwaner *et al.*, 1985), reveal an affinity to the Asian snakes. Microcomplement fixation data suggest a date of about 20 My for the separation between Australasian and Asian/African elapids. Australia must have made sufficient contact with Asia for a successful migration of snakes to take place at that time.

A Miocene migration to Australia raises the question of a land bridge extending to Asia some 20 My ago. If this were relatively unbroken one would expect more successful migrations, both to

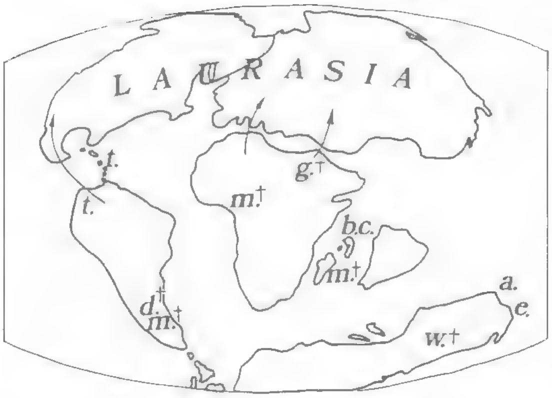

FIG. 13. Distribution of Gondwanan boids related to continental geography of the Late Cretaceous (after Rage, 1982). Fossil forms: d, *Dinilysia;* g, *Gigantophis;* m, *Madtsoia;* w, *Wonambi.* The following extant Gondwanan relicts, showing some affinities with *Wonambi*, remain isolated from suspected post-Cretaceous migration routes: a, *Acrochordus;* b, *Bolyeria;* c, *Casarea;* e, *Candoia (Enygrus).* Arrows indicate possible migration routes in the Mesozoic.

and from Asia. The evidence of faunal exchanges in the Miocene is meagre, but a one-way transfer (Australian marsupials did not establish themselves in Asia), is possibly the result of the progression of a land bridge, the Asian end disconnecting before the insular population reached Australia. This would have selectively limited the species en route from Asia, and prevented any return. If elapids arrived in Australia 20 My ago it is likely that other creatures, perhaps including the pythons, would have arrived at the same time.

Wonambi's closest affinity is undoubtedly with *Madtsoia*. Being a Gondwananan species of wide distribution it is likely that the genus *Madtsoia* radiated beyond Gondwanaland as migration routes opened up into the northern hemisphere. *Wonambi* lingered on in the isolated Australian land mass as *Madtsoia's* descendants evolved elsewhere to produce, among others, the pythons. Some of the pythons arrived in Australia during the Miocene, representing the ancestral stock of the extant species. *Wonambi* survived well into the Pleistocene, to become extinct along with much of the Australian megafauna. It is truly a ghost from the past that we have just missed seeing alive.

ACKNOWLEDGEMENTS

I am greatly indebted to the group of people who encouraged and assisted in the excavation. In particular I thank Julie Barrie, Karen, Cathlin, Paula and Wendy, F.C. and E. Holmes, A. and T. Nobes, and S. Mickan. L. and G. Henschke gave us access, often adjusting the quarry workings to aid our excavation. Dr R.T. Wells encouraged systematics and recording; Dr T.D. Schwaner gave encouragement and assisted with comparative material and literature; N.S. Pledge provided access to the *Madtsoia* specimen; H.E. Wilkinson gave critique and assistance at the excavation; M.J. Smith provided literature and encouragement to proceed with this paper; Dr O. Rieppel assisted with defining skull nomenclature. I also thank the organisers of the De Vis Symposium for the opportunity to share my experiences among others with a common interest. My wife Julie deserves the utmost praise for her unfailing support and encouragement.

LITERATURE CITED

ESTES, R., FRAZETTA, T.H. AND WILLIAMS, E.E. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward. 1. Cranial morphology. *Bulletin of the Museum of Comparative Zoology, Harvard,* **119**: 453–72.

FRAZETTA, T.H. 1966. Studies on the morphology and function of the skull in the Boidae (Serpentes). Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus. Journal of Morphology* **118**: 217–96.

HOFFSTETTER, R. 1959. Un dentaire de *Madtsoia* (Serpent géant du Paléocène de Patagonie). *Bulletin du Museum d'Histoire Naturelle, Paris* (2e ser.), **31:** 379–86.

AND GAYRARD, Y. 1964. Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). *Bulletin du Museum d'Histoire Naturelle, Paris* (2) **36:** 677–96.

MCDOWELL, S.B. 1975. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Anilioidea and Pythoninae. *Journal of Herpetology* **9**: 1–79.

PLEDGE, N.S. 1981. The Giant Rat-kangaroo *Propleopus oscillans* (De Vis), (Potoroidae: Marsupialia) in South Australia. *Transactions of the Royal Society of South Australia* **105**(1): 41–7.

RAGE, J.C. 1982. L'Histoire des serpents. *Pour la Science* **54**: 15–17.

RIEPPEL, O. 1979. A cladistic classification of primitive snakes based on skull structure. *Zeitschrift zool. Syst. Evol Forsch.* **17**(2): 140–50.

ROMER, A.S. 1956. 'Osteology of the reptiles'. (Chicago University Press: Chicago).

SCHWANER, T.D., BAVERSTOCK, P.R., DESSAUER, H.C.

AND MENGDEN, G.A. 1985. Immunological evidence of the phylogenetic relationships of Australian elapid snakes. p. 177-83 *In* 'Biology of Australasian frogs and reptiles'. (Royal Zoological Society of NSW: Sydney).

SCHWEBEL, D.A. 1983. Quaternary dune system. p. 15-24 *In* Tyler, M.J., Twidale, C.R., Ling, J.K. and Holmes, J.W. (Eds), 'Natural History of the South-East'. (Royal Society of South Australia: Adelaide).

SIMPSON, G.G. 1933. A new fossil snake from the *Notostylops* beds of Patagonia. *Bulletin of the American Museum of Natural History* **67**: 1–22.

SMITH, M.J. 1976. Small fossil vertebrates from Victoria Fossil Cave, Naracoorte, South Australia. *Transactions of the Royal Society of South Australia* **100**(1): 39–51.

UNDERWOOD, G. 1976. A systematic analysis of boid snakes. p. 151-75 *In* Bellairs, A.d'A. and Cox, C.B. (Eds), 'Morphology and biology of reptiles'. (Academic Press: London).

WELLS, R.T., MORIARTY, K. AND WILLIAMS, D.L.G. 1984. The fossil vertebrate deposits of Victoria Fossil Cave, Naracoorte: an introduction to the geology and fauna. *Australian Zoologist* **21**(4): 305–33.

FUNCTIONS OF THE TAIL IN BIPEDAL LOCOMOTION OF LIZARDS, DINOSAURS AND PTEROSAURS

TIM HAMLEY

Hamley, T. 1990 3 31: Functions of the tail in bipedal locomotion of lizards, dinosaurs and pterosaurs. *Mem. Qd Mus.* **28**(1): 153–158. Brisbane. ISSN 0079-8835.

This paper investigates the reported decrease in speed that follows tail-loss in those lizards with actively functional tails. The balance function of the tail may be less important to the bipedal locomotion of lizards than was previously suspected. Instead it is possible that the tail has an important role in regulating stride frequency. These findings may shed some light on peculiarities of tail structure in dromaeosaurid dinosaurs and rhamphorhynchoid pterosaurs.
☐ *Reptilia, Lacertilia, Theropoda, Pterosauria, bipedal locomotion.*

Tim Hamley, 609 Fairfield Road, Yeronga, Qld 4104, Australia; 1 November, 1988.

Most investigations into the role of the tail in lizard locomotion have been concerned with the effects of tail removal on speed (Pond, 1978; Ballinger *et al.*, 1979; Punzo, 1982; Daniels, 1983; Table 1). Notable exceptions include Snyder's (1949) analysis of the role of the tail in bipedal locomotion, and Ballinger's (1973) investigation of its use as an aid to balance. Except for the gecko (*Phyllodactylus marmoratus*) used by Daniels (1983), all the lizards used in those investigations were facultative bipeds and possessed what Vitt *et al.* (1977) have termed 'actively functional' tails.

Author	Year	Tail Type	Effects of Tail Removal
Snyder	1949	AF	Impaired balance (unable to run bipedally)
Ballinger	1973	AF	Impaired balance (decreased perching ability)
Pond	1978	AF	Decrease in speed
Ballinger *et al.*	1979	AF	36% decrease in speed
Punzo	1982	AF	32% decrease in speed
Punzo	1982	AF	42% decrease in speed
Daniels	1983	PF	100% increase in speed
Daniels	1985	PF	18% increase in speed

TABLE 1: Summary of previous investigations into the role of the tail of lizard locomotion. AF = Actively functional tails; PF = Passively functional tails.

Vitt *et al.* (1977) recognised two broad categories of tail function in lizards: passively functional tails, where function is primarily predator distraction via autotomy (e.g. *Phyllodactylus*), and actively functional tails that contribute to various activities such as fighting, climbing, terrestrial locomotion and swimming. Earlier studies (cited above) revealed that lizards with actively functional tails suffered a decrease in their maximum recorded speeds (by as much as 42%) following removal of the tail. By contrast, the gecko studied by Daniels (1983) almost doubled its average running speed following tail autotomy. Snyder (1949) did not report running speeds for his animals. However, he did show that abbreviation of an animal's tail impaired its bipedal ability: removal of the posterior third of the tail resulted in the lizard being unable to complete more than three strides bipedally, and when the posterior two-thirds of the tail was removed the animal was unable to run bipedally at all. The general conclusion that has been drawn from these experiments is that the actively functional tail of a running lizard acts as an organ of balance, as well as a counterbalance mechanism that moves the animal's centre of gravity closer to the pelvis and closer to the force exerted by the hindlimb (Snyder, 1962; Ballinger *et al.*, 1979; Punzo, 1982). Because of the tail's seeming importance in locomotion, its retention should be favoured in animals with actively functional tails (Vitt, 1983).

As part of a larger study of lizard locomotion I analysed the effects of partial tail loss on individuals of *Physignathus lesueurii*, the Eastern Water Dragon. These lizards are facultative bipeds attaining a snout-vent length up to 275mm. They have long tails which have a relatively low frequency of damage (see Vitt *et al.*, 1977 for an analysis of tail break frequencies), and where damage does occur it is usually restricted to the distal third of the tail.

METHODS

Locomotion in the water dragons was investigated by timing the animals as they ran along a specially constructed runway (Fig. 1). Each lizard performed a minimum of six trials on the runway, and during each trial two metres of smoked paper was placed on the floor of the runway to record the animal's footfalls. The smoked paper was later sprayed with acrylic lacquer to provide a permanent record, which was analysed with the aid of a Houston "Hi-Pad" digitizer.

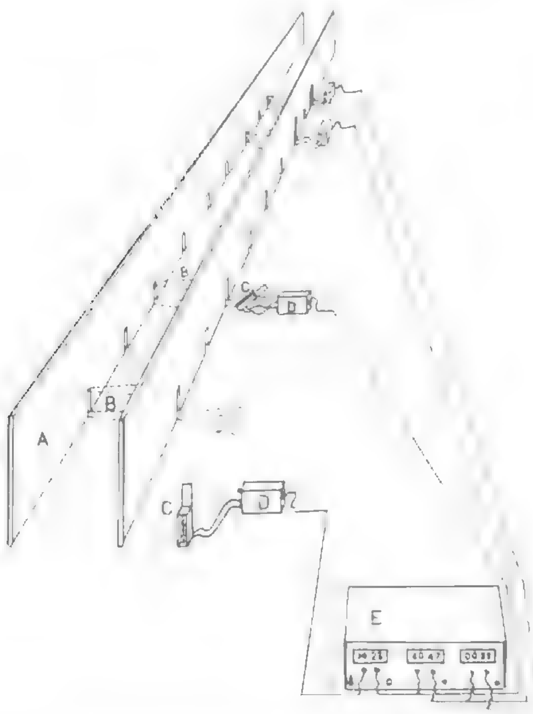

FIG. 1. Runway and timer mechanism. A = runway; B = light curtain; C = photosensitive diode array; D = electronic timer trigger; E = digital timer.

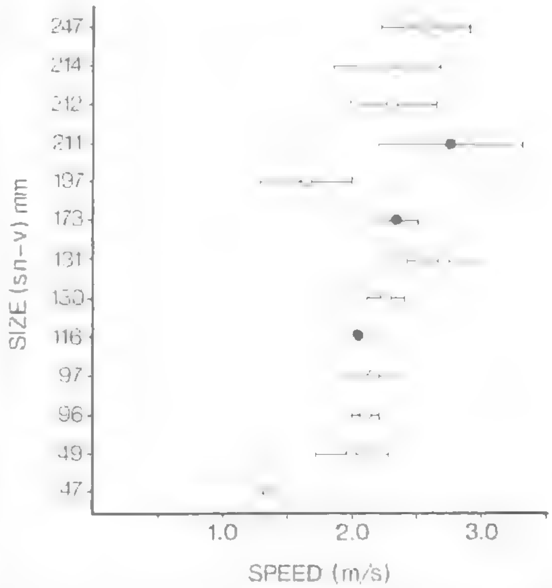

FIG. 2. Summary of locomotion data for *P. lesueurii*. The vertical axis gives the rank order of size (sn-v snout-vent length, in mm) and the horizontal axis gives the range of maximum speeds (m/s) attained by each lizard. (Closed circles denote animals with abbreviated tails).

RESULTS

The trackway results obtained for the water dragons are somewhat surprising in view of the previous studies; they provide evidence of bipedal ability in animals with as much as 40% of the tail missing. A consistent tripedal trackway was obtained from an animal that was estimated to have lost about 80% of its tail. Moreover, there was no evidence that the water dragons with damaged tails were any slower than animals with complete tails. In fact, the highest average speed recorded on the runway (3.3m/s) was achieved by a water dragon that lacked approximately 40% of its tail (Fig. 2).

DISCUSSION

Although the results shown in Fig. 2 seem to be inconsistent with those of earlier studies, the discrepancy may be explained quite simply. First, it is probable that the water dragons used in this study never achieved their maximum speeds while on the runway: most of the animals were still accelerating at the end of the trial section. Consequently it is possible that some animals might have suffered a reduction in maximum speed (as a consequence of tail loss) without it becoming

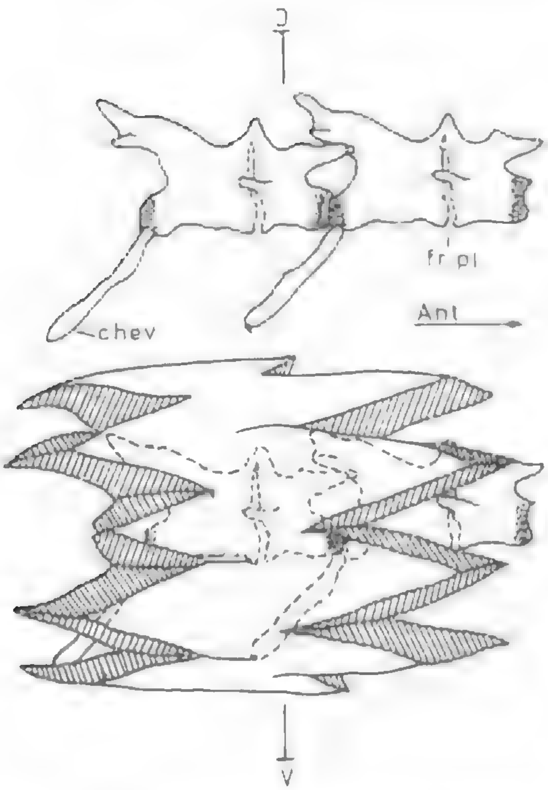

FIG. 3. Fracture planes in caudal vertebrae of autotomizing lizards and the segmental nature of caudal musculature; chev. = chevron; D = Dorsal; fr. pl. = fracture plane; V = Ventral (after Sheppard and Bellairs, 1972).

evident. Second, and perhaps more importantly, it seems that in attributing the recorded decrease in maximum speed in their animals to the fact that the centre of gravity was no longer positioned so close to the force exerted by the hindlimbs, both Punzo (1982) and Ballinger *et al.*, (1979) may have overlooked a simpler explanation. When carrying out their experiments these investigators apparently severed the animals' tails as near as possible to the vent (although this is not explicitly stated by Ballinger and co-workers in their paper). There is little doubt that tail removal in this way would affect the balance of the lizard. Here it should be remembered that the major femoral retractor muscles, the caudi- femoralis group, originate from the proximal 10 or 11 caudal vertebrae (Romer, 1922; Snyder, 1954). It seems unlikely that the tail could be removed just distal to the vent without severing some parts of this musculature, thus impairing the efficiency of femoral retraction and impairing locomotor performance. Conversely, lizards that indulge in tail autotomy are unlikely to do so at the expense of the femoral retractor muscles. This is clear from the increase in speed of the gecko after tail autotomy and the consequent loss of a considerable fraction of body weight (Daniels, 1983). In fact, autotomizing lizards generally possess fracture planes in the post-pygial vertebrae (Sheppard & Bellairs, 1972; Holder, 1960; Pratt, 1946) and the muscles in this region show a corresponding pattern of segmentation (Fig. 3). In this case the femoral retractor muscles must attach to the pygial vertebrae which are usually the first four or five of the caudal series.

It should also be noted that the investigators mentioned above used their animals within 48 hours of tail removal, a procedure that was carried out in the laboratory. Snyder (1949), for example, allowed only 15-20 minutes ("... to obviate the shock of removal") between cutting off the tails of lizards and using the animals in trials (1949, p. 136). It seems unlikely that lizards with actively functional tails would be able to run normally so soon after traumatic tail loss. By contrast, the water dragons described here had lost their tails before capture and in each case the tail was well healed and showed signs of regrowth. This difference may explain why water dragons were able to run bipedally with as much as 40% of the tail missing whereas the lizards used by Snyder were unable to do so when a third of the tail was removed.

Despite the fact that neither bipedal ability nor speed appeared to be seriously affected by less than severe tail damage, one significant effect of tail loss in water dragons was evident from the trackway records: at any given speed animals with abbreviated tails were found to take shorter strides (and axiomatically to have increased stride frequencies) than animals of the same size with complete tails (Fig. 4). To understand the significance of this increase in stride frequency it is necessary to look more closely at the relationship between the hindlimbs and the tail in sprawling tetrapods.

During lizard locomotion lateral undulations of the vertebral column generate a standing wave in the trunk region of the body. The nodes of the wave are located at the pectoral and pelvic girdles (Brinkman, 1981; Hamley, 1986). Posterior to the pelvic girdle the standing wave is transformed into a travelling wave that moves caudally along the tail. The base of the tail is flexed towards the protracted hindlimb during each cycle of hindlimb movement (Fig. 5). Then, as the hindlimb is retracted, the

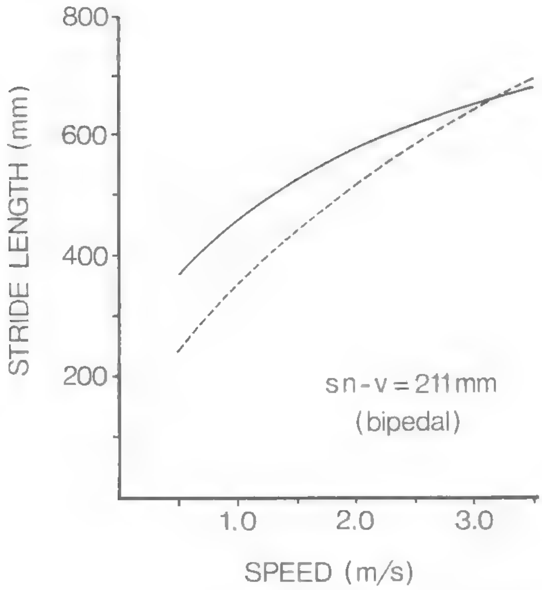

FIG. 4. Graph of stride length against speed for a lizard with partial tail loss (broken line) compared with a graph for a hypothetical animal of the same size with a complete tail (solid line).

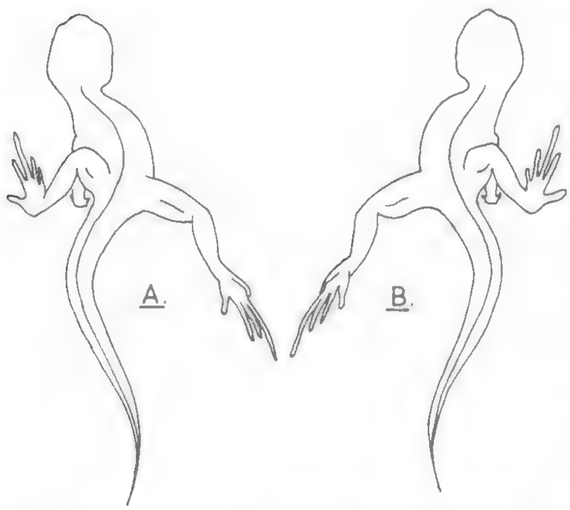

FIG. 5. Left (A) and right (B) hindlimb retraction showing extremes of tail flexion.

oscillation of the base of the tail to its opposite extreme supports what appears to be an isometric contraction of the caudi-femoralis musculature, presumably aiding in the most efficient use of the hindlimb retractor muscles. This mechanical coupling of hindlimb and tail means that the stride frequency and the frequency of tail oscillation must be equal: changes in stride frequency require corresponding changes in the frequency of tail oscillation and vice versa. If the lizard's tail is considered to be a semi-rigid bar, attached at its proximal end, then the laws of simple harmonic motion will mean that:

1. When displaced laterally the tail will have a natural frequency of oscillation
2. This frequency will be dependent on both the rigidity of the tail (controlled by the segmented caudal musculature) and the length (mass) of the tail.

Hence, a lizard wishing to increase its stride frequency (and therefore its speed) during locomotion need only "stiffen up" its caudal musculature to achieve that effect. In addition, for a given degree of tail rigidity, a lizard with a damaged tail will have a higher frequency of tail oscillation (and, therefore, of stride frequency) than will a similar-sized lizard, with a complete tail, running at the same speed.

The relationship between tail length and stride frequency explains not only the observed increase in stride frequency for lizards with damaged tails, but also the commonly noted correlation between hindlimb length and tail length in cursorial lizards. Thus it can be seen that the tail of cursorial lizards contributes more to locomotion than simply acting as a counterbalance: by adjusting the frequency of tail oscillation (via the tension in the caudal musculature) cursorial lizards can use the simple harmonic motion of the tail as an aid to femoral retraction over a range of hindlimb stride frequencies. However, it should be noted here that stride frequency in lizards has a strong negative allometry when scaled against body mass (Hamley, 1986), which probably betrays an important size constraint in the functioning of such a system. Because of this size constraint, larger animals using caudi-femoralis musculature to retract the hindlimb need to be able to generate a high degree of tail rigidity to enable them to maintain a high stride frequency at reasonable energetic cost.

These findings have some interesting implications for the locomotion of extinct bipedal reptiles. Perhaps the most extreme ability to stiffen the tail was exemplified by the dromaeosaurid theropods *Deinonychus antirrhopus* (Ostrom, 1969 a,b) and *Velociraptor mongoliensis* (Barsbold, 1983). *Deinonychus* was a small (2m), agile predaceous dinosaur with a tail that comprised 36-40 segments and made up over half the length of the body. Ostrom (1969b) described the caudal skeleton as unremarkable in all respects except two: the prezygapophyses and chevrons of

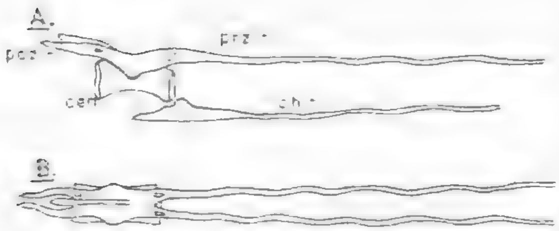

FIG. 6. Caudal vertebra of theropod dinosaur *Deinonychus antirrhopus* (after Ostrom, 1969b); prz. r. = prezygapophyseal rods; poz. r. = postzygapophyseal rods; cen. = centrum; ch. r. = chevron rods (A = right lateral view; B = dorsal view).

all but the proximal eight or nine segments were modified into extremely long bony rods that overlapped as many as ten preceding segments (Fig. 6). These bony extensions of the chevrons and prezygapophyses were nested together in such a way as to resemble the bundles of tendons that act as insertions for various caudal muscles in extant tetrapods. For example, the M. extensor caudae lateralis in lizards (such as *Iguana* and *Basiliscus*) inserts via bundles of tendons onto the extremities of the prezygapophyses, behind the fifth segment. As well, the long tendons of the M. flexor caudae in the above lizards and the M. sacrococcygeus ventralis lateralis in cats attach to the haemal arches in a way that is similar to the chevron rods of *Deinonychus*. These similarities, along with the periosteal-like histology of the rods, led Ostrom (1969b) to conclude that the caudal rods of *Deinonychus* were most probably ossified tendons.

Such bony rods would have served to stiffen the tail when extensor muscles attached to their anterior ends were contracted. However, the tail was not permanently inflexible, as is indicated by the presence of well-formed articular facets on the caudal vertebrae. What then was the function of a tail that could be stiffened to the degree indicated by the bony rods? In his descriptions of *Deinonychus*, Ostrom (1969a,b) suggested that the function of the caudal rods was to control the animal's equilibrium — that the stiffened tail of *Deinonychus* acted as a dynamic stabilizer, much like the balance pole of a tight-rope walker. Doubtless the tail of *Deinonychus* acted as a counterbalance, but it is also likely that the potential for extreme stiffening of the tail could have served to increase the natural frequency of tail oscillation, thereby allowing a greatly increased stride frequency. A predator such as *Deinonychus* might have required a reasonable degree of speed and, perhaps more importantly, an extreme degree of agility — allowing it to use its clawed hindlimbs, either independently or in concert, in dealing with its prey. It is conceivable that *Deinonychus* mauled or eviscerated its prey in much the way that a cat will — kicking and slashing repeatedly at a particularly tenacious opponent. It seems possible that the synchronisation of movements between hindlimbs and tail could have hampered this ability and the extreme stiffness of the tail in *Deinonychus* might represent an evolutionary attempt to break that relationship. In fact, the constraints imposed by this relationship may well explain the change in hindlimb retractor musculature to the birdlike pattern seen in the more advanced theropod dinosaurs (Gatesy, 1987).

In addition to *Deinonychus* and *Velociraptor*, several genera of rhamphorhynchoid pterosaurs possessed bony caudal rods (Ostrom, 1969c). Ostrom's explanation of these rods (1969c) was that they may have allowed the kite-like vane at the end of the tail to act as an inertial stabilizer, thus implying a high degree of aerial manoeuverability. Doubtless Ostrom is at least partly correct, but the presence of bony caudal rods may also have some bearing on the terrestrial mobility of rhamphorhynchoids. The cursorial ability of pterosaurs has been the subject of some controversy to date, with the main area of debate being the architecture of the pelvis and whether this indicated an 'erect' or 'sprawling' posture. Supporters of an erect posture suggest that pterosaurs were capable of fast and efficient movement, perhaps like dinosaurs (Padian, 1983). However, recent discoveries (Wellnhofer & Vahldiek, 1986; Molnar, 1987) indicate that a sprawling posture was more likely, and this has led Unwin (1987, p.13) to conclude that "most, if not all, pterosaurs could manage only a clumsy waddle . . .". The identification of a sprawling posture with a clumsy inefficient style of locomotion is a common assumption, but not necessarily correct: the lizards investigated here are 'sprawlers' yet have a high degree of cursorial and scansorial ability. If the rhamphorhynchoids were agile bipeds, perhaps obliged to achieve a fast run before taking off, then their bony caudal rods may well have served to increase stride frequency through the relationship between hindlimbs and tail. The size constraints inherent in this relationship may also explain why the bigger pterosaurs dispensed with their tails altogether.

ACKNOWLEDGEMENTS

I am indebted to Dr Tony Thulborn who supervised the research mentioned here and helped with discussions on various aspects of this paper. Dr Ralph Molnar also offered useful suggestions and helpful discussion.

LITERATURE CITED

BALLINGER, R.E. 1973. Experimental evidence of the tail as a balancing organ in the lizard, *Anolis carolinensis*. *Herpetologica*, **29**: 65–6.

NIETFELDT, J.W. AND KRUPA, J.J. 1979. An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica*, **35**: 114–6.

BARSBOLD, R. 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Transactions of the Joint Soviet-Mongolian Palaeontological Expeditions*, **19**: 1–117. [Russian]

BRINKMAN, D. 1981. The hindlimb step cycle of *Iguana* and primitive reptiles. *Journal of Zoology, London*, **181**: 91–103.

DANIELS, C.B. 1983. Running: an escape strategy enhanced by autotomy. *Herpetologica*, **39**: 162-5.

GATESY, S.M. 1987. Dinosaur limb kinematics and theropod evolution. *Journal of Vertebrate Paleontology*, 7(3): 13a.

HAMLEY, T.L. 1986. An analysis of the locomotion of two species of agamid lizard. Unpublished M.Sc. thesis, University of Queensland, Brisbane.

HOLDER, L.A. 1960. The comparative morphology of the axial skeleton in the Australian Gekkonidae. *Zoological Journal of the Linnean Society*, **44**: 300–35.

MOLNAR, R. 1987. A pterosaur pelvis from western Queensland, Australia. *Alcheringa*, **11**: 87–94.

OSTROM, J.H. 1969a. Terrible claw. *Discovery, Magazine of the Peabody Museum of Natural History*, 5(1): 1-9.

1969b. Osteology of *Deinonychus antirrhopus*, an unusual Theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History*, **30**: 1–165.

1969c. Reptilia fossils. pp. 294-8. *In*, 'McGraw-Hill Yearbook Science & Technology.' (McGRaw-Hill: New York).

PADIAN, L. 1983. A functional analysis of flying and walking in pterosaurs. *Paleobiology*, 9(3): 218–39.

POND, C.M. 1978. The effect of tail loss on rapid running in *Dipsosaurus dorsalis*. *American Zoologist*, **18**: 612.

PRATT, C.W.M. 1946. The plane of fracture of the caudal vertebrae of certain Lacertilians. *Journal of Anatomy*, **80**: 184–8.

PUNZO, F. 1982. Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *Journal of Herpetology*, **16**: 329–31.

ROMER, A.S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History*, **46**: 517–606.

SHEPPARD, L. AND BELLAIRS, A.D'a. 1972. The mechanism of autotomy in *Lacerta*. *British Journal of Herpetology*, **4**: 276–86.

SNYDER, R.C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. *Copeia*, **2**: 129–37.

1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *American Journal of Anatomy*, **95**: 1–45.

1962. Adaptations for bipedal locomotion in lizards. *American Zoologist*, **2**: 191–203.

UNWIN, D.M. 1987. Pterosaur locomotion. Joggers or waddlers? *Nature, London*, **327**: 13–14.

VITT, L.J. 1983. Tail loss in lizards: the significance of foraging and predator escape modes. *Herpetologica*, **39**: 151–62.

CONGDON, J.D. AND DICKSON, N.A. 1977. Adaptive strategies and energetics of tail autotomy in lizards. *Ecology*, **58**: 326–37.

WELLNHOFER, P. AND VAHLDIEK, B.W. 1986. Ein Flugsaurier-Rest aus dem Posidonienschiefer (Unter-Toarcium) von Schandelah bei Braunschweig. *Paläontologisches Zeitschrift*, **60**(3/4): 329–40.

A PLEISTOCENE LONGIROSTRINE CROCODILIAN FROM RIVERSLEIGH: FIRST FOSSIL OCCURRENCE OF CROCODYLUS JOHNSTONI KREFFT

P.M.A. WILLIS AND M. ARCHER

Willis, P.M.A. and Archer, M. 1990 3 31: A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Mem. Qd Mus.* 28(1): 159–163. Brisbane. ISSN 0079–8835.

A dentary of a longirostrine crocodile, recovered from Pleistocene deposits on Riversleigh Station, northwestern Queensland, represents the first fossil occurrence and the oldest record of *Crocodylus johnstoni*. The age of this specimen and its geographic location are consistent with the hypothesis that *C. johnstoni* evolved from a more generalised, saltwater-tolerant species some time after the Pliocene.

☐ *Crocodilia, Crocodylus, Pleistocene, Australia.*

P.M.A. Willis and M. Archer, School of Biological Science, University of New South Wales, PO Box 1, Kensington, NSW 2033, Australia; 13 September, 1988.

A longirostrine crocodilian dentary was collected from Pleistocene deposits on Riversleigh Station by members of the University of New South Wales 1986 Riversleigh Expedition. It is described here in detail because, although it appears to be referable to *Crocodylus johnstoni*, it displays several features that invite broader comparisons bearing on the affinities of this species. QM = Queensland Museum.

MATERIAL

QM F13115, an incomplete left dentary, with four teeth (Fig. 1).

LOCALITY AND SEDIMENTS

"Terrace Site", the source locality, is a perched and dissected river-terrace deposit 5 km downstream from the crossing of the Gregory River and the Lawn Hill road, along the west bank of the Gregory River, Riversleigh Station, northwestern Queensland. More precise locality data are available on application to the Queensland Museum or the University of New South Wales. The unnamed deposits at this site are fluviatile sediments, mostly unconsolidated sands, clays and conglomerates which are locally indurated by a light carbonate cement.

ASSOCIATED FAUNA

The "Terrace Site" material is referred to the Terrace Site Local Fauna (Archer *et al.* 1989). Aside from the crocodilian described here, other taxa in this fauna include: *Diprotodon optatum*, unidentified macropodids, an unidentified rodent, a varanid, another crocodilian, a large elseyan turtle and freshwater molluscs.

AGE

The "Terrace Site" at Riversleigh is considered to be Pleistocene in age because it contains premolars and molars of *Diprotodon optatum*, a species which is unrecorded from pre-Pleistocene deposits (Archer, 1984). Charcoal and shell suitable for radiocarbon dating were retrieved from the level containing QM F13115 but these have not yet been dated.

DESCRIPTION

QM F13115 is an almost complete left dentary of a longirostrine crocodilian (Fig. 1). It is crushed and incomplete posteriorly, and the anterior part of the symphysis is also missing. Although the dentary fragment is large (183 mm long), it is slender and gracile in form. The mandibular symphysis extends to the level of the sixth tooth, while the splenial contact extends to the level of the seventh tooth and thus does not participate in the symphysis. The surface of the dentary is lightly sculptured with indistinct pits.

Fourteen alveoli are preserved but more may have been present further back in the missing portion of the dentary. The buccal rim of the tooth row undulates, but only very slightly. All alveoli are similar in size and round in cross-section. The fourth, ninth and tenth teeth are preserved *in situ*, and an unerupted tooth was recovered from the fifth alveolus. These teeth are slender, with weak

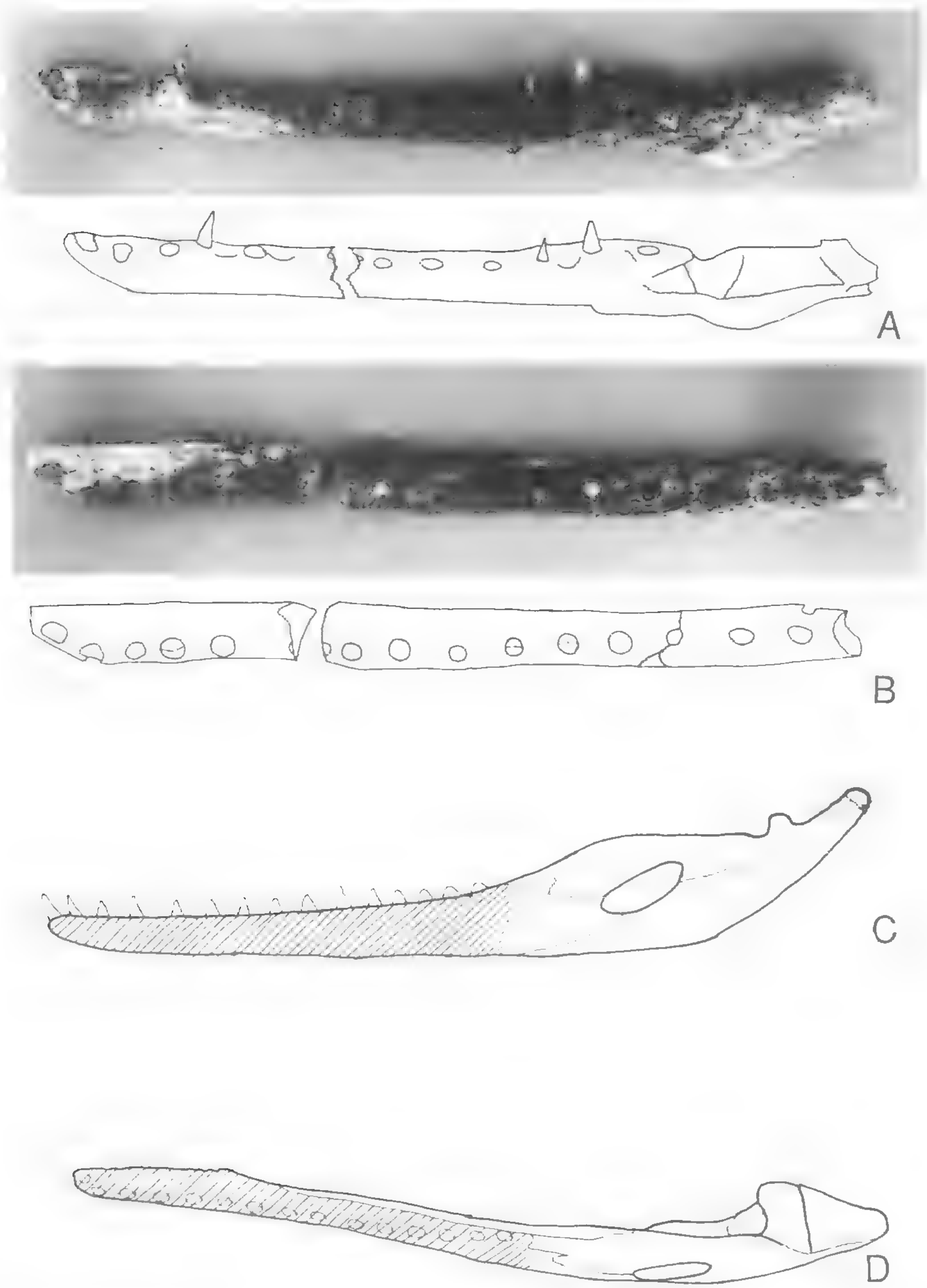

FIG. 1. QM F13115, left dentary of *Crocodylus johnstoni*: a, lateral view; b, dorsal view. Overall length 183 mm. Line drawing reconstructions shown under each view. The left mandible of *C. johnstoni*: c, lateral view; d, dorsal view. Hatching shows portion represented by QM F13115.

anterior and posterior carinae and are striated parallel to the long axis of the crown.

COMPARISONS

Although QM F13115 was initially compared with material or descriptions of all crocodilians, detailed comparisons were eventually narrowed down to specimens of *Crocodylus porosus*, *C. johnstoni* and *C. novaeguineae*. These are the only species that bear close resemblance to this Riversleigh crocodile and the only crocodiles that still survive in the region.

The slender, gracile form of QM F13115 is unlike the heavy, robust dentaries seen in undescribed Miocene crocodilians from Riversleigh and in *Pallimnarchus pollens* (Molnar, 1982a). The dentary of *Quinkana fortirostrum* (Molnar, 1981) is not known, but one would expect a more heavily built, broader dentary for this species than QM F13115. *Pallimnarchus* and *Quinkana* are the only late Cainozoic fossil crocodilians described from Australia. In its overall form, the orientation of the alveoli and the length of the mandibular symphysis the Riversleigh form is clearly different from *'Gavialis' papuensis* (Molnar, 1982b) from Woodlark Island.

QM F13115 is more gracile than the dentary of a similar-sized *C. porosus*. The shape and almost uniform size of the teeth, the barely-undulating tooth row and the narrowness of the dentary distinguish QM F13115 from both *C. porosus* and *C. novaeguineae*.

QM F13115 is indistinguishable from *C. johnstoni* in all features except three: 1, it represents an individual that would be unusually large for this species; 2, the dentary appears to be relatively narrower than that of *C. johnstoni*; and 3, there is a large gap between the fifth and sixth alveoli, not seen in *C. johnstoni*.

Although QM F13115 would represent a very large specimen of *C. johnstoni*, a *t*-test indicates that it is not significantly larger than a sample of *C. johnstoni* (n = 17, mean = 116.1, sd = 35.8, P 0.05). The *t*-test did, however, indicate that QM F13115 probably approaches the predicted extreme in size for this species. No modern specimen known to us exceeds this fossil in size. Presuming that it represents *C. johnstoni*, there are two possible explanations for the large size of QM F13115. First, crocodiles have for some time been hunted for their skins, large specimens being the most intensely sought. Because of this, awareness of the pre-European size range of the freshwater crocodile (and that of most specimens available for study) may be misleadingly low.

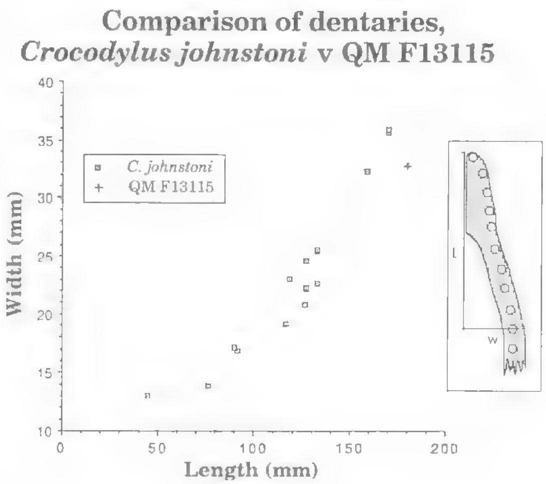

FIG. 2. Length to width ratios of *Crocodylus johnstoni* dentaries. Inset shows measurements on a typical right jaw of *C. johnstoni*. All measurements in mm. Length is measured from the anterior tip along the midline to the level of the tenth tooth; width is measured from the tenth tooth to the midline. These arbitrary measurements are necessary because QM F13115 is distorted posterior to the tenth tooth. Open circle indicates QM F13115; crosses indicate comparative examples of *C. johnstoni*.

A second possible explanation for the large size of QM F13115 involves the hypothetical evolutionary history of the species. It has been suggested by Longman (1925) that *Crocodylus johnstoni* probably descended from a larger, brevirostrine species such as *C. porosus*. Ancestral *C. johnstoni* might then be expected to have been, on average, larger than modern individuals.

The apparent narrowness of the dentary of QM F13115 may be an illusion resulting from its large size. Figure 2 shows that the dentary of modern *C. johnstoni* has a length to width ratio that follows a linear relationship (length = 5.52 width, n = 17, mean = 5.52, sd = 0.46). QM F13115 has a length to width ratio of 5.5. A *t*-test reveals that QM F13115 is not significantly different in this measurement from the comparative sample (P 0.05). Although a non-linear relationship between the length and width of the dentary may exist, the sample size of modern *C. johnstoni* is too small to detect such a relationship.

The large gap between the fifth and sixth alveoli may be nothing more than individual variation and cannot be presumed to have taxonomic or phylogenetic significance. Iordansky (1973) noted that irregular positioning of teeth is a common anomaly in many crocodilian species.

In summary, the three features in which QM F13115 appears to differ from *C. johnstoni* are not sufficient grounds for recognizing this specimen as a different species.

Discussion

As the first known fossil of *Crocodylus johnstoni*, QM F13115 establishes a minimum age for the species, which Longman (1925) suggested had evolved in northern Australia from more generalised crocodiles. The freshwater habitat of this species restricts its distribution, which is currently limited to the Australian mainland. Salt-tolerance studies of crocodilians (e.g. Taplin, 1984) indicate that some species of crocodilians have a much greater tolerance for salt water than others. This fact, coupled with interpretations of phylogenetic divergence sequences based on studies of blood proteins (Densmore, 1981; Densmore & Dessauer, 1982), prompts the following model as an explanation for the evolutionary history of the genus *Crocodylus* in Australia. By at least Pliocene times, a generalised, salt-water tolerant, ancestral species such as *C. porosus* or *C. acutus* may have dispersed across ocean barriers to estuarine habitats around the world. Some of its descendants subsequently invaded freshwater habitats and speciated into forms intolerant of saltwater, including *C. johnstoni*.

Chronologically the Riversleigh specimen is within the time framework established by protein divergence studies suggesting that *C. johnstoni* and *C. porosus* have diverged since Pliocene time. The large size of the specimen described here is consistent with descent from a larger form like *C. porosus*. Molnar (1979) has described, as *C. porosus*, an early Pliocene crocodile from the freshwater sediments of the Allingham Formation of northeastern Queensland (Archer & Wade, 1976). Clearly *C. porosus* was in Australian freshwater habitats early enough to have given rise to the freshwater crocodile, *Crocodylus johnstoni*.

ACKNOWLEDGEMENTS

We wish to acknowledge the vital financial support given to the Riversleigh Project by: the Australian Research Grant Scheme (Grant PG A3 851506P); the National Estate Grants Scheme (Queensland); the Department of the Arts, Sport, the Environment, Tourism and Territories; Wang Australia Pty Ltd; ICI Australia Pty Ltd; the Queensland Museum; Ansett Wridgways Pty Ltd; the Australian Museum; the Australian Geographic Society; Mount Isa Mines Pty Ltd; and Surrey Beatty & Sons Pty Limited. Critical logistical support in field and laboratory was received from the Riversleigh Society, the Friends of Riversleigh, the Royal Australian Air Force, the Australian Defence Force, the Queensland National Parks and Wildlife Service, the Riversleigh Consortium (Riversleigh being a privately owned cattle station), the Mount Isa Shire, the Burke Shire, the Northwest Queensland Tourism and Development Board, the Gulf Local Development Association, PROBE, and many volunteer workers and colleagues - including Henk Godthelp who helped recover and prepare the specimen for study. Alan Rackham Snr and Alan Rackham Jnr discovered the "Terrace Site".

Dr R.E. Molnar, Prof. G. Grigg, Mr A. Wood, Mr H. Godthelp and Mr C. Manolis provided advice and suggestions or provided access to comparative material.

LITERATURE CITED

Archer, M. 1984. The Australian marsupial radiation. p. 633-808 *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Carlisle, Western Australia)

Archer, M., Godthelp, Hand, S.J. and Megirian, D. 1989. Fossil mammals at Riversleigh, north-western Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 29–65.

Archer, M. and Wade, M. 1976. Results of the Ray E. Lemley Expeditions, part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* 17: 379–97.

Densmore, L.D. 1981. Biochemical and Immunological systematics of the order Crocodilia. Unpublished Ph.D. thesis, University of Houston.

Densmore, L.D. and Dessauer, H.C. 1982. Low protein divergence of species within the circumtropical genus *Crocodylus* — result of a post-Pliocene transoceanic dispersal and radiation? *Fed. Proc.* (Abstract). 41(4): 4293.

Iordansky, N.N. 1973. The skull of the Crocodilia. p. 201-62 *In* Gans, C. and Parsons, T.S. (Eds), 'Biology of the Reptilia. 4. Morphology D'. (Academic Press: London).

Longman, H.A. 1925. *Crocodilus johnstoni* Krefft. *Memoirs of the Queensland Museum* 8: 95–102.

Molnar, R.E. 1979. *Crocodylus porosus* from the Pliocene Allingham Formation of north Queensland. *Memoirs of the Queensland Museum* 19: 357–65.

1981. Pleistocene ziphodont crocodilians of Queensland. *Records of the Australian Museum* **33**: 803–34.

1982a. *Pallimnarchus* and other Cenozoic crocodiles of Queensland. *Memoirs of the Queensland Museum* **20**: 657–73.

1982b. A longirostrine crocodilian from Murua (Woodlark), Solomon Sea. *Memoirs of the Queensland Museum* **20**: 675–85.

TAPLIN, L. 1984. Evolution and zoogeography of crocodilians; a new look at an ancient order. p. 361-70 *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Carlisle, Western Australia).

NOTE ADDED IN PROOF:

A second fossil mandible of *Crocodylus johnstoni* (QM F17479) was located in the collections of the Queensland Museum by P. Willis. This mandible was found by M. Archer and H. Godthelp at 'Leichhardt 3', a locality on Floraville Station, on the Leichhardt River. The specimen is Late Pleistocene or post-Pleistocene in age (Godthelp, pers. comm.), so that the specimen described in the text of the paper probably represents the oldest known *Crocodylus johnstoni*. (R.E. Molnar.)

AN EVALUATION OF DE VIS' FOSSIL BIRDS

G.F. VAN TETS AND PAT V. RICH

Van Tets, C.F. and Rich, P.V. 1990 3 31: An evaluation of de Vis' fossil birds. *Mem. Qd Mus.* **28**(1): 165-168. Brisbane. ISSN 0079-8835.

This paper provides a generalized summary and revision of the numerous fossil birds that were described by C.W. de Vis between the years 1885 and 1911. Most of de Vis' fossil birds may be referred to extant taxa, but as many as six genera and 12 species may prove to be valid.
☐ *Aves, Pliocene, Quaternary, Australia.*

G.F. Van Tets, CSIRO Division of Wildlife & Ecology, PO Box 84, Lyneham, ACT 2602, Australia; Pat V. Rich, Department of Earth Sciences, Monash University, Clayton, Victoria 3168, Australia;

Around the turn of the 19th century Charles de Vis described and named many fossil birds. These were listed in full by Rich and Van Tets (1982, 361-6) with museum catalogue numbers, elements, localities and publications by de Vis and revisers. A checklist by Van Tets (1984) of the extinct fossil birds of Australasia includes the de Vis names. Revision of some of these names is still in progress, and updated versions of the table and checklist will be published in forthcoming editions of the books in which they originally appeared. His fossil material came mainly from southeastern Queensland and northeastern South Australia. In the absence of any radiometric dates, the material was considered by Rich and Van Tets (1981) to be Pliocene to Quaternary in age, on the basis of relative dates for associated mammalian faunas. Three-quarters of a century after de Vis (1911) published *Palaeolestes gorei*, his last fossil bird, it is interesting to reconsider his work. Isolated in Australia, de Vis worked during the period when the international rules of zoological nomenclature were being formulated (Stoll, 1961). The rules (Anon., 1905) were published too late to have any effect on de Vis' names. A typological rather than a population approach prevailed in de Vis' time and the classification of birds was very different from that with which we are now familiar. Unlike Lydekker (1891), de Vis appears to have assumed that all his fossil birds were extinct. His reference collection of modern bird bones at the Queensland Museum was far from complete and was arranged element by element, with rarely more than one specimen of an element per species. A few of his modern bird bones were misidentified. Similarly, the fossils consisted of dissociated bone and bone fragments, with rarely two or more similar specimens of the same species. Hence, it was impossible from the available modern and fossil bone collections for de Vis to obtain an appreciation of intraspecific variation. The results of our subsequent examinations of the fossil birds of de Vis are discussed below, at the generic level and classified by order.

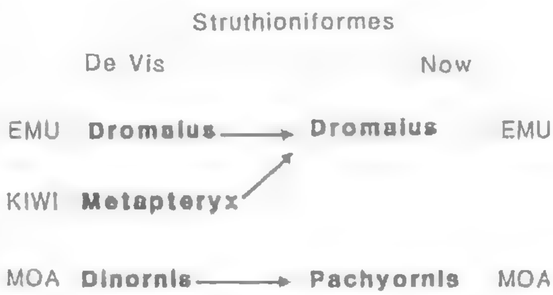

FIG. 1. De Vis' and present generic identifications of fossil Struthioniformes.

STRUTHIONIFORMES (Fig. 1)

De Vis named two emus (1888a, 1892, 1905), a kiwi (1892) and a moa (1885). Both emus and the "kiwi" are referable to the extant emu (Patterson & Rich, 1987); the moa is indeed a moa, but its supposed Queensland locality is in error, and it has since been shown to have come from New Zealand (Scarlett, 1969). According to de Vis (1891c), a Mr Daniels picked up the moa bone in Kings Creek, Darling Downs, and presented it with other fossils to the Queensland Museum.

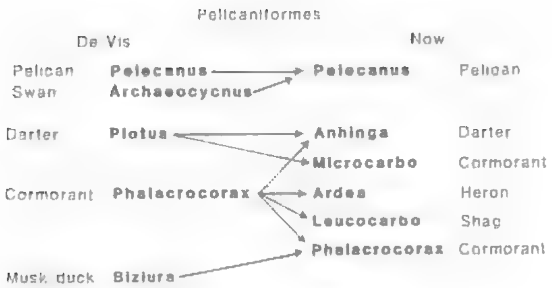

FIG. 2. De Vis' and present generic identifications of fossil Pelicaniformes.

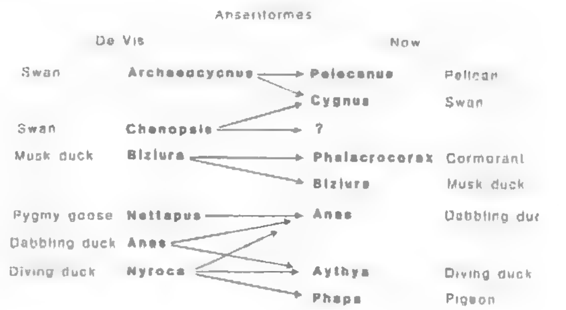

FIG. 4. De Vis' and present generic identifications of fossil Anseriformes.

PELECANIFORMES (Fig. 2)

De Vis named three pelicans (1892, 1894, 1905), two darters (1888a, 1905) and two cormorants (1905). A pelican and a darter may be extinct species, but the rest appear to be referable to extant species (Miller, 1966; Rich & Van Tets, 1981; Van Tets, in prep.).

ANSERIFORMES (Fig. 4)

De Vis named two swans (1905), a musk duck (1905), a pygmy goose (1905), three dabbling ducks and four diving ducks (1888a, 1905). One of the swans may be an extinct species and the identity of the other remains to be determined (Van Tets, in prep.). The remainder of the Anseriformes may be referred to extant species of musk duck, dabbling duck, diving duck (Olson, 1977) and an extant genus of pigeon (Van Tets & Rich, 1980).

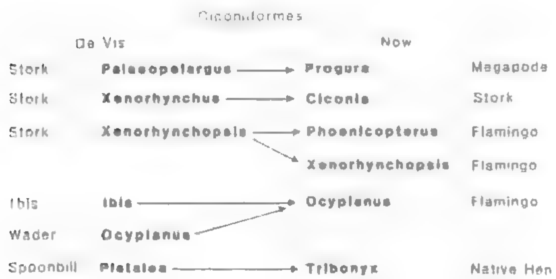

FIG. 3. De Vis' and present generic identifications of fossil Ciconiiformes.

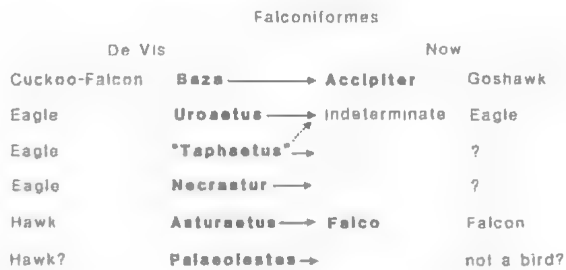

FIG. 5. De Vis' and present generic identifications of fossil Falconiformes.

CICONIIFORMES (Fig. 3)

Four storks (1888a, 1892, 1905), a spoonbill (1892) and an ibis (1905) were named by de Vis. One of the storks may be extinct, but the rest represent three extinct flamingoes plus one that is extant overseas (Rich *et al.*, 1987), a locally extinct nativehen (Olson, 1975) and an extinct megapode (Van Tets, 1974).

FALCONIFORMES (Fig. 5)

A cuckoo-falcon (1905), two hawks (1905, 1911) and three eagles (1890, 1891b, 1905) were named by de Vis. The "cuckoo-falcon" appears to be an extant goshawk (Van Tets, in prep.). One of the "hawks" is an extant falcon (Rich *et al.*, 1982), but the other is probably not even a bird. One of the eagles is indeterminate to genus and species, and the other two are under study by the authors.

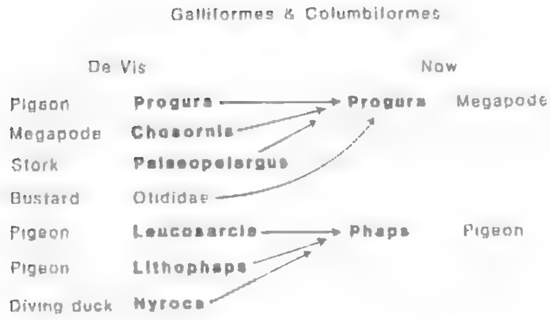

FIG. 6. De Vis' and present generic identifications of fossil Galliformes and Columbiformes.

GALLIFORMES and COLUMBIFORMES (Fig. 6)

Three pigeons (1888b, 1891a, 1905) and a megapode (1889) were named by de Vis. The megapode and one of the "pigeons" represent an extinct megapode (Van Tets, 1974). The other two pigeons belong to an extant genus (Van Tets & Rich, 1980).

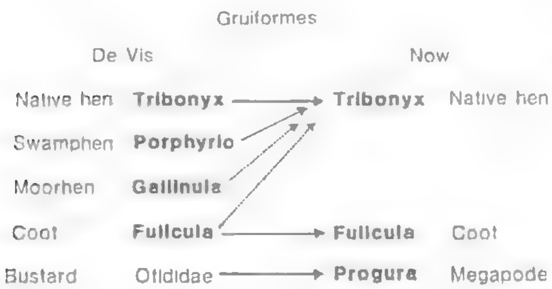

FIG. 7. De Vis' and present generic identifications of fossil Gruiformes.

GRUIFORMES (Fig. 7)

De Vis named a native hen 1892, two swamphens (1888a, 1892), two moorhens 1888a, 1892), a coot (1888a), and described, but did not name, a bustard (1888a). The native hen, the "swamphens" and the "moorhens" are referable to a single species of a locally extinct native hen (Olsen, 1975) and the "bustard" to an extinct megapode (Van Tets, 1974). The coot is an extant species of coot (Rich & Van Tets, 1982).

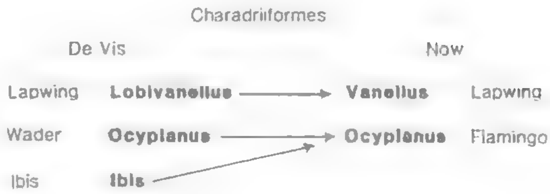

FIG. 8. De Vis' and present generic identifications of fossil Charadriiformes.

CHARADRIIFORMES (Fig. 8)

De Vis named a wader (1905) and an ibis (1905), and described but did not name a lapwing (1892). The "wader" and the "ibis" are an extinct species of flamingo (Rich *et al.*, 1987), and the lapwing may be referred to an extant form (Van Tets, in prep.).

We conclude that most of the fossil birds named by de Vis may be referred to modern species, though six of 12 genera and 12 of the 49 species that he named are still valid. Some of these, however, are in doubt and deserve further study. Fortunately the types were superbly illustrated and described by de Vis. Almost all of them are still available for study at the Queensland Museum, and a few are at the South Australian Museum (Rich & Van Tets, 1982).

LITERATURE CITED

ANON. 1905. Regles internationales de la Nomenclature zoologique. Paris 63 pp.

DE VIS, C.W. 1885. The Moa (*Dinornis*) in Australia. *Proceedings of the Royal Society of Queensland* 1: 23-8.

1888a. A glimpse of the post Tertiary avifauna of Queensland. *Proceedings of the Linnean Society of New South Wales* (2)3: 1277-92.

1888b. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland*, 5: 127-31.

1889. Additions to the list of fossil birds. *Proceedings of the Royal Society of Queensland* 6: 55-8.

1890. On a bone of an extinct eagle. *Proceedings of the Royal Society of Queensland* 6: 161-2.

1891a. On the trail of an extinct bird. *Proceedings of the Linnean Society of New South Wales* 6: 177-22.

1891b. Note on an extinct eagle. *Proceedings of the Linnean Society of New South Wales* 6: 123-5.

1891c. The moa in Australia. *New Zeuland Journal of Science* 1: 97-101.

1892. Residue of the extinct birds of Queensland as yet detected. *Proceedings of the Linnean Society of New South Wales* 6: 437–56.
1894. *Pelicanus validipes* n. sp. p.21, pl. II, fig. 5, 6. *In* Etheridge, R. Official Contributions to the Palaeontology of South Australia. No. 6 — Vertebrate remains from the Warburton or Diamantina River. *In* Brown, H.Y.L. 'Report of the Government Geologist for the year ended June 30, 1894'. (Government Printer: Adelaide). 26pp.
1905. A contribution to the extinct avifauna of Australia. *Annals of the Queensland Museum* 6: 3–25.
1911. *Palaeolestes gorei* n. sp. An extinct bird. *Annals of the Queensland Museum* **10**: 15–17.
LYDEKKER, R. 1891. 'Catalogue of the fossil birds in the British Museum (Natural History) London'. (British Museum (Natural History): London). 368pp.
MILLER, A.H. 1966. An evaluation of the fossil anhingas of Australia. *Condor* **68**: 315–20.
OLSON, S.L. 1975. The fossil rails of C.W. de Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* **75**: 49–54.
1977. The identity of the fossil ducks described from Australia by C.W. de Vis. *Emu* **77**: 127–32.
PATTERSON, C. AND RICH, P.V. 1987. The fossil history of the Emus, *Dromaius* (Aves : Dromaiinae). *Records of the South Australian Museum* 21: 85–117.
RICH, P.V. AND VAN TETS, G.F. 1981. The fossil pelicans of Australasia. *Records of the South Australian Museum* **18**: 235–64.
AND VAN TETS, G.F. 1982. Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. P.235–84. *In*: Rich, P.V. and Thompson, E.M. (Eds), 'The Fossil Vertebrate Record of Australasia'. (Monash University Offset Printing Unit: Clayton).
AND VAN TETS, G.F. (Eds) 1985. 'Kadimakara, extinct vertebrates of Australia'. (Pioneer Design Studio: Lilydale). 284pp.
VAN TETS, G.F. AND MCEVEY, A.R. 1982. Pleistocene records of *Falco berigora* from Australia and the identity of *Asturaetus furcillatus* de Vis (Aves : Falconidae). *Memoirs of the Queensland Museum* **20**: 687–93.
VAN TETS, G.F., RICH, T.H.V. AND MCEVEY, A.R. 1987. The Pliocene and Quaternary flamingoes of Australia. *Memoirs of the Queensland Museum* **25**: 207–25.
SCARLETT, R. 1969. On the alleged Queensland Moa, *Dinornis Queenslandiae* de Vis. *Memoirs of the Queensland Museum* **15**: 207–12.
STOLL, N.R. 1961. Introduction. pp.vii-xvii. *In* Stoll, N.R. (Chairman of Editorial Committee), 'International Code of Zoology Nomenclature adopted by the XV International Congress of Zoology'. (International Trust for Zoological Nomenclature : London).
VAN TETS, G.F. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* de Vis. *Transactions of the Royal Society of South Australia* **98**: 213–24.
1984. A checklist of extinct fossil Australasian birds. P.469–75. *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate zoogeography and evolution in Australasia'. (Hesperian Press: Carlisle).
AND P.V. RICH, 1980. A review of the de Vis' fossil pigeons of Australia. *Memoirs of the Queensland Museum* **20**: 89–93.

MAMMAL-LIKE REPTILES OF AUSTRALIA

R.A. THULBORN

Thulborn, R.A. 1990 3 31: Mammal-like reptiles of Australia. *Mem. Qd Mus.* **28**(1): 169. Brisbane. ISSN 0079-8835.

Until 1982 there was no evidence of therapsids, or mammal-like reptiles, in Australia. The seeming absence of these reptiles was indeed surprising, because they are among the commonest of terrestrial vertebrates in the Permian and Triassic sediments of the other Gondwana continents. Since 1982 the discovery of a half-dozen fragmentary specimens has revealed that two or three types of therapsids may have inhabited Australia during the Early Triassic.

All the specimens so far discovered are from the Arcadia Formation of southeastern Queensland. Aside from rare therapsid fragments this formation has yielded evidence of palaeoniscoids, the subholostean *Saurichthys*, lungfishes, diverse labyrinthodont amphibians, procolophonians, a thecodontian, and small lizard-like reptiles. This fauna is probably similar in age to the well-known *Lystrosaurus* Zone fauna of southern Africa and its equivalents in Antarctica and India (Thulborn, 1986).

The first therapsid specimen to be recognized was an isolated quadrate bone with morphological peculiarities unique to dicynodonts (suborder Dicynodontia; Thulborn, 1983). This specimen might actually represent the cosmopolitan zone-fossil *Lystrosaurus*, as was suggested by King (1983), though in reality there is insufficient evidence for identifying it to the level of genus. Subsequent discoveries of dicynodont material comprise a piece of squamosal, collected by Dr Mary Wade (Queensland Museum), and a portion of maxillary tusk. Neither of these fragments allows identification to genus level. While the evidence is, admittedly, rather scanty, it does indicate that at least one form of dicynodont was present in Australia during the Early Triassic. The Australian dicynodont material is tentatively assigned to the family Kannemeyeriidae, which, according to Cluver and King (1983), includes all dicynodonts of Triassic age.

The remaining three fragments are even more frustrating. Two small centra collected by Dr Anne Warren (La Trobe University) find a close match in certain cynodonts (suborder Cynodontia), though, once again, the material is so imperfect that it cannot be identified beyond "probably cynodont". The last specimen is potentially the most informative: it is the rear end of a small skull which has an occipital surface similar to that in small therapsids, including cynodonts. Unfortunately this skull fragment is embedded in haematite which is proving difficult to remove, even with the aid of thioglycollic acid.

The therapsid material discovered to date, though rare and fragmentary, does carry some interesting implications. It confirms that the vertebrate- bearing horizon of the Arcadia Formation may be broadly equivalent in age to the African *Lystrosaurus* Zone — despite its unusual preponderance of labyrinthodont amphibians over therapsids. The discovery of cynodonts, if confirmed, might indicate that mammals are just as likely to have originated in Australia as in any other continent. And, finally, the identification of Early Triassic cynodonts, in conjunction with the recent discovery of a Cretaceous mammal (Archer *et al.*, 1985), would afford reasonable hope that mammals were present in Australia through the Late Triassic and the Jurassic.

□ *Therapsida, Dicynodontia, Cynodontia?, Triassic, Queensland, Australia.*

R.A. Thulborn, Department of Zoology, University of Queensland, St Lucia, Queensland 4067, Australia; 4 March, 1988.

LITERATURE CITED

ARCHER, M., FLANNERY, T.F., RITCHIE, A. AND MOLNAR, R.E. 1985. First Mesozoic mammal from Australia: an Early Cretaceous monotreme. *Nature, London* **318**: 363–6.

CLUVER, M.A. AND KING, G.M. 1983. A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Annals of the South African Museum* 91: 195-273..

KING, G.M. 1983. First mammal-like reptile from Australia. *Nature, London* **306**: 209.

THULBORN, R.A. 1983. A mammal-like reptile from Australia. *Nature, London* **303**: 330–1.

1986. Early Triassic tetrapod faunas of southeastern Gondwana. *Alcheringa* **10**: 297-313.

PSEUDOMYS VANDYCKI, A TERTIARY MURID FROM AUSTRALIA

Henk Godthelp

Godthelp, H. 1989 3 31: *Pseudomys vandycki*, A Tertiary Murid from Australia. *Mem. Qd Mus.* **28**(1): 171–173. Brisbane. ISSN 0079-8835.

Pseudomys vandycki sp. nov. is described from the Tertiary Chinchilla Sand, Chinchilla, and is the first Tertiary murid described from Australia. *Pseudomys vandycki* differs from all other murids in the morphology of T1 on M^1 which is large rectangular and swept back to lie almost perpendicular to the T2,3 complex. *P. vandycki* most closely resembles the extant species *Pseudomys albocinereus* in aspects of dental morphology. The position of *P. vandycki* in the genus *Pseudomys* is considered tentative pending a resolution of the paraphyly within *Pseudomys*. The arrival date of murids into Australia is discussed and a date of approximately 7mya is proposed.
☐ *Muridae, Pseudomys vandycki, Pliocene, Chinchilla, Queensland.*

Henk Godthelp, School of Zoology, University of New South Wales, PO Box 1, Kensington, N.S.W. 2033; 1 June 1988.

The fossil record of Australian murids is very poor. Curiently, an isolated incisor from he middle Pliocene Allingham Formation and a few isolated teeth from the middle to late Pliocene Chinchilla Sands (Archer, 1978; Hand, 1984) are all that are recorded in the literature. The Chinchilla specimens are referred to as pseudomyine (Mahoney, pers. com., in Archer, 1978). Collections made in 1983 from Pliocene conglomerates at the Chinchilla Rifle Range have provided additional murid specimens and enabled the description of a new and distinctive rodent, *Pseudomys vandycki.*

All measurements are metric. The dental terminology follows Missone (1968). The author has examined actual specimens, casts or photographs of all known species of Australian modern and fossil murids. Where actual specimens or casts were not available photographs were used in conjunction with published descriptions.

SYSTEMATICS

Holotype

Queensland Museum F16834, a right maxillary fragment with M^1 and M^2, collected in 1983 by Godthelp, Archer, Gillespie and Blandford. Figure 1.

Type Locality

Main Gully System, Chinchilla Sand, Chinchilla Rifle Range, Chinchilla, southeastern Queensland.

Etymology

Named in honour of Stephen Van Dyck, Curatorial Officer (Mammals) at the Queensland Museum, who has had a long term involvement in advancing the phylogenetic systematics of Australian mammals.

Diagnosis

Pseudomys vandycki is a medium-sized rodent that differs from all outer murids in that the T1 of M^2 is large and has a rectangular occlusal surface, which is swept back so as to be aligned almost perpendicular to the T2,3 complex. It is most similar in aspects of dental morphology to *Pseudomys albocinereus* but differs in the relative size of T1 to the other cusps and the degree to which this cusp is swept back. The molars of *Pseudomys vandycki* are also larger and more elongate than those of *Pseudomys albocinereus.*

Description

Maxilla: Very little of the maxilla is preserved. The holotype does retain the posterior buccal edge of the incisive foramen, which ends slightly posterior to T1 on M^2.

The molars (Table 1) are three rooted, elongate, cuspidate and brachydont. The edge of T1 is positioned in front of the posterior edge of T2 and the anterior edge is positioned slightly anterior to the anterior edge of T5. The T2 is large and semicircular. Its posterior edge is concave and there is some thickening of the enamel at the apex of the anterior edge. The T3 is absent or incorporated into

A

B

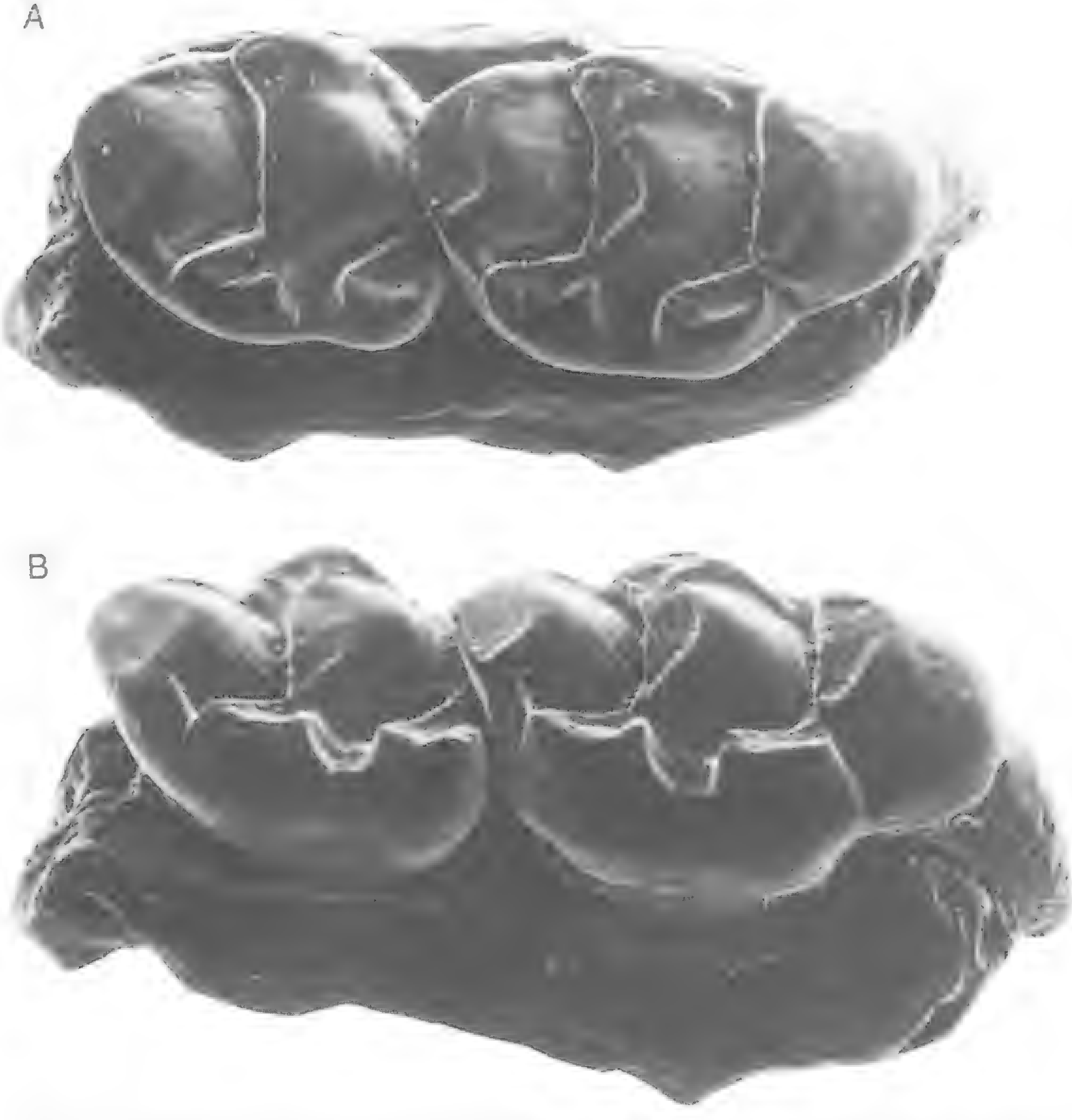

FIG. 1. A, Occlusal view of holotype (QMF 16834) of *Pseudomys vandycki.* B, Oblique occlusal view from a lingual aspect.

a T2,3 complex. The T4 is moderately large and isolated from T5. The T4 is almost perpendicular to T4,6 complex. The occlusal surface of T4 is nearly rectangular, tapering slightly in the posterior quarter. The anterior edge is level with the posterior edge of T5 and the posterior edge is level with the anterior edge of T8. The semicircular T5, although smaller than T2, is large. Its posterior edge is concave and there is some enamel thickening on the apex of the anterior edge. T6 is the smallest cusp present. The occlusal surface is triangular in shape and connected to T5 at an early stage of wear. The T7 is absent. The T8 is large and elliptical with a convex posterior edge. The T9 is absent or incorporated into the T8 complex.

M^2: The T1 is isolated and triangular in occlusal view. The T2 and T3 are absent. The T4 is equal in size to T1. It is positioned almost perpendicular to the T5,6 complex to which it is joined by a narrow wear facet. The T5 is large and triangular with a

M^1 length	2.71 mm
M^1 width	1.41 mm
M^2 length	1.93 mm
M^2 width	1.44 mm

TABLE 1: Measurements. (All measurements represent maximums)

concave posterior edge. The T6 is smaller than T5 to which it is joined. The T7 is absent. The T8 is large and elliptical and there is some enamel thickening along its anterior edge. The T9 is absent or incorporated into the T8 complex.

DISCUSSION

Pseudomys vandycki is only tentatively referred to the genus *Pseudomys*. This referral is based on its overall similarities to other species currently placed in the genus (Tate, 1947; Watts and Aslin, 1981) and in particular to *Pseudomys albocinereus*. *Pseudomys vandycki* shares features with some species of the genus *Pseudomys* which can be considered diagnostic at the generic level: three rooted M^1; relatively elongate molars; poorly developed buccal series of cusps; absence of T7; and lack of buccal displacement of the T5,6 complex.

The genus *Pseudomys* is generally accepted to be paraphyletic (Watts and Aslin, 1981). It contains many essentially plesiomorphic species that share few synapomorphies with other species in the genus. Morphological evidence (Lidicker and Brylski, 1987) from extant species and evidence from other, as yet undescribed, Tertiary murids from the Riversleigh deposits in northwestern Queensland (Godthelp in prep.) suggest that *Pseudomys* is polyphyletic. This concept, in so far as it can be checked for living species referred to the genus, is supported by genetic data (Baverstock *et al.*, 1981). Thus it is possible, pending a thorough revision of the genus, that *P. vandycki* may fall outside *Pseudomys sensu strictu*.

There is a particularly close resemblance between this species and *P. albocinereus*. Both species have isolated T1 and T4 which are positioned postero-lingual to the first and second cusp complexes. If this reflects monophyly, it suggests that *P. vandycki* and *P. albocinereus* form a distinct species group within *Pseudomys*.

Recent estimates of the time of entry of murids into Australia have been placed at 4.5 My (Archer, 1978, based on the oldest record then known) and 5-7 My ago (Watts and Aslin, 1981). The high diversity of murids, approximately 15 species, recently collected from the middle to late Pliocene of Queensland (Godthelp, 1987) suggests a entry time predating the middle Pliocene, possibly as early as 7 My ago.

It has also been assumed that murids came into Australia via rainforest corridors and only subsequently spread into the more arid environments. However the only rodents that are found in Australian rainforests today are those that appear to have entered Australia from New Guinea during the Pleistocene — *Melomys, Uromys, Pogonomys* and *Rattus* (Simpson, 1961; Taylor and Horner, 1973; Watts, 1981). It seems at least as probable that the murids entered Australia via xeric corridors which still persist in the northwest of the continent.

LITERATURE CITED

ARCHER, M. AND BARTHOLOMAI, A. 1978. Tertiary mammals of Australia: a synoptic review. *Alcheringa* **2**: 1–19.

BAVERSTOCK, P.R., WATTS, C.H.S., ADAMS, M. AND COLE, S.J. 1981. Genetical relationships among Australian Muridae. *Aust. J. Zool.* 29: 289–303.

GODTHELP, H.J. 1987. Rackhams Roost: The Beginnings of the Modern World. P. 81-3. *In* Hand, S. and Archer, M. (Eds.), The Antipodean Ark (Angus and Robertson, Sydney).

LIDICKER, W.Z. Jr AND BRYLSKI, P.V. 1987. The Conilurine rodent radiation of Australia, analysed on the basis of phallic morphology. *J. Mamm.* **68**(3): 617–41.

MISONNE, 1969. African and Indo-Australian Muridae. Evolutionary trends. *Mus. Roy. L'Afrique Cent. Tervren, Zool.* **172**: 1–219.

SIMPSON, G.G. 1961. Historical zoogeography of Australian mammals. *Evolution* **15**: 431–446.

TAYLOR, M.J. AND HORNER, E.B. 1973. Systematics of native Australia *Rattus. Bull. Amer. Mus. Nat. Hist.* **150**(1): 5–124.

WOODBURNE, M.O., TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Spec. Publ., S. Aust. Dept Mines and Energy*, **5**: 347–363.

FIRST TERTIARY MOLOSSID (MICROCHIROPTERA : MOLOSSIDAE) FROM AUSTRALIA: ITS PHYLOGENETIC AND BIOGEOGRAPHIC IMPLICATIONS

SUZANNE J. HAND

Hand, S.J. 1990 3 31: First Tertiary Molossid (Microchiroptera : Molossidae) from Australia: its Phylogenetic and Biogeographic Implications. *Mem. Qd Mus.* 28(1): 175-192. Brisbane. ISSN 0079-8835.

Petramops creaseri n.gen., n.sp. is described from Middle Miocene freshwater limestones on Riversleigh Station in northwestern Queensland. One of 25 new bat species identified among fossil remains recovered from the Riversleigh deposits, it is Australia's first Tertiary molossid. Its affinities appear to lie outside the modern Australian molossid radiation. It seems likely that bats of the *Petramops* lineage were proficient long-distance fliers which colonized Australia before the Miocene. Subsequent or coincident colonizations of Australia by molossids would have involved species of *Nyctinomus*, *Chaerephon* and *Mormopterus*.
☐ *Chiroptera, Molossidae, Riversleigh, Miocene, Petramops creaseri, biogeography.*

Suzanne J. Hand, School of Biological Science, University of New South Wales, PO Box 1, Kensington, NSW 2033; 14 December, 1988.

Fossil material referable to a new genus and species of molossid has recently been recovered from Tertiary freshwater limestones on Riversleigh Station, northwestern Queensland (Fig. 1). The Riversleigh fossil deposits cover an area of at least 40 sq. km and appear to comprise a sequence of sediments ranging in age from approximately 25 to 4 My ago (Archer *et al.*, 1986; Archer *et al.*, 1989).

From the remarkably mammal-rich Riversleigh Tertiary deposits, some 25 new species of fossil bats have been identified. These include *Hipposideros (Brachipposideros) nooraleebus* Sigé, Hand and Archer (Sigé *et al.*, 1982), *Macroderma godthelpi* Hand (Hand, 1985), *M.* sp. and a number of other hipposiderids, megadermatids, rhinolophids, emballonurids and vespertilionids, as yet undescribed (Hand, 1987).

The bat described here is Australia's first Tertiary molossid, the first representative of bats outside the superfamily Rhinolophoidea to be described from the Riversleigh sediments. The pancontinental family Molossidae is otherwise represented in Australia by five living species whose taxonomy is currently confused (e.g. Hill, 1961; Felten, 1964; Allison, 1978, 1983; Freeman, 1981; Honacki *et al.*, 1982; Legendre, 1984b; Mahoney & Walton, 1988).

In this study, dental morphology is used in an attempt to interpret the phylogenetic position of the Riversleigh fossil with respect to other Australian and non-Australian molossids. A biogeographic hypothesis involving the new molossid is proposed.

Specimens or casts examined in this study include representatives of all species of Australian molossids and subgeneric-level taxa of living non-Australian species. Also examined were specimens or casts of the fossil species: *Mormopterus (Hydromops) helveticus*, *M. (H.) stehlini*, *Nyctinomus (Nyctinomus) engesseri* (see below for discussion of the name *Nyctinomus*), *N. (N.) leptognathus* and *'Meganycteris monslapidensis'* (Table 2). Fossil specimens not examined but well-enough described or illustrated in the literature to be included in this study were *Cuvierimops parisiensis* (Legendre & Sigé, 1984) and *Mormopterus (Neomops) faustoi* (Legendre, 1984a, 1985). Other fossil molossids, too poorly represented to include in the phylogenetic analysis, are discussed more briefly.

Repositories of specimens are indicated by prefixes as follows: AM, Australian Museum; SAM, South Australian Museum; BMNH, British Museum (Natural History); AMNH, American Museum of Natural History; QM, Queensland

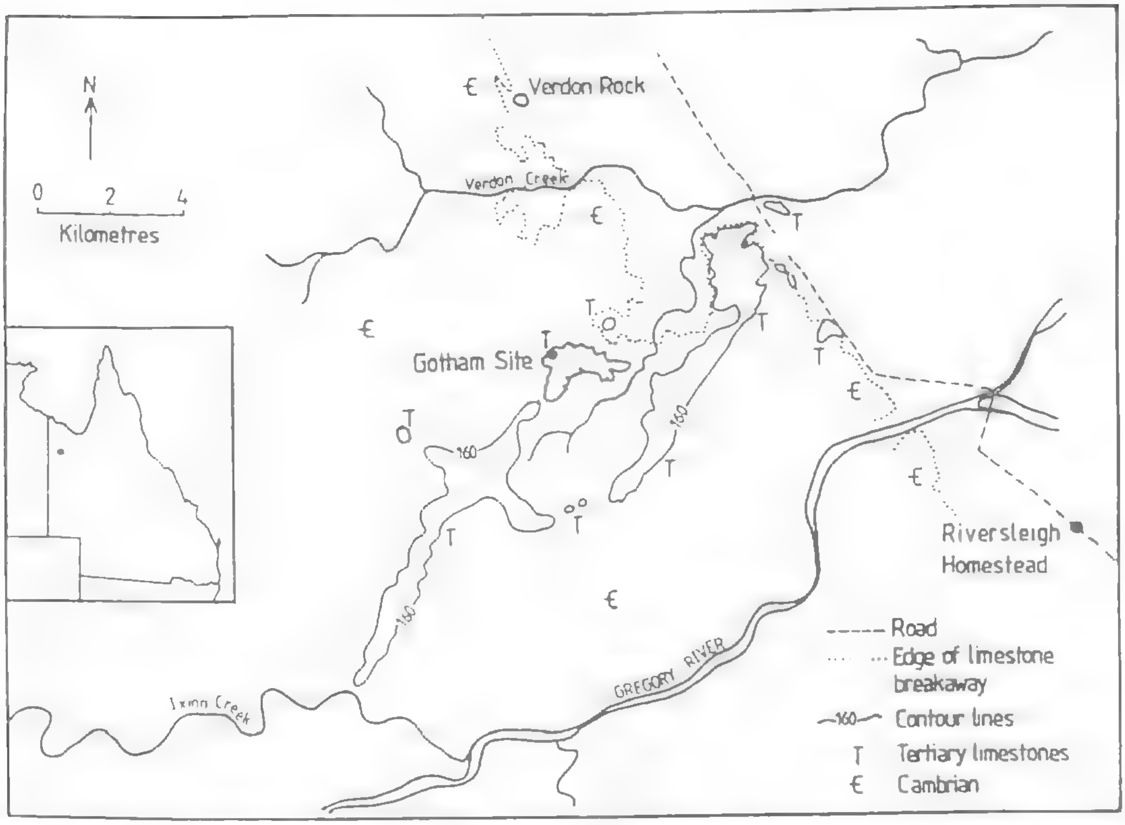

FIG. 1. Map of Riversleigh area showing location of Gotham City Site (after a map prepared by K. Gri mes and modified by H. Godthelp and M. Archer).

Museum; CG, Museum National d'Histoire Naturelle, Paris; SG, Museum d'Histoire Naturelle, Basle; 1970 XVIII, Bayerische Staatssammlung für Paläontologie und historische Geologie, München.

Dental terminology follows Legendre (1985) or is modified as in Fig. 2. Phylogenetic systematic terms used in this paper are summarized in Wiley (1981).

SYSTEMATICS

Order CHIROPTERA Blumenbach, 1779
Suborder MICROCHIROPTERA Dobson, 1875
Superfamily VESPERTILIONOIDEA Gray, 1821
Family MOLOSSIDAE Gill, 1872

Petramops creaseri n.gen, n.sp.

TYPE SPECIES

Petramops creaseri sp. nov.

ETYMOLOGY

The generic name is from the Greek *petra* (rock) and *mops* (bats), and refers to the fossil nature of this new Australian molossid; the gender is masculine.

DIAGNOSIS

This molossid genus differs from all others in the following combination of features: loss of I_3; lower molar morphology nyctalodont (as defined by Menu & Sigé, 1971; see DESCRIPTION below); P_4 with rudimentary but distinct metaconid; M^1 with distinct and well developed paraloph and metaloph; M^1 with tall conical hypocone isolated from the protocone and postprotocrista by an obliquely oriented depression; M^3 only moderately reduced, such that the premetacrista is longer than the pre- and postparacristae; lower premolars oriented longitudinally (or only slightly obliquely) in the tooth row; lower molar trigonids with marked anteroposterior compression; M_1 with

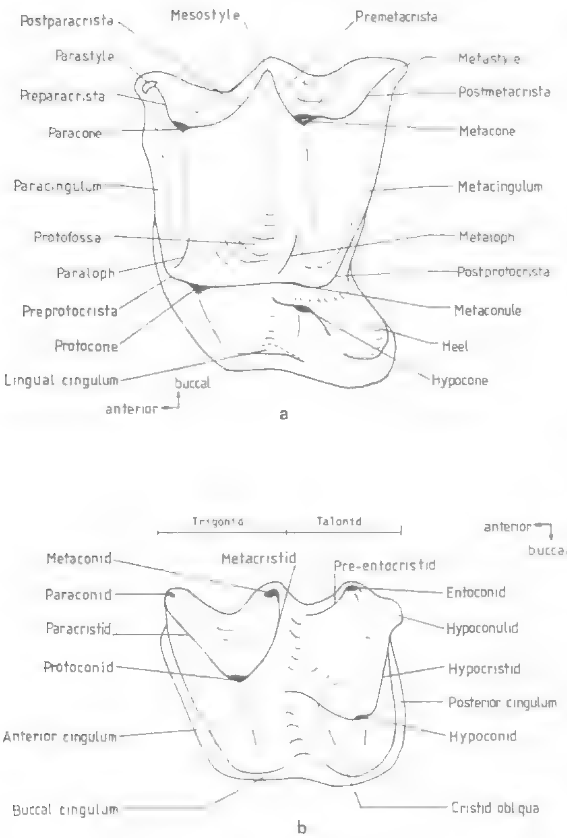

FIG. 2. Tooth terminology for molossids: A, upper tooth; and, B, lower tooth. (After Legendre, 1983; fig. 1).

well-developed paraconid; C_1 much taller than P_4; dentary depth tapering posteriorly.

Petramops creaseri n.sp.
Figs 3-4

MATERIAL EXAMINED

HOLOTYPE: QMF 13080, a left dentary containing C_1, P_4, M_1, M_2, M_3 and alveoli for P_2.

PARATYPES: QMF 13081, a right M^1, and QMF 13082, a left M^3.

ETYMOLOGY

The species is named for Mr Phil Creaser of the National Estate and World Heritage Section of the Department of the Arts, Sport, the Environment, Tourism and Territories. His untiring efforts to find support for the Riversleigh fossil bat research and his indispensable help in collecting fossil-rich limestone on Riversleigh Station are gratefully acknowledged.

DIAGNOSIS

The species diagnosis is the same as that for the genus until additional species are known.

TYPE LOCALITY, AGE, LITHOLOGY AND TAPHONOMY The type locality, Gotham City Site, occurs within the Tertiary sequence of limestone sediments on Riversleigh Station, northwestern Queensland (Fig. 1). It occurs in Ray's Amphitheatre at a level interpreted to be stratigraphically above the Gag Site (Hand, 1985) and Ringtail Site but below Henk's Hollow Site (Flannery & Archer, 1987) and Jaw Junction Site (Archer *et al.*, 1989).

On the basis of its mammal fauna (at least 24 species of marsupials and bats), the Gotham City deposit is interpreted to be of Middle Miocene age and to be younger than the Riversleigh Dwornamor and Upper Site Local Faunas and the South Australian Ditjimanka and Kutjamarpu Local Faunas (Woodburne *et al.*, 1985; Archer *et al.*, 1989) but older than the Riversleigh Henk's Hollow Local Fauna. The detailed stratigraphy of the Riversleigh sites and their relationships to those of South Australia are now under study.

The sediment is fine-grained, argillaceous freshwater limestone. Taphonomically, the Gotham fossil material is thought to represent the remains of prey collected by the megadermatid, *Macroderma* sp. The remains are consistent in size and fragmentation with prey remains recovered from roosts of the Australian megadermatid, *Macroderma gigas*, the latter's closest living relative.

DESCRIPTION

The dentary is represented by the holotype QMF 13080 (Fig. 3). It decreases markedly in depth from C_1 to below the posterior root of M_3. The large mental foramen occurs below the alveoli for P_2, the steep symphysis extending posteriorly to this same point. The mandibular foramen is not preserved. Two small foramina occur immediately adjacent to the symphysis midway between the alveolar border and the base of the dentary. The larger dorsal foramen is closer to the symphysis than the smaller, more ventral foramen. The posterior margin of the ascending ramus inclines at an angle of about 30° to the horizontal.

The lower dental formula is $I_{1,2}$ C_1 $P_{2,4}$ $M_{1,2,3}$. The incisors are unknown.

The C_1 is surrounded by a basal cingulum on which are developed minute swellings at the antero-lingual high point and postero-buccal low point of the cingulum. Postero-lingually, a very

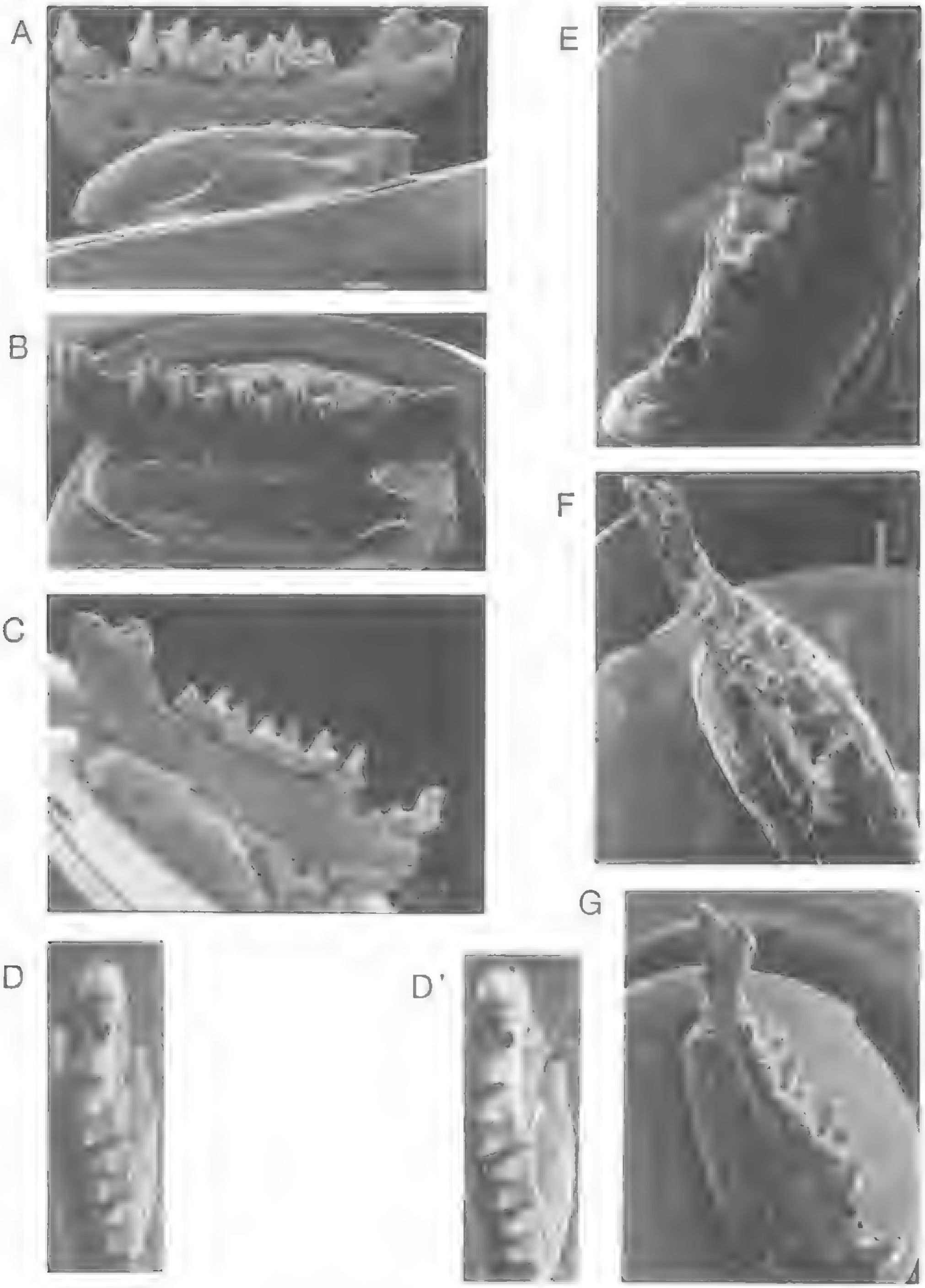

FIG. 3. *Petramops creaseri* from the Gotham City Local Fauna, Riversleigh Station, northwestern Queensland. QMF 13080, holotype, left dentary containing C_1, P_4, M_1, M_2, M_3 and alveoli for I_1, I_2 and P_2. A, buccal view; B, oblique buccal view; C, lingual view; D- D', stereopairs occlusal view; E, antero-occlusal view showing alveoli for P_2; F, anterior view showing alveoli for $I_{1,2}$; G, oblique-lingual view. Scale indicates 1 mm.

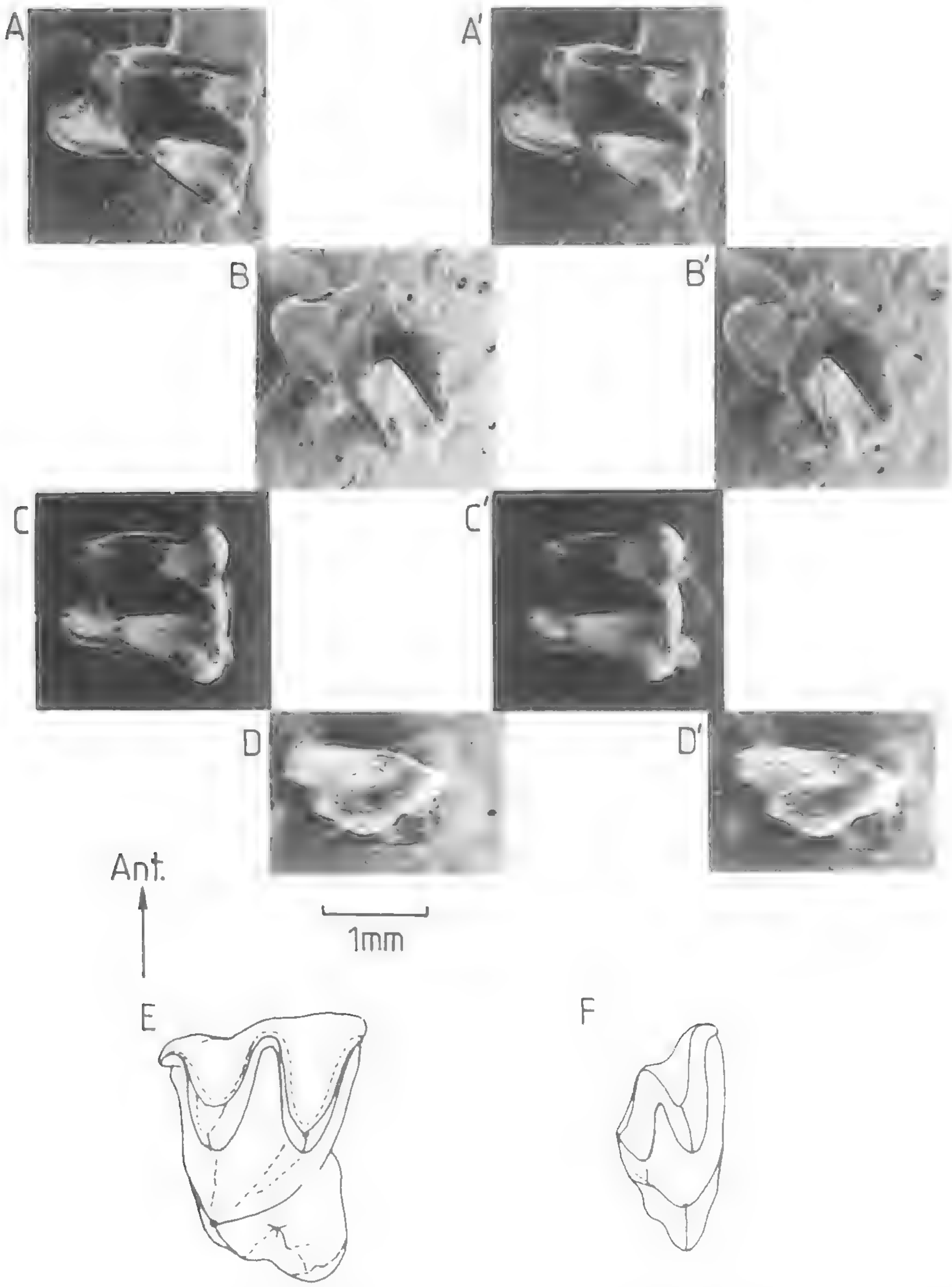

FIG. 4. *Petramops creaseri*. Paratypes. QMF 13081, a right M^1: A-A', stereopairs, oblique-occlusal view; $B\text{-}B^1$, stereopairs, oblique view; C-C', stereopairs, occlusal view. QMF 13082, a left M^3: D-D', stereopairs, oblique-occlusal view. Camera-lucida drawings (X 16) in oblique-occlusal view of, E, paratype QMF 13081 and, F, paratype QMF 13082 for comparison with camera-lucida drawings of molossid teeth in Fig. 5.

large cingular cusp contributes to the formation of a pronounced posterior heel, making the lingual face of the tooth markedly longer than the buccal face. This postero-lingual cusp is separated from the protoconid by a wide, shallow facet that passes transversely across the tooth. The lingual cingulum is much higher but narrower and less distinct than the buccal basal cingulum and at one point merges with the swollen postero-lingual edge of the protoconid. The posterior face of the protoconid is wide and conspicuously flattened, being semicircular in horizontal section. On the antero-lingual face, rising from the cingular swelling, a poorly-defined vertical crest is developed. The root of the tooth is very well-developed and posteriorly curved. The tip of the crown is missing.

The P_2 is represented only by alveoli in the holotype. The two alveoli are oblique in the tooth row, the smaller and anterior one being more buccally situated. The P_2 appears to have been a double-rooted and well developed tooth approximately the same length as P_4.

The P_4 has two roots, the posterior being longer and wider than the anterior root. There is one very large median cusp (the protoconid), a well-developed rudimentary metaconid that is approximately two-thirds the crown height of the protoconid, a tiny antero-lingual cingular cusp and a smaller postero-lingual cingular cusp. The nearly vertical anterior face of the tooth is anteriorly convex and bears a vertical crest connecting the protoconid to the antero-lingual cuspule. The protoconid is connected to the metaconid by a short transverse crest. The posterior face of the crown is flattened in a similar fashion to C_1, as is the lingual face of the metaconid. Where these two flattened faces meet, a vertical crest is formed which extends from the tip of the metaconid to the postero-lingual cingular edge of the crown. The almost angular postero-lingual corner of the crown is markedly extended such that the lingual length of the tooth is much greater than the buccal length and the posterior portion of the crown is wider than the anterior portion. The postero-lingual corner of the P_4 cradles the paraconid of M_1. The basal cingulum of the crown is much narrower and less distinct on the lingual side than on the buccal, anterior or posterior sides. In horizontal section, the crown is roughly triangular in shape with the antero-buccal face being slightly convex, the postero-buccal face flattened and the antero-lingual face gently concave. In its height the P_4 protoconid exceeds all crowns except C_1.

The M_1 has two roots and six distinct cusps, the hypoconulid being a small cingular cusp. In height the protoconid exceeds the hypoconid, which exceeds the subequal paraconid, metaconid and entoconid. The trigonid is much narrower than the talonid, in which a deep fossa is developed anteriorly. All cusps are interconnected by crests. The paracristid and metacristid are subequal in length, their paraconid, protoconid and metaconid contributions being approximately equal. The cristid obliqua is uncurved in occlusal view and contacts the trigonid just buccal to the point directly below the junction of components of the metacristid. There is an inflexion along the cristid obliqua at a point closer to the hypoconid than the trigonid. The hypocristid extends from the hypoconid directly to the hypoconulid, thus isolating the entoconid and exhibiting the nyctalodont pattern defined by Menu and Sigé (1971). An inflexion in the hypocristid also occurs closer to the hypoconid than the hypoconulid, reflecting the almost vertical rise from the talonid basin of the hypoconid before lingually recurving. The protoconid, while crescent-shaped like the hypoconid, is more lingually directed.

A steeply declining crest (pre-entocristid) links the entoconid to the trigonid at the base of the M_1 metaconid. The paracristid is orientated antero-lingually. The metacristid is close to being transverse if not also antero-lingually orientated to the long axis of the molar row, reflecting the marked compression of the trigonid. The cristid obliqua is more antero-lingually directed than the paracristid. The hypocristid parallels the metacristid. The pre-entocristid is lingually concave. There is a well-developed continuous anterior, buccal and posterior cingulum terminated near its antero- posterior end for contact with the flattened posterior face of P_4 and near its postero-lingual end by a notch for the anterior cingulum of M_2. A low cingular swelling may be discerned lingual to the trigonid basin between the bases of the metaconid and paraconid. Nevertheless, the trigonid basin is open lingually, as is the talonid at a point near the base of the trigonid.

The M_2 is described here only in so far as it differs from M_1. The M_2 is shorter than M_1, with the trigonid almost as wide as the talonid. The paracristid and metacristid are more transversely oriented with respect to the tooth row, the paraconid and metaconid more closely approaching each other on the more antero-posteriorly compressed trigonid. The cristid obliqua is slightly curved in occlusal view, this inflexion occurring approximately three-quarters of the distance from the hypoconid to the trigonid.

The M_3 is described only in so far as it differs from M_1. The M_3 is much shorter than M_1 and M_2. The trigonid is noticeably more antero-posteriorly compressed. The trigonid is subequal in width (if not wider) than the talonid. The paracristid is longer than the metacristid, its paraconid contribution being greater than the metaconid contribution to the metacristid. The point of inflexion in occlusal view in the cristid obliqua occurs very close to the metaconid.

Meristic gradients along the lower tooth row are as follows. The protoconids of M_1 and M_2 appear to be subequal in height and much higher than that cusp on M_3. The entoconids also show this pattern. The paraconids of M_1 to M_3 are subequal in height, as are the metaconids. The hypoconids appear to decline in height from M_1 to M_3. The hypoconulid of M_3 appears to be less well-developed than that of M_1 and M_2. The paracristids, metacristids and hypocristids decrease slightly in length posteriorly. The pre-entocristids of M_1 and M_2 are subequal in length, as are the cristids obliqua. These crests are markedly shorter in M_3. The angles formed between the protoconid and paraconid contributions to the paracristid of $M_{1\text{-}3}$ and the protoconid and metaconid contributions of the metacristid become more obtuse posteriorly. The angle formed between the paracristids and metacristids of $M_{1\text{-}3}$ become more acute posteriorly.

The upper dentition is known only from the paratypes, a right M^1 and left M^3.

The M^1 (QMF 13081) has three roots and six principal cusps. The metacone is taller than the broken paracone, which probably would have been slightly taller than the protocone. The protocone is taller than the very pronounced hypocone; this, in turn, is taller than the metastyle, which is taller than the parastyle. The paracone and metacone are sharply crescentic, being deeply excavated buccally. A well-developed paraloph extends lingually from the base of the paracone to the tip of the protocone. A well-developed metaloph extends antero- lingually from a point just antero-buccal of the base of the metacone to a point approximately halfway towards the protocone tip. A deep, confined protofossa is defined by the paraloph, metaloph and adjacent bases of the paracone, metacone and protocone. The pre- and postmetacristae are subequal in length and much longer than the postparacrista, which is longer than the preparacrista. The preparacrista meets the well-developed, anteriorly-oriented parastyle at a right angle. The antero-buccal flank of the massive parastyle is smoothly rounded as is the buccal side of the mesostyle and the postero-buccal flank of the metastyle. The postparacrista and premetacrista contact at the mesostyle which, however, is not cuspidate. A mesostylar shelf extends from the well-developed parastyle to the distinct but non-inflected metastyle. The angle formed between the pre- and postparacristae is approximately 55°, which is slightly greater than the comparable angle formed between the pre- and postmetacrista (approximately 45°).

Anteriorly the M^1 preprotocrista forms a broad shelf (the paracingulum) which reaches the parastyle. The postprotocrista becomes continuous with the posterior cingulum (forming the metacingulum) at a point posterior to the base of the metacone. From this point, the paracingulum continues buccally to meet the metastyle while the posterior cingulum swings slightly postero-lingually, then lingually and then anteriorly to meet the lingual cingulum at a point of pronounced cingular swelling (i.e. at the most postero-lingual point of the tooth). Together the posterior and lingual cingula enclose the well-defined, lingually-directed heel. The antero-lingual basal cingulum terminates at the posterior protocone base.

The heel of M^1 is dominated by the tall conical hypocone which is isolated from the protocone and the postprotocrista by a shallow obliquely oriented depression or valley. Approximately at a right angle to this depression a postero-lingually oriented vertical crest links the antero-buccal base of the hypocone to the hypocone tip and the most postero-lingual point of the tooth (i.e. the swollen postero-lingual portion of the basal cingulum). The heel extends anteriorly to a point level with, but basal to, the mesostyle and postero-buccally to the junction of posterior cingulum and postprotocrista. The heel is widest around the postero-lingual base of the crown and longest (antero-posteriorly) at the level of the protocone. In occlusal view, the heel is sharply-defined lingually by a conspicuous notch (or change in direction of slope) in the basal lingual cingulum. The tooth has three roots, subequal paracone and metacone roots and a larger protocone root.

The M^3 (QMF 13082) is described in so far as it differs from M^1. The metacone (which is damaged) appears to have been shorter than the paracone and subequal in height to the very poorly defined (and worn) parastyle which meets the preparacrista at a very obtuse angle. A notch for the M^2 metastyle is developed in the anterior cingulum near the

TABLE 1. Measurements (following Sigé *et al.*, 1982) of the holotype QM F13080 and paratypes QM F13081 and QM F13082 of *Petramops creaseri* from the Gotham City Local Fauna, Riversleigh Station.

CHARACTER	HOLOTYPE QM F13080	PARATYPES	
		QM F13081	QM F13082
C_1 – M_3	6.80		
P_4 – M_3	4.83		
M_1 – M_3	4.13		
C_1 length	1.19		
C_1 width	1.09		
P_4 length	0.94		
P_4 width	0.90		
M_1 length (*in situ*)	1.48		
M_2 length (*in situ*)	1.44		
M_3 length (*in situ*)	1.40		
M_1 trigonid length	0.72		
M_1 talonid length	0.83		
M_2 trigonid length	0.65		
M_2 talonid length	0.71		
M_3 trigonid length	0.48		
M_3 talonid length	0.78		
M_1 trigonid width	1.00		
M_1 talonid width	1.24		
M_2 trigonid width	1.02		
M_2 talonid width	1.22		
M_3 trigonid width	0.89		
M_3 talonid width	0.85		
M^1 length		1.54	
M^1 width		1.69	
M^3 length			0.85
M^3 width			1.62

antero-buccally oriented parastyle. There is no heel or postero-lingual development of the crown beyond the protocone. There is no postmetacrista or metastyle. The premetacrista, however, appears to remain longer than the pre- and postparacristae, and the postmetacrista may be represented by a noticeable swelling on the postero-buccal flank of the metacone.

Measurements of holotype and paratypes are given in Table 1. Measurements were made to the nearest 0.01mm using a Wild MMS 235 Digital Length-Measuring Set attached to a Wild M5A Stereomicroscope.

COMPARISONS

Petramops creaseri clearly belongs to the family Molossidae, which is distinguished by the following combination of dental and cranial features (Dobson, 1878; Miller, 1907; Hill, 1961):

1. skull low and flattened, with braincase not greatly inflated;
2. skull lacks postorbital processes;
3. posterior orifice of antorbital canal not enlarged;
4. premaxillaries with nasal branches present or absent; when present forming two palatal foramina, when absent allowing the formation of one which extends to or beyond the roots of the incisors;
5. single pair of large upper incisors occupying the centre of the space between the canines;
6. P^2 reduced or absent;
7. P^4 with well-developed anterior cingular cusp;
8. traces at least of a hypocone on M^1 and (variably) on M^2;
9. development on M^{1-3} of a paracingulum which is continuous with the preprotocrista;
10. two lower sub-caniniform premolars;
11. P_4 with postero-lingual extension that cradles paraconid of M^1.

Of these features, the last four are present in the material referred to *Petramops creaseri*.

The family comprises approximately 80 living species (Honacki *et al.*, 1982) and more than 15 fossil species (Legendre, 1985; Table 2). Living species have recently been referred to as many as 12 genera (e.g. Freeman, 1981; Honacki *et al.*, 1982) or as few as nine (e.g. Legendre, 1984b). Fossil species are referred to an additional two genera (Legendre, 1984a; 1985). Representative specimens of generic and subgeneric groups recognized in these recent studies have been examined and compared with the new Australian fossil species.

The most recent systematic revision of the family Molossidae is that of Legendre (1984b). From analysis of dental characters in living and fossil Molossidae, Legendre (1984b, 1985) recognized three subfamilies: the Tadaridinae, Molossinae and Cheiromelinae. In his revision Legendre erected the new genus *Rhizomops* in which he placed the living American tadaridine *Tadarida brasiliensis* and a number of Tertiary and Pleistocene taxa from the Old and New Worlds. Species of *Rhizomops* were considered to be more plesiomorphic than any other living tadaridines, lacking several derived features found in other species of *Tadarida*. Legendre retained *Tadarida* for all other species usually referred to that genus (e.g. by Freeman, 1981; and by Honacki *et al.*, 1982). In *Tadarida* he also included *Chaerephon* and *Mops* as subgenera. The basic taxonomic framework proposed by Legendre, including

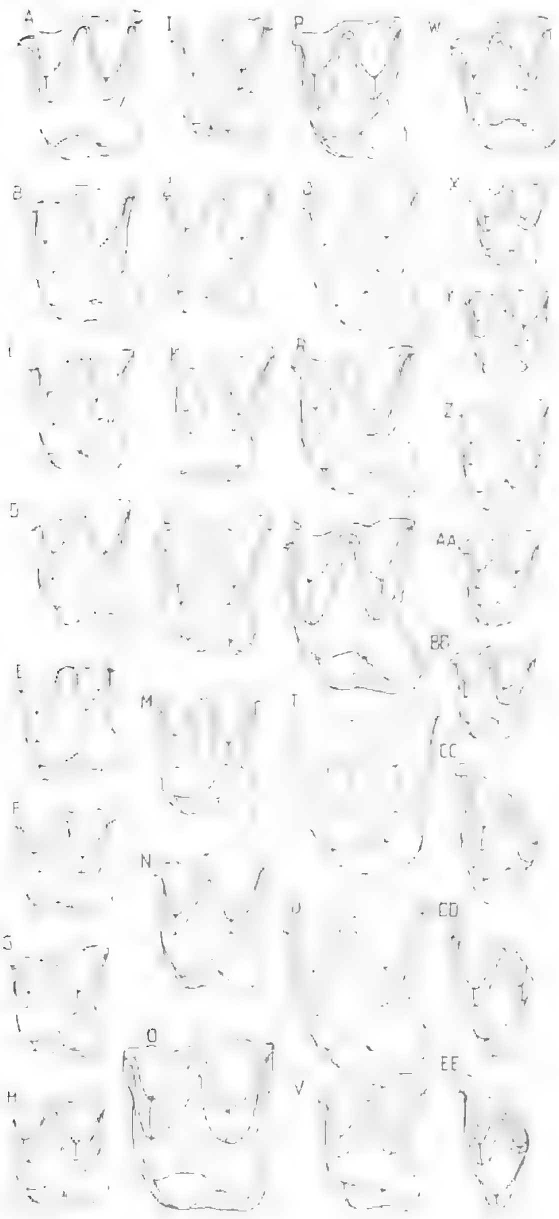

FIG. 5. Camera-lucida drawings (X 8) of M^1 in representative molossids discussed in text: A, AM M8509 *Mormopterus (Micronomus) beccarii*; B, AM M8904 *M. (M.) planiceps*; C, AM M5188 *M. (M.) loriae*; D, SAM M8372 *M. (M.) loriae*; E, AM M5041 *M. (M.) ? norfolkensis*; F, CG 1983-2257 *Mormopterus (Mormopterus)* sp. (?South American); G, CG 1983-2268 *M. (M.) minutus*; H, CG 1983-2269 *M. (M.) minutus*; I, AMNH 165626 *M. (M.) kalinowski*; J, BMNH 66.6060 *M. (M.) jugularis*; K, AMNH 217024 *M. (Platymops) setiger*; L, BMNH 73.522 *M. (Sauromys) petrophilus*; M, AM M8132 *Rhizomops brasiliensis*; N, AMNH 245636 *Nyctinomus aegyptiacus*, O, AM M7190 *Nyctinomus australis*; P, AMNH 78219 *Nyctinomops laticaudata*; Q, AM M9951 *Chaerephon pumila*; R, AM M9178 *C. plicata*; S, AM M135 *C. jobensis*; T, AMNH 88115 *Otomops martiniensis*; U, AMNH 161862 *Mops condylura*; V, AMNH 241087 *Mops (Xiphonycteris) spurrelli*; W, AMNH 181533 *Molossops temminckii* (X 4); X, AMNH 94625 *M. (Cynomops) brachymeles* (X 4); Y, AMNH 48855 *Myopterus albatus* (X 4); Z, AMNH 97022 *Eumops perotis* (X 4); AA, AMNH 178692 *Promops centralis* (X 4); BB, AMNH 123306, *Molossus ater* (X 4). Camera-lucida drawings (X 8) of the M^3 of representative molossids discussed in text: CC, BMNH 66.6060 *Mormopterus (M.) jugularis*; DD, AM M9951 *Chaerephon pumila*; EE, BMNH 73.522 *M. (Sauromys) petrophilus*.

recognition of the genus *Rhizomops*, is largely adopted in this paper (but see discussion).

Recently, however, Mahoney and Walton (1988) have noted that the name *Nyctinomus* has priority over *Tadarida* Rafinesque 1914. Evidently *Nyctinomus* was erected by Geoffroy in 1813, and not 1818 as usually reported (see Mahoney & Walton for full discussion). In this paper the name *Nyctinomus* replaces *Tadarida* throughout. Following the provision of Article 40a of the International Code of Zoological Nomenclature (1985), the subfamily Tadaridinae Legendre, 1984b is retained despite the generic seniority of *Nyctinomus* over *Tadarida*.

COMPARISON WITH LIVING FORMS

The Riversleigh fossil molossid differs from species of *Molossus*, *Molossops*, *Eumops*, *Promops*, *Myopterus* and *Cheiromeles* in its tall, conical, isolated hypocone and well-developed heel on M^1 (Fig. 5), its only moderately reduced M^3 and its antero-posteriorly compressed trigonids on M_{1-3}. In these features it is more similar to species of Legendre's (1984b, p.426) subfamily Tadaridinae, which includes all other genera of living molossids.

Among tadaridine species groups, the Riversleigh fossil probably most closely resembles in dental morphology the American species *Rhizomops brasiliensis*. It shares a number of features with *R. brasiliensis* which are not all shared with other species of *Nyctinomus*. These features include nyctalodont lower molars; P_4 with rudimentary metaconid; M^1 with well-defined paraloph and metaloph; M^3 with less well-developed paraloph; M^1 hypocone tall and isolated from protocone and postprotocrista by a depression; P_2 and P_4 oriented longitudinally rather than transversely in the axis of the lower tooth row (see Fig. 6), and M^3 only moderately reduced. The Australian fossil differs from the living American species in, among other features, its loss of I_3, marked antero-posterior compression of M_{1-3} trigonids, and less postero-lingually extended heel on M^1.

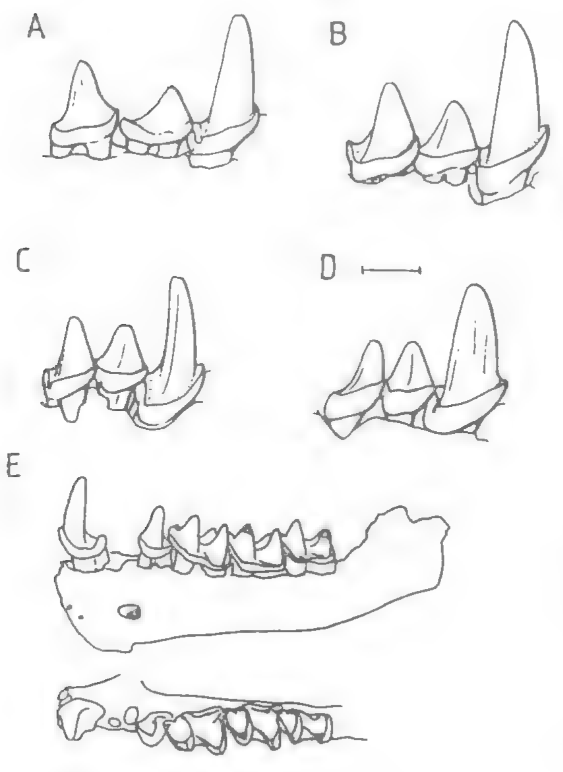

FIG. 6. Orientation of lower premolars (P_2 and P_4) in the tooth row of representative molossids: Type A, premolars longitudinal in the tooth row, e.g., *Nyctinomops macrotis* BMNH 20.7.14.33; Type B, premolars only slightly oblique to the tooth row, e.g. *Nyctinomus teniotis* BMNH 97.11.10.2; Type C, premolars more oblique to the tooth row, e.g., *Chaerephon plicata* BMNH 9.1.5.508; and, Type D, premolars transverse to the tooth row, e.g., *Mops mops* BMNH 60.1597. The Riversleigh molossid (E, buccal and occlusal views) appears to be most similar to Type B. Scale indicates 1 mm. (After Legendre, 1983; fig. 2).

With species of the tadaridine *Nyctinomops* from Central and South America, the Riversleigh fossil shares the loss of I_3; nyctalodont lower molars; a well-developed paraloph and metaloph on M^1; a poorly-developed paraloph on M^3; a tall isolated hypocone on M^1; P_2 and P_4 in the longitudinal axis of the lower tooth row, and marked antero-posterior compression of M_{1-3} trigonids. Species of *Nyctinomops* differ from the Australian fossil in the loss of the P_4 metaconid, a more reduced M^3 and convergent paraloph and metaloph on M^1.

Species of the tadaridine genus *Mormopterus* are commonly divided into three subgeneric groups: species of *Mormopterus, Sauromys* and *Platymops* (e.g. Freeman, 1981; Honacki *et al.,* 1982). Legendre (1984b) further divided the genus into the subgenera *M. (Mormopterus)* for African, Madagascan and American species of *Mormopterus* (as well as the poorly-known Asian species *M. doriae),* and *M. (Micronomus)* for Australasian species.

The monotypic southern African species *M. (Sauromys) petrophilus* differs from the Australian fossil species in, among other features, its myotodont lower molars (where the hypocristid extends from the hypoconid to the entoconid, isolating the hypoconulid), its loss of the metaloph on M^1 and its more reduced M^3.

The monotypic East African species *M. (Platymops) setiger* differs from the Riversleigh molossid in its myotodont lower molars, its loss of the metaconid on P_4, its lack of both paraloph and metaloph on M^1, and the transverse orientation of P_2 and P_4 in the lower tooth row. It further differs from the Australian fossil in the connection by crests of the anterior portion of the postprotocrista to the poorly-developed hypocone on M^1.

African and Madagascan species of *Mormopterus* (e.g. *M. jugularis*) differ from the Riversleigh molossid in retention of I_3, their myotodont or sub-myotodont lower molars, loss of the metaconid on P_4, and the connection by crests of the postprotocrista to the hypocone on M^1.

Central and South American species of *Mormopterus* (e.g. *M. kalinowski*) are more similar to the Riversleigh molossid but differ in their myotodont or sub-myotodont lower molars and the loss of the P_4 metaconid.

The poorly-known *M. doriae* from Sumatra appears to be no longer represented in world museum collections, the type specimen apparently being lost from the Genova Museum during a flood. Judging from descriptions by Anderson (1907), Hill (1961) and Legendre (1984b), this

Asian species appears to differ from the Australian fossil at least in retaining the I_3. In his comparison of *M. doriae* with other species of *Mormopterus*, Anderson (1907) concluded that it differs only slightly from the Malagasy *M. jugularis* and that it is much more similar to African *Mormopterus* species than Australasian ones.

Australasian (i.e. Australian, New Guinean and Molucca Island) species of *Mormopterus*, (*beccarii, planiceps, norfolkensis*) differ from the Riversleigh species in their loss of the P_4 metaconid, the connection of the M^1 postprotocrista and hypocone by crests, and the transverse orientation of P_2 and P_4 in the lower tooth row. *Mormopterus beccarii* further differs from the Riversleigh fossil in its myotodont lower molars.

All other living species of tadaridine bats are referred to the *Nyctinomus, Chaerephon, Mops* and *Otomops* species groups, which are considered to comprise as many as four genera (Freeman, 1981) or as few as two genera (Legendre 1984b, who includes *Chaerephon* and *Mops* as subgenera in *Nyctinomus*).

Species of *Nyctinomus (Nyctinomus)* differ from the Riversleigh molossid in the loss of the P_4 metaconid, the lack of the metaloph on M^1 and the lack of marked antero-posterior compression of the lower molar trigonids. The large African forms further differ from the Australian fossil in the connection of the M^1 hypocone to the postprotocrista by crests, lack of a paraloph on M^1 and more reduced M^3. Most *Nyctinomus* species lack the I_3, and in this way resemble the Riversleigh fossil, but one species, the Palearctic *N. teniotis*, retains the I_3.

African, Asian and Australian species of *Chaerephon* differ from the Australian fossil in the lack of the P_4 metaconid, the lack of paraloph and metaloph on M^1, the presence of crests linking hypocone to postprotocrista, a more reduced M^3 and the lack of antero-posterior compression of the lower molar trigonids.

African, Malagasy and Asian species of *Mops* (including *Xiphonycteris*), differ from the Riversleigh fossil in the same features as do species of *Chaerephon*, but in some African species a weak paraloph is present. Species of *Mops* further differ from the fossil in the transverse orientation of the P_2 and P_4 in the lower tooth row and the distal opening of the protofossa on M^1.

Afroasiatic species of *Otomops* differ from the Riversleigh fossil in the same features that *Chaerephon* does, but have a less reduced M^3. Thus, they more closely resemble both the Riversleigh fossil and non-African species of *Nyctinomus (Nyctinomus)*.

Comparison With Fossil Forms

The Miocene species from Riversleigh is one of 13 Tertiary molossids now known. These are referred to five genera: *Nyctinomus, Mormopterus, Rhizomops, Cuvierimops* and *Wallia* (Table 2).

The oldest identified molossid, the North American Late Eocene (Uintian) *Wallia scalopidens* Storer, 1984, is known from four isolated upper molars. It was originally described as a proscalopid insectivore, but was recognized as a molossid by Legendre (1985). Its affinities with other molossids are not clear, but from Storer's (1984) figures and description it appears to resemble the Riversleigh fossil in most of its features, including the separation of the hypocone from the postprotocrista by a shallow valley and its only moderately reduced M^3. However, it seems to differ in M^1 in its poor heel development, "low" hypocone and indistinct paraloph and metaloph (? para- and metaconule of Storer) and, in M^3, in its antero-lingually directed parastyle and bulbous protocone. Legendre (1985) has tentatively placed *Wallia scalopidens* in the Tadaridinae, the subfamily to which all Tertiary fossil molossids are currently referred.

Late Eocene and early Oligocene French and Spanish species of the genus *Cuvierimops* appear to be early members of the subfamily Tadaridinae (Legendre, 1985). They are characterised by: nyctalodont lower molars; P_4 with metaconid; a well-defined, conical, isolated hypocone on M^{1-2} separated from the protocone and postprotocrista; paraloph and metaloph on M^1; and slightly reduced M^3 (Legendre & Sigé, 1984) — features also shared with the Australian Miocene fossil. However, the type species *C. parisiensis* differs from the Riversleigh form in its remarkably short C_1 (which is only just taller than the P_4) and less well-developed heel and hypocone crests on the upper molars.

The late Oligocene species *Mormopterus (Neomops) faustoi* (Paulo Couto, 1956) from Brazil is the sole species of the subgenus (erected by Legendre, 1984a) and South America's oldest fossil bat (Paulo Couto & Mezzalira, 1971). It differs from the Riversleigh species in its retention of I_3, its myotodont lower molars and its lack of paraloph and metaloph on M^1.

TABLE 2. Tertiary representatives of the family Molossidae (after Hand, 1984).

		EUROPE	AFRICA	ASIA	AUSTRALIA	N.AMERICA	S.AMERICA
PLIOCENE							
MIOCENE	*Nyctinomus teniotis*[13]	X					
	?Chiroptera, cf. Molossidae[12]	X	X				
	Nyctinomus engesseri[11]	X					
	Mops monslapidensis[10]	X					
	Nyctinomus leptognathus	X					
	Tadaridinae indet.[9]	X					
	Petramops creaseri[8]				X		
	Mormopterus (Hydromops) helveticus[7]	X					
OLIGOCENE	*Mormopterus (Hydromops) stehlini*[7]	X					
	Rhizomops cf. *R. brasiliensis*[3]	X					
	Mormopterus (Neomops) faustoi[6]						X
	Tadaridinae indet.[5]	X					
EOCENE	*Cuvierimops* sp.[3]	X					
	Cuvierimops parisiensis[4]	X					
	Cuvierimops spp.[3]	X					
	Wallia scalopidens[2]					X	
	Vespertilionoidea ? Molossidae[1]					X	
PALEOCENE							

[1]McKenna *et al.*, 1962; Legendre 1985
[2]Storer, 1984; Legendre, 1985
[3]Legendre, 1985
[4]Lgendre and Sigé, 1984
[5]Sigé, 1971; Legendre, 1985
[6]Paula Couto, 1956; Paula Couto and Mezzalira, 1971; Legendre, 1984a
[7]Revilliod, 1920; Legendre, 1984a
[8]Hand and Archer, 1985
[9]Adrover, 1968; Legendre, 1985
[10]Rachl, 1983; Legendre, 1985; Mahoney and Walton, 1988
[11]Lavocat, 1961; Engesser, 1972; Rachl, 1983; Mahoney and Walton, 1988
[12]Sigé, 1982
[13]Aguilar *et al.*, 1985; Legendre, 1985; Mahoney and Walton, 1988

The first appearance of species of *Rhizomops* in the fossil record occurs in France in Oligocene-Miocene transitional sediments (Legendre, 1985, fig. 16; Table 2). This form, described as *Rhizomops* sp. cf. *R. brasiliensis*, differs from the Riversleigh fossil (and modern *Rhizomops brasiliensis)* in, among other features, the development of the metaloph which arises from the lingual base of the metacone rather than the anterior flank of the metacone (Legendre, 1985).

The French Early Miocene species *Mormopterus (Hydromops) stehlini* and the middle Miocene species *M. (H.) helveticus* from deposits in France, Germany and Switzerland, differ from the Australian Miocene species in: their myotodont lower molars; loss of the P_4 metaconid; lack of the paraloph and metaloph on M^1; presence of crests on M^1 linking the hypocone and postprotocrista; M^3 more reduced such that the premetacrista is shorter than the postparacrista; P_2 and P_4 oriented transversely in the lower tooth row, and lack of antero-posterior compression of the lower molar trigonids. Two German Steinberg species, described by Rachl (1983) as *M. kalorhinus* and *M* sp., have been synonymised with *M. (H.) helveticus* by Legendre (1985).

The Middle Miocene species *Nyctinomus engesseri* from deposits in Germany, Switzerland and Morocco, and the slightly older German *N. leptognathus*, differ from the Riversleigh molossid in their retention of I_3 and absence of P_4 metaconid. *Nyctinomus leptognathus* is further distinguished by its lack of the paraloph on M^1 and presence of crests on M^1 linking the hypocone to the postprotocrista.

The Recent species *N. teniotis* first appears in the fossil record in the Late Miocene Salobrena deposit in Spain. It differs from the Australian fossil

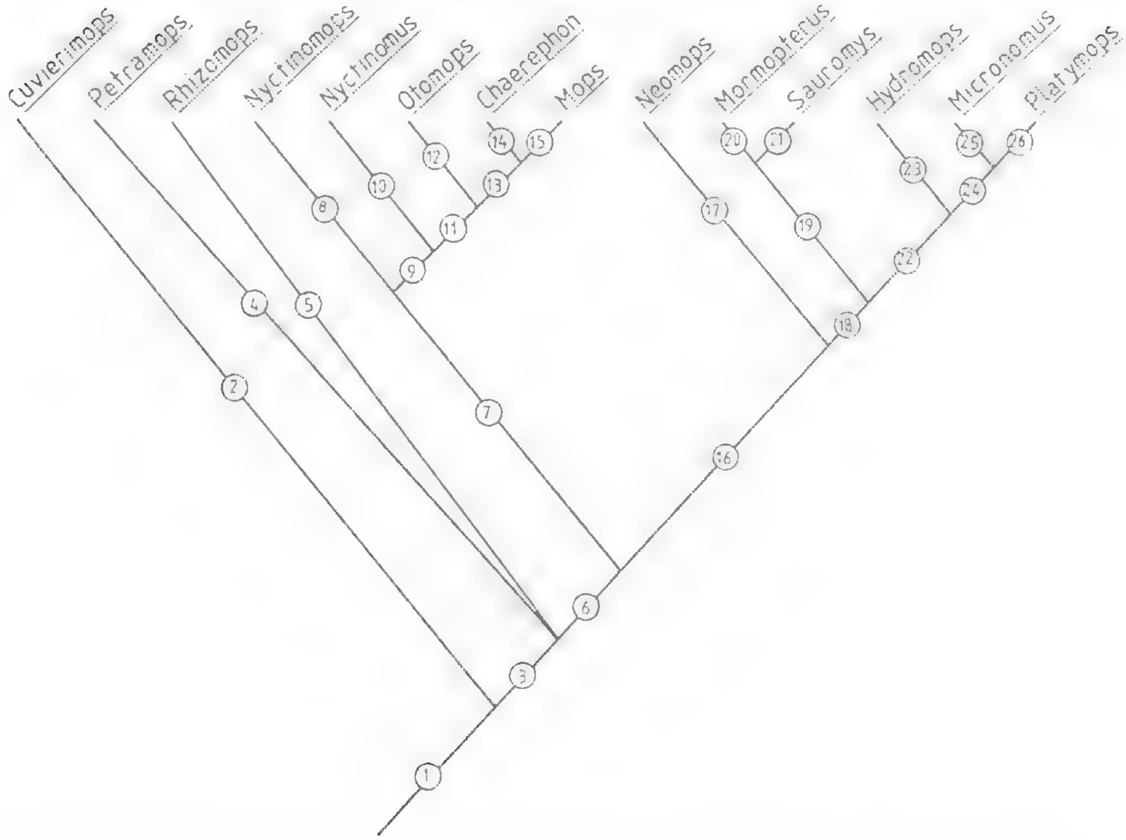

FIG. 7. Hypothesis of phylogenetic relationship of the Riversleigh fossil molossid (*Petramops creaseri*) to living and fossil molossids based on dental characters. Potential apomorphies include: 1, M^1 with heel and tall isolated hypocone, little reduced P_2, lower molars with well developed paraconids; 2, very short C_1, loss of I_3; 3, on $M^{1,2}$ hyper-development of hypocone and crests emanating from hypocone; 4, loss of I_3; 5, low coronoid process; 6, loss of P_4 metaconid; 7, low coronoid process; 8, upper incisors parallel, on M^{1-2} paraloph and metaloph convergent, M_3 reduced; 9, on M^{1-2} disappearance of metaloph, regression of paraloph and hypocone linked by crests to postprotocrista; 10, M^3 reduced; 11, upper incisors parallel, on M^{1-2} hypocone reduced and protofossa open posteriorly; 12, on M^{1-2} hypocone and heel reduced and paraloph and metaloph absent, P^2 large, P_2 elongated; 13, M^3 reduced; 14, $P_{2,4}$ relatively transverse in jaw; 15, on M^{1-2} hypocone reduced and protofossa more open posteriorly; 16, myotodonty or sub-myotodonty of M_{1-3}; 17, on M^{1-2} loss of metaloph and protofossa closed; 18, loss or reduction of P^2; 19, myotodonty of M_{1-3}; 20, on M^{1-2} hypocone crests parallel to long axis of tooth row, P^2 lost or reduced to a spicule; 21, on M^{1-2} hypocone reduced and regression of paraloph and metaloph, $P_{2,4}$ elongated, P_2 with second cusp; 22, $P_{2,4}$ transverse in jaw; 23, on M^{1-2} metaloph absent and protofossa tending to open posteriorly, M^3 reduced; 24, upper incisors with internal cingular cusp; 25, P^2 present, nyctalodont and myotodont lower molars, lower incisors with V-shaped indentation; 26, on M^{1-2} hypocone and heel reduced, upper incisors with two cusps. (See text, and also Legendre, 1984a, b, 1985).

species in features described above for living species of *Nyctinomus (Nyctinomus)*.

The Middle Miocene German *Mops monslapidensis* (Rachl, 1983; formerly *Meganycteris monslapidensis* before synonymy with *Mops* by Legendre, 1985) differs from the Riversleigh species in: lack of the P_4 metaconid; lack of paraloph and metaloph on M^1; presence of crests on M^1 linking the hypocone to the postprotocrista; reduced M^3; having P_2 and P_4 obliquely oriented in the lower tooth row; and lack of antero-posterior compression of the lower molar trigonids.

Other Tertiary molossids listed in Table 2 (Tadaridinae indet.; ?*Nyctinomus* sp.; Vespertilionoidea, ?Molossidae; and ?Chiroptera cf. Molossidae) are at present too poorly-known to allow useful comparisons with the Riversleigh fossil species.

DISCUSSION

Petramops creaseri is referred here to Legendre's (1984b, p. 426) molossid subfamily Tadaridinae on the basis of its well-developed heel on M^1 and its nyctalodont lower molars. Features that exclude it from the subfamilies Molossinae and Cheiromelinae (Legendre, 1984b, p. 425) are its tall isolated hypocone, its slightly reduced P_2 and its lower molars with well-developed paraconids.

The phylogenetic position of *Petramops* within the Tadaridinae is more difficult to determine. There is still much debate about the interrelationships of extant higher-level molossid taxa (e.g. Freeman, 1981; Legendre, 1984b) and the Tertiary history of this group is not well understood. However, on the basis of dental characters, an hypothesis of the phylogenetic relationships of *Petramops* to all other adequately-described fossil and living molossids is given in Figure 7. Characters used in this analysis were selected on the basis of their preservation in the Riversleigh material as well as their apparent value in delimiting molossid species groups (see Freeman, 1981; Legendre, 1984a, b, 1985). Polarity of character states was determined by outgroup comparison in which the family Vespertilionidae was considered to be the sister group of the Molossidae (following, for example, Miller, 1907; see also Hand, 1984).

In this hypothesis, five higher-level taxonomic groups are recognised: species of *Mormopterus* s.l., *Nyctinomus* s.l., *Rhizomops, Petramops* and *Cuvierimops*. Species of *Cuvierimops* appear to be plesiomorphic with respect to all other molossids, and *Rhizomops* plesiomorphic to all living molossids. On the basis of these features, species of *Nyctinomops, Nyctinomus, Otomops, Chaerephon* and *Mops* form a monophyletic group, as do species of *Mormopterus* s.l. The Australian Miocene taxon *Petramops creaseri* appears to be most similar to species of *Cuvierimops* and *Rhizomops*, perhaps on the basis of symplesiomorphies, and to lie outside the radiation of living Australian molossids (see below).

The hypothesis is not wholly inconsistent with alternative hypotheses of tadaridine evolutionary relationships generated by other authors (see, for example, Freeman, 1981; Legendre, 1984b, 1985). The most significant differences concern relationships of species of *Rhizomops, Otomops* and *Nyctinomops*. For example, in her review of extant species of the family Molossidae, Freeman (1981) recognized two main groups, the *Mormopterus*-like bats and the *Nyctinomus*-like bats, and considered *Nyctinomus (Nyctinomus)* (including *Rhizomops*) and *Mormopterus* s.l. to be the two most primitive groups to which all other genera can be related. In her monophyletic *Nyctinomus*-group she also included species of *Nyctinomops, Chaerephon, Mops* and *Otomops* (as well as *Eumops, Promops* and *Molossus)* and suggested close phylogenetic relationships between species of *Nyctinomus* and *Chaerephon, Chaerephon* and *Mops*, *Nyctinomus* and *Otomops* and between *Nyctinomus* and *Nyctinomops*. Freeman (1981) also placed *'Nyctinomus' brasiliensis* and *Nyctinomus aegyptiacus* phenetically close to species of *Mormopterus* and suggested a close phylogenetic relationship between species of *Nyctinomus (Nyctinomus)* and *Mormopterus* s.l. Species of *Mormopterus* (s.s. but including *Micronomus), Platymops* and *Sauromys* were recognized as a monophyletic group. Characters used in Freeman's cladistic analysis were ear shape, development of basisphenoid pits, degree of palatal emargination, wrinkling of the lips, wing shape, incisor number, reduction of P^2 and M^3, and development of M^1 metaconule (?hypocone).

Legendre's (1984b, 1985) systematic review of extant and extinct tadaridines also recognised monophyly of *Mormopterus* s.l. as well as a group containing species of *Rhizomops, Nyctinomus, Chaerephon* and *Mops*. Species of *Otomops* were suggested to lie just outside this latter group while those of *Nyctinomops* may share a close phylogenetic relationship with species of *Rhizomops*. Legendre (1985) suggested that species of *Rhizomops* may be descendants of the *Cuvierimops* lineage, a lineage which may also have spawned the *Nyctinomus* s.l. species group. Molossid stock of similar grade was thought (Legendre, 1985) to have given rise to species of *Mormopterus* s.l.

Irrespective of the true phylogenetic position of species of *Rhizomops, Otomops* and *Nyctinomops*, dental features used in this study place the Riversleigh fossil molossid outside the radiation of living Australian molossids. The Miocene fossil appears to lack several derived traits exhibited by living Australian molossids that exclude it from the *Mormopterus* s.l. and *Nyctinomus* s.l. species groups. These derived features lacking in *Petramops creaseri* include: myotodonty of lower molars; P_4 metaconid loss; loss of paraloph and metaloph on M^{1-2}; connection of M^1 hypocone to postprotocrista; transverse orientation of premolars in lower tooth row; and reduction of M^3.

Although the precise relationship of *Petramops creaseri* to species of *Rhizomops, Cuvierimops, Mormopterus* s.l. and *Nyctinomus* s.l. is not yet clear, these lineages appear to have diverged sometime between the Late Eocene and Late Oligocene (Table 2). Species of *Cuvierimops* appear in the western European fossil record during the Late Eocene and disappear in the early Oligocene. Species of *Rhizomops* are known from the latest Oligocene and Middle Miocene of western Europe as well as the Pleistocene and Recent of central America. They are thought to have diverged from ancient Old World molossid stock (possibly the *Cuvierimops* lineage) before making an Early Oligocene trans-Atlantic crossing into South America (Legendre, 1984b; fig. 18b). Species of *Mormopterus* s.l. first appear in the Late Oligocene of South America and those of *Nyctinomus* s.l. in the Middle Miocene of Europe. *Petramops creaseri* is Australia's only known Tertiary molossid, occurring in the oldest Australian fossil deposits that have produced identifiable fossil bats.

As indicated by the superbly-preserved postcranial remains of the French *Cuvierimops parisiensis*, molossids had already developed their present-day wing structure, and possibly their capacity for long, sustained flight, by the Late Eocene. Living molossids, as represented by *Rhizomops brasiliensis*, exhibit an extreme adaptation in the morphology and biochemistry of their flight muscles for high energy expenditure over extended time periods relative to all other bats (Foehring & Hermanson, 1984). Today, *Rhizomops brasiliensis* migrates seasonally over 1,300 km across the American continent to reach the warmer latitudes of Mexico for the winter months (Fenton, 1983). During the Early Oligocene, an ancestral *Rhizomops* species appears to have made a trans-Atlantic crossing between Africa and South America (Legendre, 1984a, b, c). At that time the distance between these two continents may have been as much as 3,500 km (Webb, 1978) although offshore volcanic island arcs may have served to reduce that distance considerably (McKenna, 1980).

It seems likely that members of the *Petramops* lineage, like other molossids, were proficient long-distance fliers and that while water gaps separating Australia and Eurasia in, say, the Late Eocene may have prevented molossids from reaching Australian shores, gaps existing by the Middle to Late Oligocene probably would not (Audley- Charles, 1981, fig. 4.5). Certainly, by the Early to Middle Miocene representatives of Old World bat families not recognised for sustained flight capability were well-established in Australia, the Riversleigh deposits being rich in hipposiderid and megadermatid fossil remains. In the case of at least the megadermatids, a number of independent colonization events appears to have occurred before the Early to Middle Miocene (Hand, 1985; Archer *et al.*, 1989), while the diversity of the Riversleigh hipposiderid fauna also strongly suggests that bats first entered Australia before the Early Miocene and that migration routes had been available even for bats not noted for long distance flight.

Because *Petramops creaseri* does not appear to have given rise to the groups of molossids now living in Australia, more than one colonization of Australia by molossids is envisaged. Subsequent or coincident molossid colonizations would have involved species of *Nyctinomus, Chaerephon* and *Mormopterus* (Freeman, 1981; Legendre, 1984b, c).

The family Molossidae is not well-represented in the Riversleigh fossil deposits, where it is currently known from what appears to be one individual recovered from the Gotham City Site. It is possible, however, that this may under-represent the family's status in Australia at that time. The Gotham City deposit is interpreted to comprise the remains of prey collected by the megadermatid *Macroderma* sp. Prey species apparently collected by this carnivorous megadermatid include small Miocene dasyurids, perameloids and acrobatids, juvenile petaurids, phascolarctids and pseudocheirids (these Gotham marsupials ranging from one-quarter to one-half the size of their modern counterparts), at least four hipposiderids and *Petramops creaseri*. Many mammal species preserved in the Gotham City deposit are typical of those found in contemporaneous Riversleigh deposits, but others, including *Petramops creaseri*, are unique to the Gotham City Site and appear to have been brought from outside the immediate environment by megadermatids.

The immediate palaeoenvironment of the Middle Miocene Riversleigh deposits is considered to have been dense rainforest (Archer *et al.*, 1989). Molossids (with their high aspect wings) are less capable of manoeuvring in confined spaces than, for example, hipposiderids (Hill & Smith, 1984) and, by modern analogy, would be expected to have been foraging primarily in open areas above or at the edges of the canopy rather than within the lower, more cluttered levels of the rainforest. The very large Gotham megadermatid may have been capable of feeding in both areas, ambushing vertebrate prey within the forest and at its edges as its descendant *Macroderma gigas* appears to do today (Van Dyck, 1980; Tidemann *et al.*, 1985). Nevertheless, a fast, high-flying and possibly crevice-dwelling molossid presumably would not be easy prey for a megadermatid and may explain why molossids are poorly represented in the Gotham City deposit itself. Alternatively, the Gotham molossid and megadermatid may have been sharing the same diurnal roost, although Tertiary molossids do not appear to have been as cavernicolous as their contemporaries and are more commonly preserved as whole skeletons in strictly lacustrine deposits (Sige, 1971).

In summary, *Petramops creaseri* appears to be a primitive molossid that cannot be referred to species groups now living in Australia. Its affinities probably lie with ancient lineages represented in European Eocene and Oligocene deposits, lineages which may persist in the living American species *Rhizomops brasiliensis*. If the *Petramops* lineage is assumed to have been more capable of long distance flight than its Riversleigh hipposiderid and megadermatid contemporaries, then it is likely that it first colonized Australia well before the Early Miocene.

ACKNOWLEDGEMENTS

This research was funded through the Australian Research Grants Scheme (Program Grant A3 851506P to Dr Michael Archer) and the National Estates Grants Scheme (through the Queensland Museum), and was sponsored by Wang (Australia) Pty Ltd, Australian Geographic Society, MIM Pty Ltd and ICI (Australia) Pty Ltd. During this study I was supported by a Commonwealth Post-Graduate Research Award and a Department of Arts, Heritage and Environment Research Fellowship. The Australian Museum provided funds for acid-processing of the fossil-rich limestone from the Gotham City Site. Dr M. Archer, Mr H. Godthelp and many volunteers (organized by Probe through Mr J. Courtenay and Ms M. Nixon) helped with collection of the Gotham City limestone. Modern bats vital for comparisons with the fossil molossid were kindly provided by Ms L. Gibson (Australian Museum), Mr S. Van Dyck (Queensland Museum), Dr C. Kemper (South Australian Museum), Mr J.E. Hill (British Museum (Natural History)) and Dr K. Koopman and Mr W. Fuchs (American Museum of Natural History). Ms J. Taylor produced many of the figures. Two anonymous referees provided constructive criticism and much food for thought.

LITERATURE CITED

ADROVER, R. 1968. Los primeros Micromammiferos de la cuenca valenciana, en Bunol. (Nota preliminar.) *Acta Geologica Hispanica* 3: 78–80

AGUILAR, J.-P., BRANDY, L.D. AND THALER, L. 1985. La migration de Salobrena (Sud de l'Espagne). *Paleobiologie Continentale* 14: 3-17.

ALLISON, F.R. 1978. The small molossid bats in Queensland. *Australian Mammal Society Bulletin* 5(1): 43.

1983. Little Northern Mastiff-bat, *Mormopterus loriae*. Eastern Little Mastiff-bat, *Mormopterus norfolkensis*. Beccari's Mastiff-bat, *Mormopterus beccarii*. p. 524, 525, 526 (respectively) *In* Strahan, R. (Ed.), 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson: Sydney).

ANDERSEN, K. 1904. Chiropteran notes. *Ann. Mus. Civ. Stor. Nat. Genova* 3: 1-41.

ARCHER, M., HAND, S.J. AND GODTHELP, H. 1986. 'Uncovering Australia's Dreamtime'. (Surrey Beatty and Sons: Sydney). 32pp.

EVERY, R.G., GODTHELP, H., HAND, S.J. AND SCALLY, K.B. 1990. Yingabalanaridae, a new family of enigmatic mammals from Tertiary deposits of Riversleigh, northwestern Queensland. This volume.

AUDLEY-CHARLES, M.G. 1981. Geological history of the region of Wallace's Line. p. 24-35. *In* Whitmore, T.C. (Ed.), 'Wallace's Line and Plate Tectonics' (Clarendon Press: Oxford).

BARBOUR, R.W. AND DAVIS, W.H. 1969. 'Bats of America'. (University Press of Kentucky: Lexington).

ENGESSER, B. 1972. Die obermiozane Säugetierfauna von Anwil (Baselland). *Naturforsch. Ges. Baselland, Tätigkeitsber.* 28: 37–363.

FELTEN, H. 1964. Zur Taxonomie indo-australischer Fledermäuse der Gattung *Tadarida* (Mammalia: Chiroptera). *Senck. Biol.* 45: 1–13.

FENTON, M.B. 1983. 'Just Bats'. (University of Toronto Press: Toronto).

FLANNERY, T.F. AND ARCHER, M. 1987. *Trichosurus dicksoni* and *Strigocuscus gymnotoides*, two new fossil phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. p. 527-36 *In* Archer, M. (Ed.), 'Possums and Opossums: Studies in Evolution'. (Surrey Beatty and Sons and the Royal Zoological Society of New South Wales: Sydney).

FOEHRING, R.C. AND HERMANSON, J.W. 1984. Morphology and histochemistry of flight muscles in free-tailed bats, *Tadarida brasiliensis*. *Journal of Mammalogy* 63: 388–94.

FREEMAN, P.D. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. *Fieldiana, Zoology* n.s. 7: 1–173.

GEOFFROY, É. 1813. Description des Mammiferes qui se trouvent en Égypte. p. 99-144 *In* Jomard, E.F. (Ed.), 'Description de l'Égypte on recueil des observations et des recherches qui ont été faites in Égypte pendant l'Expédition de l'armé Française. Histoire Naturelle. Tome 2, Deuxieme livre, (Volume IX), (L'Imprimerie Imperiale: Paris).

HAND, S.J. 1984. Bat beginnings and biogeography: a southern perspective. p. 853-904 *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Perth).

1985. New Miocene megadermatids (Chiroptera:Megadermatidae) from Australia with comments on megadermatid phylogenetics. *Australian Mammalogy* 8: 5–43.

1987. Phylogenetic studies of Australian Tertiary bats: a summary of PhD thesis. *Macroderma* 3: 9–12.

HILL, J.E. 1961. Indo-Australian bats of the genus *Tadarida*. *Mammalia* 25: 29-56.

1983. Bats (Mammalia: Chiroptera) from Indo-Australia. *Bulletin of the British Museum (Natural History), Zoology* 45: 103–208.

AND SMITH, J.D. 1984. 'Bats, a Natural History'. (Rigby: Adelaide).

HONACKI, J.H., KINMON, K.E. AND KOEPPL, J.W. (Eds). 1982. 'Mammal Species of the World'. (Allen Press and Association of Systematic Collections: Lawrence).

KOOPMAN, K.F. 1984. Taxonomic and distributional notes on tropical Australian bats. *American Museum Novitates* 2778: 1–48.

LAVOCAT, R. 1961. Le gisement de vertebres miocene de Beni Mellal (Maroc). Étude systematique de la faune de mammiferes. *Notes et Memoires de la Service Geologique du Maroc* 155: 29–94.

LEGENDRE, S. 1984a. Identification de deux sous-genres fossiles et compréhension phylogénique du genre *Mormopterus* (Molossidae, Chiroptera). *Compte rendu de l'Academie des Sciences, Paris* (2)298(16): 715–20.

1984b. Étude odontologique des représentants actuels du groupe *Tadarida* (Chiroptera, Molossidae). Implications phylogéniques, systématiques et zoogeographiques. *Revue suisse de Zoologie* 91: 399–442.

1984c. Essai de biogeographie phylogénique des molossidés (Chiroptera). *Myotis* 21.22: 30–36.

1985. Molossidés (Mammalia, Chiroptera) cénozoïques de l'Ancien et du Nouveau Monde; statut systématique; intégration phylogénique des donnéies. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 170: 205–27.

AND SIGÉ, B. 1984. La place du "Vespertilion de Montmartre" dans l'histoire des chiroptères molossidés. *Actes Symp. G. Cuvier* (Oct. 1982): 347–61.

MAHONEY, J.A. AND WALTON, D.W. 1988. Molossidae. pp. 146-50 *In* Walton, D.W. (Ed.), 'Zoological Catalogue of Australia'. Vol. 5. Mammalia. (Bureau of Flora and Fauna: Canberra).

MCKENNA, M.C. 1980. Early history and biogeography of South America's extinct land mammals. pp. 43-77 *In* Luckett, W.P. and Szalay, F.S. (Eds.), 'Evolutionary Biology of the New World Monkeys and Continental Drift'. (Plenum Publ. Corp.: New York).

ROBINSON, P. AND TAYLOR, D.W. 1962. Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming. *American Museum Novitates* 2102: 1–33.

MENU, H. AND SIGÉ, B. 1971. Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. *Compte rendu de l'Academie des Sciences, Paris* 272: 1735–38.

MILLER, G.S.J. 1907. The families and genera of bats. *Bulletin of the United States National Museum* 57: 1–282.

PAULA COUTO, C. de. 1956. Une chauvre-souris fossile des argiles feuilletées pléistocènes de Tremembé, etat de Sao Paulo (Brésil). *Actes 4 Congr. Internat. Quat.* 343–47.

AND MEZZALIRA, S. 1971. Nova conceituaçao geocronologica de Tremembé, Estado de Sao Paulo, Brasil. *Acad. Brasil* Cienc., An. 43: 473–88.

RACHL, R. 1983. Die Chiroptera (Mammalia) aus den mittelmiozänen Kalken des Nordlinger Rieses (Suddeutschland). Inaugural-Dissertation, Ludwig-Maximilians-Universität: München.

REVILLIOD, P. 1920. Contribution l'etude des chiroptères des terrains tertiaires. 2ᵉ partie. *Mém. Soc. pal. suisse* 44: 63–129.

SIGÉ, B. 1971. Anatomie du member antérieur chez un chiroptère molossidé (*Tadarida* sp.) du Stampien de Céreste (Alpes-de-Haute-Provence). *Palaeovertebrata* 4: 1–38.

1982. Contributions à l'étude des micromammifères du gisement miocène supérieur de Montrédon (Hérault) 4. Les chiroptères. *Palaeovertebrata* 12: 133–40.

HAND, S.J. AND ARCHER, M. 1982. An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related to Miocene representatives from France. *Palaeovertebrata* 12: 149–71.

TATE, G.H.H. 1952. Results of the Archbold Expeditions. No. 66. Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. *Bulletin of the American Museum of Natural History* 98: 563–616.

TIDEMANN, C.R., PRIDDEL, D.M., NELSON, J.E. AND PETTIGREW, J.D. 1985. Foraging behaviour of the Australian Ghost Bat, *Macroderma gigas* (Microchiroptera: Megadermatidae). *Australian Journal of Zoology* 33: 705–13.

TROUGHTON, E. le G. 1967. 'Furred animals of Australia' 9th ed. (Angus and Robertson: Sydney).

VAN DYCK, S. 1980. Ghost Bat and death cries from the rainforests of McIlwraith Range, Cape York Peninsula. *N. Qd Nat.* **45**: 3–5.

VAUGHAN, T.A. 1966. Morphology and flight characteristics of molossid bats. *Journal of Mammalogy* **47**: 249–60.

WEBB, S.D. 1978. A history of savanna vertebrates in the New World. Part II: South America and the great interchange. *Annual Review of Ecology and Systematics* **9**: 393–426.

WILEY, E.O. 1981. 'Phylogenetics: the Theory and Practice of Phylogenetic Systematics'. (John Wiley and Sons: New York).

WOODBURNE, M.O., TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication, South Australian Department of Mines and Energy* **5**: 347–63.

YINGABALANARIDAE, A NEW FAMILY OF ENIGMATIC MAMMALS FROM TERTIARY DEPOSITS OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

M. ARCHER, R.G. EVERY, H. GODTHELP, S.J. HAND AND K.B. SCALLY

Archer, M., Every, R.G., Godthelp, H., Hand, S.J. and Scally, K.B. 1990 3 31: *Yingabalanaridae*, A New Family of Enigmatic Mammals from Tertiary Deposits of Riversleigh, Northwestern Queensland. *Mem. Qd Mus.* **28**(1): 193-202. Brisbane. ISSN 0079-8835.

A new genus and species, *Yingabalanara richardsoni*, based on a single tooth is described from limestone deposits between Early and Middle Miocene in age on Riversleigh Station, northwestern Queensland. Although it represents a new family of mammals, the Yingabalanaridae, it is not clear to which higher level systematic group this family belongs. There are at least six possible contradictory interpretations of the structure of the tooth depending on whether the specimen represents a left or right lower tooth, whether or not the drepanid relationships evident in the region of the metakid are convergent on those of 'tribotheres', and whether or not it retains a plesiomorphic talonid of the kind that characterises derived 'tribotheres' and eutherians (*sensu* Gill, 1872 *nec* Huxley, 1880). It may lack a plesiomorphic talonid and hence have converged on the 'tribotherian' and eutherian condition in its development of this structure. Alternatively, presuming that it retains a plesiomorphic talonid, if it is a right molar, the autapomorphically hypertrophied talonid is higher than the relatively reduced trigonid, a combination of derived features at least superficially resembling those seen (albeit in less extreme form) in adapid primates, although in other respects it departs significantly from the primate pattern. Similarities to some phyllostomoid bats are also noted. Alternatively, if it is a left molar, the association of drepanids in the region of the metakid (metaconid) is autapomorphic and unique within Eutheria but similar to that found in some 'tribotherians' such as the Late Cretaceous *Potamotelses* of North America. However, interpreted as a left molar, it differs from all 'tribotheres' in having a relatively hypsodont talonid and a very high Hypobli quid (cristid obliqua). Other less plausible phylogenetic interpretations are considered. An omnivorous diet is indicated. This species is part of the Upper Site Local Fauna which collectively indicates a lowland rainforest biota in northwestern Queensland sometime between the Early and Middle Miocene.

☐ *Mammalia, Eutheria, Marsupialia, Placentalia, 'tribotheres', Potamotelses, Yingabalanaridae, Yingabalanara, Tertiary, Queensland, Riversleigh, thegosis, convergence, rainforest.*

M. Archer, H. Godthelp and S.J. Hand, School of Zoology, University of New South Wales, PO Box 1, Kensington, NSW 2033, Australia; R.G. Every and K.B. Scally, The Thegotics Foundation Trust, PO Box 4624, Christchurch, New Zealand; 13 December, 1988.

In June, 1985, a fossil-rich deposit in Tertiary limestone was discovered on the western flank of Godthelp Hill, Riversleigh Station, northwestern Queensland. This site was first excavated in 1986 at which time it became known as Upper Site.

Like many of Riversleigh's newly discovered sites, this one contains a diverse fauna indicative of a rainforest palaeoenvironment (Archer *et al.*, 1989). However, Upper Site material has produced a particularly diverse fauna including several forms unique to this deposit. Among the unique elements is the taxon described here as *Yingabalanara richardsoni*. Although this form is represented only by a single lower molar, we consider description appropriate at this time for two reasons: first, it represents a highly distinctive taxon indicative of a previously unrecognised clade of Australian mammals; and, second, because we have acid-processed approximately 2 tonnes of material over two years and yet obtained only the single molar, we consider it unlikely that more material will turn up in the near future, at least from Upper Site.

The dental terminology used here, where it departs from the conventional Cope-Osborn system (e.g., as applied to marsupials by Archer, 1976), follows Every (1972, 1974). The thegotic nomenclature of Every distinguishes terms for blades (= crests in more conventional terminology) by use of capital letters (e.g. Prototransversid) and those for cusps by lower case (e.g. protoakid). Also, names for cusps incorporate the stem 'aki'. Figure 2 illustrates the relationship between the thegotic and Cope-Osborn terminology as it applies to the holotype of *Yingabalanara richardsoni*. Use of thegotic nomenclature represents an effort to involve functional concepts in the nomenclature used to describe mammalian teeth (Every, 1974), something which is not implicit in the more conventional Cope-Osborn nomenclature.

We are in considerable doubt about the basic structure of this tooth. It may be: *1*, a eutherian (*sensu* Gill, 1872 — i.e. marsupial plus placental; Aplin & Archer, 1987) left molar displaying a morphological pattern unique within Eutheria; *2*, a eutherian right molar with a pattern at least superficially similar to that seen in some adapid primates and phyllostomoid bats but otherwise unknown among marsupials; *3*, a 'tribotherian' left molar resembling the Late Cretaceous *Potamotelses* but with an autapomorphically hypsodont talonid and enlarged Hypobiliquid (= cristid obliqua); *4*, a left molar of a pre-'tribotherian' mammal with a convergently developed talonid-like structure; *5*, a right molar of a pre-'tribotherian' mammal with a convergently developed trigonid-like structure; or *6*, a zalambdodont eutherian that has redeveloped a phylogenetically lost talonid. Because of this uncertainty, it is necessary to take the unusual step of providing six contradictory interpretations of the tooth.

Three of us (MA, HG and SH) initially presumed the tooth to be a left molar of a eutherian. After communicating SEM photographs plus a mold of the tooth and a draft of the proposed manuscript to Every and Scally in an effort to see what additional understanding a detailed examination of thegotic structures might provide, Every suggested that it could be a right molar of a eutherian with specialisations of the type characteristic of adapid primates (Every, 1974). Subsequently, we concluded that the animal could also be a specialised 'tribotherian' or zalambdodont mammal or even a pre-eutherian that had convergently developed a talonid.

Higher-level mammalian nomenclature follows Aplin and Archer (1987). Biostratigraphic nomenclature and concepts follow Archer *et al.* (1989).

SYSTEMATICS

Class MAMMALIA
Subclass THERIA
Infraclass indet.
YINGABALANARIDAE new family

Diagnosis

Yingabalanarids differ from all non-eutherian mammals (except monotremes, yinotherians and some 'tribotheres' *sensu* Clemens and Lillegraven, 1986) in their possession of well-developed, trigonid-like, as well as talonid-like, structures. They differ from yinotherians (*Shuotherium*: Chow & Rich, 1982) in lacking any trace of an entoakid (= entoconid) or pseudo-entoakid (= pseudo- entoconid) and in having both halves of the molar lingually open with their occlusal surfaces steeply inclined in the lingual direction. Adjacent talonid-like and trigonid-like structures are subequal in height, in contrast to the relatively much smaller size of the pseudo-talonid of yinotherians. There is also no trace of a lingual basal cingulid.

Yingabalanarids differ from monotremes (*Steropodon* and *Obdurodon*) in having widely open talonid-like and trigonid-like structure, narrow, elongate molars and no lingual or buccal cingulids.

Yingabalanarids closely resemble some 'tribotheres' (e.g. *Potamotelses*) but differ in having very high talonids and well developed and elevated Hypobliquids.

They differ from known marsupials and placentals in either having a markedly hypertrophied talonid in combination with a vestigial trigonid (if the tooth is a right molar) or in having (if the tooth is a left molar) a uniquely integrated Prototransversid (= metacristid) and Hypobliquid (= cristid obliqua).

Etymology

In the Wanyi language spoken by the Aborigines who lived on Riversleigh Station, *yinga* means "another" and *balanara* means "moon". The combination, meaning 'two moons', refers to the distinctive overlapping crescentic trigonid-like and talonid-like Triakididrepanids. The gender is masculine.

Yingabalanara gen. nov.

Type Species

Y. richardsoni sp. nov.

DIAGNOSIS

The diagnosis of the genus is that for the family until additional genera are known.

Yingabalanara richardsoni gen. et sp. nov.

DIAGNOSIS

The diagnosis of the species is that for the family until additional taxa are known.

HOLOTYPE

Queensland Museum F13016 (Fig. 1), recovered in 1987 from acid-insoluble concentrates. The limestone from which this concentrate was obtained was collected in 1986. Field notes pertaining to collection of this material are presently held in the School of Zoology, University of New South Wales, and copies will be lodged with the Queensland Museum.

ETYMOLOGY

This species is named in honour of the Commonwealth Minister for the Environment and the Arts, Mr Graham Richardson, for his determination to conserve what is left of Australia's endangered rainforest biotas of which *Yingabalanara* was once a part.

TYPE LOCALITY, AGE, FORMATION AND LOCAL FAUNA

Upper Site, Godthelp Hill, Riversleigh Station, northwestern Queensland. Precise location details of Upper Site, based on laser surveys, have been recorded by the University of New South Wales research team. In an effort to minimise the risk of vandalism before completing current biostratigraphic studies, these details are not published at this time but may be made available on request. Upper Site is an excavation in one level of a thick sequence of lacustrine carbonates. Our present understanding leads us to conclude that compared with other published Riversleigh faunas, the Upper Site Local Fauna is stratigraphically higher than the Site D Local Fauna but lower than the Dwornamor (e.g. Hand, 1985) and Henk's Hollow Local Faunas. It is regarded by Archer *et al.* (1989) to be part of Riversleigh's system B sequence. The Site D Local Fauna comes from the Carl Creek Limestone (Tedford, 1967). There is evidence (from work in preparation) to suggest that the Upper Site Local Fauna comes from an unnamed freshwater carbonate that is separated from the older Carl Creek Limestone by at least one angular unconformity.

We have previously interpreted the sequence of deposits at Riversleigh to span Middle Miocene to Late Pleistocene time (Archer, Hand & Godthelp, 1986) partly on the basis of intercontinental comparisons of bats (Sigé, Hand & Archer, 1982), intracontinental correlation of marsupials (Tedford, 1967; Archer *et al.*, 1987) and work in progress on rodents. The Upper Site Local Fauna, which comes from deposits near the base of the Riversleigh sequence, contains a wynyardiid referable to *Namilamadeta* (previously only recorded from the Tarkarooloo Local Fauna of the Frome Embayment, South Australia) and a potoroid referable to *Wakiewakie lawsoni* (previously only recorded from the Kutjamarpu Local Fauna of the Tirari Desert, South Australia). Although it has become customary to presume these central Australian deposits to be Middle Miocene in age (approximately 12-15 My: Woodburne *et al.*, 1985), more recent work based on e.g. studies of foraminiferans (Lindsay, 1987) suggests that at least some of these deposits may be as old as Late Oligocene. In view of this, we consider it probable that the Upper Site Local Fauna is between Early and Middle Miocene in age (Archer *et al.* 1989).

DESCRIPTION

Six alternative descriptions are provided (Fig. 3). Additional hypotheses about the tooth's structure are possible but less likely to be correct.

HYPOTHESIS 1. THE TOOTH IS A EUTHERIAN (MARSUPIAL OR PLACENTAL) LEFT MOLAR: This is the hypothesis that Archer, Godthelp and Hand first developed, based in part on the apparent similarities between the largest triakididrepanid of *Yingabalanara richardsoni* to the trigonids of the marsupial yalkaparidontids (Archer, Hand & Godthelp, 1988), as well as on the generalised trigonid-like (rather than talonid-like) structure of this portion of the crown of *Y. richardsoni.*

In broad construction, there are two principal overlapping sections and five principal akids (= cusps). The anterior trigonid has a buccal protoakid (= protoconid), and antero-lingual parakid (= paraconid), a mediolingual metakid (= metaconid) and a modified Prototransversid (= metacristid). The talonid displays a buccal hypoakid (= hypoconid), a medially-situated posterior cuspid presumably homologous with the hypotransversakid (= hypoconulid) of other eutherians, and a modified Hypobliquid (= cristid obliqua). There is no interdental facet on the posterior face of the crown to suggest that this tooth was not the last in the row although the absence of such a facet is no guarantee of the

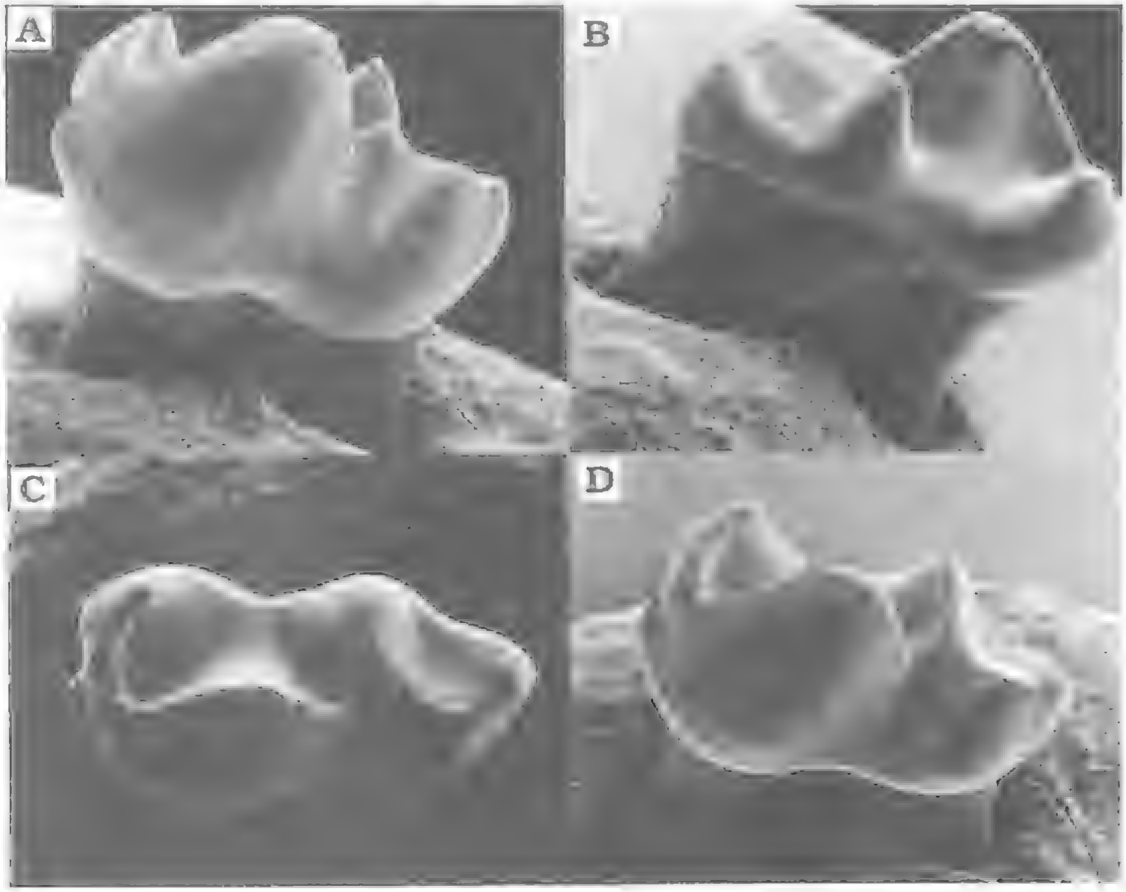

FIG. 1. SEM photographs of QMF13016, the holotype of *Yingabalanara richardsoni*, a lower molar of ambiguous orientation. Whether it is a right or left molar: A, buccal view; B, linqual view; C, occlusal view; D, buccal oblique view. Presuming it to be a left molar, the largest cusp is the protoakid (ff protocone); presuming it to be a right molar, the largest cusp is the hypoakid (ff hypoconid). Size is indicated in Fig. 2.

tooth's posterior position. The degree to which the hypotransversakid projects posteriorly suggests that it could have served as the 'tongue' to lock into a corresponding notch in the anterior cingulid of a succeeding molar. On the front of the trigonid, at the base of the crown, is a small anteriorly projecting akid or remnant cingulid. This would probably interdigitate with a corresponding groove in the posterior cingulid of the preceding molar. Just lingual to this small akid is a corresponding indentation which would represent the 'groove' for the hypotransversakid of the preceding molar. The trigonid is open lingually, and the lingual flank of the protoakid extends to the lingual side of the tooth. The postero-buccal face of the parakid, antero-buccal face of the metakid and lingual face of the protoakid all face each other to enclose the other portions of the trigonid basin.

The Protobliquid (= paracristid) is deeply concave with the parakid contribution the shorter portion of the blade. In occlusal view, the akids and drepanids of the trigonid form a bowl-shaped system of points and blades. This is because the parakid and metakid appear to be inturned towards each other on the lingual side of the trigonid. In fact, this appearance is due to the U-shaped Protobliquid and nearly U-shaped Prototransversid which anteriorly and posteriorly extend the trigonid basin. This has the effect of 'rounding' the whole trigonid and making it less like the trigonids of other tribosphenic mammals. The Protobliquid cannot be described with confidence as part of a Proto-Triakid because what we presume to be the homologue of the Prototransversid is autapomorphically complex. The protoakid end of the Prototransversid is

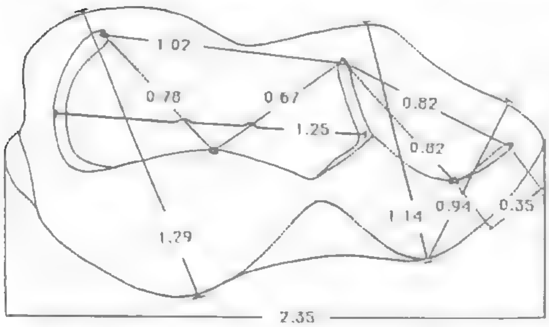

FIG. 2. Measurements (in millimetres) of QMF13016, the holotype of *Yingabalanara richardsoni*. These were made using a graticule with a Wild M3 microscope.

essentially plesiomorphic but the lingual half of the blade is not. Just lingual to the point of inflexion along the Prototransversid, the rising blade forms a right angle intersection with the crest of the Hypobliquid which extends from this intersection to the hypoakid. It is not clear whether the drepanid linking this intersection to the metakid is the homologue of the lingual half of the Prototransversid, the antero-lingual half of a conventional Hypobliquid of eutherian mammals or a novel extension of that blade linking the metakid to the postero-lingual end of the autapomorphically truncated Prototransversid. Allowing for the uncertain homology of the

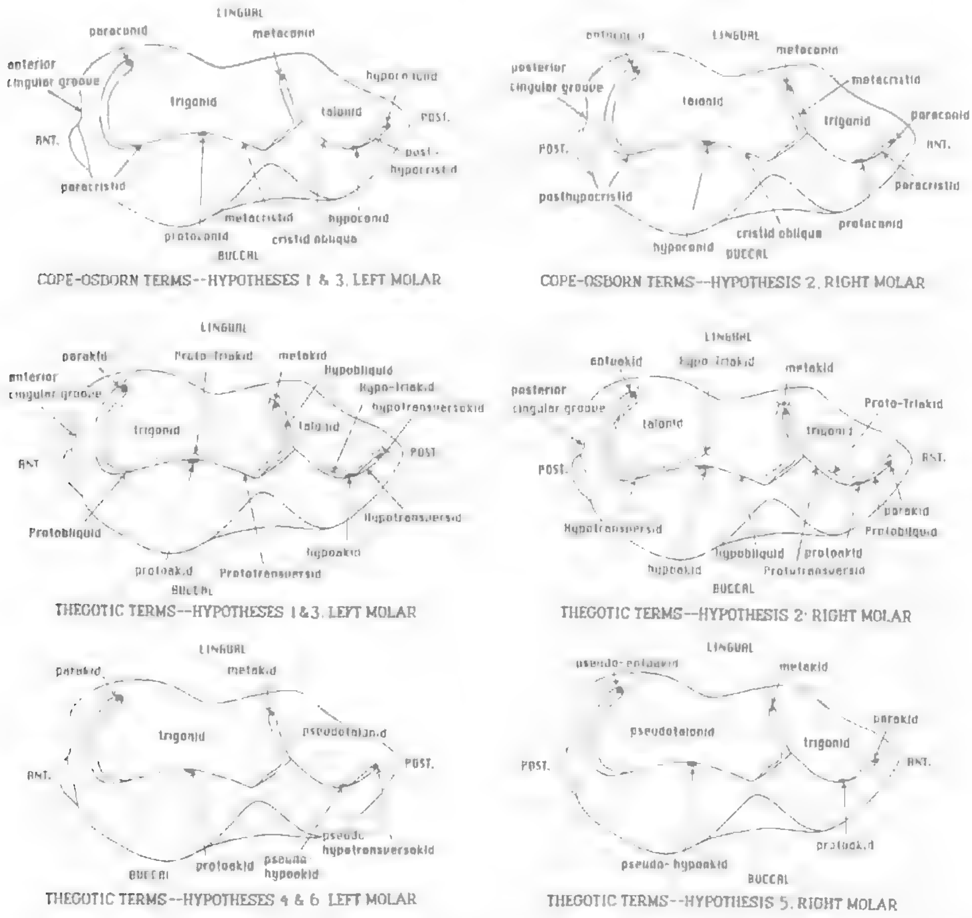

FIG. 3. Cusp homologies of QMF13016, the holotype of *Yingabalanara richardsoni*, determined according to the alternative hypotheses about its nature and orientation presented in the text. The Cope-Osbornian terminology is presented to demonstrate homology of thegotic and traditional nomenclature. The different hypotheses are: 1, it is a left molar of a eutherian; 2, it is a right molar of a eutherian; 3, it is a left molar of a 'tribothere' like *Potamotelses*; 4, it is a left molar of a pre-eutherian with a convergently evolved 'pseudotalonid'; 5, it is a right pre-eutherian with a convergently developed 'pseudotalonid'; 6, it is a zalambdodont molar (in this case a left) with a re-developed talonid ('pseudotalonid').

metakid's postero-buccal blade, the talonid displays what appears to be an autapomorphically hypsodont Hypo-Triakid. The Hypobliquid is occlusally gently concave and intersects in an uncertain manner, as noted above, the Prototransversid. The Hypotransversid (= posthy- pocristid) is much shorter and only just concave occlusally. It terminates posteriorly as the slightly swollen hypotransversakid. The talonid basin steeply slopes in a ventro-lingual direction and is open lingually, there being no evidence of an entoakid. On the other hand, although the basin is open lingually, the lingual flank of the hypoakid adjacent to the leading edge of the Hypo-Triakid served as a sloped incussive platform in opposition to the Proto-Triakid. If appropriate, food incussed on the talonid surface could have been maintained in that position by the tongue.

There are two roots below the crown: a cylindrical vertical one beneath the protoakid; and a more elongate, transversely compressed one beneath the hypoakid and metakid. The posterior root inclines postero-ventrally, as posterior roots commonly do in molars at the posterior end of the tooth row.

Interpreted in this manner, while the trigonid appears to be essentially plesiomorphic in its basic construction, the tooth is unusual among eutherians for two main reasons. First, the talonid seems to lack any clear indication that it had an incussive function, although its Hypo-Triakid was clearly involved in scissorial action with a corresponding structure in the upper molars (presumably the Proto-Triakis). Second, the unusual nature of the intersection of the Prototransversid and Hypobliquid means that the homology of the drepanid extending postero-buccally from the metakid is unclear.

HYPOTHESIS 2. THE TOOTH IS A EUTHERIAN RIGHT MOLAR: This is the hypothesis first proposed by Every. It is based in the first instance on the observation that adapid primates have hypertrophied talonids which result in similar drepanid interrelationships in the region between the metakid and hypoakid (Every, 1974). In the following description, in an effort to avoid repetition (particularly in view of the fact that all of the principal structures have been identified according to Hypotheses 1-6 in Fig. 2), we will restrict comment here to the features that would be most significantly misconstrued following Hypothesis 1.

The small trigonid (the structure identified in Hypothesis 1 as the talonid) and the large talonid are unusual in that the talonid is markedly hypertrophied with repect to the trigonid, the hypoakid being almost 50% taller than the protoakid. It is also unusual in that the talonid is very trigonid-like without any clear indication of incussive function despite its large size. The metakid, hypoakid and entoakid are all very high structures surrounding their steeply inclined and converging internal flanks which do not resolve at their base into a talonid basin. The parakid (the hypotransversakid of Hypothesis 1) is very reduced in size and restricted to a median position on the crown. In this context, there is no hypotransversakid whereas (in contrast to Hypothesis 1) there is a large entoakid. The associated blades and apex of the akid interpreted here to be the entoakid (the parakid of Hypothesis 1) are also distinctive in lacking any indication that they sheared against a protoakis-like structure in the unknown corresponding upper molar. The normal 'tongue and groove' locking mechanisms for avoiding food impaction are here but, presuming the tooth is a right molar, these structures are unconventionally reversed in position with the 'groove' occurring on the posterior face of the crown and the 'tongue' projecting from the anterior face.

The Protobliquid (= the Hypotransversid of Hypothesis 1) is less than half the length of the Prototransversid. What is interpreted here to be the Prototransversid is 'normal' in extending between the protakid and metakid. The Hypobliquid (the Prototransversid of Hypothesis 1) is about the same height (near its lingual end) as the Prototransversid and is unusual in that the two drepanids intersect at the level of their little-worn cutting edges.

Interpreted within the context of Hypothesis 2, the anterior root presents a somewhat unusual condition. This relatively narrow, transversely compressed root beneath the small trigonid inclines in an anteroventral direction. This would seem to suggest that the tooth had been positioned at the edge of a diastema with no tooth immediately in front of it.

Considering that one of the reasons for suggesting this particular structural interpretation (Hypothesis 2) is the similarity between this tooth and the molars of adapid primates, it is of interest to contrast *Yingabalanara richardsoni* with *Adapis parisiensis* (as interpreted by Every, 1974, p. 604). The basic similarities include reduced trigonid, enlarged talonid, reduced Protobliquid and intersection almost at the level of the blades of the Hypobliquid and Prototransversid. Differences include (in *A. parisiensis* but not *Y. richardsoni*): a relatively much smaller, shorter and V-shaped talonid that still functions in the 'traditional' double-function way — as an incusso-scissorial structure such that the peripheral blades cut and the mesial platform supports incussion involving the protoakis (= protocone) and the Proto-Triakis (= two drepanids sharing the protoakis); absence of a 'carnassial notch' in the Hypobliquid; a large Metastylotransversid (= metastylid crest); and a buccal Hypocingulid (buccal cingulid on the base of the hypoakid) and Protocingulid (buccal cingulid on the base of the protoakid).

Similarities have also been noted by Hand between the holotype of *Y. richardsoni* and illustrations (Miller, 1907, pl. 10) of the right molars of phyllostomoid bats of the genus *Carollia*. In both, the trigonid appears to be U-shaped and the Hypobliquid connected, directly or indirectly to the metakid. In *Carollia* the connection appears to be direct, such as occurs in aegialodontids (where it involves the 'postmetacristid'), rather than via a prior intersection with the Prototransversid such as occurs in *Y. richardsoni*. In other respects, phyllostomoids are unlike yingabalanarids in trigonid and talonid structure. However, considering the fact that phyllostomoid bats have representatives in New Zealand and South America (Hand, 1984), a possible representation in Australia would be no less probable than representation by adapid primates or 'tribotheres' (see below).

Koopman (in Daniel, 1976) suggests that phyllostomoid bats dispersed to New Zealand from South America across the South Pacific sometime before the Early Oligocene. Presumably they could have as easily dispersed from New Zealand to Australia, although we are not convinced that the similarities noted above between *Y. richardsoni* and either phyllostomoid bats or adapid primates represent anything other than convergence.

HYPOTHESIS 3. THE TOOTH REPRESENTS A 'TRIBOTHERIAN' LEFT MOLAR: This hypothesis arose after consideration by Archer, Godthelp and Hand of the Upper Cretaceous *Potamotelses* (Fox, 1972, 1975, 1976). This form, referred to by Clemens and Lillegraven (1986) as a 'tribothere', is similar to *Yingabalanara* in having a drepanid system that connects the Hypobliquid (via a 'postmetacristid') to the Prototransversid and then this conjunction to the metakid. It is also similar in its relatively elongate, U-shaped trigonid and lack of an entoakid. However, the two forms differ in that the Hypobliquid of *Potamotelses* is a low structure that descends to the base of the occlusal surface near the anterior end of the talonid before steeply rising on the posterior flank of the trigonid to contact the Prototransversid. The talonid of *Yingabalanara* is also much higher relative to the trigonid. The absence of an entoakid in *Yingabalanara* is matched in one of the lower molars referred to *Potamotelses* (Fox, 1976, fig. 7) but not the other (Fox, 1972, figs 2-6). None of the other 'tribotherians' is as similar to *Yingabalanara* as *Potamotelses*. Fox (1976) discusses the possible structurally annectant position of *Potamotelses* between Early Cretaceous aegialodontids and Late Cretaceous deltatheridiids.

HYPOTHESIS 4. THE TOOTH IS A NON-EUTHERIAN LEFT MOLAR THAT HAS CONVERGENTLY DEVELOPED A SMALL TALONID-LIKE STRUCTURE: This hypothesis should be considered because of the superficial similarity of the large trigonid to the crowns of symmetrodonts, and the demonstration provided by yinotherians (*Shuotherium*) and docodontids that some pre-eutherian groups experimented with the addition of incussive components to essentially scissorial trigonids. If the holotype of *Yingabalanara* is a left molar and displays an independently evolved talonid-like structure, it might help to explain the otherwise aberrant drepanid relationships in comparison with those of eutherians. However, without discovery of additional material or the sacrifice of sufficient enamel for ultrastructural analysis of the holotype, we are at present unable to test the hypothesis that it is not a eutherian mammal.

HYPOTHESIS 5. THE TOOTH IS A NON-EUTHERIAN RIGHT MOLAR THAT DEVELOPED A LARGE TRIGONID-LIKE STRUCTURE POSTERIOR TO THE ORIGINAL TRIGONID: As an alternative variation of Hypothesis 4, it is possible that the smaller triakididrepanid is a plesiomorphic trigonid (also proposed in Hypothesis 2) and that the larger triakididrepanid is a neomorphic structure.

However, this seems less likely than Hypothesis 4 because what would be the neomorphic structure looks considerably more like a symmetrodont trigonid than does the anterior half of the tooth — which does not resemble the teeth of any non-eutherian known to us. Hypothesis 5 is possible but would be extremely difficult to test. While ultrastructural analysis would probably determine whether or not the tooth was eutherian, if it turned out to be non-eutherian, it would be very difficult to determine which of the two halves of the tooth represented the plesiomorphic section and which the neomorphic section.

HYPOTHESIS 6. THE TOOTH IS THAT OF A ZALAMBDODONT MAMMAL THAT HAS REDEVELOPED A TALONID: The resemblance of the larger triakididrepanid of *Yingabalanara* to the molars of the zalambdodont yalkaparidontids makes this an attractive interpretation. However, because this hypothesis involves loss and subsequent redevelopment of analogous structures (the talonid-like smaller triakididrepanid), it seems less parsimonious than the five alternative hypotheses considered above.

In summary, given our present level of understanding, we cannot decide which if any of the various hypothetical interpretations of the structure of *Yingabalanara richardsoni* presented above is most likely to be correct. While some of us are inclined to favour particular interpretations, we remain open-minded about the other possibilities.

We have deferred a consideration of function pending ultrastructural examination of the tooth's thegotic facets.

DISCUSSION

Although we have become accustomed to the discovery of unusual creatures in the Tertiary sediments of Riversleigh (e.g. Archer, Hand & Godthelp, 1988), *Y. richardsoni* is markedly less 'conventional' than any Riversleigh form so far encountered. For this reason, it is important to consider an assumption that we have made but not discussed — that the tooth exhibits the standard (normal) morphology of an albeit unusual taxon. The main reason for this assumption is the presence of precise thegotic and/or wear facets on all major drepanids. These facets demonstrate that the otherwise uniquely-disposed cutting edges were being thegosed by precisely-positioned counterparts in the unknown upper dentition. If the tooth were abnormal, it would be most unlikely to have had precise structural counterparts in the corresponding upper teeth (Archer, 1975). Related to the hypothesis of normality is the obvious fact that the animal that produced this tooth lived at least long enough to develop, erupt and use the tooth.

Accepting that the holotype represents the normal molar structure of *Yingabalanara richardsoni*, we are uncertain about its phylogenetic affinities within Mammalia at all systematic levels. We have not recognised a single synapomorphic feature that would refer it unambiguously to any previously known marsupial, placental or pre-eutherian group. At the very least it represents a new species, genus and family of mammals, and possibly a new order.

If the holotype of *Yingabalanara richardsoni* is a eutherian left molar (Hypothesis 1), it exhibits particularly distinctive features: 1, an elongate U-shaped (rather than more normal V-shaped) Proto-Triakid; 2, a continuous drepanid linking the hypoakid and metakid which incorporates in an unusual (if not unique) way what may be the lingual portion of the Prototransversid or a lingual extension of the Hypobliquid; 3, a V-shaped Hypo-Triakid which shares the metakid with the Proto-Triakid a feature found in some 'tribotheres' (e.g. *Aegialodon* and *Potamotelses*) but no known marsupials or placentals (Fox, 1975); and 4, a talonid basin that is inclined and wide-open lingually without a trace of the entoakid normally present in plesiomorphic eutherians. Implicit in these observations is the hypothesis that the as yet unknown corresponding upper molar differed significantly from a plesiomorphic tribosphenid pattern in structural aspects of stylar cusp B, the Para-Triakis and Proto-Triakis.

If it is a eutherian right molar (Hypothesis 2), it exhibits among unusual features: a remarkably hypertrophied talonid; a significant departure from conventional talonid structure and function such that the talonid, although well developed, may have had no incussive function; a hypoakid that is 50% taller than the protoakid (rather than subequal to or smaller than the protoakid, which is the normal situation); a recessed 'groove' in the posterior (rather than normal anterior) basal edge of the crown for what must have been a forwardly projecting (rather than more normal posteriorly projecting) 'tongue' from an adjacent molar; and an anteriorly inclined trigonid (rather than normal talonid) root.

Alternatively, if *Yingabalanara* is a 'tribothere', yinothere, monotreme, symmetrodont or zalambdodont mammal, it exhibits striking features that would make it stand out as unique within those groups. Of these, it is most similar to the Late Cretaceous 'tribothere' *Potamotelses* and, of the two lower teeth referred to this taxon, in particular to the tooth interpreted by Fox (1976) as a possible 'M_4' (the most posterior molar in the tooth row). The features that separate *Yingabalanara* from *Potamotelses* include the hypsodont talonid and high, well developed Hypobliquid of the former. These features could, however, be autapomorphic specialisations superimposed on a *Potamotelses*-like ground plan.

Considering the Late Cretaceous age of *Potamotelses*, it is not impossible that this lineage could have had a representative in Gondwana prior to the isolation of Australia approximately 45 million years ago.

On balance, we conclude that *Yingabalanara* represents a highly distinct clade of mammals of uncertain affinities within the class. Hopefully, further work at Riversleigh will provide more information about this enigmatic creature.

The Upper Site Local Fauna contains forms indicative of a rainforest biota (Archer *et al.*, 1989). These include a high diversity of pseudocheirids, *Strigocuscus* sp. and at least one species of *Hypsiprymnodon*. The geology of the region suggests that the area exhibited only slight topographic relief and that, therefore, the vegetation would have been lowland rainforest. Aquatic vertebrates are rare, being represented by small turtles and crocodiles. Amphibians, reptiles, birds, terrestrial mammals, insects and millipedes are, however, very well represented. None of the faunal elements present in this assemblage shows any sign of having been transported and, combined with the chemical nature of the sediments and the small aquatic vertebrates, we conclude that this assemblage accumulated in a shallow, carbonate-enriched freshwater pool.

ACKNOWLEDGEMENTS

We wish to acknowledge the vital financial support the Riversleigh Project has had from: the Australian Research Grant Scheme (Grant PG A3 851506P); the National Estate Grants Scheme (Queensland); the Department of Environment and Arts; Wang Australia Pty Ltd; ICI Australia Pty Ltd; the Queensland Museum; the Australian Museum; Australian Geographic Society Pty Ltd; Mount Isa Mines Pty Ltd; Ansett Wridgways Pty Ltd; the Linnean Society of N.S.W.; the Royal Zoological Society of N.S.W. and Surrey Beatty & Sons Pty Limited. Critical logistical support in the field and laboratory has been received from the Riversleigh Society, the Friends of Riversleigh, the Royal Australian Air Force, the Australian Defence Force, the Queensland National Parks and Wildlife Service, the Riversleigh Consortium (Riversleigh being a privately owned station), the Mount Isa Shire, the Northwest Queensland Tourism and Development Board, the Gulf Local Development Association, PROBE and many volunteer workers and colleagues. Dr G. Breen (Darwin Community College) kindly allowed access to his unpublished vocabulary of the Wanyi Aborigines.

LITERATURE CITED

APLIN, K. AND ARCHER, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. p. xv-lxxii. *In* M. Archer (ed.), 'Possums and Possums: Studies in Evolution'. (Surrey Beatty & Sons: Sydney).

ARCHER, M. 1975. Abnormal dental development and its significance in dasyurids and other marsupials. *Memoirs of the Queensland Museum* 17: 251–65.

AND FLANNERY, T.F. 1985. Revision of the extinct gigantic rat kangaroos (Potoroidae: Marsupialia), with description of a new Miocene genus and species of *Propleopus*. *Journal of Paleontology* 89: 1131–49.

FLANNERY, T.F., RITCHIE, A. AND MOLNAR, R.E. 1985. First Mesozoic mammal from Australia — an early Cretaceous monotreme. *Nature* 318: 363–6.

GODTHELP, H., HAND, S.J., AND MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy correlation and environmental change. *Australian Zoologist*, 25: 29–65.

HAND, S.J. AND GODTHELP, H. 1986. 'Uncovering Australia's Dreamtime'. (Surrey Beatty & Sons: Sydney).

1988. Discovery of a new order of Tertiary zalambdodont marsupials. *Science* 239: 1528–31.

CLEMENS, W.A. AND LILLEGRAVEN, J.A. 1986. New Late Creataceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *University of Wyoming, Contributions to Geology, Special Papers* 3: 55–85.

DANIEL, M.J. 1976. Feeding by the short-tailed bat (*Mystacina tuberculata*) on fruit and possibly nectar. *New Zealand Journal of Zoology* 5: 357–70.

EVERY, R.G. 1976. 'A new terminology of mammalian teeth'. (Pegasus Press for the Centre for the Study of Conflict: Christchurch).

1974. Thegosis in prosimians. p. 579-619. *In* Martin, G.A., Walker, A.C. and Doyle, G.A. (eds). 'Prosimian Biology' (Duckworth: London).

FOX, R.C. 1972. A primitive therian mammal from the Upper Cretaceous of Alberta. *Canadian Journal of Earth Sciences* 9: 1479–94.

1975. Molar structure and function in the Early Cretaceous mammal *Pappotherium*: evolutionary implications for Mesozoic Theria. *Canadian Journal of Earth Sciences* 12: 412–42.

1976. Additions to the mammalian local fauna from the Upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences* 13: 1105–18.

HAND, S.J. 1984. Bat beginnings and biogeography: a southern perspective. p. 853-904. *In* Archer, M. and Clayton, G. (eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Perth).

1985. New Miocene megadermatids (Chiroptera: Megadermatidae) from Australia and comments on megadermatid phylogenetics. *Australian Mammalogy* **8**: 5–43.

LINDSAY, J.M. 1987. Age and habitat of a monospecific foraminiferal fauna from near-type Etadunna Formation, Lake Palankarinna, Lake Eyre Basin. *Department of Mines and Energy South Australia Rept* Bk. No. 87/93.

SIGÉ, B., HAND, S.J. AND ARCHER, M., 1982. An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related to Miocene representatives from France. *Palaeovertebrata* **12**: 149–72.

TEDFORD, R.H. 1968. Fossil mammal remains from the Tertiary Carl Creek Limestone, north-western Queensland. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* **92**: 217–37.

WOODBURNE, M.O., TEDFORD, R.H., ARCHER, M., TURNBILL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publications, South Australian Department of Mines and Energy* **5**: 347–63.

ADDENDUM

Since completing the original analysis of the holotype, R.G. Every has more extensively examined the tooth. As a result, it seems appropriate to append here the following interpretation as a distinctive variant of Hypothesis 1.

Every's first suggestion that the tooth is a right lower molar was made from only SEM photographs and a poor-quality cast of the crown. Since he has had access to the original specimen, however, it is now clear that the facet on the secondary suprastegid (the buccal aspect of the tongue-and-grove feature) defines this tooth as a left lower molar. The suggestion of similarity with the right lower molar of *Adapis parisiensis* is nonetheless illuminating. Here the process of Hypo-Triakid/Proto-Triakid levelling has resulted in the loss of the parakid and the restriction of the Protobliquid to the buccal side of the contact point (a new protobliquakid replacing functionally the parakid). In *Y. richardsoni* the scissorial function of the Protobliquid is likewise restricted to an area buccal to the contact point, yet the remainder of the blade to the parakid is retained, this non-scissorial segment being curved around to enclose the markedly hollowed out escapement of the Protobliquid. The contrasting junction of the Hypo-Triakid with the Proto-Triakid in the two species is again illuminating. In the primate scissorial function of the Prototransversid is not only maintained but extended (Metastylo-transversid). In *Y. richardsoni*, however, the opposite has occurred. Here the Hypo-Triakid/Proto-Triakid levelling has raised the hypobliquakid right to the cutting edge of the (original) Prototransversid. Scissorial action on the blade's linqual arm extending to the metakid is no longer possible and therfore is lost, its function remaining incusive solely — the explanation of its puzzling worn edge and orientation (for it also encloses a hollowed out escapement; i.e., that of the now modified Prototransversid). Because of the restriction of scissorial function to the buccal arm of the (original) Prototransversid, this segment has now developed its own drepanid with a prototransversakid (replacing functionally the metakid) and mid-blade fissure, the new akid virtually joining the hypobliquakid as a synakid. The loss of scissorial function has, however, been somewhat compensated for by the blade's markedly oblique orientation. The Hypo-transversid is correspondingly oblique. In fact, when the specimen is examined directly in line with the scissorial action both triakididrepanids appear as straight-sided, equi-angled, inverted V's. Close examination of the lingual arm of the Protobliquid also reveals an incusive edge. All this would seem to predict an upper molar with an extensive incusive feature in the hypoakis area as well as one anterolingual to the obliquely angled Prototransversis. Possibly, also, it is because of this marked obliquity that a function for an Entoakid has been crowded out.

NIMBACINUS DICKSONI, A PLESIOMORPHIC THYLACINE (MARSUPIALIA: THYLACINIDAE) FROM TERTIARY DEPOSITS OF QUEENSLAND AND THE NORTHERN TERRITORY

J. MUIRHEAD AND M. ARCHER

Muirhead, J. and Archer, M. 1990 3 31: *Nimbacinus dicksoni*, a plesiomorphic thylacine (Marsupialia: Thylacinidae) from Tertiary deposits of Queensland and the Northern Territory. *Mem. Qd Mus.* **28**(1): 203–221. Brisbane. ISSN 0079-8835.

A new Tertiary thylacinid, *Nimbacinus dicksoni*, shows features unique to the Thylacinidae, while retaining many other features that are plesiomorphic within the group. *Nimbacinus dicksoni* expands the diversity of the family to two genera and three species and extends its history to the Late Oligocene or Early Miocene. *Nimbacinus dicksoni* provides support for the monophyly of a group combining the Thylacinidae and Dasyuridae but suggests that these two families diverged before the Late Oligocene.
☐ *Nimbacinus dicksoni, Marsupialia, Thylacinidae, Riversleigh, Oligocene, Miocene.*

J. Muirhead and M. Archer, University of New South Wales, PO Box 1, Kensington, NSW 2033, Australia.

The Thylacinidae is a family of dasyuroids known to contain only one modern species, *Thylacinus cynocephalus*, and one extinct species, *T. potens*. *Thylacinus potens,* from the Late Miocene Alcoota Local Fauna (Woodburne, 1967), provides little insight into the history of the group because in many respects it is almost as specialised morphologically as the modern *T. cynocephalus* (Woodburne, 1967; Archer, 1982b).

A new thylacinid from the older Tertiary deposits of Riversleigh (Queensland) and Bullock Creek (Northern Territory) is described here. It is the oldest and most plesiomorphic thylacinid known and as such encourages a re-evaluation of thylacinid phylogeny. Dental nomenclature follows Archer (1978, 1982b).

Institutional abbreviations: NTM, Northern Territory Museum; QM, Queensland Museum; AR, Archer Collection, University of New South Wales.

SYSTEMATICS

Family THYLACINIDAE Bonaparte, 1838
Nimbacinus n. gen.

TYPE AND ONLY SPECIES

Nimbacinus dicksoni n. gen. and n. sp.

GENERIC DIAGNOSIS

Nimbacinus differs from all other thylacinids in the following combination of features: 1, extremely small metaconids on all lower molars; 2, an unreduced stylar shelf region with prominent stylar cusps B and D as well as smaller cusps C and E on M^2 and M^3; 3, protoconule and metaconule present on M^2-M^4 and prominent on M^3 and M^4; 4, prominent protocristae and talonid basin ridges. *Nimbacinus* differs from plesiomorphic dasyurids (e.g. species of *Murexia*) in possessing: 1, much smaller metaconids; 2, much smaller paracones; 3, smaller stylar cusps B and E; 4, greater degree of ectoflexus on M^4; 5, smaller entoconids; 6, smaller talonid basins and protocones; and 7, longer postmetacristae and paracristids.

ETYMOLOGY

Nimba is a Wanyi Aboriginal word from the Riversleigh area meaning "little" (G. Breen, pers. comm.); *cinus* is from the Greek *kyon* meaning "dog" in reference to the dog-like shape of thylacinids. The gender is masculine.

Nimbacinus dicksoni n. sp.

HOLOTYPE

QMF16802 (formerly AR6670) a left M_2 collected in 1984 by M. Archer, H. Godthelp and S. Hand; chosen as the holotype because it is the only tooth represented in all isolated thylacinid populations from Riversleigh and Bullock Creek.

TYPE LOCALITY

Henk's Hollow Site, the Gag Plateau, Riversleigh Station, NW Queensland; Henk's

Hollow Local Fauna, Middle to Early Late Miocene (Archer *et al.*, 1989).

PARATYPES

QMF16803 (AR7852), a right maxillary fragment with P^3, M^2-M^4; QMF16804 (AR5568), a right maxillary fragment with M^2-M^4; QMF16805 (AR4056), an M^4; QMF16806 (AR9041), an M^4; QMF16807 (AR7712), an M^5; QMF16809 (AR1834), a broken right M_3, and Northern Territory Museum fossil collection number NTMP85553-3, a right dentary fragment containing P_1, P_2 and M_2.

PARATYPE LOCALITIES

All Riversleigh paratypes are from the type locality — except QMF16809 which is from D-Site, Riversleigh Station, NW Queensland (Riversleigh Local Fauna), Late Oligocene, Early Miocene, P85553-3 is from Bullock Creek, Camfield Station, Northern Territory (Bullock Creek Local Fauna).

SPECIFIC DIAGNOSIS

As for genus.

AGE, STRATIGRAPHY AND LOCAL FAUNA

The Henk's Hollow Local Fauna (Hand, 1985) is Middle to Early Late Miocene in age (Archer *et al.*, (1989). It was recovered from an unnamed freshwater limestone apparently overlying the Carl Creek Limestone which contains the Riversleigh Local Fauna (Tedford, 1967). Age estimation is based in part on the occurrence, in the Henk's Hollow Local Fauna, of a species of *Litokoala*, a phascolarctid genus otherwise known only from the Kutjamarpu Local Fauna (Woodburne *et al.*, 1985). The age of the central Australian local faunas is in doubt. Although the Ditjimanka and Etadunna local faunas have most commonly been regarded as Middle Miocene in age (Woodburne *et al.*, 1985), there are now reasons to conclude that they may be Late Oligocene (M. Lindsay, pers. comm.; Archer *et al.*, 1989, 1990; Flannery, 1990). The Kutjamarpu Local Fauna, which has been regarded to be Middle Miocene in age (Woodburne *et al.*, 1985), is more reasonably regarded as Late Oligocene to Early Miocene. On this basis, the faunal similarities between the Riversleigh Local Fauna (the oldest mammal-bearing fauna from the Riversleigh region and source of paratype QMF16809) and the Kutjamarpu Local Fauna suggest a comparable Late Oligocene to Early Miocene age for the Riversleigh Local Fauna. The Henk's Hollow Local Fauna (the type locality of *Nimbacinus dicksoni)*, as currently understood, is younger than the Riversleigh Local Fauna, but how much so is unclear. Based on the apparent absence in this Local Fauna of wynyardiids, ilariids, the rarity of balungamayine macropodoids and the abundance of balbarine kangaroos combined with the stratigraphic proximity to the Jaw Junction Local Fauna (which contains an unnamed zygomaturine similar to *Kolopsis,* a genus otherwise only known from relatively derived Late Miocene species), the Henk's Hollow Local Fauna is probably between Middle to Early Late Miocene in age. The age of the Bullock Creek Local Fauna (source of NTM P85553-3) is also uncertain but, on the basis of biocorrelation (the presence of a species of *Neohelos*, a plesiomorphic species of *Wakaleo* and the absence of wynyardiids, ilariids and other groups characteristic of the older Riversleigh mammal-rich assemblages) it also probably is Middle to Early Late Miocene in age.

DESCRIPTION

The lower molars from the Henk's Hollow samples are represented by a left M_2, QMF16802 (Fig. 1). (Paratypes QMF16809 and P85553-3 also include lower molars, but these are described and discussed separately). QMF16802 crown roughly rectilinear with anterior portion slightly narrowed. Roots of equal width. Protoconid largest cusp, followed (in decreasing order) by hypoconid, paraconid, hypoconulid, entoconid and metaconid. Metaconid positioned postero-lingual to protoconid. Paracristid longest crest followed (in decreasing order) by posthypocristid, metacristid, cristid obliqua, preentocristid and postentocristid. Crests all relatively straight. Straight lingual face on crown with small bulge around anterior end of paraconid. Posterior crown surface straight with relatively small bulge protruding posteriorly as hypoconulid. Buccal flank has posterior bulge extending from base of protoconid around crown meeting midway at posterior bulge of hypoconulid. Flanks of talonid basin converge low in centre of basin. Basin width extends slightly beyond metaconid and slightly beyond protoconid.

Maxilla represented by QMF16804 and QMF16803. QMF16803 is more complete and is the basis for this description (Fig. 2). Maxilla preserved anteriorly to alveoli for P^2, dorsally to infraorbital canal and postero-dorsally to suture with jugal. Infraorbital canal not completely enclosed by bone and opening above M^3. Very small foramen occuring slightly anterior and ventral to infraorbital canal.

Right P^3 represented by QMF16803. Crown longer than wide, roughly triangular in occlusal

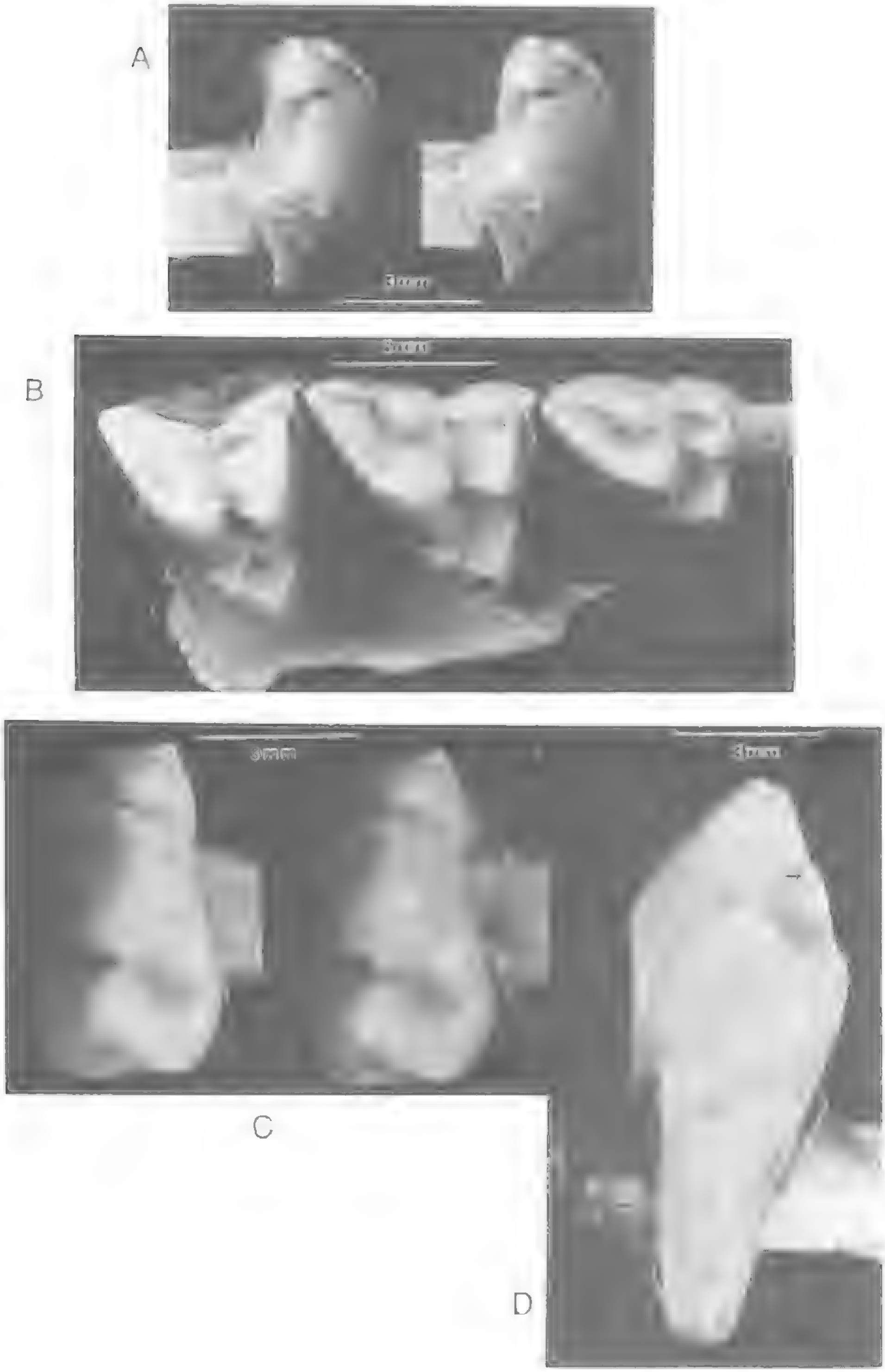

FIG. 1. *Nimbacinus dicksoni*. A, paratype QMF16809, broken right lower M_3 in occlusal view. B, paratype QMF16804, right maxillary fragment with M^2-M^4 in occlusal view. C and D, QMF16802 holotype left M_2. C, occlusal view; D, posterior view showing metaconid.

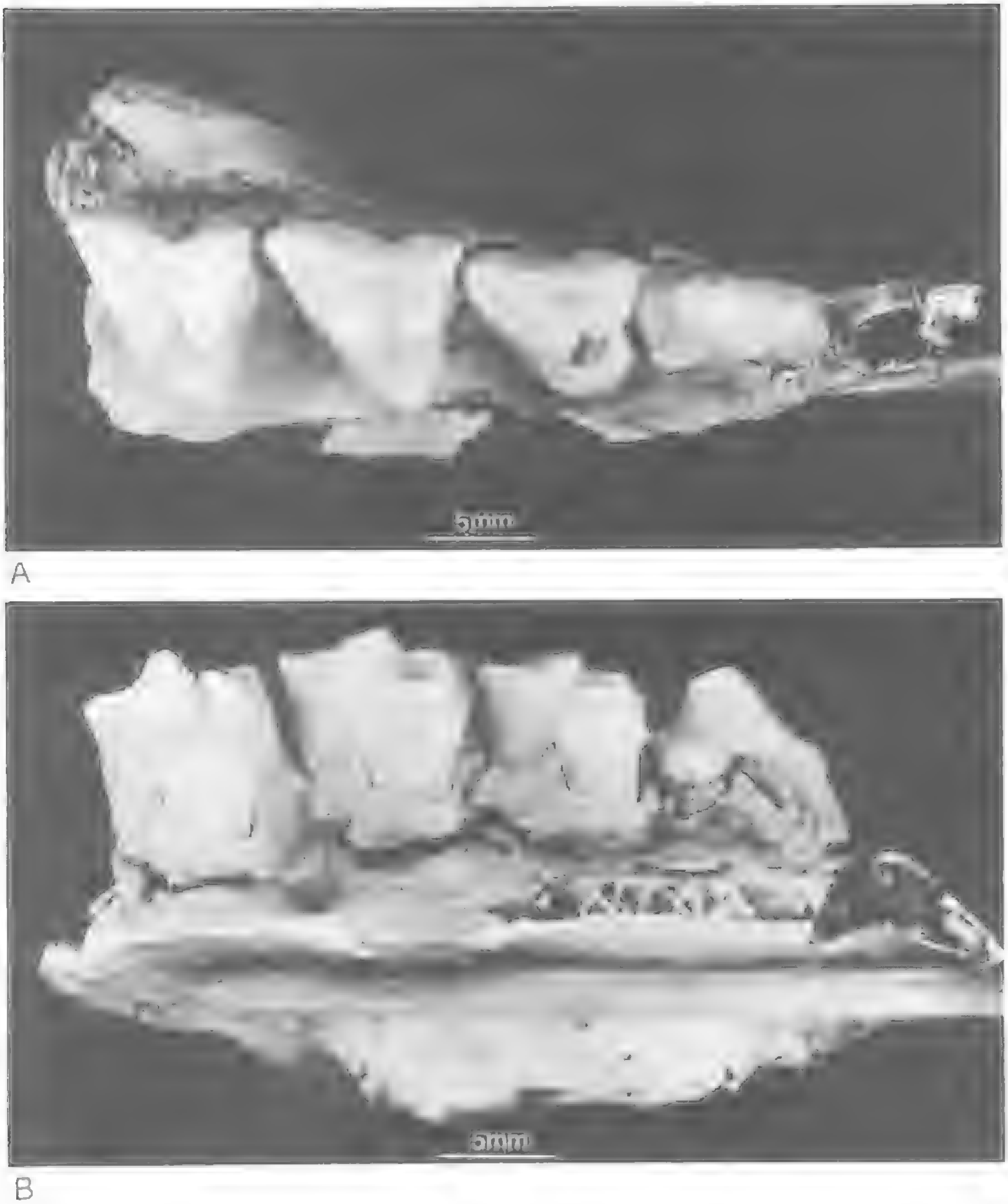

FIG. 2. *Nimbacinus dicksoni*, paratype QMF16803, right maxillary fragment. A, occlusal view; B, lingual view.

view and increasing in width posteriorly. Anterior root more massive and more nearly vertical than posterior root. Paracone medially positioned, tip worn. Tiny postero-lingual basal cuspule and posterior cuspule present. Tiny cuspule at anterior edge of crown may represent vestigial anterior cingulum. Paracone flank curved in posteriorly convex arc, continuing inclination of anterior root. Anterior surface of paracone rounded towards tip with anterior vertical crest only at base. Posterior crest extends from paracone to posterior cuspule and steeply concave in occlusal view.

M^2 represented by QMF16803 and QMF16804. Description here based on QMF16804 because this specimen is less worn. Three roots of M^2 much thinner than roots of P^3 and equal in size to each other. Each root directed vertically from each of three corners of crown. Triangular outline of crown (in occlusal view) has greatest width anteriorly. Buccal crown length exceeds anterior crown width and is exceeded by distance between protocone and metastylar corner of crown. Major cusps (in order of decreasing height) metacone, stylar cusp D, paracone, stylar cusp B, protocone. Parastylar crest present, tiny stylar cusp C in valley between stylar cusps B and D, tiny stylar cusp E on buccal edge of tooth, tiny protoconule and tiny metaconule. Small antero-buccal cingulum extends from paracone to parastylar crest. No other cingula present. Postmetacrista well-developed and longest of principal crests, followed (in decreasing length) by postprotocrista, preprotocrista, preparacrista, premetacrista and postparacrista. Major crests all meet at right angles. Postmetacrista linear, extending from metacone to metastylar corner. Preparacrista convex, connecting paracone to stylar cusp B. Postparacrista and premetacrista straight, not as well-developed as postmetacrista and meet in valley between paracone and metacone. Preprotocrista and postprotocrista are straight and approximately equal in length. These meet at tip of protocone. Postprotocrista extends posteriorly to terminate at postero-lingual base of metacone and connects to metaconular ridge. Similarly preprotocrista extends anteriorly to link with protoconular ridge at lingual base of paracone. Buccal crest runs posteriorly from stylar cusp B to posterior metastylar corner. Prominent vertical ridges extend anteriorly from stylar cusp B and lingual side of protocone. Lower buccal edge of crown bulges at base of stylar cusps B and D, producing small rounded concavity (ectoflexus) adjacent to stylar cusp C and valley between paracone and metacone. Lower lingual edge of crown rounded around protocone and forms 'U' shape when viewed occlusally. Region between paracone, metacone and stylar cusps appears enamel-free thereby facilitating removal of tooth material from the leading flanks of principal buccal shearing blades.

Right M^3 represented in QMF16804 and QMF16803. Wear is most pronounced on QMF16803 and description is based primarily on QMF16804. M^3 similar to M^2 except as follows. Crown dimensions of M^3 larger, with triangular shape of crown being less equidimensional. Metacone well-developed, distinctly higher than stylar cusp D. Protoconule, metaconule and stylar cusp C much larger on M^3. Enlargement of conules results in termination of postprotocrista and preprotocrista at tips of conules rather than at base of metacone and paracone. Stylar cusp E smallest cusp present. Preprotocrista exceeds postprotocrista in length. Preparacrista longer on M^3 than on M^2. Relative size of principal crests (from longest to shortest) are postmetacrista, preparacrista, premetacrista, preprotocrista, postprotocrista and postparacrista. Junction of preparacrista to postparacrista at paracone forms acute angle. All major crests on M^3 relatively straight including preparacrista which curves convexly at termination at stylar cusp B. Ectoflexus on M^3 greater than that of M^2. Buccal bulges of stylar cusps B and D do not extend to ends of crown. Metastylar tip forms more acute angle than in M^2. Lingual edge of tooth at base of protocone more angular than in M^2 and has prominent vertical ridge producing 'V' shape on lingual flank.

Right M^4 represented in QMF16803, QMF16804 and QMF16806. Isolated left M^4 represented in QMF16805. QMF16804 and QMF16806 show least wear and description is based on these. M^4 similar to M^2-M^3 except as follows. M^4 larger than M^2 but comparable in some dimensions to M^3. Stylar cusp D not well-developed and smaller than M^3 or M^2. Paracone second largest cusp followed by stylar cusp B. Stylar cusp D shows variation in height on M^4. QMF16806 has stylar cusp D subequal to stylar cusp B; on QMF16804 (showing similar wear pattern to QMF16806) stylar cusp D is smaller than stylar cusp C and metastylar crest. No stylar cusp E present on M^4. Paraconule and metaconule larger than on M^2 and subequal to M^3. Postmetacrista longest of crests followed (in order of decreasing length) by preparacrista, postprotocrista, preprotocrista, postparacrista and premetacrista. Junctions of these crests form sharper angles than on M^2. No buccal crest on stylar shelf region, which is reduced to greater degree. Lingual vertical ridge from protocone sharply pronounced. Lingual surface of tooth 'V'-shaped rather than 'U'-shaped as in M^2. Buccal surface of M^4 shows marked difference from that surface on M^2. Ectoflexus strongly developed. Bulges at base of stylar cusps B and D on M^2 reduced on M^4 and concavity between these enlarged and extended to anterior and posterior corners of crown. Buccal surface forms a broad 'V'-shaped concavity.

M^5 represented by isolated right tooth, QMF16807. Crown broken and similar to M^2, M^3 and M^4 except as follows. Occlusal shape of crown roughly linear with metastylar region reduced. Most prominent cusp is paracone from which extends straight preparacristid to parastylar crest at antero-buccal edge of crown. Postparacrista shorter than preparacrista and extends posteriorly to reduced metacone. Crests make wide angle at junction on the paracone. Protocone present but metaconule and protoconule reduced. No stylar shelf present. Occlusal surface at postero-buccal end of crown falls from crests after concave slope.

Meristic gradients from M^2 to M^4: postmetacristae length increases posteriorly; preparacristae length increases posteriorly; premetacristae length decreases posteriorly; lingual surface and junction between preprotocristae and postprotocristae becomes sharper posteriorly; degree of ectoflexus increases posteriorly; buccal crown length increases from M^2 to M^3, then decreases to M^4.

The Bullock Creek Specimen

Specimen NTMP85553-3 is a right dentary fragment preserving a region extending from P_1 to M_2. Mental foramen occurs under diastema between P_1 and P_2. A larger foramen occurs under anterior alveoli of P_3. Symphysis extends below posterior alveoli for P_3. Small (2 mm) diastema occurs between P_1 and P_2. Diastema between P_2 and alveoli for P_3 is slightly smaller. No diastema apparent between P_3 and M_2.

Crown on P_1 linear with maximum width at middle. Anterior root roughly equidimensional in cross-section and inclined posteriorly in its alveolus. Posterior root more massive than anterior root but inclined to same degree and linear in cross-section. Protoconid positioned in middle of anterior half of crown. It supports a slight anterior cristid running lengthwise from tip of protoconid.

Roots of P_2 similar to those of P_1. Crown morphology of P_2 also resembles that of P_1, differing only in following features. P_2 has triangular-shaped crown increasing in width posteriorly from protoconid. Protoconid height almost double that of same cusp on P_1 and lies in more posterior position on crown. Anterior cristid prominent, and posterior cristid also present. Posterior half of crown does not flatten to same degree as in P_1 because of increased height of protoconid and more posterior position. In centre of posterior edge of crown is minute cuspid.

Two broken alveoli represent P_3. Size and position of these suggest a tooth similar in size to P_2.

Crown size and general morphology of M_2 resembles that of QMF16802 from Henk's Hollow sample. The following description concentrates on features that differ between the two samples.

Bullock Creek M_2 very worn. Postero-lingual surface has slightly better-developed shelf with corner of crown extending out at sharper angle than in Henk's Hollow specimen; therefore posterior width of Bullock Creek tooth slightly greater. Antero-lingual surface of Bullock Creek crown has circular curvature. Bullock Creek specimen has greater anterior thickness than Henk's Hollow specimen which thins anteriorly to greater degree.

COMPARISON OF SAMPLES

Henks Hollow Material

Material representing *Nimbacinus dicksoni* from the Henk's Hollow Local Fauna includes the holotype QMF16802, and paratypes QMF16803, QMF16804, QMF16805, QMF16806 and QMF16807. These are presumed to represent a single taxon for the following reasons. QMF16803 and QMF16804 are both right maxillary fragments containing M^2, M^3 and M^4 and are very similar in size and morphology. The only significant difference between the two specimens is the degree of wear. QMF16806 and QMF16805 are isolated molars but they are virtually identical to the M^4 of QMF16803 and QMF16804. QMF16807 is an isolated M^5. No other thylacinid M^5 has been recovered from the Henk's Hollow deposit. Size and morphology, however, support the hypothesis that QMF16807 is an M^5 of *Nimbacinus dicksoni.* QMF16802 is the holotype and hence *N. dicksoni* by designation. Size and morphology suggest that this lower left molar represents the same species as the rest of the Henk's Hollow material. No other dasyuroid of comparable size has been recovered from this deposit despite preparation of a large amount of material. QMF16802 is the only thylacinid lower molar from the Henk's Hollow sample. This tooth corresponds perfectly to the occlusal features of upper molars (from the other side, QMF16803 and QMF16804). Meristic trends in *Thylacinus cynocephalus* suggest that QMF16802 is a left M_2 for the following reasons:

1) The M_2 of *T. cynocephalus* has a very reduced, simple anterior cingulum while the M_3 and M_4 have well-developed anterior cingula with a notch for the hypoconulid of the preceding molar. The Henk's

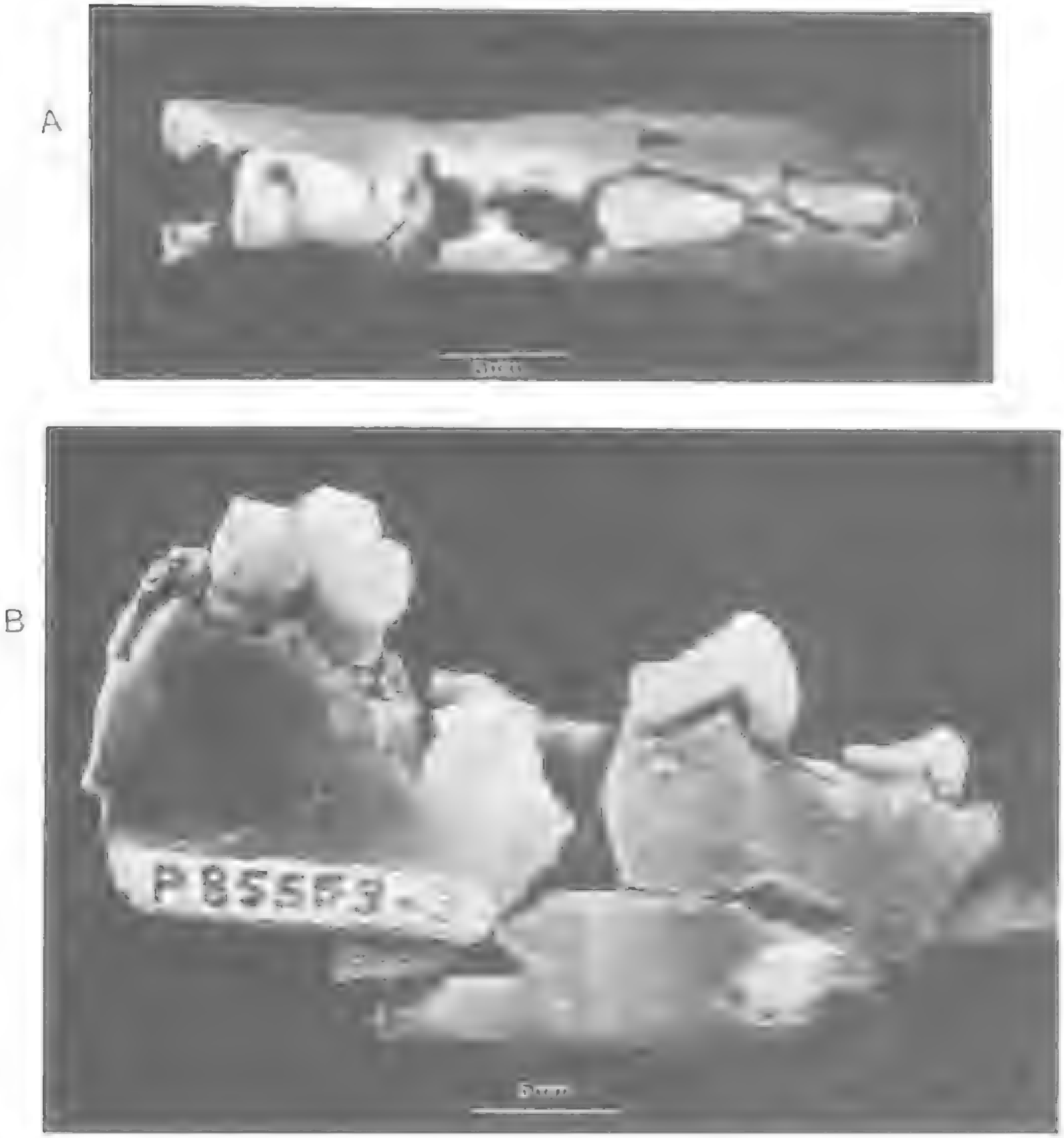

FIG. 3. *Nimbacinus dicksoni* paratype P85553-3. Right dentary fragment; A, occlusal view; B, buccal view.

Hollow lower molar has a proportionally larger single anterior cingulum but a much smaller and proportionately less well-developed cingulum than occurs on either the M_3 or M_4 of *T. cynocephalus*.

2) In *T. cynocephalus*, the paraconid of M_2 is poorly developed when compared with the paraconid of M_3 and M_4. The Henk's Hollow tooth also exhibits a relatively poorly developed paraconid.

3) In *T. cynocephalus*, the M_2 is subequal in crown length to that of M^2. Similarly, the M_3 and M_4 correspond in size to M^3 and M^4 respectively. The M_2, however, is much smaller than M^3 or M^4. The maxillary fragments from Henk's Hollow, although from the opposite side of the mouth, permit crown length comparisons with the lower molar which is subequal in size to M^2 and much smaller than M^3 and M^4.

4) Protocone and talonid width are directly correlated because they occlude. Direct correlation could not be demonstrated because upper and lower teeth are from opposite sides, but the talonid

width of the lower molar is subequal to the protocone width of the M^2 of the maxillary fragments.

THE BULLOCK CREEK MATERIAL

Specimen NTMP85553-3 (Fig. 3) was collected by P. Murray and party from the Camfield Beds of Victoria Downs Station, Northern Territory. The faunal assemblage from this formation, known as the Bullock Creek Local Fauna (Plane & Gatehouse, 1968), has been interpreted on the basis of biochronology to be middle Miocene in age (Woodburne *et al.*, 1985). The overall morphology of the M_2 in the Bullock Creek specimen NTMP85553-3 is very similar to the holotype from Henk's Hollow, and is therefore considered to represent *Nimbacinus dicksoni*.

THE SITE D SPECIMEN

QMF16809 is a right lower anterior molar fragment from the Carl Creek Limestone. It was collected by G. Clayton, S. Hand and M. Archer at Site D Locality (Tedford, 1967), Riversleigh Station. It is the anterior half of a right lower molar and is the only thylacinid material recovered from this site. Conclusions about meristic homology (as an M_2) and the specific identity of the tooth need qualification. It is equal in size to the M_2 of *Nimbacinus dicksoni* but two morphological features suggest that this tooth could not be an M_2. First, the anterior cingulum is strongly developed in the Site D molar. This produces a distinct 'V'-shape on the anterior surface of the crown, a feature found in M_3-M_5 of many marsupials as an adaptation to prevent food from lodging between adjacent molars. This feature is never found on M_2. Second, paraconid development increases posteriorly along the lower molar row in didelphids, dasyurids and thylacinids. The paraconid is typically poorly developed on M_2. The Site D molar has a very strongly developed paraconid, much larger than that seen in the Henk's Hollow or Bullock Creek specimens.

These features suggest that the Site D specimen, although comparable in size to the M_2 of the Henk's Hollow sample, must be either an M_3 or M_4. Thus the Site D specimen, which displays an extremely reduced metaconid for a posterior molar (a unique feature of thylacinids) must represent a smaller individual than those represented by the teeth from the Henk's Hollow and Bullock Creek samples. This is, therefore, also reason to suspect that the Site D thylacinid might represent a different, smaller species than *Nimbacinus dicksoni*.

Three morphological differences between the Site D tooth and those from the other two samples could be interpreted as indications of specific level distinction: the relatively small metaconid size, the less well developed antero-buccal margin of the crown and smaller overall size. The first two differences are not predictable attributes of a more posteriorly situated molar in dasyurids or thylacinids although the differences could represent intraspecific variation within *N. dicksoni*, a possibility that cannot be tested until larger samples are available. The possibility that the Site D specimen is specifically distinct on the basis of its small size, however, can be examined. Variation in a total combined *N. dicksoni* sample (including the Site D specimen) may be compared with that in *Thylacinus cynocephalus*, the latter being the only thylacinid represented by large samples (Ride, 1964; Dawson, 1982). The Site D tooth is not an M_2 for reasons noted above and is therefore either an M_3, M_4 or M_5. However, the further along the tooth row (i.e., closer to M_5) the tooth is, the greater the size difference between it and samples of *N. dicksoni* because the molars of thylacinids increase in size from front to back. If we presume that it is an M_3 rather than an M_4, this increases the probability that it and the other samples of *N. dicksoni* represent a single species. In order to see if the Site D tooth (presumed here to be an M_3) and the Henk's Hollow and Bullock Creek teeth could represent a single species no more variable than *T. cynocephalus*, differences between trigonid width of the smallest M_2 and that of the largest M_3 were compared in samples of modern (Tasmanian) and Pleistocene (Wellington Caves) *T. cynocephalus*. These differences are expressed below as a function of the length of the M_2 crown in order to standardise the measure. Tooth length is taken as the greatest antero-posterior dimension of the enamel crown. Tooth width equals the transverse width across the widest part of the trigonid. Thus the ratio for each sample is: (smallest M_3 width - largest M_2 width) / M_2 length. *Nimbacinus dicksoni* (all samples plus Site D specimen): (2.85-3.18) / 6.57 = 0.05 (where 2.85 and 6.57 are the dimensions of QMF16809 and QMF16802 respectively, and 3.18 the width of the Site D trigonid). Modern *T. cynocephalus*: (5.03-4.95) / 2.91 = 0.01 (where 5.03 and 4.95 represent AR8409 and S789 respectively and 9.21 represents S789). Pleistocene plus modern populations of *T. cynocephalus*: (5.03-6.23) / 12.53 = 0.10 (where 5.03 and 12.53 represent AR8409 and MF308 respectively and 6.23

represents MF308); (for specimen details see Appendix).

It can be seen that the combined range of the *Nimbacinus dicksoni* sample (with the Site D tooth included) exceeds that of modern *T. cynocephalus*. However, the size range ratio of *T. cynocephalus* when Pleistocene and modern samples (the two being regarded to represent *T. cynocephalus* by Ride, 1964 and Dawson, 1982) are combined is 0.10. This value is higher than that for the modern specimens alone and exceeds that for the combined *N. dicksoni* sample. Thus on the basis of size alone, the Site D tooth cannot be excluded from *N. dicksoni*. This tooth may, however, represent a smaller population of the species than that which occurred in the Henks Hollow and Bullock Creek deposits. As is evident from these calculations, the same magnitude of size difference exits between modern plus Pleistocene samples of *T. cynocephalus*.

CHARACTER ANALYSIS

Phylogenetic systematic methodology was used to examine the relationships of *Nimbacinus dicksoni* within the Thylacinidae. This analysis used the method of out-group comparison elaborated by Watrous and Wheeler (1981) in order to determine character state polarities within the Thylacinidae. Richardson, Baverstock and Adams (1986) suggest that the out-group should consist of several species which are distantly related yet as close as possible to the group under study. Dasyurids have been determined to be the most appropriate out-group on the basis of morphological, serological and other studies of thylacinid and dasyurid relationships (e.g. Simpson, 1941, 1945; Marshall, 1977; Archer, 1982a; Szalay, 1982; Sarich *et al.*, 1982). Of the dasyurids, the relatively most plesiomorphic and unspecialised species of *Murexia* were interpreted (*fide* Archer, 1976) to represent the plesiomorphic states of polymorphic characters within the Dasyuridae.

CHARACTERS CONSIDERED AND THEIR CHARACTER-STATE POLARITIES

1. Paracone Height: In the oldest and most plesiomorphic marsupials (e.g. species of the genera *Alphadon*, *Pediomys* and *Didelphodon*), the paracone is lower than the metacone, a condition that appears to represent an autapomorphic feature of marsupials. Some dasyurids, most borhyaenoids, sparassocynids and thylacinids, however, show further reductions of paracone height considered to be apomorphic within the Marsupialia (Archer, 1982a). Of thylacinids, *T. cynocephalus* exhibits extreme paracone reduction while *T. potens* shows less but still marked reduction of the paracone. In *Nimbacinus dicksoni*, the height of the paracone relative to the metacone is slightly lower than that for most dasyurids and therefore represents an apparently plesiomorphic state within the Thylacinidae.

2. Stylar Cusp B: Stylar cusp B is present and large in almost all plesiomorphic marsupials. This appears to be the plesiomorphic state among dasyuroids being present in, for example, species of *Murexia*. In dasyurids, loss of stylar cusp B from M^2 is a synapomorphy of several morphologically specialised lineages such as the dasyurines (Archer, 1976). In *Thylacinus cynocephalus* stylar cusp B is extremely reduced on M^2 and minute on M^3 and M^4 (Archer, 1976). In *Thylacinus potens*, there is a similar reduction of stylar cusp B on M^4 but its condition is indeterminate on the other molars because of poor preservation. Stylar cusp B in *N. dicksoni* is also reduced although not to the same degree as in species of *Thylacinus*. Stylar cusp B is small on M^2 but prominent on M^1 and M^4. On M^4 it is the third largest cusp on the crown. In this condition *N. dicksoni* displays a more plesiomorphic condition than the species of *Thylacinus*.

3. Stylar Cusp C: Some Caenozoic didelphids exhibit a reduction of stylar cusp C in contrast to the condition of peradectids. A small stylar cusp C has been considered to be plesiomorphic within the Marsupialia (e.g. Archer, 1976). *Thylacinus cynocephalus* shows no sign of stylar cusp C on any molars. *T. potens* shows a small stylar cusp C on M^4. The preservation of M^2 and M^3 of *T. potens* is too poor to determine the size of this cusp on these teeth. In *N. dicksoni* stylar cusp C is minute on M^2 and slightly larger on M^3 and M^4. On M^4 it is comparable in size to stylar cusp D (which is relatively more prominent on M^2 and M^3). Stylar cusp C on the M^4 of *N. dicksoni* is relatively larger than that seen on M^4 of *T. potens*. This suggests that, in this regard, *N. dicksoni* displays a more plesiomorphic condition than any other thylacinid.

4. Stylar Cusp D: Stylar cusp D is present in didelphids and dasyurids. In dasyurids this cusp tends to be largest on M^2 and M^3 (Archer, 1976). *Thylacinus cynocephalus* has lost this cusp on all molars. *T. potens* shows a reduced stylar cusp D on M^4 which is larger in height than stylar cusp C. The damaged M^3 of *T. potens* suggests a better-developed stylar cusp D than that on M^4.

Stylar cusp D on the M^4 of *Nimbacinus dicksoni* is only slightly larger than that seen in *T. potens*. However, on the M^2 and M^3 of *N. dicksoni*, stylar cusp D is very large and comparable to that of dasyurids. This condition in *N. dicksoni* is therefore interpreted to represent a more plesiomorphic condition while the reduced state of stylar cusp D in other thylacines is interpreted as the apomorphic condition.

5. Stylar Cusp E: Stylar cusp E is present in some peradectids and many dasyurids (Archer, 1976). *Thylacinus cynocephalus* has a small cusp in the position of stylar cusp E on M^2 and M^3 and is the largest of the cusps present. No stylar cusp E occurs on M^4. Stylar cusp E does not occur on any of the molars of *T. potens*. Specimen QMF16804 of *N. dicksoni* exhibits very little wear and reveals a vestigial stylar cusp E on M^2 and M^3. No stylar cusp E is present on M^4 of this species. Reduction of stylar cusp E is considered an apomorphic condition within the Thylacinidae but the complete loss of this cusp in *T. potens* appears to represent an autapomorphic condition.

6. Protoconules: Almost all Cretaceous peradectids display protoconules and metaconules. These are also present in most didelphids and many dasyurids. The presence of these cuspules is therefore considered to be plesiomorphic and their reduction or loss apomorphic.

In dasyurids, if a protoconule is present a metaconule is usually also present. In rare cases a protoconule is present without the simultaneous presence of a metaconule (e.g. *Thylacinus potens*). The opposite is also seen to occur. A very reduced metaconule may be present without the presence of a protoconule. Clearly the two conditions can vary independently and should be analysed separately.

Thylacinus cynocephalus lacks the protoconule on all molars. The presence of a protoconule on the M^2 of *T. potens* is indeterminate. The M^4 of *T. potens* appears to have a reduced protoconule. *Nimbacinus dicksoni*, in contrast, has a large and distinct protoconule on M^3 and M^4. The M^2 has an extremely small protoconule, a common condition for the M^2 of dasyurids. *N. dicksoni* thus appears to display the plesiomorphic condition while *T. potens* and *T. cynocephalus* exhibit apomorphic states.

7. Metaconules: The metaconule is present in all Cretaceous peradectids, most didelphids and many dasyurids. The presence of a well-developed metaconule is considered plesiomorphic and the loss or reduction of this cusp apomorphic. Metaconules are absent on the teeth of *T. cynocephalus*. Similarly, *T. potens* has no distinguishable metaconules on any molar. *Thylacinus potens* therefore displays the variable loss of one conule without loss of the other. *Nimbacinus dicksoni* has a large and distinct metaconule on M^3 and M^4 but not on M^2. It therefore exhibits a relatively plesiomorphic condition while *T. potens* and *T. cynocephalus* display an apomorphic condition.

8. Pre- and Postprotocristae: Presence of distinct preprotocristae and postprotocristae occurs in peradectids, most didelphids and plesiomorphic dasyurids and is therefore considered to be the plesiomorphic state within dasyuroids. Variation in these features does not appear to be correlated with the size of the protoconules and metaconules because some dasyurids, such as species of *Phascogale*, exhibit distinct pre- and postprotocristae while the proto- and metaconules are very reduced. Reduction of the pre- and postprotocristae is an apomorphic condition in *Thylacinus cynocephalus*. Protocristae are extremely reduced on M^4 but are more evident on M^3. The M^2 shows an almost total loss of protocristae. *T. potens* shows less extreme reduction of the protocristae of M^4 in contrast to the condition seen in *T. cynocephalus*. The M^3 of *T. potens* also shows reduction of the protocristae while the condition on M^2 is unclear. *Nimbacinus dicksoni* displays the plesiomorphic condition with sharp and distinct protocristae on both M^3 and M^4. The protocristae of M^2 are slightly less pronounced.

9. Preparacristae and Postmetacristae: Archer (1982b) considered the proportional size reduction of the preparacristae to be associated with a functional complex correlated with elongation of the postmetacristae. *Thylacinus cynocephalus* shows this correlation in that the preparacristae are small relative to tooth size while the postmetacristae are extremely elongate.

The proportional size of the preparacristae in peradectids, didelphids and unspecialised dasyurids is approximately half the length of the anterior tooth surface of the M^2 and M^3 while the preparacrista of M^4 is slightly longer. This condition is considered to be the plesiomorphic state. *Nimbacinus dicksoni* and *T. potens* show the plesiomorphic state. *Thylacinus cynocephalus*, in contrast, shows relatively shorter preparacristae which are much less than half the width of the anterior tooth surface of M^2, M^3 and also M^4. This reduction in *T. cynocephalus* appears to be autapomorphic.

Elongation of the postmetacristae is an apomorphic state displayed by borhyaenids, thylacosmilids and specialised dasyurids (Archer, 1982b). *Nimbacinus dicksoni* displays the same relative size of the postmetacristae seen in primitive dasyurids such as peradectids, didelphids and species of *Murexia*. *Thylacinus potens*, however, shows apomorphic elongation of the postmetacristae. *T. cynocephalus* displays a similar but more exaggerated elongation of the postmetacristae, these crests being slightly larger than they are in *T. potens*. Thus, the two *Thylacinus* species share the apomorphic state of postmetacristae elongation.

10. Angle Between the Preparacrista and Postmetacrista: The angle made by the intersection of lines projected along the preparacrista and postmetacrista varies among dasyurids and thylacinids. This angle is markedly acute and reasonably constant throughout the peradectids, didelphids, most dasyurids and *Nimbacinus dicksoni*. This acute condition is therefore considered plesiomorphic. The two *Thylacinus* species show a proportional increase in the size of this angle. *Thylacinus potens* displays a significant increase in this angle while this feature in *T. cynocephalus* is further increased to approximately a right angle. Thus the species of *Thylacinus* display apomorphic conditions. The increase in this angle results from an antero-posterior shift in the orientation of the preparacristae and postmetacristae. This shift is particularly well-developed in *T. cynocephalus* where the molars, especially M^4, are not equidimensional in crown outline as are those of peradectids, didelphids, dasyurids and *N. dicksoni*. This suggests that in this feature *T. cynocephalus* is the most derived member of the family.

11. Ectoflexus: Well developed ectoflexus is a feature of dasyurids. The M^4 of *Nimbacinus dicksoni*, however, exhibits better-developed ectoflexus than occurs in any dasyurid. This may reflect the reduced size of stylar cusp D in *N. dicksoni*. However, complete loss of stylar cusp D in *Thylacinus cynocephalus* has not resulted in an increase in the extent of ectoflexus. *T. potens* has very pronounced ectoflexus resulting in a 'V'-shaped buccal surface. This ectoflexus is more marked than that which occurs in dasyurids and *N. dicksoni* and may, therefore, be considered autapomorphic rather than plesiomorphic although the increased ectoflexus of *N. dicksoni* and *T. potens* may constitute a synapomorphic condition.

Thylacinus cynocephalus, in contrast to dasyurids and other thylacinids, has extremely limited ectoflexus, the buccal surface of the crown being almost straight. This condition appears to be autapomorphic within this family. Thus *N. dicksoni* and *T. potens* appear to show one apomorphic state (hypertrophied ectoflexus) while *T. cynocephalus* displays another (extreme reduction of ectoflexus), both conditions contrasting with the presumed plesiomorphic state that would have more clearly resembled that seen in dasyurids.

12. Metaconid: The metaconid of peradectids, didelphids and most dasyurids is conspicuous and unreduced. All marsupial carnivores possess metaconids except most borhyaenids and thylacinids (Archer, 1982b). Metaconid reduction on M_2 occurs in three separate dasyurid lineages (Archer, 1976) but this cusp is rarely absent. Reduction and loss of the metaconid is considered to be an apomorphic state. *Thylacinus cynocephalus* has no trace of metaconid on any of its molars. Woodburne (1967) describes *T. potens* as having no metaconid. *Nimbacinus dicksoni*, however, possesses a very reduced metaconid. In this regard, *N. dicksoni* appears to represent a condition intermediate between that of dasyurids and other thylacinids.

13. Entoconid: All peradectids and almost all didelphids (an exception being, e.g. *Monodelphis dimidiata*) possess a well developed entoconid. Most dasyurids possess an entoconid, although it is absent in several otherwise apomorphic dasyurid lineages such as species of *Planigale* and *Pseudantechinus* (Archer, 1976; 1982a). Presence of a well developed entoconid is thus presumably the plesiomorphic state.

Thylacinus cynocephalus exhibits a very reduced entoconid. This is minute on M_2 and M_4. Woodburne (1967) described *T. potens* as possessing an entoconid on the M_4. Although it is probable that the entoconid also occurs on at least M_3-M_4 of *T. potens*, Woodburne (1967) made no comment about this condition.

Nimbacinus dicksoni has an extremely small entoconid on at least the M_2. The appearance of a relatively larger entoconid in *T. cynocephalus* may be the result of reduction of surrounding cristids in this species. These cristids are well developed in *N. dicksoni* and almost completely encompass the entoconid. The relative height of the entoconid from the base of the crown in *N. dicksoni* is similar to that of *T. cynocephalus*. Thus, while all three thylacinids exhibit synapomorphically reduced entoconids this cusp is more conspicuous in *T. cynocephalus* possibly because of the autapomorphic loss of adjacent cristids.

TABLE 1. Character state polarity

Character	Plesiomorphic State	Apomorphic State (see text for details)
1 Paracone height	Prominent but < metacone	A1(red.), A2(red.+), A3(red.++)
2 Stylar cusp B	Large	A2(red.), A2(red.+)
3 Stylar cusp C	Present	A1(red.), A2(lost)
4 Stylar cusp D	Large	A1(red.), A2(lost)
5 Stylar cusp E	Present	A1(red.), A2(lost)
6 Protoconule	Prominent	A1(red.), A2(lost)
7 Metconule	Prominent	A1(lost)
8 Pre- and Postprotocrista	Prominent	A1(red.), A2(red.+)
9 Preparacrista and Postmetacrista	Long and Short (resp.)	A1(red. prepara, elong. postpara) A2 (as for A1+)
10 Angle between Prepara- & Postmetacrista	Sharp, acute	A1(acute+), A2(> 90°)
11 Ectoflexus	Present	A1(enlarg.), A2(enlarg., A3(red.), A4(red.+)
12 Metaconid	Large	A1(red.), A2(lost), A1.5(red.+)
13 Entoconid	Large	A1(red.)
14 Talonid basin ridge	Large	A1(red.)
15 Talonid basin and protocone size	Large	A1(red.), A2(red.+)

Abbreviations: red. = reduced; red.+ = reduced more than red.; red.++ = reduced more than red.+; elong. = elongated; elong.+ = elongated more than elong.; enlarg. = enlarged; enlarg.+ = enlarged more than enlarg.; elarg.++ = enlarged more than enlarg.+; A1 = 1st state of apomorphy; A2 = 2nd state of apomorphy; A3 = 3rd state of apomorphy.

14. Talonid Basin Ridge: Most plesiomorphic dasyurids have a low talonid basin surrounded by cristids. *Nimbacinus dicksoni* shares this feature with dasyurids, the talonid basin being enclosed by cristids. Woodburne (1967) described a ridge on M_3 of *Thylacinus potens* that connects the hypoconulid to the hypoconid and entoconid, thereby creating an enclosed talonid basin. *Thylacinus cynocephalus* has a very flat talonid basin. The only distinct cristid that surrounds the basin is the posthypocristid. The only structure that defines the lingual edge of the basin is the tiny entoconid. The floor of the basin slopes down towards the lingual side. *Thylacinus cynocephalus* thus displays, among thylacinids, the most apomorphic condition.

15. Talonid Basin and Protocone Size: The protocone and talonid basin occlude and are correlated as a character complex. The smaller size of both is a synapomorphy of thylacinids, borhyaenoids and some dasyurids such as *Sarcophilus* (Archer, 1982b).

Nimbacinus dicksoni has a small talonid basin compared to most dasyurids. The antero-posterior length of the protocone is also slightly smaller in this species than in dasyurids. *Thylacinus cynocephalus* has even smaller talonids and protocones. Talonid basin size in *T. potens* is uncertain but the protocone is of a similar size to *T. cynocephalus*. Thus, *N. dicksoni* is more apomorphic than dasyurids but is more plesiomorphic than *T. cynocephalus* and *T. potens*.

Summary of Cladistic Analysis and Results

Table 1 presents the characters considered above with an indication of the plesiomorphic state for each; table 2 summarizes the polarity of character states for each of the four groups analysed.

Only the distribution of potential synapomorphic states is considered because these may represent features shared in a common ancestor. Thus, character 14 (talonid basin ridge) provides no information useful for interpreting phylogenetic relationships within Thylacinidae because only one of the three thylacinid taxa

TABLE 2. Character state distribution

Character	D	d	p	c
1	P	A1	A2	A3
2	P	A1	A2	A2
3	P	P	A1	A2
4	P	P	A1	A2
5	P	A1	A2	P
6	P	P	A1	A2
7	P	P	A1	A1
8	P	P	A1	A1
9	P	P	A1	A2
10	P	P	A1	A2
11	P	A1	A2	A3
12	P	A1	A2	A2
13	P	A1	A1	A1
14	P	P	?	A1
15	P	A1	A2	A2

Characters identified by number in Table 1. Abbreviations for taxa: D = plesiomorphic dasyurid (e.g. *Murexia* spp.); d = *Nimbacinus dicksoni*; p = *Thylacinus potens*; c = *Thylacinus cynocephalus*. Abbreviations for character states: P, plesiomorphic; A1-A3, as in Table 1.

displays an undoubted apomorphic (hence autapomorphic) condition.

Hypotheses about Thylacinid Phylogeny

Figure 4 shows the twelve different dichotomous cladograms possible for the four groups considered in the analysis. Of these only trees 1 and 3 are substantiated by the distribution of synapomorphies. Tree 3 is supported by one out of fifteen characters — stylar cusp E. Tree 1 is supported by the remaining fourteen characters. These results are summarised in Table 3.

The presence of a prominent stylar cusp E (Character 5) has been considered above to represent the plesiomorphic state and its reduction or loss as apomorphic states. If correctly interpretated in terms of polarity, the condition in *Thylacinus cynocephalus* would be plesiomorphic in contrast to the condition seen in all other thylacinids. *Nimbacinus dicksoni,* which in all other characters appears to be the most primitive thylacinid, has only a vestigial stylar cusp E on M^2 and M^3; and the cusp is entirely lost in *T. potens.*

It is possible, however, that the cusp identified here as stylar cusp E in *T. cynocephalus* is incorrectly identified. Archer (1982b) considered that this cusp might in fact be stylar cusp D in an unusually posterior position. This alternative interpretation of the homology of this cusp appears to be supported by the development and occurrence of stylar cusps D and E within the Thylacinidae. If this cusp is stylar cusp D rather than E, it may represent a stage in the reduction of stylar cusp D and the enlargement of the posterior region of the teeth, a trend supported by the overall morphology of all other thylacinids.

Stylar cusp D is very well-developed on the M^2 and M^3 of dasyurids. This condition is found in *N. dicksoni* where, as in dasyurids, it is the largest of the stylar cusps. The M^4 in both cases has a relatively smaller stylar cusp D. *Thylacinus potens* appears to have a better-developed stylar cusp D on M^3 than on M^4. The better development of this cusp on M^2 and M^3 in contrast to its size on M^4 appears to be a size relationship characteristic for stylar cusp D in dasyurids. With the phylogenetic increase in development of the posterior region of the tooth in thylacinids, the stylar cusps may have shifted posteriorly and what we at first interpreted to be stylar cusp E in *Thylacinus cynocephalus* may in fact be stylar cusp D. This conclusion would remove any support for Tree 3 leaving Tree 1 as the only one to be supported by the character analysis (Fig. 5).

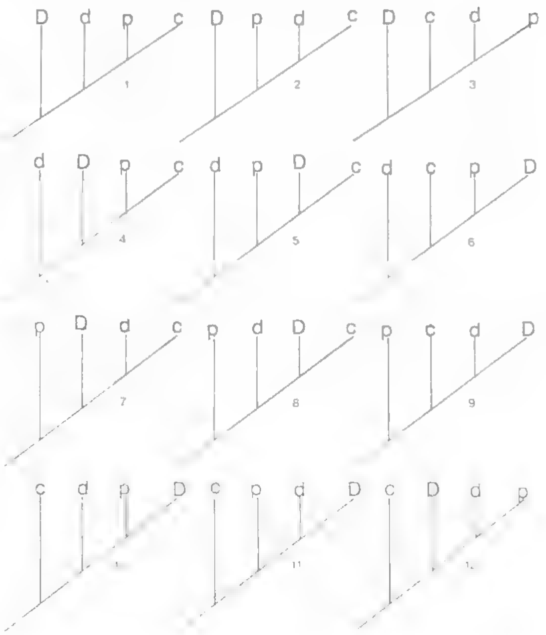

FIG. 4. Twelve possible cladograms involving dasyurids and thylacinid species. D, dasyurids (e.g. species of *Murexia*); c, *Thylacinus cynocephalus*; p, *Thylacinus potens*; d, *Nimbacinus dicksoni.*

TABLE 3.

Tree	Characters in Support	Characters Against
1	1,2,3,4,6-15	5
2	none	all
3	5	1,2,3,4,6-15
4-12	none	all

DISCUSSION

The results of the character analysis suggest that *Nimbacinus dicksoni* is more specialised than peradectids, didelphids and most dasyurids (except *Sarcophilus*) in the reduction of the paracone, stylar cusps B and E, metaconid, entoconid, protoconid and talonid basin. It is more plesiomorphic than *Thylacinus* species in which these same features are further reduced or lost. It is also more plesiomorphic than *Thylacinus* species in the lack of enlargement of the postmetacrista and the angle formed between this crest and the preparacrista. These are carnivorous adaptations that transform the shearing structures of the molars from short transverse to more elongate longitudinal blades, features well-developed in

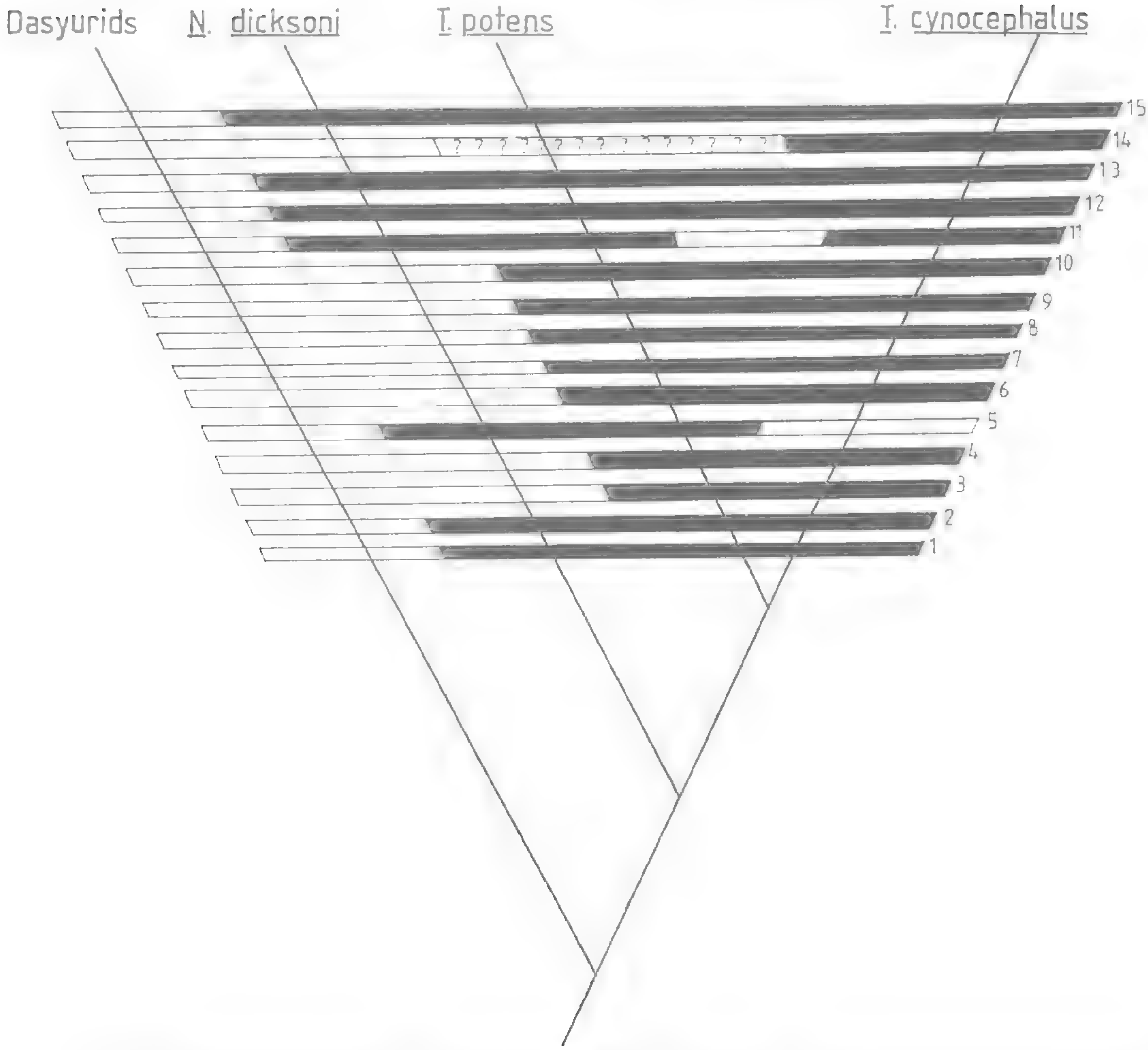

FIG. 5. The supported hypothesis of thylacinid relationships (Tree 1). Solid bar = plesiomorphic state; empty bar with question marks indicate unknown state. For character 11, there are two alternative apomorphic states (an autapomorphic condition occurring in *T. cynocephalus*; see text).

Thylacinus (among thylacinids) and *Sarcophilus* (among dasyurids).

Nimbacinus dicksoni also retains many plesiomorphic features common in peradectids, didelphids and dasyurids but which have been reduced or lost in *Thylacinus*. These are: presence of stylar cusp C; a large stylar cusp D; prominent protoconule and metaconule; prominent preprotocrista and postprotocrista; and a talonid basin ridge. Similarly, *N. dicksoni* retains a very large third premolar which is a plesiomorphic feature common in peradectids, didelphids and thylacinids but lost in all except the most plesiomorphic dasyurids (e.g. species of *Murexia)*.

Nimbacinus dicksoni shares some derived features with the more specialised carnivorous dasyurids such as *Sarcophilus harrissi* including: the reduction of the protocone; reduction of the talonid basin and its ridge; reduction of the stylar shelf region; elongation of the postmetacrista; and the increase in angle between the preparacrista and postmetacrista.

A morphocline involving progressively better-developed carnassial adaptations such as those seen in *Nimbacinus* links *Dasyurus maculatus* through *Sarcophilus moornaensis* to *S. harrissi*. This dasyurid lineage is distinct from *Nimbacinus dicksoni* in its retention of plesiomorphic features such as large metaconid and entoconid and its synapomorphic loss of P3. If *Nimbacinus dicksoni* is not part of this dasyurid radiation, the features that make it similar must have been independently acquired and thus convergent. This hypothesis is all the more probable because these are features that have been convergently developed in other marsupial groups (e.g. borhyaenoids; see Archer, 1982b).

Nimbacinus dicksoni also shares features with *Dasylurinja kokuminola* which is represented by a very small isolated right M^4 from the Late Oligocene Yanda Local Fauna, South Australia. Archer (1982a) concluded that it is a distinct dasyurid lineage unrelated to any previously known dasyurid subfamily. The features shared by both *D. kokuminola* and *Sarcophilus*, *Dasyurus* and *Satanellus* were considered by Archer (1982a) to be the result of convergence because *D. kokuminola* appears to be more autapomorphic than species of these three genera (e.g. in the extent of reduction of the metaconule, protoconule and the paracone).

Archer (1982a,b) did not consider possible relationship of *D. kokuminola* to thylacinids. It shares with thylacinids an antero-posteriorly compressed protocone, a reduced paracone and extreme enlargement of the postmetacrista. *Nimbacinus dicksoni* shares additional (presumably plesiomorphic) features with *D. kokuminola*, including the presence of stylar cusps B, D, E and possibly C, a combination of stylar cusps not found in any other dasyurid group. *Dasylurinja kokuminola*, however, shows a more extreme apomorphic state than *N. dicksoni* in its greater reduction of the metaconule and protoconule. *D. kokuminola* cannot, therefore, be an actual ancestor to *N. dicksoni* unless this condition has been secondarily acquired. Apomorphic reduction of the metaconule and protoconule is, however, also seen in species of *Thylacinus* and there is no feature of *D. kokuminola* that rules out the possibility of it being ancestral to species of *Thylacinus*. Similarly, *N. dicksoni* may be ancestral to *D. kokuminola*. However, the much larger size of *N. dicksoni* makes this hypothesis less likely.

Stirton, Tedford and Miller (1961) considered material subsequently described as *Apoktesis cuspis* from the Late Oligocene Ngapakaldi Local Fauna, to be ancestral to species of *Thylacinus*. Their conclusion was based on shared premolar size gradients which increase from P_1 to P_3 and the lack of a metaconid on M_2.

The premolar size gradient exhibited by *Apoktesis cuspis* is a plesiomorphic state present in unspecialised dasyurids such as species of *Murexia* (Archer, 1976, 1982a). The apomorphic reduction of the metaconid in *A. cuspis* only occurs on its M_2; the metaconids on its other molars are better developed. Reduction (and sometimes loss) of the metaconid on M_2 but large size on M_3-M_5 is common in dasyurids (e.g. some species of *Pseudantechinus*, *Dasyurus* and *Parantechinus*). Thylacinid species, in contrast, are unique in showing equivalent metaconid reduction on all molars.

Other features of *Apoktesis cuspis* noted by Stirton, Tedford and Miller (1961) do not appear to be synapomorphies with *Thylacinus* (Archer, 1976). Similarly *Nimbacinus dicksoni* shows no other features comparable to *A. cuspis*. Metaconid reduction on M_2 of *A. cuspis* and thylacinids is therefore concluded to be convergent.

It is possible, although less parsimonious, that *N. dicksoni* is a dasyurid lineage convergent on thylacinids. Although this would require an extreme degree of convergence, the possibility cannot be dismissed because comparable convergence has taken place between thylacinids and borhyaenids (e.g. Archer, 1982b).

Nimbacinus dicksoni is placed in the family Thylacinidae because it shows a combination of features otherwise unique to thylacinids: reduction of the metaconid on all lower molars; reduction of the stylar shelf by the independent reduction of the stylar cusps; reduction of the entoconid of the lower molars; reduction of the talonid basin and protocone; and an infraorbital canal posteriorly delimited by the jugal.

Loss of the metaconid together with the loss of the talonid basin ridge, reduction in talonid basin size and its lingual orientation places emphasis on the antero-posterior linear orientation of the cusps and crests of the lower molars. These adaptations of the lower molars are matched in the uppers by reduction of the protocone, reduction of the stylar shelf and the overall antero-posterior lengthening of the tooth. In combination these carnivorous adaptations are unique to species of *Thylacinus* and partially developed in *N. dicksoni*.

Considering phylogenetic relationships of the family Thylacinidae, *Thylacinus cynocephalus* and *T. potens* are concluded to be sister-species of a monophlyetic group rather than transformational members of an anagenetic lineage. The impropriety of considering *T. potens* as the actual ancestor of *T. cynocephalus* is indicated by the suite of autapomorphic features in *T. potens* (e.g. the enlargement of the ectoflexus) absent in *T. cynocephalus*.

So far as known, *Nimbacinus dicksoni* exhibits no feature that would prohibit it from being a direct ancestor to all species of *Thylacinus*. Similarly, no feature precludes *Dasylurinja kokuminola* from being ancestral to species of *Thylacinus*. Thus there are at least three plausible phylogenetic hypotheses involving thylacinids and *Dasylurinja*: 1, all three genera could be members of a monophyletic group in which none is the direct ancestor of any other (a trichotomy); 2, *N. dicksoni* could be a direct ancestor of *Thylacinus* with the common ancestor of this group sharing a common ancestor with *D. kokuminola*; or 3, *N. dicksoni* could be ancestral to *D. kokuminola* which in turn was ancestral to species of *Thylacinus*. The possibility of species of *Thylacinus* being ancestral to *N. dicksoni* and *D. kokuminola* is remote because of the many autapomorphic features of *Thylacinus*.

Nimbacinus dicksoni appears to represent the earliest record of the family Thylacinidae. It is a relatively unspecialised thylacinid sharing features with plesiomorphic dasyurids. Apart from *N. dicksoni*, the oldest known thylacinid is the Late Miocene *Thylacinus potens* (Woodburne, 1967).

Nimbacinus dicksoni is regarded as generically distinct from species of *Thylacinus* because the difference between it and any other species of *Thylacinus* is much greater than that exhibited between the other species of *Thylacinus* or between the species of any other dasyuroid genus.

Accepting that *N. dicksoni* is a thylacinid, the concept of the Thylacinidae must be revised as follows. Thylacinids are dasyuroids with the following unique combination of features: extreme reduction of the metaconid on all lower molars; reduction of the entoconid; reduction of the stylar shelf, especially stylar cusps B and E; reduction in the size of the talonid basin and protocone; retention of a large, unreduced P3; and posterior definition of the infraorbital canal by the jugal. Of these features, metaconid reduction on all molars is a uniquely thylacinid feature.

Thylacinids differ from myrmecobiids in many features, including the reduction of the metaconid and entoconids on all molars and the presence of a well-developed postmetacrista, molariform and tritiberculo-sectorial molars. Myrmecobiids also differ from thylacinids in their common possession of five adult molars while thylacinids retain only four.

The phylogenetic relationships of thylacinids have long been the centre of debate. Two main proposals have been: 1, thylacinids are part of the Australian radiation, having diverged from ancestral dasyurids (supported by Matthew, 1915; Simpson, 1941, 1945; Tate, 1947; Marshall, 1977; Archer, 1982b, 1984; Aplin & Archer, 1987); and 2, thylacinids share their closest ties with the South American borhyaenids (proposed by Sinclair, 1906, and supported by Scott, 1913; Gidley, 1915; Loomis, 1921; Osgood, 1921; Wood, 1924; and Archer, 1976). Bensley (1903) was uncertain, but considered that thylacinids were a "foreign" element in the Australian fauna. The oldest previously named thylacinid, the Late Miocene *Thylacinus potens*, unfortunately provides little insight into thylacinid relationships, being almost as distinct from dasyurids as is *T. cynocephalus* (Woodburne, 1967; Archer, 1982b).

A morphological study of tarsal bones by Szalay (1982) identified features that appeared to separate thylacinids from borhyaenids and to ally them with australidelphian marsupials. Serology provided further support for separation of thylacinids and borhyaenids. Sarich *et al.* (1982) examined albumin taken from dried museum specimens and concluded that the living dasyurids examined and the Thylacine shared a common ancestor approximately 7 million years ago.

The rate of evolution at the molecular level has been suggested to be relatively constant (e.g. Kimura and Ohta, 1971). For this reason albumin serology has been used to provide a molecular clock (Sarich, 1977). Error in this method for estimating divergence times may occur however, if the rate of change in proteins is not always constant (Vawter *et al.*, 1980). Richardson *et al.* (1986) discuss reasons for doubting the reliability of molecular clocks. Large measures of genetic distance give a very poor estimate of time while small distances are susceptible to varying rates of evolution due to the 'bottleneck effect' (Schmitt, 1978). Thus the molecular clock is subject to error and caution must be used in its application in phylogenetic analysis.

The 7 My date of separation for thylacinids from dasyurids proposed by Sarich *et al.* (1982) is clearly in error because: 1, *Thylacinus potens* from the late Miocene is already a highly specialised thylacinid (Woodburne, 1967); and 2, *Nimbacinus dicksoni* from sediments between Late Oligocene and Middle Miocene in age is evidently a thylacinid, albeit a relatively plesiomorphic member of the family. *Nimbacinus dicksoni* provides further support for the hypothesis that thylacinids are closely related to dasyurids in its possession of many features that appear to be intermediate between those of plesiomorphic dasyurids and species of *Thylacinus*.

ACKNOWLEDGEMENTS

We wish to acknowledge the vital financial support the Riversleigh Project has had from: the Australian Research Grant Scheme (Grant PG A3851506); the National Estate Grants Scheme (Queensland); the Department of Arts, Sport, the Environment, Tourism and Territories; Wang Australia Pty Ltd; ICI Australia Pty Ltd; the Queensland Museum; the Australian Museum; the Australian Geographic Society; Mount Isa Mines Pty Ltd; Ansett Wridgways Pty Ltd; and Surrey Beatty & Sons Pty Ltd. Critical logistical support in the field and laboratory has been received from the Riversleigh Society, the Friends of Riversleigh, the Royal Australian Air Force, the Australian Defence Force, the Queensland National Parks and Wildlife Service, the Riversleigh Consortium (Riversleigh being a privately owned station), The Mount Isa City Council, the Northwest Queensland Tourism and Development Board, the Gulf Local Development Association, PROBE and many volunteer workers and colleagues. Dr G. Breen (Darwin Community College) kindly allowed access to his unpublished vocabulary of the Wanyi Aborigines. Photographs were taken by Mr R. Arnett and Ms R. Murphy. Ms L. Gibson and Dr A. Ritchie provided access to material in the collections of the Australian Museum. Use of Bullock Creek material was kindly provided by Dr P. Murray and Mr D. Megirian. Dr L. Dawson kindly provided access to additional measurement data.

We would also like to acknowledge the support given to J. Muirhead by the Queen Elizabeth II Silver Jubilee Trust For Young Australians and the Australian Postgraduate Award Scheme.

LITERATURE CITED

APLIN, K.P. AND ARCHER, M. 1987. Recent advances in marsupial systematics with a new syncretic classification. p. xv-lxxii *In* M. Archer (Ed.) 'Possums and opossums: Studies in Evolution. (Surrey Beatty and Sons and the Royal Zoological Society of New South Wales: Sydney).

1976. The dasyurid dentition and its relationship to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina: Marsupialia). *Australian Journal of Zoology, Supplementary Series* 39: 1–34.

1978. The nature of the molar-premolar boundary in marsupials and interpretation of the homology of marsupial cheekteeth. *Memoirs of the Queensland Museum* 18: 157–64.

1982a. Review of the dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. p. 397-443. *In* M. Archer (Ed.) 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

1982b. A review of Miocene thylacinids (Thylacinidae Marsupialia), the phylogenetic position of the Thylacinidae and the problem of apriorisms in character analysis. p. 445-76. *In* M. Archer (Ed.) 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

EVERY, R.G., GODTHELP, H., HAND, S.J. AND SCALLY, K.B. 1990. Yingabalanaridae, a new family of enigmatic mammals from the Tertiary deposits of Riversleigh, northwestern Queensland. This volume.

GODTHELP, H., HAND, S.J., AND MEGIRIAN, D. 1989. Fossil mammals at Riversleigh, north western Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 29–65.

BENSLEY, B.A. 1903. On the evolution of the Australian Marsupalia with remarks on the relationships of marsupials in general. *Transactions of the Linnean Society of London (Zoology)* 9: 83–217.

DAWSON, L. 1982. Taxonomic status of fossil thylacines (*Thylacinus*, Thylacinidae, Marsupialia) from late Quaternary deposits in eastern Australia. p. 527-36. *In* M. Archer (Ed.) 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

FLANNERY, T.F. 1990. Dating the great New Guinea - Australia vicariance event: new evidence for the age of Australia's Tertiary mammal faunas. This volume.

GIDLEY, J.W. 1915. An extinct marsupial from the Fort Union. *Proceedings of the United States National Museum* 48: 395–402.

HAND, S.J. 1985. New Miocene megadermatids (Chiroptera: Megadermatidae) from Australia with comments on megadermatid phylogeny. *Australian Mammalogy* 8: 5–43.

KIMURA, M. AND OHTA, T. 1971. Protein polymorphism as a phase of molecular evolution. *Nature* 229: 467–69.

LOOMIS, F.B. 1921. Origin of South American faunas. *Bulletin of the Geological Society of America* 32: 189–90.

MARSHALL, L.G. 1977. Cladistic analysis of dasyuroid, borhyaenoid and thylacinid affinity. *Systematic Zoology* 26: 410–25.

MATTHEW, W.D. 1915. Climate and evolution. *Annals of the New York Academy of Science* 24: 229–83.

OSGOOD, W.H. 1921. Monographic study of the American Marsupial *Caenolestes*. *Field Museum of Natural History, Zoology* 14: 1–156.

PLANE, M.D. AND GATEHOUSE, C.G. 1968. A new vertebrate fauna from the Tertiary of northern Australia. *Australian Journal of Science* 30: 272–73.

RICHARDSON, B.J., BAVERSTOCK, P.R. AND ADAMS, M. 1986. 'Allozyme Electrophoresis'. (Academic Press: London).

RIDE, W.D.L. 1964. A review of Australian fossil marsupials. *Journal and Proceedings of the Royal Society of Western Australia* 47: 97–131.

SARICH, V.M. 1977. Electrophoresis in evolutionary studies: rates, sample sizes and the neutrality hypothesis. *Nature* 265: 24–8.

LOWENSTEIN, J.M. AND RICHARDSON, B.J. 1982. Phylogenetic relationships of *Thylacinus cynocephalus* (Marsupialia) as reflected in comparative serology. p. 707-9. *In* M. Archer (Ed.) 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

SCHMITT, L.H. 1978. Genetic variation in isolated populations of the Australian Bush Rat. *Evolution* 32: 1–18.

SCOTT, W.B. 1913. 'History of Land Mammals in the Western Hemisphere'. (MacMillan: London).

SIMPSON, G.G. 1941. The affinities of the Borhyaenidae. *American Museum Novitates* 1118: 1–6.

1945. The principles of classification and the classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–350.

SINCLAIR, W.J. 1906. Mammalia of the Santa Cruz Beds (Marsupialia). *Report of the Princeton Expedition to Patagonia* 4: 333–460.

STIRTON, R.A., TEDFORD, R.H. AND MILLER, A.H. 1961. Cenozoic stratigraphy and vertebrate palcontology of the Tirari Desert South Australia. *Records of the South Australian Museum* 14: 19–61.

SZALAY, F.S. 1982. A new appraisal of marsupial phylogeny and classification. p. 621-40 *In* M. Archer (Ed.) 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

TATE, G.H.H. 1947. Results of the Archbold Expeditions. No 56. On the anatomy and classification of the Dasyuridae. *Bulletin of the American Museum of Natural History* 88: 97–156.

TEDFORD, R.H. 1967. Fossil mammals from the Carl Creek Limestone, northwestern Queensland. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 92: 217–36.

VAWTER, A.T., ROSENBLATT, H.R. AND GORMAN, G.C. 1980. Genetic distances among fishes of the Caribbean: support for the molecular clock. *Evolution* 34: 705–711.

WATROUS, L.F. AND WHEELER, Q.D. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30: 1–11.

WOOD, H.E. 1924. The position of the "sparassodonts": with notes on the relationships and history of the Marsupialia. *Bulletin of the American Museum of Natural History* 51: 77–101.

WOODBURNE, M.O. 1967. The Alcoota Fauna, Central Australia: an integrated palaeontological and geological study. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 87: 1–187.

TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication, South Australian Department of Mines and Energy* 5: 347–63.

APPENDIX

Pleistocene *Thylacinus cynocephalus* dental measurements:

	Tooth Length (mm)			
Specimen Number	M/2	M/3	M/4	M/5
SAM P20451	11.0	13.2	15.8	17.6
SAM P20453	10.0	12.3	—	—
SAM P20452	10.5	13.0	15.0	—
SAM P16750	c.10.0	13.5	—	—
SAM Unregistered 1	9.6	—	14.6	16.5
SAM Unregistered 2	8.0a	—	—	13.0a
SAM Unregistered 3	8.2	—	—	—
SAM P13827	9.0	c.11.0	12.5	15.0
SAM P13728	—	12.3	14.6	17.3
SPS/ANU Unreg. 1	—	—	—	9.1
SPS/ANU MM5	—	—	11.6	13.6
SPS/ANU Unreg. 2	—	11.5	13.8	14.5
ANU/NCA/B/3	8.2	10.5	11.6	
QMF1737	—	—	16.5	
QMF730	10.5	13.6	14.3	16.9
AMMF413	9.2	11.3	13.3	15.5
F57929	—	—	14.51	18.16
F16550	11.14	—	16.23	18.14
F57875	—	13.38	15.21	—
F16504	—	10.97	14.69	13.57
F57857	10.05	12.47	—	—
F57857	—	—	15.34	—
MF308	12.53	15.35	—	—
F57850	10.29	—	—	—
SAM P20451	—	—	7.5	8.2
SAM P204553	4.8	—	—	—
SAM P204552	5.2	6.3	6.7	—
SAM P16750	—	6.1	—	
SAM Unregistered 1	4.4	—	6.0	7.8
SAM Unregistered 2	—	—	—	—
SAM Unregistered 3	3.9	—	—	—
SAM P13827	4.5	5.3	5.5	7.0
SAM P13728	—	6.0	—	7.8
SPS/ANU Unreg. 1	—	—	—	—
SPS/ANU MM5	—	—	4.9	6.4
SPS/ANU Unreg. 2	—	5.5	c.5.5	7.0
ANU/NCA/B/3	4.0	5.5	6.0	—
QMF1737	—	—	7.9	—
QMF730	5.7	6.4	7.4	7.8a
AMMF413	4.4	5.6	6.9	8.1
F57929	—	—	6.91	7.28
F16550	5.15	—	7.33	7.35
F57875	—	5.89	6.46	—
F16504	—	7.07	8.40	7.43
F57846	5.86	6.03	6.63	—
F57857	—	—	7.61	—
MF308	6.23	7.30	—	—
F57850	4.88	—	—	—

All data other than F and MF numbers from Dawson (1982). (a = approximately).

(1982) for other specimen details. F and MF specimens from Australian Museum collections (a = approximately).

Nimbacinus dicksoni detail measurements:

Lowers (mm)											
	1	2	3	4	5	6	7	8	9	10	11
QMF16802	6.57	3.75	3.18	2.70	1.66	3.04	2.79	4.81	2.26	1.84	1.01
QMF16809	—	—	2.85	2.55	1.39	2.76	—	—	—	—	—
P85553-3 P1	4.38	1.68	1.52								
P2	5.88	2.85	2.05								
M2	6.75	4.03	3.05	2.54	1.52	3.42	3.32	5.19	2.80	2.49	worn

Uppers (mm)					
	1	2	3	4	5
QMF16803 P3	8.06	4.14			
M2	7.46	5.89	2.70	2.85	2.67
M3	8.19	7.55	3.19	4.11	3.09
M4	7.35	8.77	4.81	5.84	2.68
QMF16804 M2	6.82	5.39	2.47	3.63	2.74
M3	7.65	7.40	3.33	4.81	3.01
M4	6.82	8.28	4.15	5.09	2.23
QMF16805 M4	7.83	8.86	5.06	4.40	2.48
QMF16806 M4	7.80	7.89	3.80	4.74	3.30
QMF16807 M5	4.56	7.84	4.04	3.40	2.08

Key to dental dimensions for *Nimbacinus dicksoni* specimens:

Lowers

1 = greatest length along axis of tooth; 2 = greatest width of talonid (perpendicular to long axis); 3 = greatest width of trigonid (perpendicular to long axis); 4 = protoconid to paraconid; 5 = protoconid; 5 = protoconid to metaconid; 6 = paraconid to metaconid; 7 = hypoconid to protoconid; 8 = hypoconid to paraconid; 9 = hypoconid to metaconid; 10 = hypoconid to hypoconulid; 11 = hypoconid to entoconid.

Uppers

1 = greatest antero-posterior length; 2 = greatest width perpendicular to 1; 3 = protocone to paracone; 4 = protocone to metacone; 5 = paracone to metacone.

Modern *Thylacinus cynocephalus* dental measurements:

Tooth Length (mm)						
	LM/2	LM/3	LM/4	RM/2	RM/3	RM/4
AR1045	10.25	12.50	14.92	10.36	12.42	15.00
AR8409	9.10	11.04	12.78	—	—	—
M217	9.80	11.91	14.41	10.00	12.26	14.25
778	9.22	11.52	13.24	9.10	11.60	13.33
767	9.54	12.21	14.34	9.10	11.82	13.91
S402	8.83	11.10	13.14	—	11.30	12.28
S1180	8.69	11.32	13.14	9.45	12.00	13.66
768	9.95	12.56	14.18	9.96	11.82	14.72
770	9.52	12.82	14.73	9.09	11.96	14.51
M822	8.76	11.56	13.40	8.81	11.40	13.54
S403	8.70	11.19	13.19	8.66	11.20	12.92
M1129	9.30	12.16	13.83	9.26	12.12	13.93
S401	11.35	12.97	14.84	11.58	12.64	15.09
775	8.59	11.32	13.75	9.22	11.29	13.84
S789	8.35	11.32	13.96	9.21	11.48	13.09
776	10.01	12.21	14.35	9.90	12.19	14.15
769	9.59	12.22	14.98	9.85	12.51	—
Tooth Width (mm)						
	LM/2	LM/3	LM/4	RM/2	RM/3	RM/4
AR1045	4.61	5.59	6.61	4.34	5.50	6.70
AR8409	4.15	5.03	5.85	—	—	—
M217	4.42	5.74	6.52	4.48	5.54	6.55
778	3.98	5.29	6.14	4.21	5.31	6.00
767	4.61	5.76	6.61	4.66	6.00	6.76
S402	4.30	5.32	6.19	—	5.32	6.10
S1180	4.32	5.38	6.30	4.34	5.53	6.16
768	4.86	5.94	6.32	4.61	5.62	6.48
770	4.67	5.86	7.12	4.57	5.82	6.74
M822	4.12	5.32	6.14	4.29	5.32	6.07
S403	4.23	5.27	5.89	4.21	5.26	5.96
M1129	4.32	5.32	6.31	4.24	5.47	6.21
S401	4.75	6.00	7.03	4.80	5.89	6.92
775	4.15	5.34	6.01	4.10	5.50	6.00
S789	4.26	5.50	6.33	4.85	5.44	6.22
776	4.56	5.56	6.64	4.75	5.54	6.72
769	4.62	5.44	6.61	4.64	5.74	—

All specimens other than AR numbers are from the Australian Museum collection of Tasmanian *T. cynocephalus*. AR specimens from Archer's Reference collection.

FOSSIL MAMMALS OF THE COIMADAI LOCAL FAUNA NEAR BACCHUS MARSH, VICTORIA

WILLIAM D. TURNBULL, ERNEST L. LUNDELIUS, JR. AND RICHARD H. TEDFORD

Turnbull, W.D., Lundelius, E.L., Jr. and Tedford, R.H. 1990 3 31: Fossil Mammals of the Coimadai Local Fauna near Bacchus Marsh, Victoria. *Mem. Qd Mus.* 28(1): 223–245. Brisbane ISSN 0079-8835.

De Vis (1898) first published on Coimadai fossil vertebrate specimens, recognizing vombatids, macropodids and diprotodontids. His identifications are updated, and specimens recovered since de Vis' day are assessed. The locality, which is now partly submerged by the waters of the Marrimu Reservoir, appears to be early Pliocene in age. The hardest, normally most resistant, calcified tissues were destroyed preferentially, apparently by solution. The geological and stratigraphical evidence for a pre-Bullengarook Pliocene age of relationship of the sediments (including Coimadai Limestone) to the Rowsley-Fault, and on the eruption of Mt Bullengarook. Of the seven post-Miocene genera, five are extinct (*Kurrabi, Protemnodon, Troposodon, Euowenia* and *Zygomaturus*), and two have species living today (*Vombatus* and *Macropus*) □ *Victoria, Pliocene, Marsupials, Taphonomy.*

William D. Turnbull, Field Museum of Natural History, Chicago, Illinois 60605; Ernest L. Lundelius, Jr., The University of Texas, Austin, Texas 78712; Richard H. Telford, American Museum of Natural History, New York, New York 10024; 8th August, 1988.

Ninety years ago, de Vis, (in Appendix A to Officer & Hogg 1898), reported a sample of 22 fossil marsupials from lacustrine (usually dolomitic) and fluviatile limestones at Coimadai, Victoria that had been collected by Officer, Hogg and Ferguson of the Victoria Mines Department. Other specimens reported here were collected incidental to the quarry operations of the late 19th and early 20th centuries. We report on all of the material from the various Coimadai quarries which are in the collections of Melbourne University Geology Department (MUGD), the Victoria Mines Department (VMD) and the Museum of Victoria (NMV). The VMD materials are now incorporated into the NMV collection (nos P186781-186806). Opportunity for collecting additional materials is nil, the quarries having been nearly exhausted, and the remnants of the formation are now submerged by Lake Merrimu, one of several reservoirs in the Warribee drainage. In addition to reporting on the fossils, we describe the locality in so far as is possible at this late date, using photographs taken by two of us (WDT & ELL) in 1963-4. The locality, about 10 km NNE of Bacchus Marsh, is in the valley of Pyrete (Coimadai) Creek, a tributary of the Warribee River. It is about 3 km E of the Rowsley Fault, the major N-S fault in the area which was active in the Early Pliocene (Gill, 1964). Coulson's (1924) map shows three of the quarries immediately S and E of a much smaller fault, the E-W trending Coimadai Fault of Fenner (1918). The map provided by Officer and Hogg (1898) covers a larger area N-S, and shows the path of the Lava tongue from Mt Bullengarook (12 km to the N) that filled the former Bullengarook Creek (or River) valley with a resistant basalt. Subsequent drainage was thus diverted to the E and W sides of the former creek to form Pyrete and Goodman's Creeks (Officer & Hogg, 1898, Sec. V). Their map also shows the straight E-W trending southern margin of the N block of the Ordovician sandstone (labelled Silurian by Officer & Hogg, 1898) that is part of the evidence for the Coimadai Fault (Hart, 1908; Fenner, 1918). The unnamed quarry shown by Officer and Hogg (1898) is probably Alkemade's Quarry to judge by its position. We have modified Coulson's map (Fig. 1) to show these features. For reasons given later, the limestones mapped as Pleistocene by Coulson, the same quarried limestones that produced the fossils, are most likely Pliocene in age.

There is some confusion about the quarries that we cannot resolve. The three shown on Coulson's 1924 map (and Fig. 1), Alkemade's, Hjorth's and Burnip's, are the only ones with precisely known locations, if he has not erred. Bennett's and Davies' are mentioned by Officer and Hogg (1897) and Gill (1964) respectively, without indication of exact location. Another problem is that Officer and Hogg (1897) mentioned (but did not designate) two

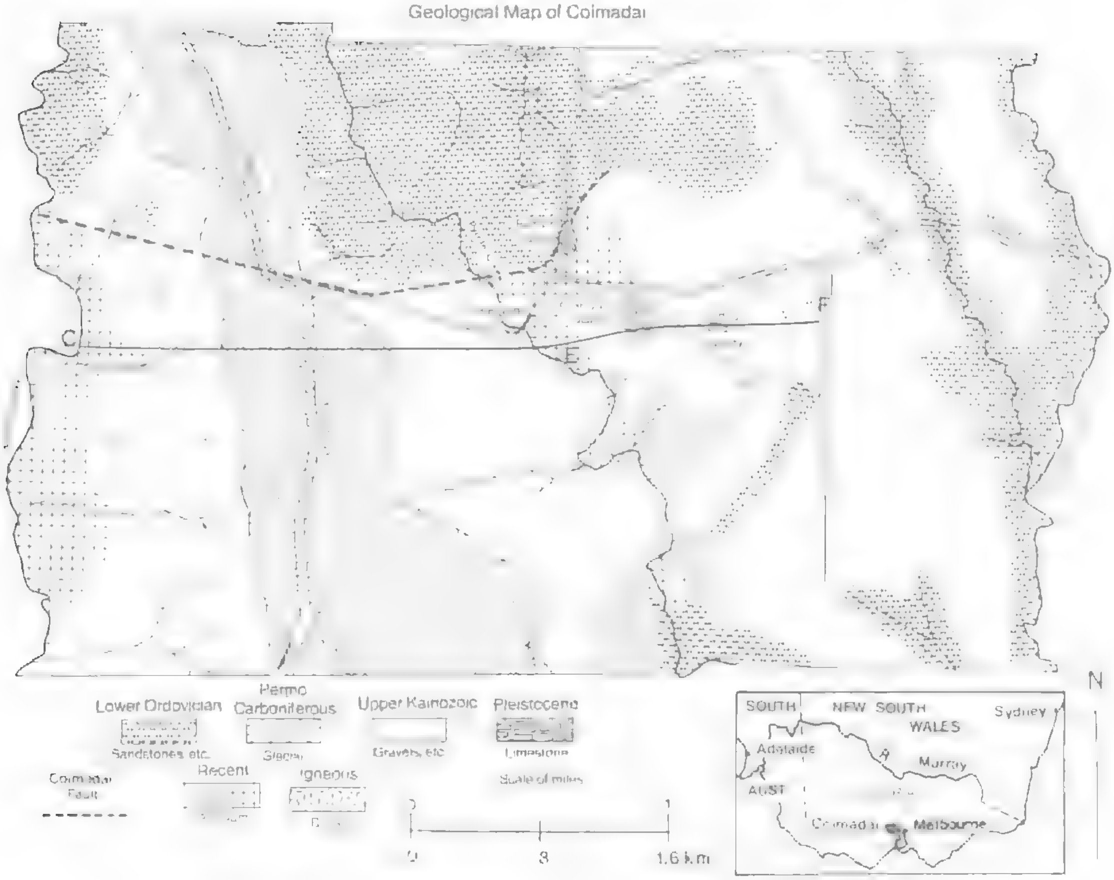

FIG. 1. Coulson's (1924) geologic map of the Coimadai area slightly modified, showing three of the quarries, the Coimadai Fault, the Bullengarook Basalt Flow within the channel of the ancient Bullengarook Creek and the modern drainages.

large quarries, Alkemade's and Bennett's, "on the eastern side of Pyrite Valley", and they go on to say, "a third and smaller quarry (Birnip's)" [spelled Burnip's on Coulson's map where the three are labelled] is "on the west side of the valley". All are on the E side of the valley. In as much as his study relied heavily on Officer and Hogg (1897-8) and followed theirs by a quarter century, we tend to accept the detail given by Coulson. In addition to this confusion, or perhaps because of it, we either misunderstood or were misinformed as to the identity of Burnip's and Hjorth's quarries when Edmund Gill showed us the locality in 1963. Our notes show the two reversed. Whichever is correct, the Alkemade quarry is by far the most important, having produced the majority of the specimens and there does not seem to be any doubt about its location. Figures 2 and 3A show the Alkemade quarry. Figure 3B shows the remnant of Burnip's, and Figure 4 gives two views of the Hjorth quarry; all show conditions as of 1964.

STRATIGRAPHY AND GEOLOGY

Since the earliest studies by Ferguson (1894) and Officer and Hogg (1897-8), the geology at the Coimadai quarries has been reported by several workers including Summers (1923) and Keble (1925). Uncertainties still remain as to interpretation of the geology and the timing of some events. Officer and Hogg (1897) distinguished five "formations" in the district: (1) Silurian [Ordovician in most subsequent works]; (2) Permo-Carboniferous Glacial beds; (3) Coimadai limestones, gravels, conglomerates, etc.; (4) Newer Basalt; (5) Post-Tertiary and Recent beds. Of these, items (3) and (4) concern us here.

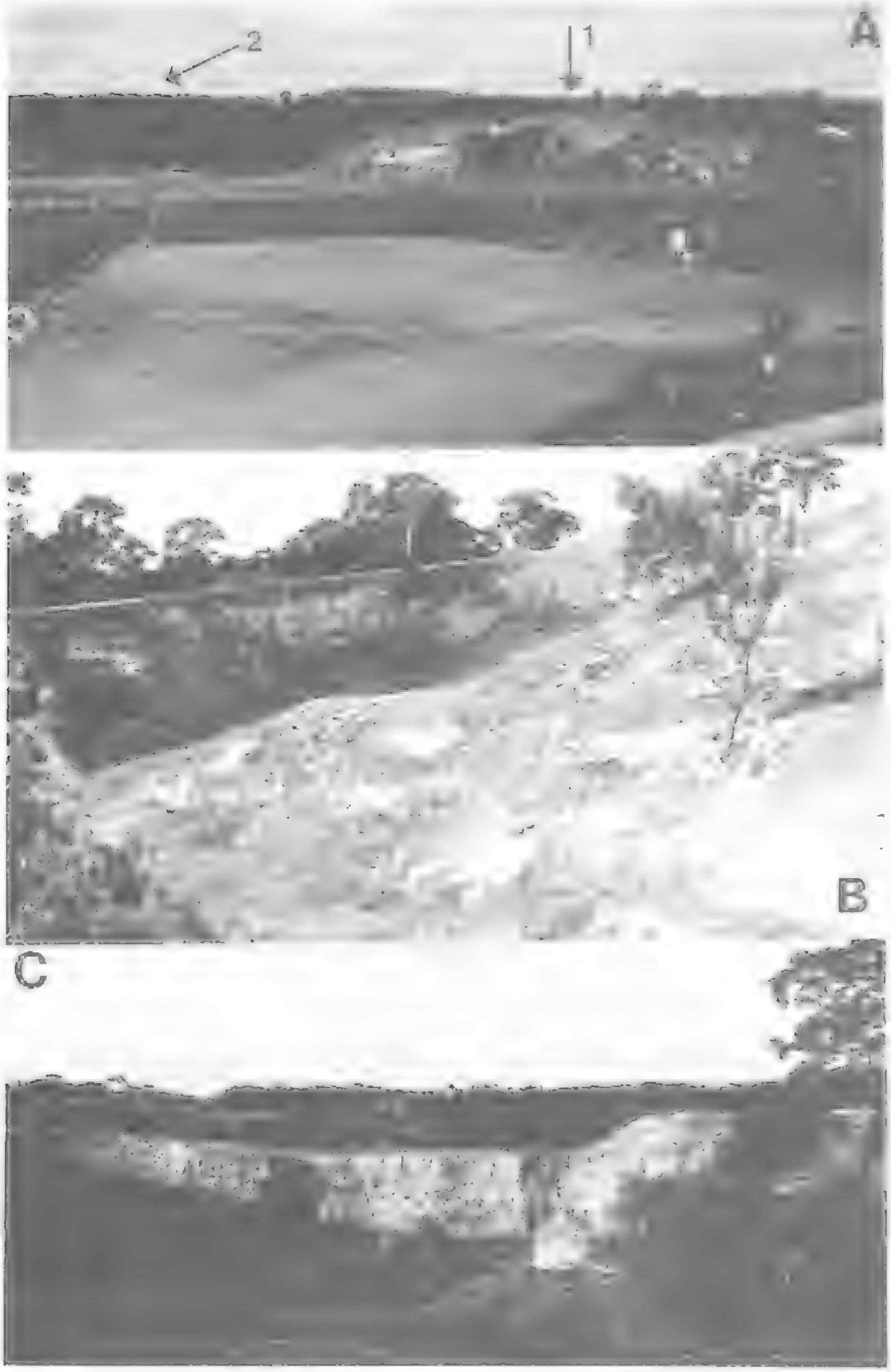

FIG. 2. Three views of Alkemade's Quarry. A, as seen from Burnip's Quarry, looking SE; arrow -1 points to Alkemade's Quarry, arrow -2 to approximate site of Hjorth's Quarry, hidden by trees. B, C, views within the quarry; the old working-face is in the distance, with mixture of overburden and rubble in middle and foreground.

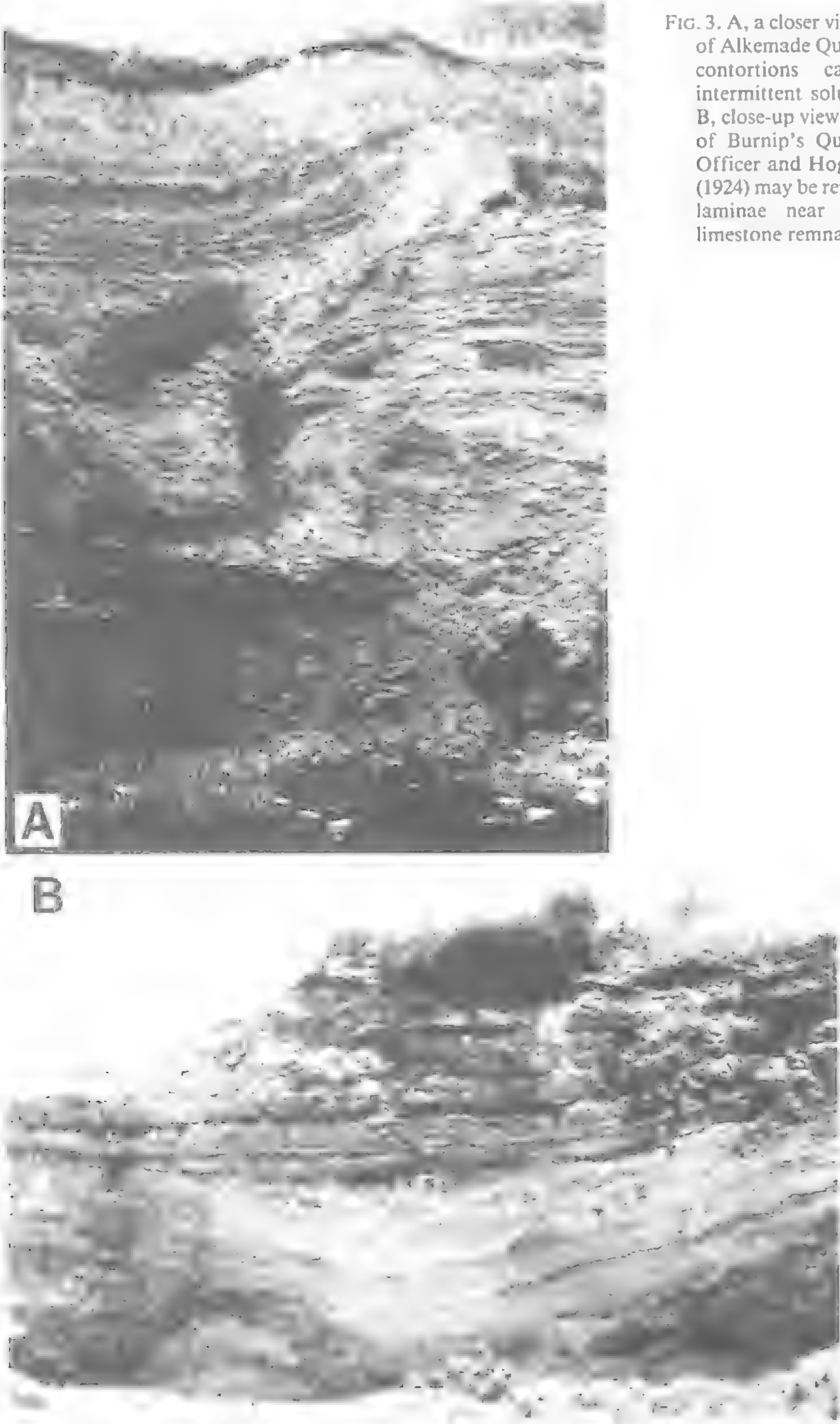

FIG. 3. A, a closer view of old working-face of Alkemade Quarry, showing bedding contortions caused by irregular, intermittent solution- collapse events. B, close-up view of face at the remnant of Burnip's Quarry; the ash bed of Officer and Hogg (1898) and Coulson (1924) may be represented by one of the laminae near the middle of this limestone remnant

FIG. 4. A, face of the small Hjorth Quarry, from the nearest point permitting the entire face to be included. B, a closer view showing bedding irregularities; according to Officer and Hogg, the ash bed was observed in this quarry too, but it was not identified in this study (perhaps covered by slump). Scale indicated by Marsh pick with 51 cm handle.

It is difficult to see close parallels between the 13.5 m (44 ft) section of Officer and Hogg (1897) and Gill's (1964) 11 m (36 ft) one measured in 1958, wherein he proposed names for the formations he recognized — Alkemade Siltstone (above) and Coimadai Dolomite. Erosion, slump and other changes during the 60 intervening years, coupled with the fact that the measurements were taken at quite different places within Alkemade's quarry, surely account for the lack of close correspondence. Most curious is the lack of mention by any worker other than Coulson (1924) of the 15 cm (6 inch) volcanic ash marker-bed 4 of Officer and Hogg (1897). Coulson noted its presence, giving mineralogical details. In their section Officer and Hogg (1898) indicate that most mammalian bones came from a 1 m (3 ft) unit of calcareous sand situated 2 m - 3 m (7-10 ft) below the ash, and in their section V (DEF on their map) the letter (a) keys the "thin bed of volcanic ash interstratified with limestone containing Marsupial bones". Two other geological problems concern the two faults. Gill's observation (1964) regarding the timing of activity of the Rowsley Fault as, "epi-Timboon Terrain (Lower Pliocene)" fits well with his notion that the deposits at Coimadai (and elsewhere E of the fault) began as alluvial fans that were generated by rejuvenation of the drainages of the upthrown western block. This in turn caused overloading of the drainages of the downthrown block (including Bullengarook Creek) causing them to aggrade. Levees and shallows developed in the aggrading parts of the Bullengarook flood-plain, and the shallows formed the lake(s) within which deposition of the limestones, limey muds and silts took place. The valley of concern was that of the ancient Bullengarook Creek, not Coimadai Creek, as Gill had stated (1964, p. 351). Then the Bullengarook lava flow filled the youngest, highest channel and thus ended that stream's existence, causing the twin streams to form. Gill (1964) did observe that the Bullengarook lava, "is higher than the deposits in the valley".

The Coimadai Fault also would have contributed to the overloading of the drainage to the S of the fault in the Coimadai area. However, in a footnote to his brief statement rejecting Fenner's (1981) explanation of the formation of the Coimadai lake "by the Bullengarook lava flow blocking the drainage", Gill (1964) questioned the existence of the Coimadai Fault, stating "The Coimadai Fault of Fenner (1918) probably does not exist since the platform cut on the Ordovician bedrock is at similar elevations on the N. and S. sides of the Coimadai valley". But he gave no topographic data to substantiate this, and by itself the point seems inadequate for rejecting the fault's existence. Coulson (1924) realized that the basaltic lava flows followed some sedimentation in the lake but was "preceded by the outburst of fine ash which was only preserved in the limestone lake". He appears to have been the first to point out the probable connection of the two features to the same event (Bullengarook eruption) although his dating of the beds as Pleistocene differs from Gill's and ours as (post-earliest) Pliocene. By drawing upon these observations of Coulson (1924) and Gill (1964), it now appears that Officer and Hogg (1893) may have provided the most informative geological summary with their schematic Section V, redrawn here (as Fig. 5) to trace a nearly E-W line located near to, but mostly just S of, the Coimadai fault,

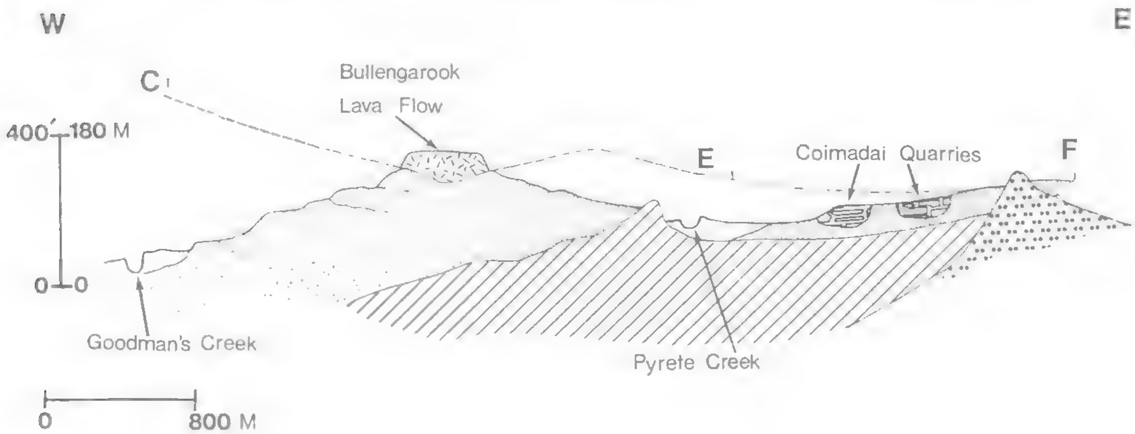

FIG. 5. Schematic section based on the Officer and Hogg (1898) map and their sections I and V, of the Coimadai area. It follows a line from about their point C to E and on to F. Geological symbols as in Fig. 1.

from their point C to points E and F. The section shows the modern streams (Goodman's and Pyrete Creeks), the Pliocene alluvial fan deposits and related fluviatile and lacustrine beds (Coimadai Limestone, including the Alkemade Siltstone and Coimadai Dolomite), the Coimadai quarries and the basalt-filled channel of the ancient Bullengarook Creek, with a suggested probable surface topography of that period (dashed lines). Two radiometric dates have been reported for the Bullengarook basalt, 3.31 and 3.64 Ma (two determinations, P. Roberts, pers. comm. to RHT, 1983). Thus the Coimadai local fauna dates from about that time since most of the bones came from just below the thin ash bed that Coulson correlated with the Mt Bullengarook eruption. Additional evidence supporting this interpretation comes from the maps of Coulson and of Officer and Hogg, wherein it can be seen that the lower area to the S of the Coimadai Fault captured much more of the post-Rowsley alluvial fan and related Upper Cainozoic (Pliocene) deposits than did the erosional upstream area to the N of that fault.

SYSTEMATIC PALAEONTOLOGY

De Vis (1898) considered that three marsupial families are represented in the Coimadai materials. This study, using additional material and benefiting from modern preparation of all the material, supports de Vis' conclusion and refines the identifications. Many specimens were preserved as vugs which were prepared by injecting epoxy resin to form artificial casts of the bones.

Class MAMMALIA
Subclass THERIA
Infraclass METATHERIA (MARSUPIALIA)
Order DIPROTODONTA
Family VOMBATIDAE

Apparently two taxa of wombats were present at Coimadai. The following materials are assigned to the family — (MUGD 1671, 3570, 3585, NMV P23219) probably to *Vombatus*, but specific assignment is uncertain.

MUGD 1671 is the right ramus with full dentition that de Vis had assigned to *Phascolomys parvus* (Owen, 1871), a taxon never widely accepted (Dawson, 1983). It persisted until Merrilees (1967) carefully examined the matter and rejected it as valid taxon. He synonymized *P. parvus* with *Vombatus hirsutus*, considering it to be a juvenile of the modern taxon. Merrilees demonstrated the unusual degree of variation in dental size that accompanies developmental stages in wombats. More recently, Wilkinson (1978) strongly supported this stance. However, we note here, for the first time, one feature not previously considered which suggests that Merrilees' conclusion may need to be altered. The Coimadai jaw, which is well within the size range of juveniles of *V. hirsutus*, has the typical form of modern adult wombats; it is swollen throughout the length of the horizontal ramus, and the ventral margin is smoothly curved (Fig. 6A). This is an important point, for in one very young modern specimen of *V. hirsutus* (FMNH 123652), the ventral margin of the jaw is extremely thin beneath each forming cheek tooth (perforate in one spot) and decidedly uneven, giving a hummocky appearance all along that margin of the ramus (Fig. 6B). The Coimadai jaw is slightly smaller overall than that of this very young juvenile *V. hirsutus* although its cheek teeth are slightly larger. In marked contrast, because there has been some minor damage to the fossil, one can see that the bone of its ventral margin is thick and has a well-developed, multi-layered compacta structure, an indication of some age and not of a juvenile condition. An X-ray (Fig. 6E) of the juvenile specimen clearly shows the bases of the forming, very hypsodont, teeth to be in close contact with the bone of the ventral jaw margin. This results in the thinning of the bone in the immediate area of each developing tooth and in bulging these regions out beyond the curve of the jaw margin to give the associated hummocky condition. X-rays of the fossil provided by T. Rich (Museum of Victoria) are included for comparison (Fig. 6C-D). From this we conclude that the Coimadai *P. parvus* was not a juvenile, yet compared with the dimensions given by Merrilees (1967; and Table 1), it falls within the range of values for juveniles of *V. hirsutus*. (The cheektooth row length, from the anterior alveolus of P_4 to the posterior of M_4, of the four smallest female juveniles in Merrilees' sample of *V. hirsutus*, from his graphs, is 29.4, c.38, c.41 and 41+mm. For FMNH 123652 the value is 35.6mm, and for the *P. parvus* fossil it is 37.5mm.) Thus it does not appear to be a normal variant of that taxon. Additional evidence that this *P. parvus* specimen was not a juvenile comes from four other adult, or at least more mature, conditions that it possesses: 1) The masseteric fossa is a deep pocket (Fig. 6A), not just a shallow indentation (Fig. 6B) as is seen in juveniles before growth and/or extensive chewing gives rise to the adult form; 2) The incisor tooth is relatively deep in its cross section (again compare

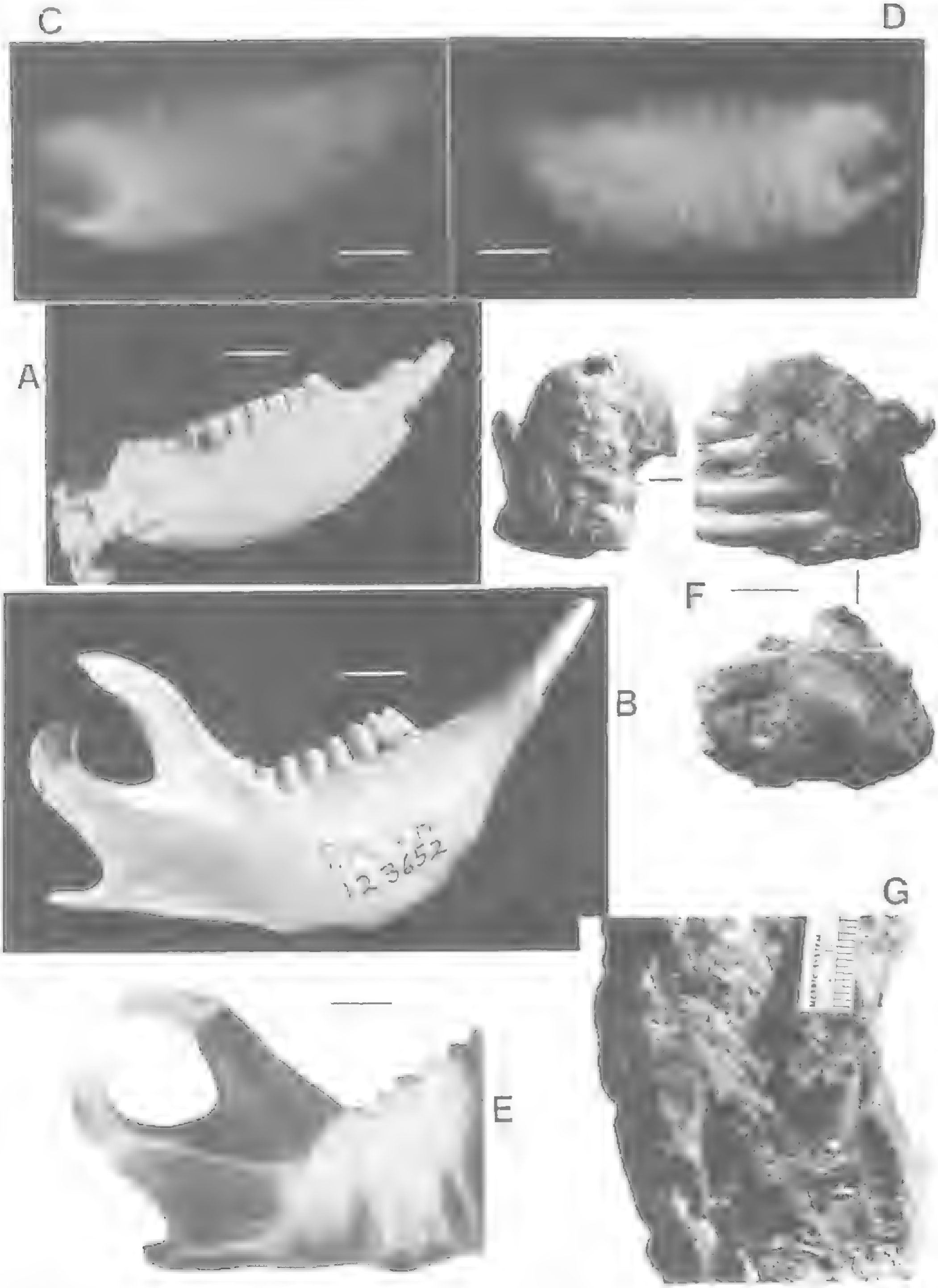

FIG. 6. Three Coimadai fossil wombat specimens, and very young juvenile of the modern *Vombatus hirsutus*. A, buccal side of right mandible, MUGD 1671, which de Vis (1898) identified as *Phascolomys parvus*. B, corresponding view of FMNH 123652, very young juvenile of *V. hirsutus*. C-E, X-rays of same specimens (at nearly the same scale) to show features discussed in text. F, G, specimens referred to cf. *V. hirsutus* (MUGD 3570 and NMV P23219 respectively). Scale = 2 cm.

A & B of Fig. 6); 3) All cheek teeth are decidedly tapered from their forming bases to the occlusal surfaces in juveniles, especially in the latter area, but the fossil shows only very slight tapering (Fig. 6A-D); and 4) seen in side view, the cheek teeth of the fossil all are truncated by wear at their occlusal ends so that a flat, nearly straight, horizontal surface has resulted. In the juvenile, although most details of the initial crown structure quickly wear away, a vestige remains in that there is a right-angled groove between the anterior and posterior moieties of each molar (even M_3 has a notch), as well as a groove between adjacent teeth (Fig. 6A & B) so that the whole occlusal surface has many angles to it and is not reduced to a flat planar surface.

From this it is clear that at Coimadai at least, the "*P. parvus*" specimen represents a species of *Vombatus* other than *V. hirsutus*. For a conclusive decision it will be necessary to examine a large series of modern juvenile wombats of both *Lasiorhinus latifrons* and again to compare directly the Coimadai specimen with Owen's holotype of *P. parvus*. We tentatively accept Merrilees' (1967) assignment of the holotype of *P. parvus* to the genus *Vombatus*, but leave the decision as to its specific assignment open, for *parvus* may yet prove to be a dwarf species of *Vombatus*.

The other three wombat specimens are teeth that are well within the size range of modern adult *V. hirsutus*. MUGD 3570 consists of M_3-M_4 and the impression of the M_2. Without any clear-cut diagnostic features, size and Merrilees' criterion of greater angulation of the outline of molar occlusal surface suggest assignment to *V. hirsutus*. Antero-posterior and posterior width measurements are given in Table 1 and the specimen is illustrated (Fig. 6F).

TABLE 1. Dental and mandibular measurements of Coimadai vombatids and of a modern specimen of *Vombatus hirsutus*. All measurements in mm.

	MUGD 3570 cf. *V. hirsutus*	MUGD 1671 '*Phascolomys parvus*'	FMNH 123652 *V. hirsutus*
Diastema L. (I-P_4)	–	>13.5	19.9
P_3 L.	—	3.5	3.2
W.	—	2.4	2.2
M_1 L.	—	6.5	5.5
W.	—	4.0	3.7
M_2 L.	—	7.0	7.0
W.	—	4.2	4.3
M_3 L.	9.3	7.5	6.7
W.	6.2	4.3	4.2
M_4 L.	7.9	5.8	5.6
W.	3.9	3.3	3.0

The last two specimens are listed as cf. *Vombatus* sp., probably *V. hirsutus*. MUGD 3585 consists of four associated fragments, two of which join, but we do not know which teeth they are. NMV P23219 is an isolated tooth, probably a lower molar, still partly encased in its travertine matrix (Fig. 6G) its antero-posterior measurement is 10.8 mm and its height from occlusual surface to the broken edge near its forming end is 31.1 mm.

Family MACROPODIDAE
Subfamily MACROPODINAE
Kurrabi sp.

MATERIAL

MUGD 3567, NMV P23160, 23218, and 186806.

DESCRIPTION

Two of the most complete and best-preserved, hence most informative specimens, MUGD 3567 and NMV P186806, are left mandibular rami which seem to represent the same species (Fig. 7A, B). They differ in ontogenetic age, and possibly sex. The older of the two (NMV P186806) has a longer diastema, but in size of ramus, position of mental foramen and length of tooth row, the two are nearly identical. MUGD 3567 is the more informative specimen, although enamel (actually an epoxy cast of the natural mould) is retained only on the M_2 talonid, the M_3 and the M_4 talonid. In size and morphology the best match is with *Kurrabi merriwaensis*. The smaller P_3 has the characteristic form of *Kurrabi*, first described from the Bow Local Fauna, New South Wales (Flannery & Archer, 1984). It seems lower-crowned than *K. merriwaensis*, more like the Hamilton form (Flannery, pers. comm., 1988), although it is hard to evaluate with so little enamel remaining. From the description of *K. merriwaensis*, the Coimadai specimens agree with that taxon, even to details such as the shallow concavity on the posterior side of the hypolophid lingual to the midline. *Macropus dryas* also occurs in the Bow Local Fauna and, although comparable in size to *Kurrabi* sp., the dentition is higher-crowned and has better-developed links. Table 2 gives measurements for the teeth of the Coimadai specimens of *Kurrabi* sp. compared with those of *K. merriwaensis* and

FIG. 7. Three left rami of *Kurrabi* sp. from the Coimadai Local Fauna, each in (stereo) occlusal view. A, MUGD 3567, with all cheek-teeth, also shown in buccal view. B, NMV P186806, with parts of all cheek-teeth. C, NMV P23160, edentulous fragment with much of symphysis and alveoli of P_3-M_3. Scale = 2 cm.

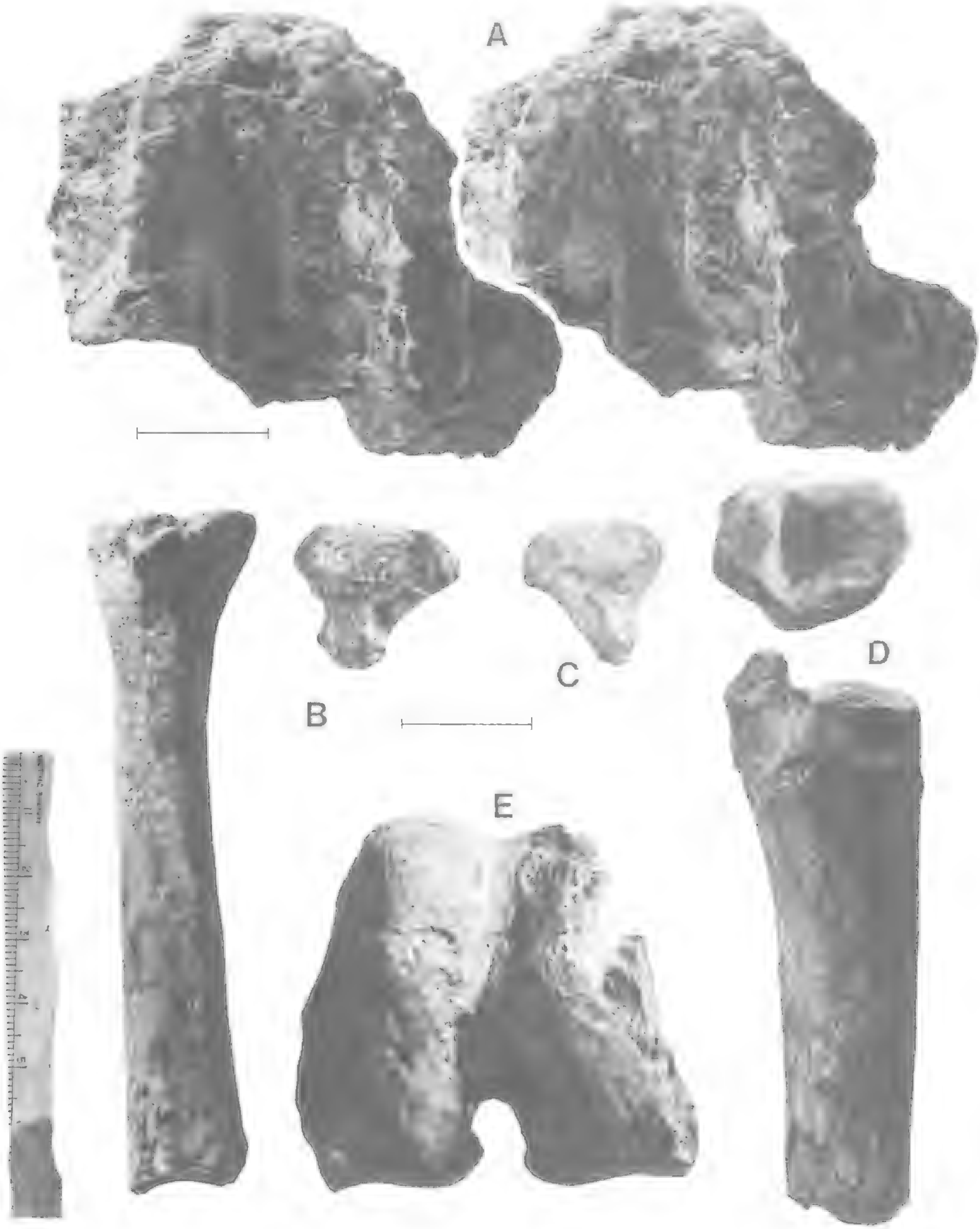

FIG. 8. Five Coimadai specimens referred to *Kurrabi* sp. A, NMV P23218, palate lacking crowns of all teeth, but with some of roots and crown-bases cast from remnants of the natural moulds; in ventral (stereo) view. B, NMV P23187, proximal two-thirds of right metatarsal IV, in ventral and proximal views. C, MUGD 3576, proximal articular end of left metatarsal IV. D, MUGD 3578, distal end and posterior views of partial left tibia. E, MUGD 3562, distal end-view of partial right femur (see also Fig. 9A). Scale = 2 cm.

TABLE 2. Dental and mandibular measurements of Coimadai and other macropodids. All measurements in mm. Measurements of tooth width were taken at posterior of tooth. Symbols: a, measurement of alveolus; b, measurement of dentine core; e, estimated; r, measurement of roots. *Kurrabi* sp., specimen NMV P23160, may comprise P_2-M_2 rather than P_3-M_3; ranges for *Macropus dryas* from Bartholomai, 1975 (T 21, Chinchilla) and 1978 (T 8, Bluff Downs); ranges for *K. merriwaensis* from Flannery & Archer, 1984 (Bow Local Fauna); measurements for *Troposodon* sp. include P_2 in place of P_3.

	MUGD 3567	NMV P 186806	NMV P 23160	NMV P 23208	T3	T21	T8	MUGD 3568	MUGD 3571	MUGD 3573	NMV P 186781	NMV P 23199	MUGD 3569
P_3 Length	11.3	10.5^{e}	10.0^{e}	$\sim 10.5^{a}$	10.2-11.2	10.2-11.7	10.5-11.7	11.2^{a}	~14.5	14.0^{ae}	$\sim 14.1^{a}$	—	$\sim 12.0^{a}$
P_3 Width	3.8^{a}	3.0^{e}	3.0^{e}	3.0^{ar}	—	3.6-4.2	3.6-4.2	3.9^{e}	5.4	—	6.0^{a}	—	4.2^{a}
M_2 Length	9.0	8.0^{e}	$\sim 7.0^{e}$	9.8^{a}	8.1-10.4	9.7-11.4	8.7-9.9	8.8^{r}	~7.3	9.0^{ar}	7.5^{a}	—	$\sim 7.7^{a}$
M_2 Width	~6.5	$\sim 6.0^{a}$	5.5^{e}	6.9^{a}	—	—	—	—	—	—	7.3^{a}	—	—
M_3 Length	10.0	9.6^{ea}	$\sim 9.0^{e}$	9.9^{a}	9.0-9.9	10.4-12.7	10.0-12.5	9.8^{r}	~11.0	11.0^{e}	10.0^{a}	9.5^{a}	8.6^{a}
M_3 Width	7.6	6.9^{a}	8.8^{e}	8.5^{a}	—	—	—	—	—	—	8.1^{a}	7.0^{e}	7.2^{a}
M_4 Length	11.2	10.9^{e}	—	12.3^{a}	10.2-10.9	11.9-14.0	12.2-13.6	10.5^{r}	13.9	11.4^{e}	12.9^{a}	11.2^{e}	12.5^{e}
M_4 Width	8.7	7.8^{a}	—	9.8^{a}	—	—	—	—	8.7	7.3^{e}	8.1^{a}	8.3^{e}	8.1^{r}
M_5 Length	11.5	12.0^{e}	—	12.5^{a}	11.8-11.9	13.8-15.7	13.4-13.8	11.8^{r}	—	11.0^{er}	12.5^{a}	14.3^{a}	12.0^{e}
M_5 Width	7.8	6.5^{ar}	—	9.6^{a}	—	—	—	—	—	—	7.9^{a}	$\sim 8.4^{e}$	8.1^{e}
Diastema I-P_3	~30.0	43.6	29.4	—	—	—	—	~26.0	—	—	~24.0	—	—

Macropus dryas (two samples of the latter taxon reported by Bartholomai 1975, 1978). If NMV P23160, a left ramus fragment with broken incisor and alveoli of three cheek teeth (Fig. 7C), is interpreted correctly as representing P_3-M_3 (there is no bulge in the ramus beneath the anterior teeth for a forming P_3) then it compares well with MUGD 3567 and can also be identified as *Kurrabi* sp. NMV P23218 is a palate with roots only of the right M^2-M^3 and the left P^3-M^5 (Fig. 8A). The palate extends posteriorly to opposite the anterior root of M^4, and the narial incision must be located behind this point. The palate is wide (31.6 mm at M_2) and the tooth rows do not converge markedly to the anterior. The palatine foramen lies opposite the anterior root of M^5 and the root of the zygoma is opposite M^4-M^5. P^3 is not as wide as M^2. The small size of P^3 relative to the molars suggests that this is a palate of *Kurrabi* rather than *Protemnodon.*

cf. **Kurrabi** sp.

MATERIAL

MUGD 3561-2, 3575-6, 3578: NMV P23161, P23187, and P186791.

DESCRIPTION

These specimens are all postcranial pieces assigned only tentatively to the genus. They probably belong to the same undetermined species as the previously listed cranial fragments. It is possible that they represent other genera not recognized from the cranial materials (*Halmaturus* sp., *Macropus dryas, Prionotemnus palankarinnicus).* Since the appropriately-sized cranial specimens all appear to be *Kurrabi* sp. we think this tentative assignment is the most probable of the alternatives. MUGD 3561 is the distal end of a left femur, consisting of little more than the condyles. An old label reads *Halmaturus anak* Owen. It is of a size appropriate for *Kurrabi.* MUGD 3562 is the distal end of a right femur with an old label reading *H. dryas* de Vis. It too is of a size appropriate to *Kurrabi*, or *Macropus dryas*, (Figs 8E, 9A). MUGD 3575 is a complete left metatarsal IV; shown in Fig. 14C, it measures 123.8 mm in length. MUGD 3576 is the proximal end of a left metatarsal IV (Fig. 8C) and NMV P23187 is the proximal end of a right metatarsal IV (Fig. 8B). These three examples of metatarsal IV also seem to be of a size appropriate for *Kurrabi.* They are smaller than those we refer to cf. *Macropus* sp. (below) and their proximal articular surfaces are triangular in shape, indicative of a strong metatarsal V. A left metatarsal V, lacking distal epiphysis, NMV P23161, is of suitable size (Fig. 11E). These bones are about the size of *Prionotemnus palankarinnicus* Stirton (1955) and thus could also be *Kurrabi* sp., as could MUGD 3578, the distal end of a left tibia (Fig. 8D). NMV P186791 is a part of a right pelvis with the acetabulum and base of the ilium (Fig. 9B). It has a macropodine form with a large pectineal process, and is of a size appropriate to *Kurrabi*

Protemnodon sp.

MATERIAL

MUGD 3568, 3571, 3573, NMV P186781.

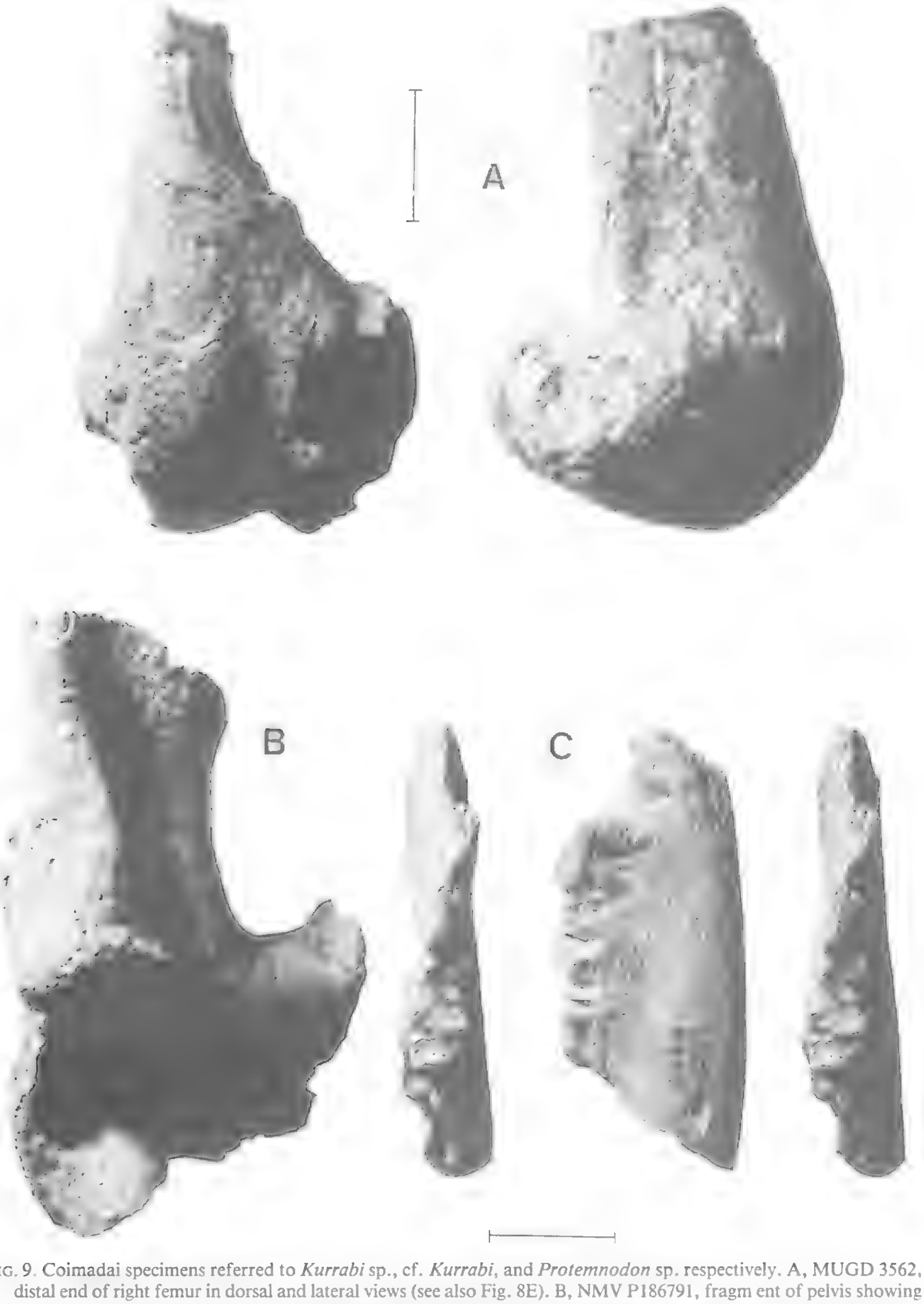

FIG. 9. Coimadai specimens referred to *Kurrabi* sp., cf. *Kurrabi*, and *Protemnodon* sp. respectively. A, MUGD 3562, distal end of right femur in dorsal and lateral views (see also Fig. 8E). B, NMV P186791, fragm ent of pelvis showing view into the right acetabulum. C, *Protemnodon* sp., MUGD 3571, a fragmentary right ramus with P3-M4; shown in occlusal (stereo) and buccal views. Scale = 2 cm.

Description

These four ramus fragments are slightly larger than those described for *Kurrabi* and *Troposodon minor*. MUGD 3568 is an edentulous right ramus with alveoli showing that P_3 was relatively elongate and that the molars were of appropriate proportions for the genus. The buccal groove of the jaw was distinct and long. Only a few alveolar measurements could be taken (Table 2). MUGD 3571 has the dentine cores of the right P_3, M_2-M_4 preserved (Fig. 9C). MUGD 3573 (Fig. 10B) is edentulous, with alveoli for the left P_3, M_2-M_5. NMV P186781 is a right ramus with dentine cores of P_3, M_2-M_4 (Fig. 10D). They correspond reasonably well with *P. chinchillaensis* in size, relative length of P_3 (Table 2), position of mental foramen and length of buccal mandibular groove (from posterior root of P_3 to posterior root of M_3 or anterior root of M_4).

cf. **Macropus** sp.

Material

MUGD 1476, 3560A&B, 3563-4, 3574, 3577, 3579, NMV P23165-6, P23178-9, P23189(T), P23196-7, P23199, P186782, P186784, P186786 and P186794.

Description

A number of fragmentary bones and some associated materials all seem to represent a macropodine kangaroo about the size and morphology of the living *M. giganteus* or the extinct *M. titan*. They surely represent a derived macropodine. The most informative bone is a complete left metatarsal IV,NMV P186794, 171.4 mm in length (Fig. 14B). The proximal end of another left metatarsal IV,MUGD 3574, is nearly identical in size, as is NMV P23189(T), a vug that preserved the form of the proximal end of a metatarsal IV. MUGD 1476, the proximal two-thirds of a right femur, was presented by R.J. Alkemade in 1933 and identified by E.S. Hills the same year as *Macropus* sp. (Fig. 11C). MUGD 3564 is the shaft and part of the cnemial crest of a left tibia (Fig. 11B). MUGD 3563 and 3577 are distal ends of left femora, the latter with a relatively large medial malleolus. MUGD 3560 is the articulated partial left forelimb (Fig. 11A), with much of each long bone preserved as natural moulds.

NMV P23197 consists of both articulated partial forelimbs preserved in two apparently associated concretions, every bone preserved as a vug. Now epoxy-filled, the left elements are the distal halves of the radius and ulna, the carpals, metacarpals II-V, some of the phalanges and several sesamoids; the right elements are the distal epiphyses of radius and ulna, the carpals and metacarpals II-V, proximal phalanges of digits II-IV and some other phalanges and at least 6 sesamoids. Fig. 12 shows the partial left forelimb in dorsal aspect and the right manus in palmar aspect. Correspondence to forelimb and manus of *Macropus* is fair. MUGD 3579 is a part of a large pelvis with massive bone but a relatively small acetabulum. NMV P23165-6 are scapular fragments that may belong together, but if so the contact has been lost. NMV P23178 (Fig. 14D) and P23196 each consist of the mid and distal portions of the shaft of a humerus preserving part of the deltoid ridge and the entepicondylar foramen. NMV P23179, a concretion with several vugs seeming to represent a terminal phalanx and parts of astragalus and calcaneum. NMV P186782 is another hollow (natural mould with most of the bone gone); now epoxy-filled and prepared, it is the distal end of a tibia with a poorly-preserved epiphysis. NMV P186784 and P186786 are also pieces of tibial shafts, the first about 18 cm long, the other 14 cm long. The only jaw fragment tentatively referable to *Macropus* is an edentulous left ramus, NMV P23199 (Fig. 14A), with alveoli for M_3-M_5. The strong molar size gradient and increasing jaw depth anteriorly support this identification.

Subfamily STHENURINAE
cf. **Troposodon** sp.

MUGD 3569, a nearly complete edentulous left ramus with dentine cores, roots or alveoli is here interpreted as representing P_2, M_1-M_5 (Fig. 10B, Table 2). The dental formula, showing eruption of M_5 before P_3, is typical of sthenurines. The crest of P_2 is lingually directed and the specimen is about the size of *T. minor*. It is referred to *Troposodon* because the jaw is relatively shallow beneath M_4-M_5; the symphysis procumbent and the mandible, although wide at M_4-M_5, is not as robust throughout as in *Sthenurus*. It is slightly larger than the specimens here assigned to *Protemnodon*; the cheek-tooth row is longer (in spite of a shorter premolar) and the last two molars are larger and somewhat more massive.

MACROPODIDAE gen. et sp. indet.

Material

MUGD 3565-6, 3580-1, NMV P23162, P23164, P23170, P23181, P23188, P23194-5, P186783,

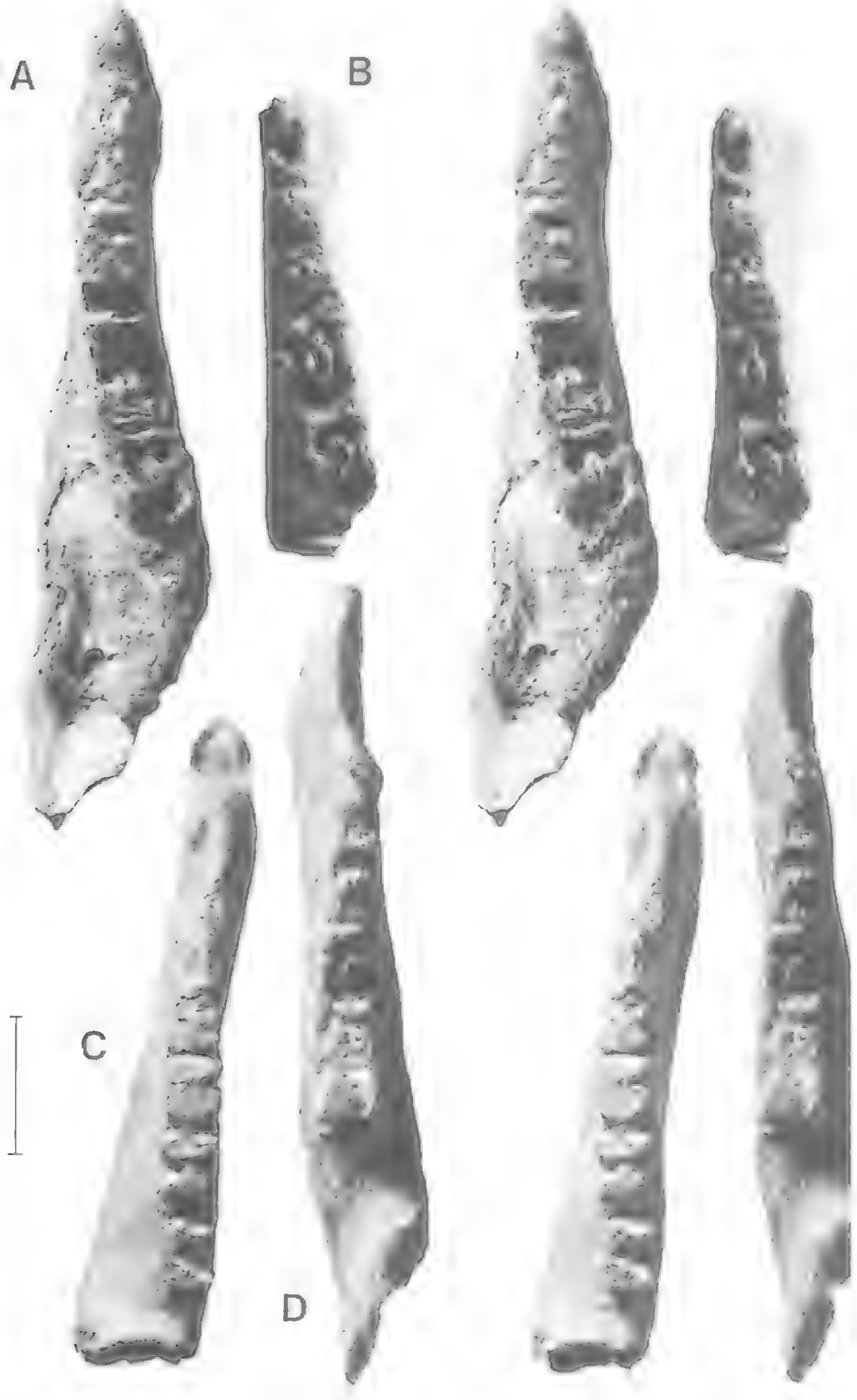

FIG. 10. Four of the Coimadai jaw rami referred to *Troposodon* sp. (A), and to *Protemnodon* sp. (B-D), all in (stereo) occlusal view. A, MUGD 3569, left ramus with parts of P_3-M_3 and alveoli of M_4-M_5. B, MUGD 3573, an edentulous left ramus fragment with alveoli of P_3-M_4. C, NMV P186781, a left ramus with part of P_3 and most of M_2-M_5. D, MUGD 3568, an edentulous right ramus with alveoli of cheek-teeth. Scale = 2 cm.

FIG. 11. Various Coimadai specimens. A-C are referred to cf. *Macropus* sp., D is indeterminate (probably Marsupialia), and E is referred to *Kurrabi* sp. A, MUGD 3560, casts of articulated partial left forelimb, taken from natural moulds. B, MUGD 3564, proximal two-thirds of left tibia, showing cnemial crest. C, MUGD 1476, proximal two-thirds of right femur, in posterior view. D, NMV P23183- 4, joined fragments of fragile medullary trabeculae from a long bone; all the dense compacta bone has been destroyed. E, NMV P23161, a stout left metatarsal V, which articulates almost perfectly with another *Kurrabi* specimen (MUGD 3575). Scale = 2 cm.

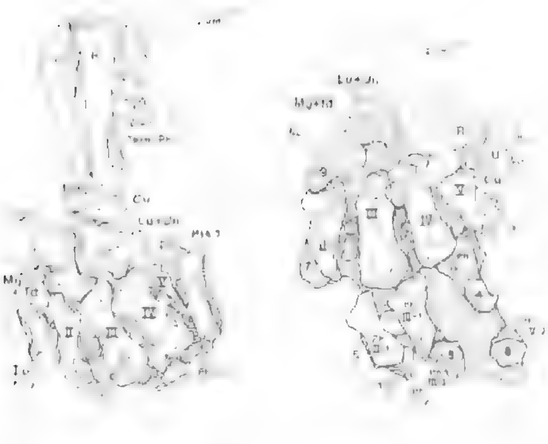

FIG. 12. Articulated partial front limbs of NMV P23197, cf. *Macropus* sp.; preserved as hollow natural moulds that are now epoxy-filled and prepared in relief on their matrix base (stipple). At left is the partial left forelimb in dorsal aspect; at right, the right manus in palmar aspect. Scale = 2 cm. Abbreviations and symbols: wavy lines with or without arabic numerals, openings into the vugs at the weathered surface of blocks before preparation; Roman numerals I-V, metacarpals and digits; phalanges (Ph) also shown with Roman II-IV and arabic numerals to indicate position; Cu, cuboid; Lu + Un, lunar + unciform; Mg + Td, magnum + trapezoid; Pis, pisiform; R, radius; s, sesamoid; Sc, scaphoid; Term Ph, terminal phalanx; Tz, trapezium; U, ulna.

P186789-90, P186792-3 (T), P186795, P186798, P186800, and P186802 (T).

DESCRIPTION

The first two, MUGD 3565-6, are 16-18 cm long pieces of tibial shafts. MUGD 3580-1 are two pieces of the midshaft region of longbones. MUGD 3580 had been designated as a humerus on its old label, but this is doubtful as all surface compacta is gone and only the trabecular pattern of the spongiosa remains. NMV P23162 and P23164 are both tibial midshaft bits. NMV P23170 is a 7 cm length of rib. NMV P23181 is a 6 cm long piece of the midshaft of a longbone, with its open medullary tract now epoxy-filled. It could be a piece of femur, tibia, or humerus. NMV P23188 is the distal end of a fibula. NMV P23194-5 are two femoral midshaft pieces, each preserving some of the bicipital tuberosity. NMV P186783 consists of two bones: number 2 is the proximal end of the shaft of a large left femur with part of the lesser trochanter and the bicipital tubercle; and number 2A is a bit of the shaft of a tibia. The associated label specifies *Halmaturus dryas*, but this is doubtful. They could be from a large *Macropus* or a *Protemnodon*. NMV P186789 is the proximal two-thirds of the shaft of a right humerus, from the epiphysis to beyond the deltoid crest at about the narrowest point of the shaft. NMV P186790 (T) is the distal third of a large left femur (Fig. 14E). It includes most of the shaft distal to the bicipital tuberosity but is lacking the distal extremity and the condyles. All surface bone is gone, but the trabeculae within (and the plaster-filled medullary tract) show the supracondyloid fossa and the raised bony shelf that led to the condyles. NMV P186792 (T) and P186793 are two distal ends of tibial shafts. The first was a hollow 10 cm long that was plaster-filled and prepared, but that early attempt to save the bone was not successful (Fig. 13C). A better procedure would be to sacrifice the bone and to cast from the natural mould. NMV P186795 is from the midshaft of a long bone whose sections suggest that it may be an ulna. NMV P186798 consists of two joined pieces of rib. NMV P186800 and P186802 (T) are both midshaft pieces of large diameter long bones, probably femora, the latter with very leached, punky bone with questionable indication of the bicipital tuberosity. NMV P186801 is a bit of the proximal end of the shaft of a tibia.

Family DIPROTODONTIDAE
Subfamily DIPROTODONTINAE
Euowenia sp.

NMV P23202-3 are both edentulous rami which belong to the same mandible and show the whole tooth row, parts of the symphysis and ascending ramus (Fig. 13A). Comparative measurements (Table 3) show that NMV P23202-3 is similar in size to the Late Miocene *Pyramios alcootensis* and to the Pliocene *Meniscotherium mawsoni* and *Euowenia grata*. Like those of *Pyramios* and *Euowenia*, the mandible is deep, particularly at the posterior end of the symphysis, and tapers markedly to the rear. The symphysis does not extend behind the anterior part of M_2, as in *Euowenia* and *Pyramios* and unlike *Meniscotherium* or *Nototherium*, which have long symphyses (extending to the anterior part of M_2 in *Meniscotherium* or M_3 in *Nototherium*). The posterior end of M_5 in the Coimadai specimen is not significantly overlapped by the edge of the ascending ramus, as in *Pyramios*, not as in the other genera. The posterior opening of the dental canal lies at the end of a long post-alveolar crest, above the alveolar border and probably above the crowns

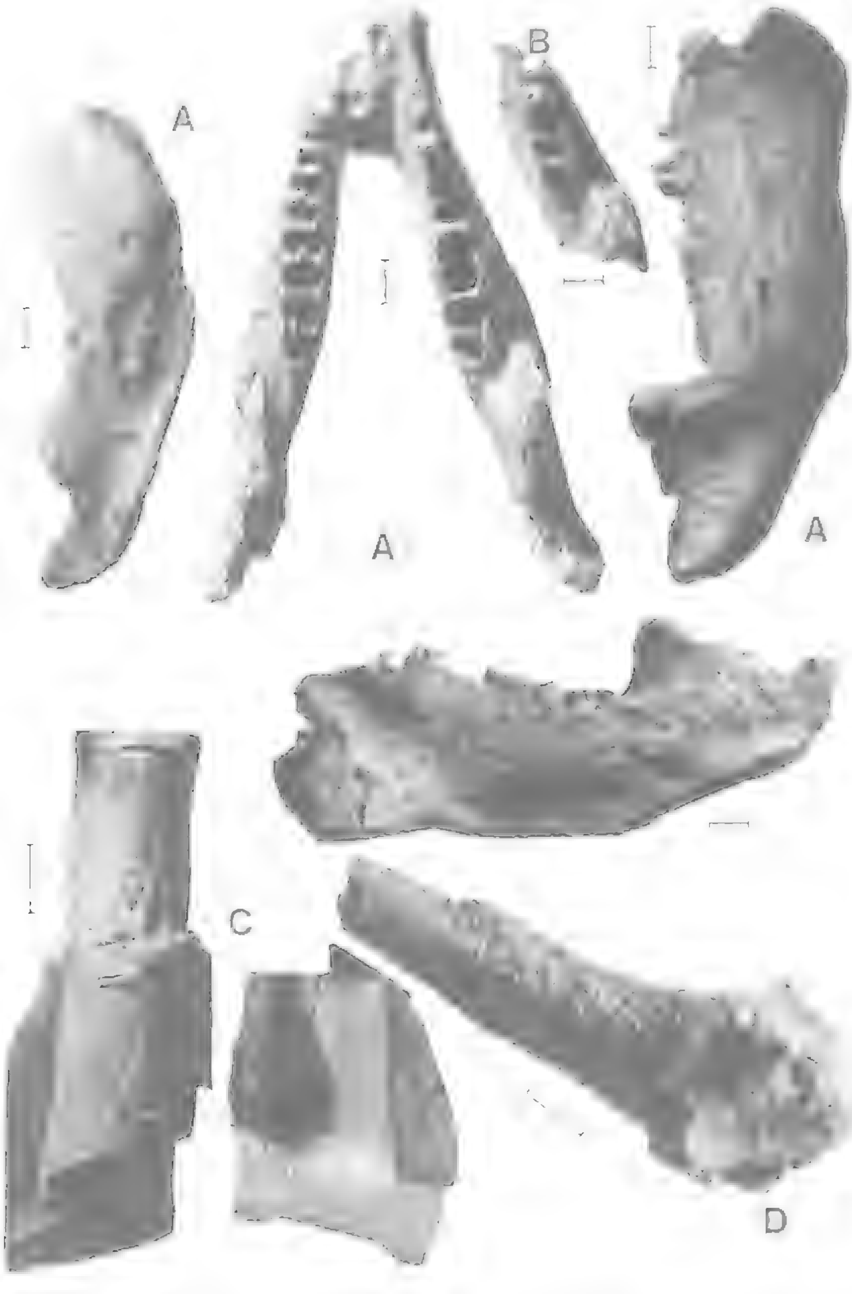

FIG. 13. Two of the Coimadai diprotodontid specimens (A, B), and indeterminate pieces (C, D) that illustrate preparation problems and two common styles of preservation. A, *Euowenia* sp., NMV P23202-3; nearly edentulous pair of jaws, associated but without contact, shown in dorsal and lingual views; the right ramus is also shown in buccal view. B, NMV P23198; edentulous jaw fragment identified as cf. *Zygomaturus;* evidently with a broad talonid to M_5, to judge from comparison with the alveolus of M_5 in *Euowenia*, fig. 13A. C, NMV P186792, part of the shaft of a long bone identified as cf. indet. macropodid; used to determine the best means of preparation when a hollow concretion contained fragile bone around the void. It was plaster-filled and the upper half prepared as usual. For the lower half the bone of one side was sacrificed and a cast of the exposed natural mould proved to be the best means of obtaining the bone's surface detail. D, NMV P23200, indet. vertebrate, probably Marsupialia; another specimen of taphonomic interest in that all dense bone has been resorbed, leaving only the spongiosa and some of the inner trabeculae of the compacta. Scale = 2 cm.

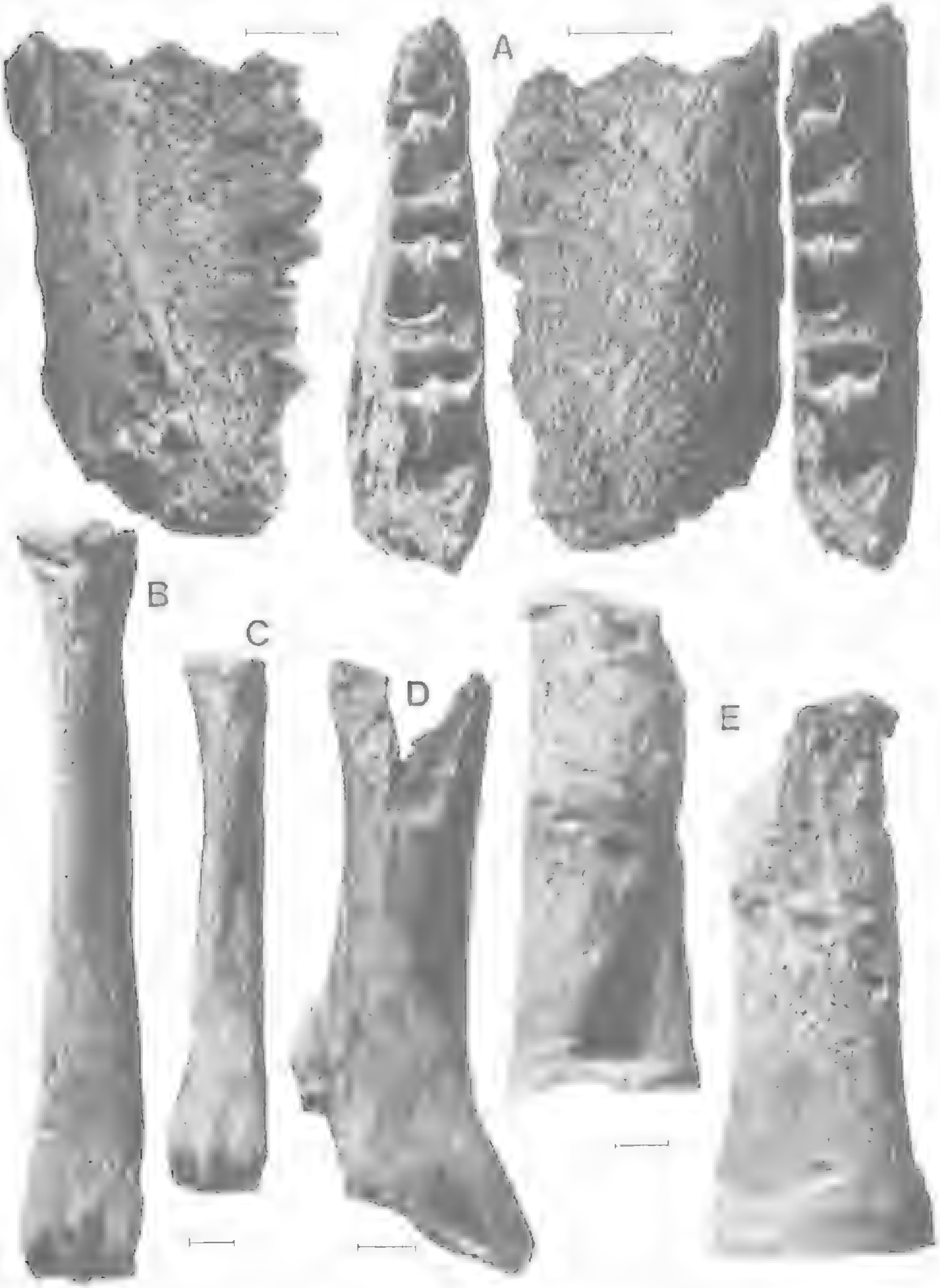

FIG. 14. Five additional Coimadai fossils. A, NMV P23199, an edentulous left ramus fragment identified as cf. *Macropus* sp., in dorsal (stereo), buccal and lingual views. It shows a condition commonly seen in Coimadai materials, where all tooth tissues and dense surface bone are gone, leaving the trabecular bone matrix pattern. B, NMV P186794, complete left metatarsal IV identified as cf. *Macropus* sp., in postero-ventral view. C, MUGD 3575, *Kurrabi* sp., complete left metatarsal IV, also in postero-ventral view. C, NMV P23178, cf. *Macropus* sp., a partial right humerus in antero-dorsal view. E, NMV P186790, a heavily-leached piece of macropodid femur, prepared by filling the open medulla with plaster and removing the superficial matrix. Little of the original compacta remains, but the overall shape is sufficient to permit identification of the large supracondyloid fossa. Scale = 1 cm.

of the teeth as in *Nototherium*, not at or below this level as in *Euowenia*, *Meniscotherium* or *Pyramios*. The digastric process on the inferior border of the ramus lies just behind M_5 as in *Euowenia*, *Pyramios* and *Meniscotherium*, rather than markedly behind as in *Nototherium*. The symphysis is fused, its shape at mid-suture being oval with the long axis at about 40° to the alveolar border of the cheek teeth, as in *Euowenia*. There is a lower gradient in *Pyramios*, *Nototherium* and *Meniscotherium*. The lower incisor root is very large, as in *Euowenia*. It is directed at a low angle to the alveolar plane at this level but it probably curves dorsally as in *Euowenia* for the I_1-P_3 distance cannot be much over 70 mm, as in *Euowenia* (113 in *Meniscotherium;* 99-130 in *Pyramios*). The incisor alveoli indicate the roots to be widely open, not tapering significantly posteriorly as in *Pyramios* and not reaching the anterior root of P_3 as in *Euowenia*, *Nototherium* and *Pyramios*. The incisor cross-section shows an internal ridge delimited by two sharp grooves apparently as in *Euowenia*, but not the other genera. The alveoli of the cheek teeth show a strong gradient in length extending to M_4, the longest tooth, as in the other genera compared. The posterior root of the M_4 has a lower inter-radicular crest than the anterior and is narrower transversely indicating a markedly narrower talonid for this tooth as in *Euowenia*. The conclusion reached from these comparisons is that the Coimadai mandible is a diprotodontine diprotodontid, sufficiently resembling *Euowenia* in mandibular form to be assigned to that genus.

Subfamily ZYGOMATURINAE
cf. **Zygomaturus** sp.

Another diprotodontid, probably a zygomaturine, is indicated by NMV P23198, an edentulous fragment of a right ramus showing alveoli for M_4-M_5. The mandible is wider than that attributed to *Euowenia*, and the M_5, judging from its alveoli, is slightly shorter than M_4 and had a talonid as wide as the trigonid (Fig. 13B).

DIPROTODONTIDAE
Genus indeterminate

One specimen, NMV P23214, is so assigned on the basis of its large size. It probably is the proximal

TABLE 3. Dental and mandibular measurements of selected diprotodontids in comparison with the Coimadai *Euowenia* specimen. All measurements in mm. Includes data from de Vis, 1887 *(Euowenia grata)*; Stirton, 1955 *(Meniscolophus mawsoni)*; Woodburne, 1967, tables 4-6 *(Pyriamos alcootensis)*.

	cf. *Euowenia* NMV P23202-3	topotypes *Pyriamos alcootensis*	*Meniscolophus mawsoni*	*Euowenia grata*
Length P_3	~15 alv.	13.5-15.4	17.2	14.5
Length M_2	~18 alv.	20.9-21.2	29.0	—
Length M_3	~25 alv.	24.4-29.7	32.4	—
Length M_4	~32 alv.	27.2-36.1	36.4	34.5
Length M_5	~32 alv.	30.1-35.8	37.1	—
Incisor Length	~37	20.7-28.9	—	32.0
Incisor Width	26	9.4-13.1	—	26.5
Mandible depth				
at P_3	~93	—	—	105.5
at M_2	~86	67.1-95.6	70.0	—
at M_4	~80	63.6a-95.5	61.0	—
Mandible length from rear of symphysis to digastric process	~135	121.2	—	—
Mandible length P_3-M_5	~123	119.5-121.0	130.3	—
Mandible length M_2-M_5	~116	—	133.4	135.5

end of a left femur lacking the head and trochanters, but conceivably could be the proximal end of a tibia or humerus.

Indeterminate vertebrate remains

Nearly half the specimens fall into this category. We have identified them as closely as possible; many are of taphonomic significance, the most important being indicated in the listings with the code-letter (T) — as was done also with some of the more definitively assigned specimens above.

MATERIAL.

Australian Museum F1236, MUGD 3582-4, NMV P23163, P23167-9(T), P23171-5(T)-7, P23182-4(T) (Pl. IX D), P23190-1, P23193, P23200(T) (Pl. X D)-1(T), P23215, P186785, P186787-8, P186796, P186799(T), and P186803-5. All are either mere bone scraps with no diagnostic features, or they are so leached and eroded that we assign them as ? Mammalia, probably Marsupialia.

Two large-diameter rib pieces now joined, NMV P23180 and P23192, suggest a pachyostotic condition somewhat like that seen in ribs of dugongs, although it is not nearly as well-developed. They are of an appropriate size for a dugong, but more probably are pieces of a small diprotodont.

One macropodid ramus with 2½ teeth (?M_2-M_4), MUGD 3572, we suspect is not from any of the Coimadai quarries. Its preservation is different from all of the others, resembling more that at Lake Colongulac.

A final lot of specimens are all concretions, some with faint traces of bone that could represent nuclei, but most show no trace of bone or any other nucleating source. These are: NMV P23185-6, P23204-13 and P23216-7.

TAPHONOMY

The generally poor state of preservation of tooth and bone at Coimadai deserves attention. Usually the hardest and most resistant vertebrate tissues persist the longest. This is not so in this situation, where tooth enamel succumbs first (Figs 7A-C, 10A-D) to whatever diagenetic or other destructive agents are operating, then dentine (Fig. 10A,C), then dense bone such as compacta, leaving only the most fragile-appearing bony materials as final remnants — the medullary trabeculae of the spongiosa (Fig. 14A) and the trabecular groundmass pattern of internal bone fabric (Figs 13D, 14E). Finally all trace of the original tissues disappear and only empty limestone or lime-mud hollows remain (Figs 11A, 12), natural moulds of the original exterior surfaces. There are exceptions to this usual sequence of destruction, especially when subaerial surface weathering persists for long periods. Behrensmeyer (1978) has characterized six bone-weathering stages for one East African region, the Amboseli Basin. At first glance many of the Coimadai fossils appear to match the conditions she described. However, we do not think that the comparison properly applies in this case, for many of our specimens were entombed and fossilized quickly as is evidenced by the fact that some were in articulation and many of the natural moulds preserve unweathered bone surfaces in good condition. Surface weathering apparently was not the primary destructive agency involved. Instead unusual ground water chemistry seems a more likely cause.

CONCLUSIONS

Restudy of fossil material from the Coimadai limestone quarries and of the geological relationships of the quarries confirms the presence of three families of marsupials in the fauna but indicates that the age is Pliocene rather than Pleistocene as originally thought by de Vis (1898) and later by Coulson (1924). Despite the difficulties of identification posed by the unusual preservation of the Coimadai fossils, it has been possible to gain some knowledge of the more abundant taxa. There is a mixture of genera, both extant (*Vombatus, Macropus*) and extinct (*Kurrabi, Protemnodon, Troposodon, Euowenia* and *Zygomaturus*). Such mixtures are known only from post-Miocene assemblages in Australia (Woodburne *et al.*, 1985). Some of the extinct genera (e.g. *Kurrabi, Euowenia*) have chronological ranges restricted to the Pliocene, and the most comparable species within *Protemnodon* are also Pliocene taxa. The Coimadai Local Fauna thus seems clearly of Pliocene age and, if comparable to the Chinchilla and Bow faunas as indicated above, it probably is of Early or Middle Pliocene age. These biochronological results are in harmony with, and thus help support, the geological inferences that the lacustrine environment in which the fauna was entombed was in existence prior to disruption of the local drainage by deposition of extensive alluvial fans E of the Rowsley Fault. The uplifted, rejuvenated western side of the fault contributed the material of the fan deposits, but the stream (Bullengarook Creek) aggraded to accommodate the added material until the Bullengarook eruption filled its channel with a basalt flow (3.3 – 3.6 Ma) that formed a resistant cap. This forced development of two parallel drainage systems, one (Pyrete or Coimadai Creek) E of the old Bullengarook Creek and the other (Goodman's Creek) on its W side. The influx of detritus continued until well after the Bullengarook flow (well into the Pleistocene) before the present erosional phase became dominant. The Coimadai quarries exposed both pre- and post-Bullengarook flow deposits including the Coimadai Limestones with their fossils, the majority of which came from a few metres below the reported ash bed that Coulson (1924) correlated with the Bullengarook flow. There are a few Early Pliocene assemblages from Victoria (Rich *et al.*, 1982; Woodburne *et al.*, 1985) that likewise can be related to the dated Newer Basalt Province, or can be tied to marine strata for independent age-assessment. Some of these faunas lack systematic treatment and the best known, the Hamilton Local Fauna, of earliest Pliocene age (4.47 Na) lacks an adequate representation of comparable large forms (Turnbull & Lundelius, 1970). However, several of the same macropodid genera occur at Hamilton (*Kurrabi, Troposodon, Protemnodon*) (Flannery, pers. comm.) as at Coimadai, setting the earliest known limits to the chronological range of those taxa in Australia. The small vombatid, which has been assigned to *Phascolomys parvus* by de Vis (1898) and others, and was considered to be a juvenile assignable to *Vombatus hirsutus* by Merrilees (1967), has a number of characters that suggest that it may in fact represent a dwarf species. Further study and comparison with the type will be necessary to assess its relationships.

ACKNOWLEDGEMENTS

The late Edmund Gill of the (National) Museum of Victoria introduced two of us (ELL & WDT) to the Coimadai quarries and other potentially fossiliferous localities in 1963-4, arranged for loans and shipment of materials and helped in many other ways. Marlene Werner, Zbigniew Jastrzabski, Ronald Testa, Sophia Anastasion-Wasik and Clara L. Richardson of the Scientific Support Services Staff and/or Division

Photography of the Field Museum aided with the illustrations. William Simpson (Chief Preparator) aided Turnbull in the development of the epoxy injection technique. Moulding and casting was done by John Harris. We thank Thomas Rich for X-rays of the *Phascolomys parvus* specimen. Barrie Smith, Assistant Chief Construction Engineer on the Lake Marrimu Project, made it possible for Turnbull to revisit the Coimadai site in May 1987. The investigation at Coimadai was carried out under NSF grant GB975, with additional support from both the Field Museum and the University of Texas at Austin.

LITERATURE CITED

BEHRENSMEYER, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150–62.

BARTHOLOMAI, A. 1975. The genus *Macropus* Shaw (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 17: 195–235.

1978. The Macropodidae (Marsupialia) from the Allingham Formation, northern Queensland. Results of the Ray E. Lemley Expeditions, Part 2. *Memoirs of the Queensland Museum* 18: 127–42.

COULSON, A.L. 1924. The geology of the Coimadai area, Victoria, with special reference to the limestone series. *Proceedings of the Royal Society of Victoria* 36: 163–74.

DAWSON, L. 1983. The taxonomic status of small Fossil Wombats (Vombatidae: Marsupialia) from Quaternary Deposits and of related modern Wombats. *Proceedings of the Linnean Society of New South Wales* 107 (1982):99–121.

DE VIS, C.W. 1898. On the marsupial bones of the Coimadai Limestone. *Proceedings of the Royal Society of Victoria* 10: 198–201.

FENNER, C. 1918. The physiography of the Werribee River area. Proceedings of the Royal Society of Victoria 31: 176-313.

FERGUSON, W.H. 1894. "Notes on the occurrence of limestones at Merrimu". *Geological Survey of Victoria. Progress Report* 8: 69–70.

FLANNERY, T.F. AND M. ARCHER. 1984. The macropodoids (Marsupialia) of the early Pliocene Bow Local Fauna, central eastern New South Wales. *Australian Zoologist* 21: 357–83.

RICH, T.H.V., TURNBULL, W.D. AND LUNDELIUS, E.L., JR in prep. The Macropodoidea of the early Pliocene Hamilton Fauna, Victoria, Australia.

GILL, E.D. 1964. Rocks contiguous with the basaltic cuirass of western Victoria. *Proceedings of the Royal Society of Victoria* 77: 331–55.

HART, T.S. 1908. The Highlands and Main Divide of Western Victoria. *Proceedings of the Royal Society of Victoria*, new series 20: 257–8.

KEBLE, R.A. 1925. Tertiary magnesian limestone at Coimadai. *Records of the Geological Survey of Victoria* 4: 441–3.

MERRILEES, D. 1967. Cranial and mandibular characters of modern mainland Wombats (Marsupialia, Vombatidae) from a paleontological viewpoint, and their bearing on the fossils called *Phascolomys parvus* by Owen (1872). *Records of the South Australian Museum* **13**: 399–418.

OFFICER, G. AND HOGG, E.G. 1897. The geology of Coimadai, Part I. The Coimaidai limestones and associated deposits. *Proceedings of the Royal Society of Victoria*, new series **10**: 60–74.

1898. The geology of Coimaidai, Part II. The Silurian and Glacial Beds with appendices by de Vis and Hall. *Proceedings of the Royal Society of Victoria*, new series **10**: 180–203.

OWEN, R. 1871. On the fossil mammals of Australia. Part 6. Genus *Phascolomys* Geoffr. *Philosophical Transactions of the Royal Society of London* **1872**: 173–96.

RICH, T.H.V., ARCHER, M., PLANE, M.D., FLANNERY, T.F., PLEDGE, N.S., HAND, S. AND RICH, P.V. 1982. Australian Tertiary mammal localities. P. 525-72. *In* Rich, P.V. and Thompson, E.M. (Eds), 'The Fossil Vertebrate Record of Australasia'. (Monash University Offset Printing Unit: Clayton).

STIRTON, R.A. 1955. Late Tertiary marsupials from South Australia. *Records of the South Australian Museum* **11**: 247–68.

SUMMERS, M.S. 1923. The geology of the Bacchus Marsh and Coimadai district. *Handbook of the Pan-Pacific Congress* **1923**: 97–112.

TURNBULL, W.D. AND LUNDELIUS, E.L., Jr. 1970. The Hamilton Fauna, A Late Pliocene mammalian fauna from the Grange Burn, Victoria, Australia. *Fieldiana: Geology* **19**: 1–163.

WILKINSON, H.E. 1978. Synonymy of the fossil wombat *Vombatus pliocenus* (McCoy) with the living species *Vombatus hirsutus* (Perry). *Memoirs of the National Museum of Victoria* **39**: 93–100.

WOODBURNE, M.O. 1967. Three new diprotodontids from the Tertiary of the Northern Territory. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **85**: 53–103.

TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS E.L., Jr. 1985. Biochronology of the continental mammalian record of Australia and New Guinea. p. 347-63 *In* Lindsay, J.M. (Ed.), 'Stratigraphy, Paleontology, Malacology, Papers in Honour of Dr Nell Ludbrook'. *Special Publication of the South Australian Department of Mines and Energy*, **5**.

THE UPPER FOSSIL FAUNA OF THE HENSCHKE FOSSIL CAVE, NARACOORTE, SOUTH AUSTRALIA

NEVILLE S. PLEDGE

Pledge, N.S. 1990 3 31: The Upper Fossil Fauna of the Henschke Fossil Cave, Naracoorte, South Australia. *Mem. Qd Mus.* **28**(1): 247–262. Brisbane. ISSN 0079-8835.

The Henschke Fossil Cave was discovered in a quarry near Naracoorte in 1969. The fossiliferous silt was excavated systematically from the upper levels of the cave during the next eleven years. The resulting fossils from each designated area and arbitrary level were analysed for species, and minimum numbers calculated. Relative abundance of each species was calculated for each level in the combined central areas of the deposit, and is presented graphically. Opposing trends of relative abundance are revealed for some species, and might reflect environmental changes. Age determinations on charcoal indicate that this part of the cave filled between 32,000 and 40,000 years ago, before becoming sealed. Interpreted environmental changes from a wetter, denser, forest to drier, more open, shrubby woodland, agree with climatic and vegetational data obtained elsewhere in the region. Comparisons are made with the fauna of the nearby Victoria Fossil Cave.

☐ *Pleistocene, Henschke Fossil Cave, taphonomy, Anura, Lepidosauria, Chelonia, Aves, Monotremata, Marsupialia, Eutheria.*

Neville S. Pledge, South Australia Museum, Adelaide, SA 5000, Australia; *1 June 1988.*

The Henschke Fossil Cave was discovered in 1969 as the result of quarry operations on the outskirts of Naracoorte, South Australia (Fig. 1, 2a, 2b) and was reported to the South Australia Museum.

FIG. 1. Locality map. SE South Australia with major towns and stranded beach ridges.

The southeastern region of South Australia is underlain by the Oligocene-Miocene Gambier Limestone, and in the Naracoorte region, this is capped by the resistant early-mid Miocene Naracoorte Limestone Member of the Gambier Limestone (Ludbrook, 1961). Following regional uplift in the later Miocene, when karst features were developed (Wells et al., 1984), there was a brief period of inundation during the Pliocene. Pleistocene sea-level fluctuations, combined with steady uplift, left a distinctive signature of stranded beach ridges on the landscape (Hossfeld, 1950; Sprigg, 1952, 1959; Cook *et al.*, 1977; Idnurm & Cook, 1980). In the Naracoorte area caves tend to be associated with these aeolian ridges, particularly the Naracoorte East Range, which sits upon a scarp of Naracoorte and Gambier Limestones associated with the buried Kanawinka Fault. The present caves are apparently elaborations on exhumed Miocene karst features, although no trace of cave sediment older than Late Pleistocene has been recognised.

The several quarries around Naracoorte owe their existence to uplift along the Kanawinka fault; all show karst features - "pot-holes" filled with Pliocene Parilla Sand (Wells *et al.*, 1984) or small caves (e.g. Daily, 1960). In 1969, Henschke's Quarry broke into another small cave. At the far end of the cave a few bones of extinct species of

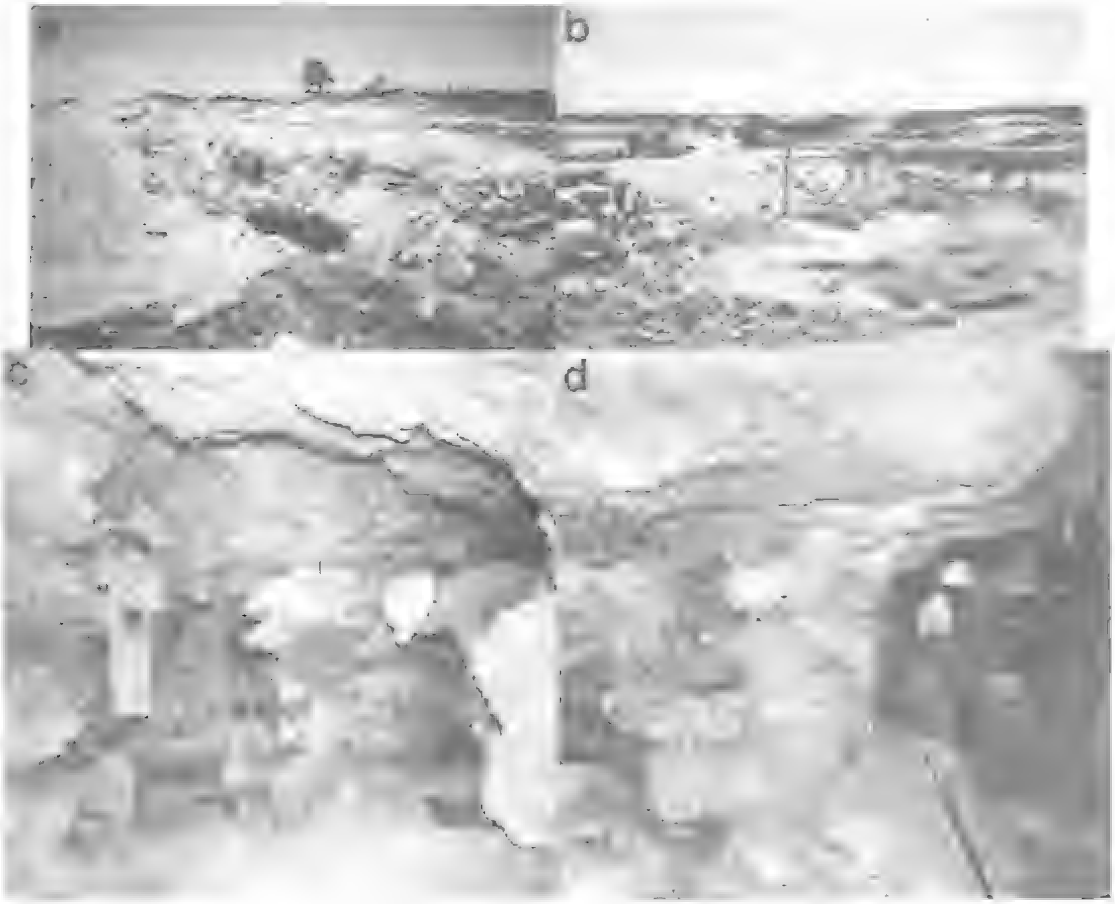

FIG. 2. a) View to SE along the line of the Henschke Fossil Cave, showing a figure in the second entrance and the cap rock of Naracoorte Limestone. b) View to NW along the line of the Henschke Fossil Cave, with the excavated natural entrance in foreground, and Naracoorte in the background separated by a marshy interdune valley. c) Main passage, looking NW from the natural entrance. Silt filled this passage almost to the top of the photo. d) View from the main passage to the natural entrance, which was used as the major means of access during later phases of the excavation.

marsupials lay on the surface of a deep, red silt deposit.

METHODS

Excavation techniques evolved during the eleven years of work in the cave. Initially, working from a point where the quarry had accidentally broken in a second time, digging proceeded along the tunnel in 1 m areas. A centre-line was established in this part of the tunnel after the cave had been surveyed by Mr F.W. Aslin. Notable finds were plotted relative to this line as no distinctive bedding could be discerned. The survey showed that an access hole could be dug from the surface through about 2 m of roof rock to a blind shaft almost directly above the farthermost open area of silt. It also showed that just beyond the perceptible limit of the tunnel there was a large shallow surface depression.

After about 5 m of the tunnel had been excavated, operations moved to a point below the access shaft, and an area (A1, see Fig. 3) 0.9 m^2 was dug out in arbitrary 7.5 cm layers. The silt was brought to the surface and sieved through a garden sieve (6 mm mesh), all teeth, jaws and unusual bones being kept. Analysis showed no perceptible sedimentary layering, nor any obvious faunal differences through the 1.8 m depth of the pit, which ended in broken rock. This may have been due to the small area being sampled. The

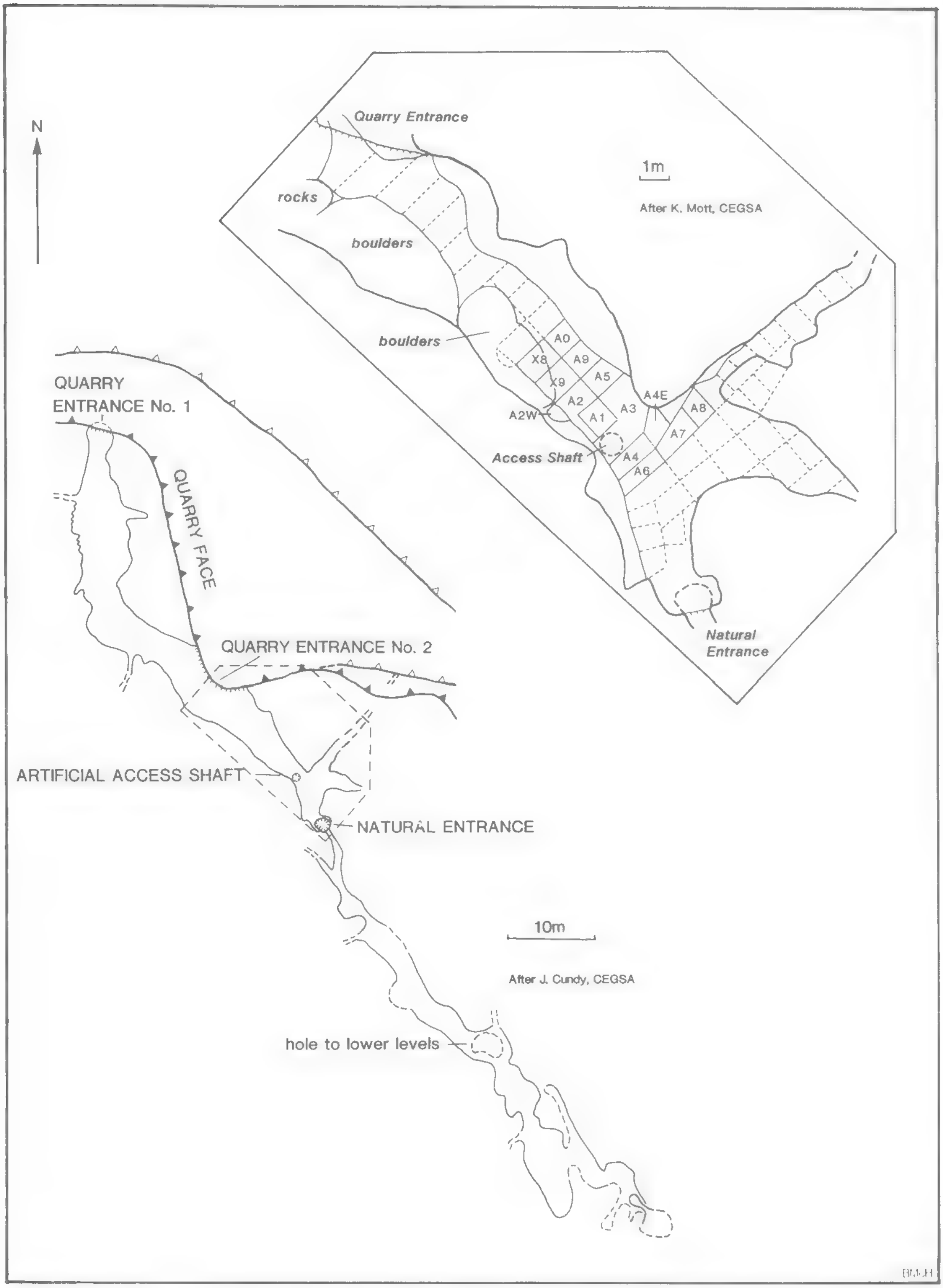

FIG. 3. Henschke Fossil Cave. Plan of upper cave, with detail of excavated area. Census areas designated.

excavation was therefore extended laterally in discrete areas of about 1 m^2, in layers 15 cm thick. In this way most of the tunnel and its accessible offshoots were excavated. The surface depression was considered to be an infilled entrance, and excavation eventually proved this, disclosing a pot hole about 1 m X 1.5 m X 3 m deep. The tunnel was found to continue to the SE for another 60 m, but no bones were seen on the surface. The cave was resurveyed and mapped by the Cave Exploration Group of South Australia. (Fig. 3).

It was soon realised that small items were being overlooked in the sieves because they were coated with mud. Therefore, the concentrate in the sieves was kept, dried and later screen-washed through flymesh. Occasional unsieved samples were also screen-washed to check for particularly small specimens. The identifiable teeth and bones from each layer of each area were kept separate for later analysis, and also to facilitate possible correlation of associated elements. Charcoal was collected wherever it was in sizeable lumps or concentrations, and two samples were eventually submitted for dating.

Subsequently, teeth and jaws, and bones of some taxa, were identified as closely as possible. Minimum numbers of individuals of each mammal taxon in a layer sample were calculated by pairing jaws, and counting them *plus* the excess. If represented only by isolated teeth, a species was recorded as "present". Ultimately, census was done for an area of about 7 m along the tunnel (Fig. 3). Gross numbers for each 15 cm layer were added, percentages of the total identifiable mammal fauna calculated and the results tabulated.

All specimens are house in the Palaeontological collections of the South Australian Museum, prefix SAM P.

THE CAVE

Being in a working quarry, it was inevitable that the cave would be destroyed. However, through the good offices of the owners, Henschke Industries, this was delayed until 1981 when our excavations had been completed as far as was practicable.

As first seen, the cave was a simple tunnel about 50 m long trending roughly NW-SE, with a southward dog-leg bend about halfway along. The floor of the first half was littered with large fallen boulders. At about the bend, reddish fossiliferous silt began to appear below these boulders, which increased in size but disappeared after another 8 m. The silt floor gradually rose towards the far end which narrowed impassably and pinched out. A narrow side passage extended to the east.

On excavation it was found the silt reached a maximum depth of over 3 m, near the natural entrance pothole. Here the cave expanded laterally so that the entrance was bell-shaped, and, therefore, almost escape-proof: a natural pit-fall trap. In this, the cave resembles McEachern's Cave (Wakefield, 1967), but differs in having been sealed before the Holocene.

The sediment is primarily a red-brown silty sand, with a small but annoyingly appreciable clay component (which continually caused the sieves to clog), and occasional coarse sand. It is apparently derived from the Pleistocene Bridgewater Formation, an aeolian sand forming the beach dune ridges such as the East Naracoorte Range. (A fortuitous rainstorm during the excavation of the natural entrance showed how readily the cave sediment could accumulate: sheet wash from a relatively small area — less than one hectare — of gently sloping hillside emplaced more than a metre of sediment in the pit). Rare laterite pebbles suggest also some reworking of the Pliocene Parilla Sands (Firman, 1967). Rockdust and fragments from the cave roof formed a variable component of the sediment. The lowest parts of the deposit tended to be gritty and rather greenish-yellow, apparently with breakdown products from the limestone.

Although a large longitudinal section of the sediment was cleared, no bedding planes of more than 1 m could be seen, in contrast to McEachern's Cave (Wakefield, 1967). Evidence of non-depositional episodes was rare, but occasionally spectacular, such as the articulated skull and jaws of a *Protemnodon* (Fig. 4a), found buried slightly nose-down in the middle of the main passage. The front part of the skull was perfectly preserved, but no trace remained of the cranium or back of the lower jaws. Also, an early rockfall seemed to have been cemented with a thin flowstone crust before being buried by later silt.

During later quarry operations lower extensions of the cave were found and excavated by John Barrie (this volume).

The internal geometry of the cave was manifestly important in the distribution of the fossils. It was found, for instance, that there were few (and mostly large) bones in the central zone of the passage, except in the lee of fallen rocks. Hydrodynamic sorting into size classes occurred, and bones were concentrated, apparently by stream flow, in alcoves along the walls or in the lee of boulders. This may also be an effect of the movement of animals that had survived the fall —

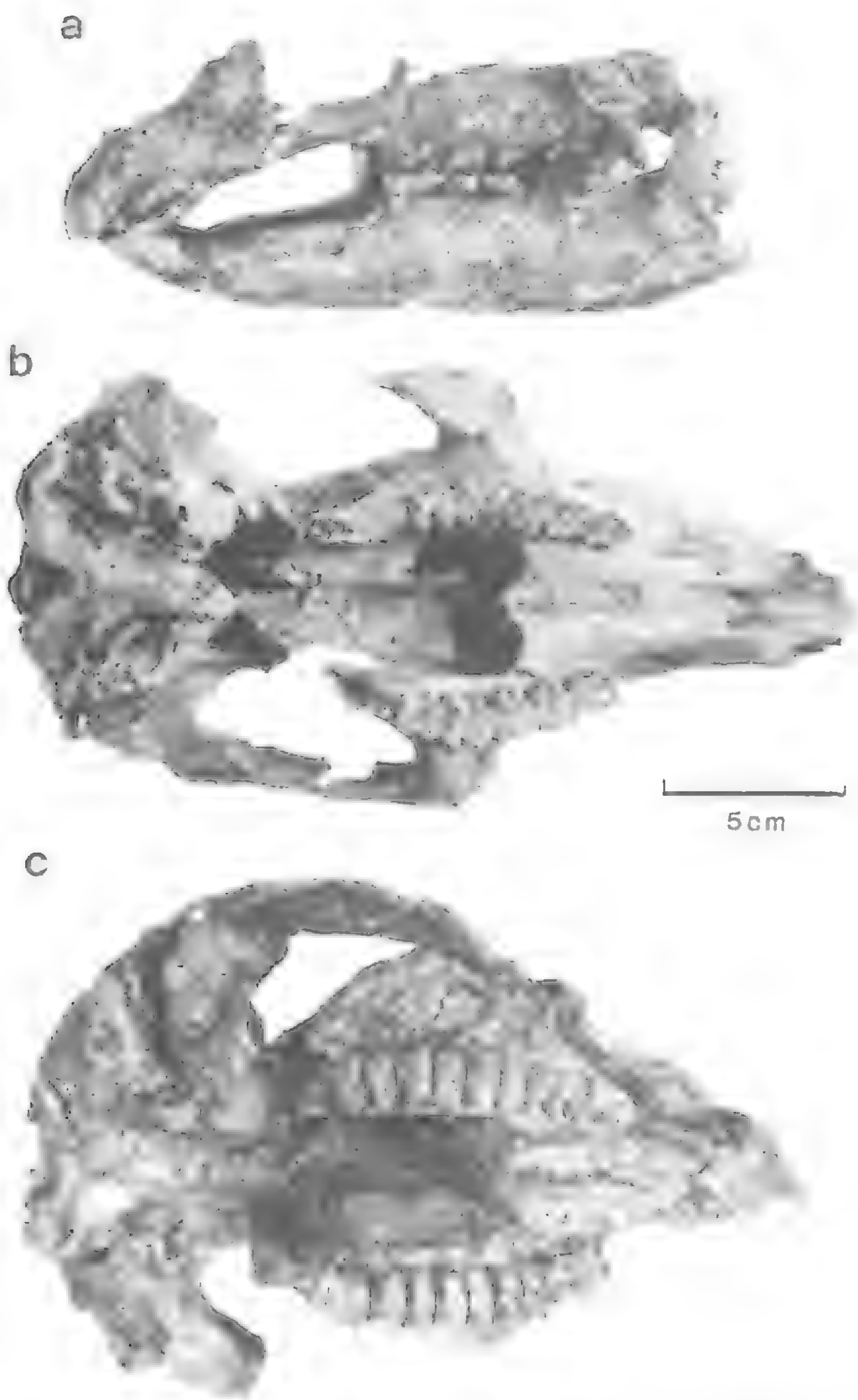

FIG. 4. a) Articulated upper and lower jaws of *Protemnodon roechus* (SAM P22845) showed evidence for erosion which removed all trace of the posterior part of the skull (from Area A2/7). b) Skull of *Sthenurus atlas* SAM P29570 (from Area A10/16). c) Skull of *Simosthenurus occidentalis* SAM P18644, discovered during excavation of the natural entrance shaft. All to same scale. Photos: R. Ruehle.

up to 5 m — into the cave, crushing or kicking aside the remains of earlier victims.

That animals could survive the fall is seen in the partial skeletons of a turtle (*Chelodina*) and a (?)swan found together behind a large rock about 15 m from the pitfall entrance where it is unlikely they would have been washed intact. Many, if not most, remains come from animals that fell into the cave and were trapped, while the few sparse and fragmentary specimens of *Diprotodon* indicate that its remains were washed in from the surrounding hillside. In any case, an adult *Diprotodon* would have stuck in the entrance. There is no convincing evidence that any animal freely inhabited the cave during this last phase of its existence, except possibly during periods when tree trunks or branches had fallen into the entrance to act as ladders. No "fossil" wood has been found, but numerous tubular, branching holes have been interpreted as moulds of twigs, and a large (5 cm diameter) charcoal-lined cavity with a woody-like surface texture presumably represented a charred branch washed in after a bushfire.

Finely disseminated and chunky pieces of charcoal occurred irregularly through the sediment, though very little was found in either the uppermost or lowermost layers. Two aggregated samples were dated by the Radiocarbon Laboratory, University of Sydney (Gillespie & Temple, 1979) as follows:

SUA-140. Area A3, depth 105–120 cm, gave a background result. Age greater than 35,000 years. δC14: −997.7 +/− 4.0; and

SUA-234. Area A1, depth 30–75 cm. Age 33,800, +2,400/−1,850. δC14: −985.1 +/− 3.9.

Archer (1974) has shown the difficulties of dating fossils from associated charcoal, and it must be stressed that the above dates should be regarded as indicative rather than definitive, in view of the small charcoal sample sizes obtainable for dating, and the possibility of contamination of far older charcoal.

Extrapolating these charcoal age values suggests a deposition span for this part of the cave system of about 8,000 years, ceasing when the natural entrance finally became permanently blocked by its own talus pile perhaps 32,000 years ago. Periods of non-deposition may have occurred when the entrance became temporarily blocked. Ponded mud and water from heavy rains would eventually have softened and overcome the obstruction and released a mudflow of debris as described by Wells *et al.* (1984). Evidence of such flows may be interpreted in the jumbled orientations of bones. Such events undoubtedly have caused perturbations in the species abundance charts, but these effects would have been outweighed by other factors affecting the data.

THE FAUNA

The fauna is listed in Tables 1 and 2, together with aggregate totals of the mammals in the volume of census. Note that many fragmentary jaws of smaller taxa were not identified to species level. No attempt was made to estimate numbers of non-mammalian vertebrates.

Amphibia

Tyler (1977) identified and discussed collections of fossil frog ilia from the Victoria Fossil Cave and the Henschke Fossil Cave. Subsequently *Geocrinia laevis* was recognised in further material from the latter cave, but *Limnodynastes* cf. *L. dumerili* is still absent there. There are other notable absences, as discussed by Tyler (*ibid.*).

Reptilia

Smith (1976) lists twelve reptile species from the Victoria Fossil Cave at Naracoorte: five snakes and seven lizards. Most specimens from the upper Henschke Fossil Cave have not been identified or studied in detail, but there is no reason to expect any significant difference.

There are two notable exceptions, however. The giant python *Wonambi naracoortensis* Smith is not present in the upper part of the Henschke cave system. Barrie, however, reports (this volume) on almost complete material from the lowest levels.

TABLE 1. Faunal List: non-mammal species.

AMPHIBIA: *Geocrinia laevis; Limnodynastes tasmaniensis; Litoria ewingi; Ranidella signifera*
REPTILIA: *Chelodina longicollis; Amphibolurus* spp.; *Tiliqua rugosa;* Scincid undet.; *Varanus* sp. cf. *V. gouldii; Pseudonaja* sp.
AVES: *Dromaius novaehollandiae; Progura naracoortensis* (extinct); *Cygnus* (?) sp. or *Anseranas* n. sp.; *Turnix varia; Hirundo neoxena;* Corvidae undet.

TABLE 2. Faunal List: mammal species, with minimum number of individuals within census areas (A0-A8).

MAMMALS	
SPECIES	AGGREGATE NUMBER OF INDIVIDUALS
*Zaglossus ramsayi***	6
Dasyurus viverrinus	54
Antechinus cf. *A. minimus* } *Sminthopsis leucopus* }	34
Phascogale sp.	1
*Sarcophilus laniarius laniarius***	6
*Thylacinus cynocephalus***	12
Perameles cf. *P. gunni* } *Perameles* cf. *P. bougainville** }	469
Isoodon obesulus	96
Phascolarctos cf. *P. cinereus*	2
Vombatus ursinus	8
Lasiorhinus cf. *L. latifrons***	18
*Diprotodon optatum***	5 tooth fragments
*Zygomaturus trilobus***	3
Petaurus breviceps	2
Pseudocheirus peregrinus	1 tooth
Cercartetus nanus	(1)
Trichosurus vulpecula	(1 tooth)
*Thylacoleo carnifex***	46
*Propleopus oscillans***	1
Potorous tridactylus } *Potorous* cf. *P. apicalis* } *Potorous* cf. *P. platyops** }	280
Bettongia cf. *B. gaimardi* } *Bettongia* cf. *B. penicillata* } *Bettongia* cf. *B. lesueur*(?)* }	137
Aepyprymnus rufescens	2
*Lagorchestes leporides**	58
Wallabia cf. *W. bicolor*	5
Macropus cf. *M. giganteus/titan***	147
Macropus cf. *M. rufogriseus**	335
*Protemnodon roechus***	8
Procoptodon cf. *P. rapha***	(1)
*Sthenurus atlas/andersoni***	16
*Simosthenurus gilli***	32
*Simosthenurus occidentalis***	12
*Simosthenurus brownei***	1
*Simosthenurus maddocki***	5
*Simosthenurus pales***	6
Nyctophilus cf. *N. geoffroyi*	1
Mastacomys fuscus } *Conilurus** }	114
"*Rattus*" spp.	224
"*Pseudomys*" spp.	30
Hydromys chrysogaster	3

*Extinct on mainland
**Totally extinct
Numbers for census volume only (areas AO to A8)
Figures in parenthesis recorded only outside the area.

Fragments of shell referred to the turtle *Chelodina longicollis* occur widely through the deposit, and an almost complete carapace and plastron were found in a situation suggesting the animal might have survived its fall into the cave. The presence of this species here is interesting, as Smith (1976) does not report turtles from the Victoria Fossil Cave, and Wells *et al.* (1984) only list cf. *Emydura macquarii*. Presumably the turtles migrated up from the marsh and swamp a few hundred metres away to lay their eggs in the sandy slopes of the East Naracoorte Range.

Dermal scutes of *Tiliqua rugosa* and various reptilian vertebrae are locally abundant in the deposit, and jaws of *Tiliqua* sp. indicate it was the most common taxon. The scarcity or absence of varanids and gekkonids suggests that they were able to escape the pitfall trap that held their less scansorial brethren.

AVES

By far the most abundant bird fossils represent the extinct giant mallee fowl *Progura naracoortensis* (van Tets, 1974) which seems to have been more common here than in the Victoria Fossil Cave. This may be because its poor flying ability made it more susceptible to being trapped in the narrow pothole funnel than in the large entrance which Wells delineated (Wells *et al.*, 1984). It is, therefore, rather surprising that there is such limited and fragmentary emu material - enough only to suggest it was derived from scattered surface debris.

Other birds also are rare. The swallow *Hirundo neoxena* probably nested in the entrance and the quail *Turnix varia* may have come from an owl pellet. Both are represented only by a few isolated bones. By contrast, the swan, (?)*Cygnus*, being studied by van Tets, comprises most of the skeleton, and seems to be a new species.

Compared with the Victoria Fossil Cave, with 17 species (van Tets & Smith, 1974) the Henschke Fossil Cave upper fauna is markedly depauperate in birds, with possibly only four species in common. This difference probably reflects a difference in mode of accumulation, for van Tets and Smith postulated a large avian predator component, which is not evident here.

MAMMALIA

MONOTREMATA. Although bones of *Tachyglossus aculeatus* may be present, they have not been distinguished from those of *Zaglossus ramsayi*, the giant long-beaked echidna (Pledge, 1980). Bones of the latter are widely scattered through the deposit and are locally common, suggesting associated material from a single individual. Two near-complete skulls have been found, but the number of limb bones suggests more individuals were present. Barrie (pers. comm., 1987) has found associated remains, including skulls, of several specimens in the lower levels of the cave.

MARSUPIALIA

DASYURIDAE. The most common dasyurid is *Dasyurus viverrinus*, which is fairly evenly scattered throughout the deposit. As Smith (1972) has noted, it is difficult to distinguish *D. viverrinus* from *D. geoffroyi* without having complete, undamaged palates, but tooth dimensions favour the former species. Species of *Antechinus* and *Sminthopsis* together are almost as common and evenly distributed. Only a few have so far been provisionally identified to species level, but these differ from those listed by Smith (1972). A single jaw, bearing only the canine, is referred to *Phascogale*.

Sarcophilus is notable for its markedly skewed stratigraphic distribution (Fig. 5). Most specimens are within the top 15 cm of the deposit. They are uniformly large and massive, more so than modern comparative material at hand, and should therefore be known as *S. laniarius laniarius* (Werdelin, 1987; see also Dawson, 1982a). Only isolated teeth, some of which may have been misidentified thylacine teeth, were found below 60 cm.

In contrast, *Thylacinus cynocephalus* occurred fairly uniformly, though rarely, throughout the deposit. As most jaws were from young juveniles, the abundance could be greater, because there were numerous isolated teeth that had not developed solid roots or showed signs of wear, and had therefore come from disintegrated juvenile jaws. The collection also includes one of the largest dentaries, of an aged individual, I have seen. It exceeds any modern specimen in the South Australian Museum's collections. However, such size differences are not worthy of specific distinction (Dawson, 1982b).

PERAMELIDAE. Bandicoots are overwhelmingly abundant, particularly in the lower parts of the deposit (though this may be an artefact of hydrodynamic sorting, where they were preserved preferentially in alcoves towards the floor of the tunnel). There is a general decrease in abundance of both *Perameles* spp. and *Isoodon obesulus* from bottom to top of the deposit. No separation was made of the different *Perameles* species but the larger *P. gunni* seemed to be the more common. Each was more abundant than *Isoodon*. Most specimens were toothless, and frequently broken. Counts were therefore made by pairing only those dentaries retaining the ascending ramus, whether or not they bore teeth. Both species of *Perameles* are now extinct in the Naracoorte area, but *Isoodon* is still found there.

PHASCOLARCTIDAE. Koalas are rare in the deposit, and mostly represented by isolated teeth. The jaws discovered vary slightly from most modern representatives, but the latter are so variable between different wild and zoo populations that they encompass these fossil specimens.

VOMBATIDAE. Most wombats come from the upper 60 cm of the deposit. *Lasiorhinus* is found throughout the sequence but mainly in these top levels, and appears to have coexisted with *Vombatus ursinus* which has a more even distribution. The specific identity of *Lasiorhinus* is uncertain. It differs markedly from the modern *L. latifrons* in having a much larger upper incisor relative to the other teeth. The relative abundance of this presumed open-country animal at the top of the deposit comes as something of a surprise, but coincides with upsurges or reductions of several other species, and must be considered to reflect some major ecological/climatic change around 32,000 years ago. *Lasiorhinus* is not reported from the Victoria Fossil Cave (Wells *et al.*, 1984).

DIPROTODONTIDAE. *Diprotodon* is a very minor component of the cave deposit. Only three fragments of molar, showing the distinctive rugose enamel, and pieces of an upper incisor have been identified. Very poorly preserved vertebrae and limb fragments may pertain to this species, but equally well could belong to *Zygomaturus*. It is apparent that these fragmentary remains were washed piecemeal into the cave from the surrounding hillside. None has been recorded from Victoria Fossil Cave, nor any other cave in the area, but a specimen was collected by E.C. Mais last century during the building of the railway from Mt. Gambier to Millicent, about 100 km from Naracoorte (U.S. National Museum of Natural History specimen, pers. obs., 1972). Another was excavated from a stream deposit near Kingston, SE S.A.

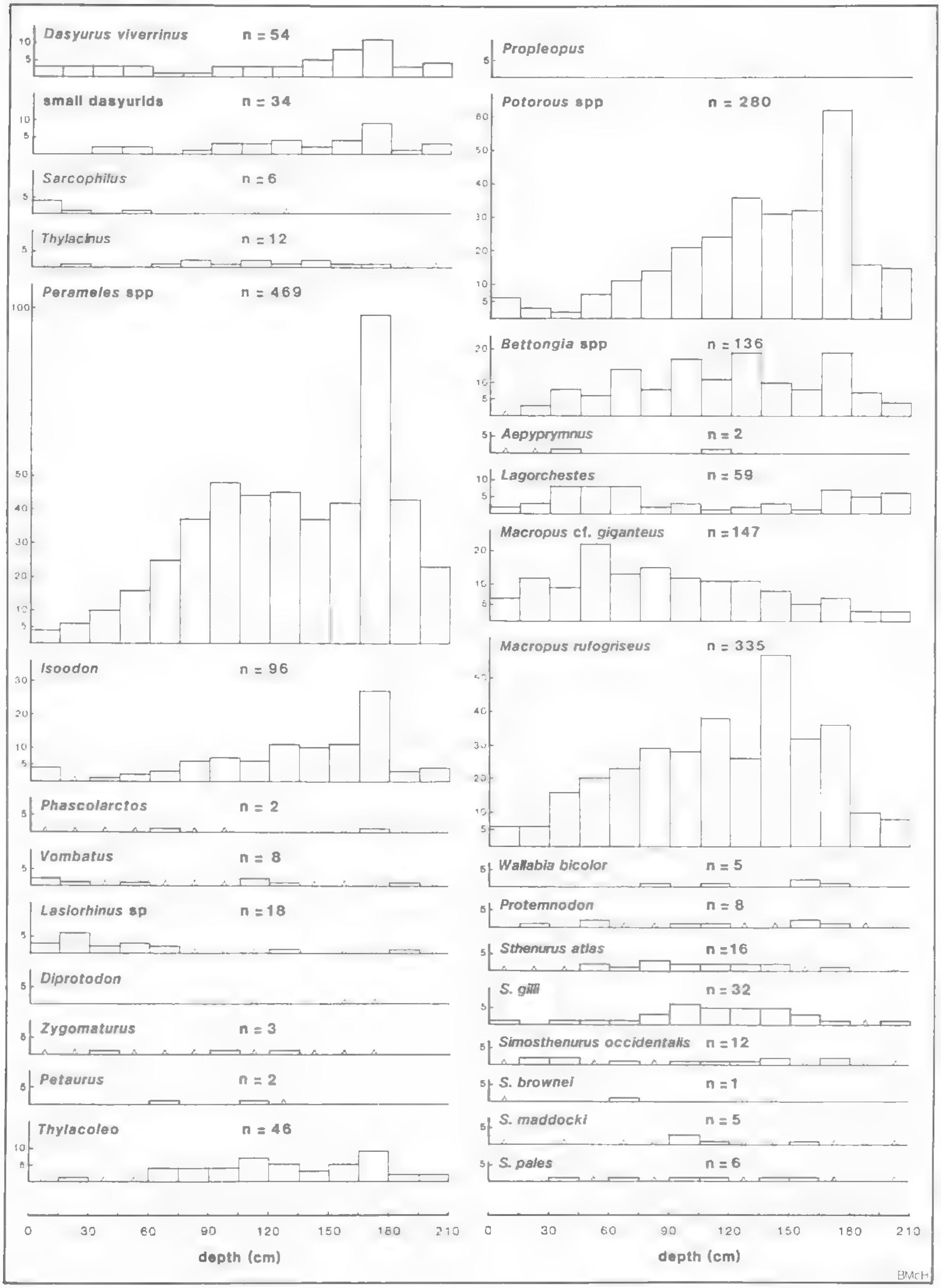

FIG. 5. Absolute abundances with depth of marsupial species in the census areas. Bars represent minimum numbers based on jaws; ticks represent presence of isolated teeth only.

By contrast, *Zygomaturus trilobus* is relatively common, being represented by numerous isolated or associated teeth, jaw fragments and some limb bones. Again, however, these remains were probably garnered from the surrounding slope by flash floods, the entrance being too small to accommodate a live animal. This is unlike the Victoria Fossil Cave, where a partial skeleton has been found (pers. obs.).

POSSUMS. The smaller arboreal marsupials are notably rare in the deposit. The Petauridae are represented by two dentaries of *Petaurus breviceps*, the Pseudocheiridae by a solitary lower molar of *Pseudocheirus* cf. *P. peregrinus*, and the Burramyidae by a single dentary of *Cercartetus nanus*. The presence of the phalangerid *Trichosurus* is uncertain as it is based on a single molar. In isolation, such molars are very similar to those of bettongs.

As with the small dasyurids, the rarity of these species is probably best explained by their scansorial abilities, allowing them to escape from the cave. The fragmentary smaller remains may be derived from owl pellets. Smith (1971) records *Pseudocheirus, Petaurus* and *Cercartetus* as relatively abundant in the Victoria Fossil Cave, and considers their presence to be the result of predation, possibly by owls. It should be noted that *Pseudocheirus* and *Trichosurus* are particularly common in modern cave deposits in the area.

THYLACOLEONIDAE. The thylacole or marsupial "lion", *Thylacoleo carnifex*, is relatively common for its size and presumed trophic position as top carnivore. It is notable, however, that a large proportion seem to be juvenile, (Fig. 8b) an age distribution seen also in *Thylacinus*. It is considered that this age distribution reflects the inexperience of the young animals, leading them to try to scavenge on animals trapped in the pit — the "baited-trap mechanism".

It must be noted, however, that very few bones bear any sign of the cut marks attributed elsewhere to *Thylacoleo* (cf. Wells *et al.*, 1982). The preponderance of *Thylacoleo* below 60 cm depth probably reflects its ability to climb out of the cave once the silt floor had reached close to the walls of the tube.

POTOROIDAE. Potoroids are almost as abundant as bandicoots. Four genera are recognised, with at least six species. One of the rarest species in this deposit, and in fact countrywide, is the giant musk rat-kangaroo *Propleopus oscillans*. It is known here from a handful of scattered isolated molars, a premolar, lower incisor and a possible humerus (Pledge, 1981). Barrie (pers. comm., 1987) has found better material in the lower levels of the cave. It has not yet been found in the Victoria Fossil Cave.

Another rare species, known from two fragmentary dentaries, is the rufous rat-kangaroo, *Aepyprymnus rufescens*. This also has not been recorded by Smith (1971) or by Wells *et al.* (1984).

Species of *Potorous* are the most abundant of the potoroids. They include *P. apicalis, P. platyops* and *P. tridactylus*, the last of which was not recorded by Smith (1971). Nor did she list *Bettongia* cf. *B. lesueur*, which occurs at Henschke's together with *B. gaimardi* and *B. penicillata*. The uncertainty of identity of *B.* cf. *B. lesueur* is because the otic bullae are not as inflated as in the modern species. No attempt has been made to assign all the material to separate species for census purposes, as much of it is broken and incomplete.

MACROPODIDAE. This family is overwhelmingly dominated by species of *Macropus*, more than half of which have been ascribed to *M. rufogriseus*. These appear to be a larger race than the modern form, being up to 20% larger than specimens from the SE of South Australia. *Macropus* cf. *M. giganteus*, which is only half as abundant, is also about 20% larger than the modern form, but additionally possesses an elongate I^3 almost as long as that of *M. titan*. *Macropus titan* has also a greatly enlarged pocket on the rear of the hypolophid of the lower molars, but this is reduced in the Henschke specimens which seem to represent an intermediate form between it and the modern *M. giganteus*. This Pleistocene gigantism has been noted before (e.g. Marshall, 1974). Close relationship between *M. titan* and *M. giganteus* is indicated by Bartholomai (1975). The extinct *M. greyi*, which Wells *et al.* (1984), record as rare, has not been recognised.

Wallabia cf. *W. bicolor* is distinguished primarily by its premolars, which resemble small versions of those of *Protemnodon* (Stirton, 1963). Only five widely scattered jaws retaining premolars were found in this deposit, but others lacking those diagnostic teeth may have been confused with *M. rufogriseus*. *Wallabia bicolor*, which now prefers wet sclerophyll forest, is not found in the region today. Wakefield (1963b) reports it as subfossil from the Portland area of Victoria.

The hare wallaby, *Lagorchestes leporides* is relatively common in the deposit, but its abundance fluctuates in a manner that does not correspond with any other species. Wells *et al* (1984) record only its larger sister species, *L* cf. *L. conspicillatus*; this is rather surprising as this latter now lives only in northern Australia, whereas *L. leporides* existed in the Murray Basin in historic times (Tedford, 1967).

The giant wallaby, *Protemnodon roechus* Owen, is evenly distributed, although rare, in the deposit. There are a relatively high number of juvenile or immature, suggesting less ability to avoid the pitfall trap. One specimen preserves the articulated upper and lower jaws, complete with incisors, of a mature animal (Fig. 4a). The post-nasal part of the skull had been exposed for some period and removed presumably by "bioerosion" — the passage of other animals during a period of non-deposition.

Associated molars and pieces of maxilla and dentary of a single individual are all the evidence of *Procoptodon* in this deposit, but the specific identity is uncertain. In size and premolar and molar morphology, the specimen agrees with *P. rapha* Owen, but the lower molar tooth row is distinctly curved, unlike illustrated specimens. The dentary of *P. pusio* illustrated by Stirton and Marcus (1966, fig. 6) shows slight curvature of the tooth row, but the molars of this species are noticeably smaller than the Henschke specimen. *Procoptodon rapha*, is recorded from Victoria Fossil Cave (Wells *et al.*, 1984).

The other sthenurine kangaroos, species of *Sthenurus* and *Simosthenurus*, are not common in the fauna, although isolated teeth make them seem so, and their abundance is fairly constant throughout the sequence. Several skulls have been found, despite their fragility. *Sthenurus atlas* (Fig. 4b) and *S. gilli* seem to be slightly more common in the middle part of the sequence; *Simosthenurus occidentalis* (Fig. 4c) is more common towards the top, but with abundances of less than 4% in any one 15 cm interval, this is difficult to prove. Certainly, in absolute numbers, *S. gilli* is most common (Table 2). Because of the often fragmentary nature of the remains, and an apparent variability in tooth morphology, many identifications are uncertain. For instance, Wells *et al.* (1984) listed *S. andersoni* as being more common than *S. atlas*. Direct comparison with some of those specimens, and with Tedford (1966), showed the Henschke material to have characters in common with both species, and intermediate tooth dimensions. Similarly, *S. brownei* is listed as more common that *S. occidentalis* in Victoria Fossil Cave, whereas it has been difficult to distinguish in Henschke's. It is notable that the megadont *S. pales*, not reported by Wells *et al.* (1984), is more common, albeit as fragmentary jaws, than the microdont *S. maddocki* which is reported there.

PLACENTALIA

CHIROPTERA. A single bat jaw has been recovered. Jaw and molar structure are reminiscent of *Nyctophilus geoffroyi*, but this identification requires confirmation. It is obvious that the cave never met requirements for breeding or overwintering, and must at best have been visited only rarely.

RODENTIA. Because of the difficulty of identifying often toothless rodent jaws, no detailed census was undertaken, beyond dividing them into size classes: large *(Mastacomys, Conilurus)*, "rats" (*Rattus* etc.) and "mice" (*Pseudomys* etc.). In addition, several specimens of *Hydromys* were found. The *Mastacomys* group had fairly uniform relative abundance, increasing slightly towards the top of the deposit. The *Rattus* group initally had an abundance fluctuating between 5% and 10% but rapidly increased in the upper third of the deposit to nearly 30% at the top, while the "*Pseudomys*" group showed low abundance at first, gradually decreasing upwards. The latter trend is perhaps a preservational bias, as protective alcoves were more common and larger at depth, but this does not explain the reverse trend of the *Rattus* group.

POPULATION ANALYSIS

The gross census figures of the marsupials were processed to give relative abundances of species in each 15 cm interval. These figures involve considerable error, in view of the different areal size of each interval, the uncertainty of correlating even adjacent excavation areas, the certainty of frequent reworking of surface layers by flash floods, sheet wash and mudflows (e.g. Archer, 1974), and other taphonomic factors, such as scavenging and biological disturbance.

Despite all these difficulties, however, opposite trends are seen in some species that must reflect external factors of climatic or environmental change. Notable are the distributions of *Perameles* spp., *Isoodon obesulus* and *Potorous* spp. against *Macropus giganteus, Lasiorhinus* sp., and *Sarcophilus laniarius*, or *Isoodon* against *Lagorchestes leporides*. These data are shown in Fig. 6.

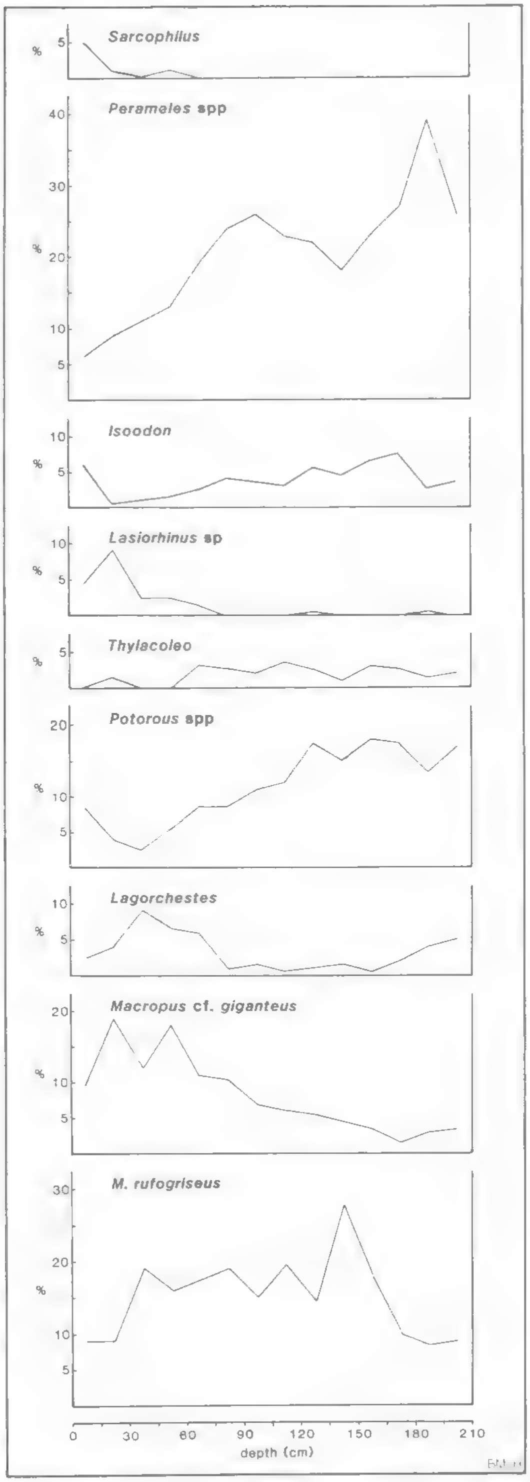

FIG. 6. Relative abundance of selected species, expressed as percentage of total marsupial population of each arbitrary 15 cm layer.

ENVIRONMENTAL ANALYSIS

Wells *et al.* (1984) attempted to relate their deposit on the basis of radiocarbon ages with hydrological and vegetational parameters defined by Bowler *et al.* (1976) and Dodson (1977) respectively. A similar exercise for the Henschke Fossil Cave places the deposit in a wet-drier-wet cycle, with eucalypt forest and dry heath (Fig. 7). More detail is perhaps obtainable by considering the habitat preferences of those species still living. For this purpose, the work of Strahan (1983) has been heavily used. Only species having distinctly non-uniform abundance are considered here (summarised below), as the others apparently were not affected by any climatic/environmental changes.

Dasyurus viverrinus — dry sclerophyll forest, scrub, heathland; forest-grassland mosaic.

Sarcophilus harrissi — sclerophyll forest, coastal scrub.

Vombatus ursinus — forest, woodland, scrub and heathlands, with grass; temperate, humid.

Lasiorhinus spp. — drier open woodlands, scrub and grasslands.

Potorous tridactylus and *P. apicalis* — sclerophyll forest, with thick ground cover, coastal heath, high rainfall.

P. platyops (*P. morgani*) — scrubby woodland, heath (on Kangaroo Island).

Bettongia penicillata — open forest, woodlands, tussock grass understorey.

B. gaimardi — dry sclerophyll forest, grassy understorey, higher rainfall.

B. lesueur — open woodland, grassland, sandy soil, semiarid.

Lagorchestes leporides — open tussock grass plains (Murray Basin).

Macropus rufogriseus — open eucalypt forest with shrubby understorey, tall coastal heath.

M. giganteus — semiarid mallee scrub, forest with open grass, rainfall more than 250 mm.

Hydromys — permanent water.

Conilurus — eucalypt woodland, low hollow branches for nesting.

Mastacomys — alpine to subalpine heathland, open woodland, dense undergrowth in wet sclerophyll forest, sedgelands.

The overall picture is one of scrubby woodland with patches of thick understorey and some open grassy areas becoming larger. Heath may have existed on the lower slopes adjacent to the still existing swamp.

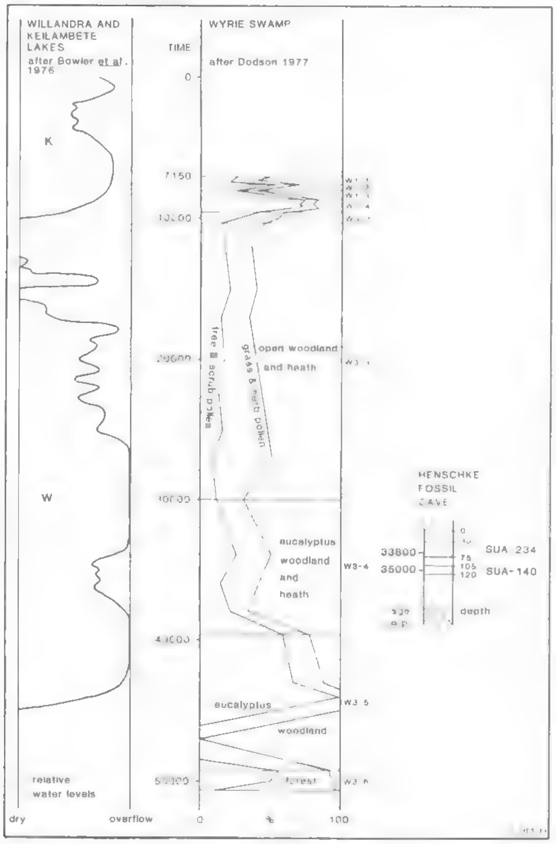

FIG. 7. Henschke Fossil Cave sequence compared with late Quaternary environmental parameters (after Bowler *et al.*, 1976; Dodson, 1977).

DISCUSSION

Comparison of the Henschke fauna (Table 2) with that of the Victoria Cave (Wells *et al.*, 1984) shows a close correspondence in species, with only minor differences, although their relative abundances differ. In contrast, analysis of the Pleistocene mammals in McEachern's Cave (Wakefield, 1967) shows a different, much less diverse faunal composition, with fewer extinct species present. Carbon-dated on bone at 15,200 +/- 320 years B.P. (Gak 509) this fauna may reflect the unfavourable environmental conditions at the end of the Ice Age, despite Wakefield's belief that this was a pluvial period.

Palaeoecological interpretations are fraught with problems arising from the generally undefinable effects of taphonomic processes on the fossils available for study, as well as the ability of some species to survive in less desirable habitats. Wells (1978) has summarised these problems. Notwithstanding these difficulties, it is considered that the opposing trends and changes of relative abundance shown by certain species reflect actual climatic and/or environmental changes during the filling of the Henschke Fossil Cave. On comparing these habitat preferences, it is apparent that the collection has sampled a mosaic of environmental types, as might be expected of a sandy ridge adjacent to a swampy plain. However, a general trend from wetter, denser vegetation to drier, more open vegetation may be discerned.

Although the age and depth of the dated charcoal samples are of limited value, if they are extrapolated, one obtains an approximate date of about 40,000 years B.P. for the start of deposition in this part of the cave complex, and about 32,000 years B.P. when the cave was finally sealed. This span (Fig. 7) compares favourably with the environmental picture indicated by Bowler *et al.* (1976) and Dodson (1977).

It would seem that at the time of accumulation of fossils in the Henschke Fossil Cave, the East Naracoorte Range was well vegetated with sclerophyll forest and patches of thick undergrowth, but the forest gradually thinned and diminished, to provide more open, grassy areas. Relict patches of dense forest may have persisted nearer the permanent swamp, besides heath and sedgelands.

The pitfall form of the original cave entrance, as a probably sand funnel-rimmed pot-hole that expanded into a bell-like chamber, argues for catastrophic accumulation of most animals represented in the deposit. However, an arbitrary sample of *M. rufogriseus* jaws (layer 8, i.e. roughly 105-120 cm depth; 49 jaws) was analysed for age structure by determining the stage of eruption of molars. The results are shown in Fig. 8a. Except for the absence of extreme juveniles, the histogram approaches that typical of an attritional mortality sample (e.g. Voorhies, 1969). It suggests that most bones were washed into the cave, or perhaps that a predator had concentrated on one size class — about 15 kg. The absence of very young individuals may be explained by the great fragility of their bones, so that measurable jaws were not preserved. This distribution curve is in contrast to the catastrophic one obtained by Wells *et al.* (1984) for the same species. The only obvious difference in situation is the size and shape of the natural entrance: much larger for the Victoria Fossil Cave, which therefore took a broader sample of the population.

Other departures from the typical attritional curve may be the result of some catastrophic

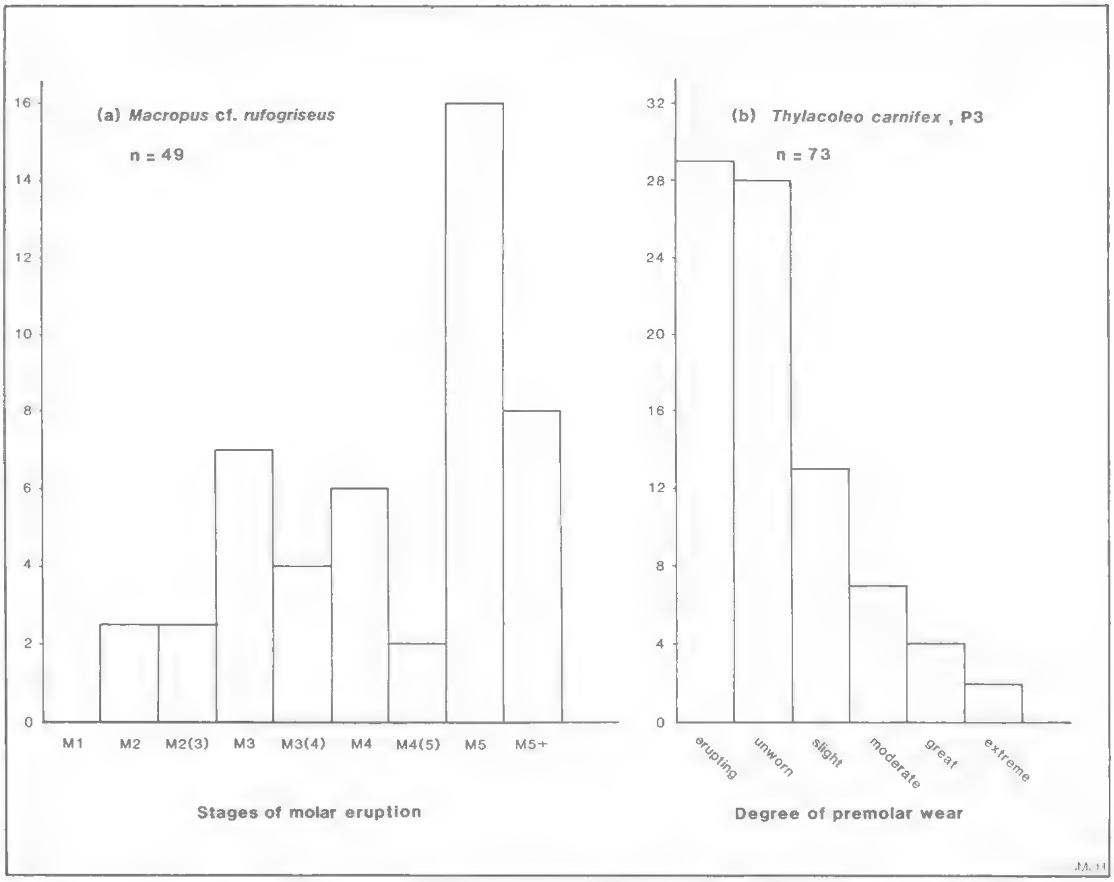

FIG. 8. Age distribution curves of two selected species, based on degree of tooth eruption and/or wear. a) *Macropus* cf. *M. rufogriseus*, layer 8, minimum number n = 49. b) *Thylacoleo carnifex*. Lower premolars P_3, n = 73, not corrected for minimum numbers. Total excavated area.

component. There is clear evidence, in the frequent occurrence of charcoal dust and fragments, for occasional bushfires. In such events, animals tend to flee with less care than normally, and would blunder into the pit-fall trap in greater numbers.

By comparison, analysis of *Thylacoleo* (n = 55 not corrected for minimum numbers) from throughout the deposit, based on the degree of eruption and wear of the lower premolars, shows a typical catastrophic mortality curve (Voorhies, 1969; Fig. 8b). This suggests that either *Thylacoleo* was attracted to the cave by the sound and smell of dying animals, or *Thylacoleo* was able to use the cave as a den. The latter hypothesis is unlikely except for rare occasions, as when a fallen tree or branch in the entrance shaft could act as a ladder for exit from the cave.

In summary, the presence or, particularly, the absence of a species must be weighed against its known body-size, habits and habitat. Small scansorial animals may be rare because of their ability to escape the trap, and because there was little predator input into the deposit. Large animals may be rare because they could avoid the relatively small entrance, or because they preferred a more open environment (e.g. *Diprotodon*). Absence of others (e.g. *Palorchestes azael*) may be because of their general rarity in the fauna. Most species samples are the result of a combination of attritional and catastrophic accumulation. Despite reworking of surface material, changes in species abundances indicate environmental changes during a period of about 30,000 to 40,000 years ago.

ACKNOWLEDGEMENTS

This work could not have been done without the efforts of the indefatigable Fred W. Aslin of Mt Gambier, who brought the site to the attention of the South Australian Museum, organised volunteers and supervised the excavations (particularly in the early years). Detailed surveys of the cave and the surrounding quarry were made by Mr Kevin Mott and Mr Jim Cundy. I am indebted to the numerous volunteers, many of them members of the Cave Exploration Group of South Australia (CEGSA), who often maintained their active interest for years, and to the forebearance of the quarry owner, Mr L.A. Henschke, and his sons, during this period.

LITERATURE CITED

ARCHER, M. 1974. Apparent association of bone and charcoal of different origin and age in cave deposits. *Memoirs of the Queensland Museum* 17: 37–48.

BARTHOLOMAI, A. 1975. The genus *Macropus* Shaw (Marsupialia : Macropodidae) in the Upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* 17: 195–235.

BOWLER, J.M., HOPE, G.G., JENNINGS, J.N., SINGH, G.E. AND WALKER, D. 1976. Late Quaternary climates of Australia and New Guinea. *Quaternary Research* 6: 359–94.

COOK, P.J., COLWELL, J.B., FIRMAN, J.M., LINDSAY, J.M., SCHWEBEL, D.A. AND VON DER BORCH, C.C. 1977. The late Cainozoic sequence of southeast South Australia and Pleistocene sea-level changes. *BMR Journal of Australian Geology and Geophysics* 2: 81–8.

DAILY, B. 1960. *Thylacoleo*, the extinct marsupial lion. *Australian Museum Magazine* 13: 163–6.

DAWSON, L. 1982a. Taxonomic status of fossil devils (*Sarcophilus*, Dasyuridae, Marsupialia) from late Quaternary in eastern Australian localities. p. 517-25. *In* Archer, M. (Ed.), 'Carnivorous Marsuplals' (Royal Zoological Society of New South Wales: Sydney).

1982b. Taxonomic status of fossil thylacines (*Thylacinus*, Thylacinidae, Marsupialia) from late Quaternary deposits in eastern Australia. p. 527-36. *In* Archer, M. (Ed.), 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

DODSON, J.R. 1977. Late Quaternary palaeoecology of Wyrie Swamp, southeastern South Australia. *Quaternary Research* 8: 97–114.

FIRMAN, J.B. 1967. Stratigraphy of Late Cainozoic deposits in South Australia. *Transactions of the Royal Society of South Australia* 91: 165–80.

GILLESPIE, R. AND TEMPLE, R.B. 1979. Sydney University natural radiocarbon measurements V. *Radiocarbon* 21: 95–106.

HOSSFELD, P.S. 1950. The Late Cainozoic history of the South-East of South Australia. *Transactions of the Royal Society of South Australia* 73: 232–79.

IDNURM, M. AND COOK, P.J. 1980. South Australian stranded beach ridges and the Milankovitch theory of ice ages. *Nature* 2867: 699–702.

LUDBROOK, N.H. 1961. Stratigraphy of the Murray Basin in South Australia. *Bulletin of the Geological Survey of South Australia* 36: 1–96.

MARSHALL, L.G. 1974. Late Pleistocene mammals from the "Keilor Cranium site", southern Victoria, Australia. *Memoirs of the National Museum of Victoria* 35: 63–86.

PLEDGE, N.S. 1980. Giant echidnas in South Australia. *South Australian Naturalist* 55: 27–30.

1981. The Giant Rat-Kangaroo *Propleopus oscillans* (De Vis) (Potoroidae : Marsupialia) in South Australia. *Transactions of the Royal Society of South Australia* 105: 41–7.

SMITH, M.J. 1971. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. I. Potoroinae (Macropodidae), Petauridae and Burramyidae (Marsupialia). *Transactions of the Royal Society of South Australia* 95: 185–98.

1972. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. II. Peramelidae, Thylacinidae and Dasyuridae (Marsupialia). *Transactions of the Royal Society of South Australia* 96: 125–37.

1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. IV. Reptiles. *Transactions of the Royal Society of South Australia* 100: 39–51.

SPRIGG, R.C. 1952. The geology of the southeast province, South Australia, with special reference to Quaternary coast-line migrations and modern beach development. *Bulletin of the Geological Survey of South Australia* 29: 1-120.

1959. Stranded sea beaches and associated sand accumulations of the Upper South-East. *Transactions of the Royal Society of South Australia* 82: 183–93.

STIRTON, R.A. 1963. A review of the macropodid genus *Protemnodon*. *University of California Publications in Geological Sciences* 44: 97–162.

AND MARCUS, L. 1966. Generic and specific diagnoses in the gigantic macropodid genus *Procoptodon*. *Records of the Australian Museum* 26: 349–59.

STRAHAN, R. 1983. (Ed.) 'The Australian Museum Complete Book of Australian Mammals'. (Angus & Robertson: London). 530 pp.

TEDFORD, R.H. 1966. A review of the macropodid genus *Sthenurus*. *University of California Publications in Geological Sciences* 57: 1–72.

1967. The fossil Macropodidae from Lake Menindee, New South Wales. *University of California Publications in Geological Sciences* 64: 1–156.

TYLER, M.J. 1977. Pleistocene frogs from caves at Naracoorte, South Australia. *Transactions of the Royal Society of South Australia* 101: 85–9.

VAN TETS, G.F. 1974. A revision of the fossil Megapodidae, including a description of a new species of *Progura* De Vis. *Transactions of the Royal Society of South Australia* 98: 213–24.

AND SMITH, M.J. 1974. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. III.

Birds (Aves). *Transactions of the Royal Society of South Australia* **98**: 225–7.

VOORHIES, M. 1969. Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska. *University of Wyoming Contributions to Geology, Special Papers* **1**: 1–69.

WAKEFIELD, N.A. 1963a. Sub-fossils from Mount Hamilton, Victoria. *Victorian Naturalist* **79**: 323–30.

1963b. Mammal sub-fossils from near Portland, Victoria. *Victorian Naturalist* **80**: 39–45.

1967. Preliminary report on McEachern's Cave, S.W. Victoria. *Victorian Naturalist* **84**: 363–83.

WELLS, R.T. 1978. Fossil mammals in the reconstruction of Quaternary environments with examples from the Australian fauna. p. 1033- 124. *In* Walker, D. & Guppy, J.C. (Eds), 'Biology and Quaternary Environments'. (Australian Academy of Sciences: Canberra).

HORTON, D.R. AND ROGERS, P. 1982. *Thylacoleo carnifex* Owen (Thylacoleonidae, Marsupialia): marsupial carnivore? p. 573–86. *In* Archer, M. (Ed.), 'Carnivorous Marsupials'. (Royal Zoological Society of New South Wales: Sydney).

MORIARTY, K. AND WILLIAMS, D.L.G. 1984. The fossil vertebrate deposits of Victoria Fossil Cave. Naracoorte: an introduction to the geology and fauna. *Australian Zoologist* **21**: 305–33.

WERDELIN, L. 1987. Some observations of *Sarcophilus laniarius* and the evolution of *Sarcophilus*. *Records of the Queen Victoria Museum* **90**: 1–27.

PLEISTOCENE DEPOSITS AND FOSSIL VERTEBRATES FROM THE "DEAD HEART OF AUSTRALIA"

RICHARD H. TEDFORD AND R.T. WELLS

Tedford, R.H. and Wells, R.T. 1990 3 31: Pleistocene Deposits and Fossil Vertebrates from the "Dead Heart of Australia". *Mem. Qd Mus*, 28(1): 263-284. Brisbane. ISSN 0079-8835.

The first vertebrate fossils from central Australia were found in Quaternary deposits in the eastern Lake Eyre Basin, South Australia, at the end of the last century. Substantial collections were made by the J.W. Gregory expedition early this century. Further collecting and geologic observations along with the earlier collections permit reconstruction of this area's history for the latter part of the Pleistocene. Two major periods of sediment accumulation are recognized. The older (Kutjitara Formation) is associated with the penultimate glacial period, and the younger (Katipiri Formation) with the last glacial period. The Kutjitara Formation comprises fluviatile deposits derived locally from distributary stream systems ("prior streams") that drained the hinterlands of pre-Quaternary rocks surrounding the Lake Eyre Basin. Interbedded within this sequence are salt-lake sediments and groundwater deposits of gypsum indicative of dry periods, though there is no evidence of dune development. The Katipiri Formation is also largely of fluviatile nature but represents a more integrated drainage system similar to that existing today. The Katipiri sediments are the "ancestral" rivers of the Cooper and Warburton drainages. These rivers were very sinuous, similar to their present-day descendants, and preserve a record of decreasing discharge. They also drained into the Lake Eyre salina. The aeolian facies of the Katipiri Formation is represented by transverse and longitudinal dunes derived from river sediments and formed in the arid phase associated with the last glacial maximum. The reorganization of the drainage system from Kutjitara to Katipiri times is related to tectonic subsidence.

Fossil vertebrates were recovered from both the Kutjitara and Katipiri Formations. The last appearance of many forms, particularly the large species, is associated with the hyper-arid environments of the last glacial maximum. "Disharmonious" vertebrate faunas of extant taxa are recorded in central Australia as well as around the margins of the continent during the last glacial. The geographic dispersal of their components is indicative of habitat changes affecting the centre of the continent.

☐ *Pleistocene, Marsupialia, Aves, Reptilia, Pisces, Geomorphology.*

R.H. Tedford, American Museum of Natural History, New York; R.T. Wells, Flinders University, South Australia 5000, Australia;

South Australia State Geologist H.Y.L. Brown discovered Pleistocene vertebrates in central Australia in 1892. His collection was obtained on the Warburton River "between Toopawarrina waterhole and Kalamurina station", and included fossil "reptilian teeth; scales, and bones, apparently of crocodiles and turtles; teeth of diprotodon-one upper jaw, having all the teeth (five in number) in a good state of preservation-bones of the diprotodon, the largest of which is a thigh-bone, 15 inches in circumference, and bones and teeth of smaller marsupials, kangaroos etc". These remains were submitted to R. Etheridge, Jr, then Palaeontologist of the Geological Survey of New South Wales, who confirmed (1894) the presence of *Diprotodon* (represented by a left maxillary fragment with P/3M2-5). This, along with the other marsupial and some reptilian remains, was presented to the South Australian Museum in 1899 but not further described. Etheridge (1894), in consultation with C.W. de Vis, Curator of the Queensland Museum, described and figured a thoracic and a lumbar vertebra of the giant varanid lizard *Megalania*, crocodilian scutes and coprolites identified by de Vis as "an alligator", *Pallimnarchus pollens*, turtle shell fragments (Chelidae in Gaffney, 1981, p. 16), and the distal end of a right tarsometatarsus of a pelican — which de Vis described as *Pelicanus validipes* n. sp. (De Vis in Etheridge, 1894, p. 21, pl. 2, fig. 5, 6; later referred to the living *P. conspicillatus* by Rich & Van Tets, 1981). Brown (1892, p. 5) gave three sections showing the stratigraphy at the fossil sites and commented that, although the specimens had been found in the bed of the Warburton River, "they appear to have been washed out of the sand and clay banks by the floods, although . . . none [were observed] *in situ* in these banks".

These reports, and those of Debney (1881a, b) and Tate (1886), concerning fossils from the lower Cooper Creek, stimulated J.W. Gregory, Professor of Geology, Melbourne University, and Director of the Geological Survey Branch of the Mines Department of Victoria, to make a more comprehensive search for vertebrate fossils east of Lake Eyre in South Australia. Gregory (1906, p. 145) explained in a statement that remains a succinct rationale for all the subsequent palaeontological work in the area, that "the objects of the expedition to Lake Eyre were to secure a collection of the fossils of that area, to determine with greater precision the age of the giant marsupials that once lived there, to gain further information as to the geological history of Central Australia; and to see what light geology could throw on the legends and original home of the aborigines". Accordingly, in December 1901 and January 1902, Gregory, his assistant H.J. Grayson, and five Melbourne University students explored the lower reaches of Cooper Creek and the Warburton River, east of Lake Eyre, South Australia, and secured a collection of fossil vertebrates from these water-courses in the same manner as H.Y.L. Brown. This heroic trip, conducted without serious incident in mid-summer heat and near the peak of the devastating turn-of-century drought, was described in Gregory's famous work "The Dead Heart of Australia" (1906), the title contributing to the vernacular of Australia. The collections obtained by Gregory's pioneer party were never fully described beyond de Vis' (1905) account of the smaller birds which became part of the Queensland Museum collection (see Rich & Van Tets, 1982, Table 5 for summary). The remaining fossil vertebrates were deposited in the Hunterian Museum of Glasgow University by Gregory on his return to Scotland in 1905. These collections were studied by W.E. Swinton in the early 1920s (unpublished report, Hunterian Museum). Except for White's (1925) description of the lungfish remains, the Gregory collection received no further notice in the literature.

Fifty years later, R.A. Stirton and R.H. Tedford, then at the University of California, inspired by Gregory's narrative, retraced his journey, collected further fossils and studied the stratigraphy associated with them. Their work (with palaeornithologist Alden Miller), summarized in 1961, gave the first faunal list for the collections obtained on Cooper Creek. Gregory, like Brown, did not find material *in situ* and made no detailed studies of the stratigraphy exposed in the banks of the Cooper and Warburton. Stirton, Tedford and Miller (1961) determined the local stratigraphic sequence and found sufficient material *in situ* to identify the source of the fossils.

TABLE 1. Equivalent Nomenclature for Fossil Localities, Cooper Creek.

Swinton ms	J.W. Gregory 1906	Reuter 1901 ms	Lands Dpt. S. Aust
Hunterian Museum	Text (T), Map (M)	Map	Pastoral Maps
Lower Cooper Locality 1			
Lower Cooper Locality 2			
Lower Cooper Locality 3			
Lower Cooper Locality 4			
Lower Cooper Locality 5	Eli Hartig's Soak (T:85)		
Undusoumpa	Unduwumpa (T:84)	Wunduwompana	
	Unduwumpa (M)		
Lower Cooper Locality 6	Patara Mordu (T:84)	Pataruwordu	
	Pataramordu (M)		
Lower Cooper Locality 7	Kuttipirra (T:84)	Katipiri	Cuttupirra
	Kutupirra (M)		
Emu Camp	Emu Camp (T:80, M)	Malkuni	Malcoona (1897)
	Markoni (T:80, M)		Malgoona (1974)
	Malkuni (T:80)		
Pearam (East of)	Piaranni (T:78)	Pijari	Pirranna Soak
	Piranni (M)		
	Palankarinna (T:78)	Parlangunku	White Crossing

In subsequent years additional study of the youngest deposits in the Lake Eyre Basin has been undertaken while working on the Tertiary rocks, and in 1980 and 1983 a special study by the authors and their colleagues amplified and greatly extended this early work. The purpose of this report is to provide further historical documentation of the Gregory expedition so that their collections can be localized, and thus incorporated in a synthesis of the Stirton data with results of our more recent research.

ABBREVIATIONS: FUAM, field catalogue of Flinders University-American Museum of Natural History collections 1980, 1983 ultimately to be catalogued in the South Australian Museum collection; HM, Hunterian Museum, Glasgow University; LDSA, Lands Department, South Australia; QM, Queensland Museum; SAM, South Australian Museum; UCMP, University of California, Museum of Paleontology. Serial identification of marsupial cheek teeth follows Archer (1978). Ka, indicates dates in thousands of years ago; BP, before present; Coll, collections.

THE GREGORY EXPEDITION, 1901-2

Documentation of the itinerary of the Gregory party comes primarily from the narrative in the "Dead Heart of Australia" (Gregory, 1906, pp. 17-154, apparently reprinted from a series of letters submitted to the "Melbourne Age") and the accompanying map. The map is a generalization based on "pastoral plans of the Surveyor General of South Australia", and was modified along the routes of march, presumably from local observations. Native place-names on this map do not necessarily correspond with those in the text as to orthography; nor do they match phonetically similar forms used in the map accompanying the contemporary study of the Dieri people by J.G. Reuther (published in 1981). The various names for fossil sites are explained in Table 1. Gregory's fossil collections were documented only with place names and site numbers, using a system apparently adopted in the field. These names were used by de Vis (1905), and also by W.E. Swinton in his catalogue of the collection and his "Description of the vertebrate remains collected by Professor J.W. Gregory, D. Sc., FRS in the Lake Eyre district of South Australia", (ms, ca 1924). Despite wide enquiry we have not been able to find Gregory's journal of this expedition.

The narrative and map allow fairly accurate knowledge of the itinerary of the Gregory party, especially the route along Cooper Creek, where camp sites can be located approximately on a modern planimetric base (Figs 1 and 2). Appendix I (by C.W. de Vis) in Gregory (1906) indicates that a system of numbering localities was adopted by the Gregory party for sites in the lower reaches of Cooper Creek. This system is also reflected in Swinton's catalogue; his manuscript reveals some correspondence between numbered sites that were also given names, e.g. Lower Cooper Locality 5 = Eli Hartig's Soak (Gregory 1906, p. 85; "Harty's" in Swinton ms., p. 11); Lower Cooper Locality 6 = Patara Mordu (Gregory 1906, p. 84; Swinton ms., p. 14). These sites occur in reverse numerical order downstream, indicating that the numbering proceeded upstream and that there are four sites further downstream. One of these must be the site mentioned in the text: "our collecting ground next morning was the richest we found during the expedition" (Gregory, 1906, p. 93). This site can be located because of the full description of the previous day's march from Camp 5 (Fig. 2), and from the fact that this site, Lower Cooper Locality 4, produced more specimens (93) than any other locality. The remaining three localities were further downstream; each was a sand bar in the channel, most likely just downstream from prominent outcrops of Quaternary deposits cut by the river in flood. Their approximate locations are shown in Fig. 2. Other Cooper Creek localities can be matched to place names on the maps consulted. The most important site for the Gregory party (and later workers) is near Emu Camp (227 catalogued specimens in the Gregory Coll.), which from the description includes the bars downstream from Malkuni Waterhole. Gregory's party did not camp at Emu Camp (in 1980 still marked by a yard of coolibah logs), but in the coolibahs at the eastern end of the "Markoni" Waterhole.

From Cooper Creek the Gregory party moved directly NNE in the interdune valleys to Kalamurina homestead (then, as now, deserted) on the Warburton (called "Diamantina" by Gregory). Leaving most of the party at Kalamurina to collect in the vicinity of the homestead, Gregory, Grayson, a guide and another assistant travelled up the Warburton to the stony crossing at Ulabarinna (Oolabarrina of LDSA, Pastoral Plan 16S, 1897), one of the sites from which the Brown Coll. had been obtained (Fig. 1). Only 23 specimens were obtained from this site, where Quaternary deposits overlie a silcrete developed on Tertiary rocks. A larger collection (159 specimens) was obtained by the main party in the vicinity of Kalamurina. Specimens were probably obtained beneath

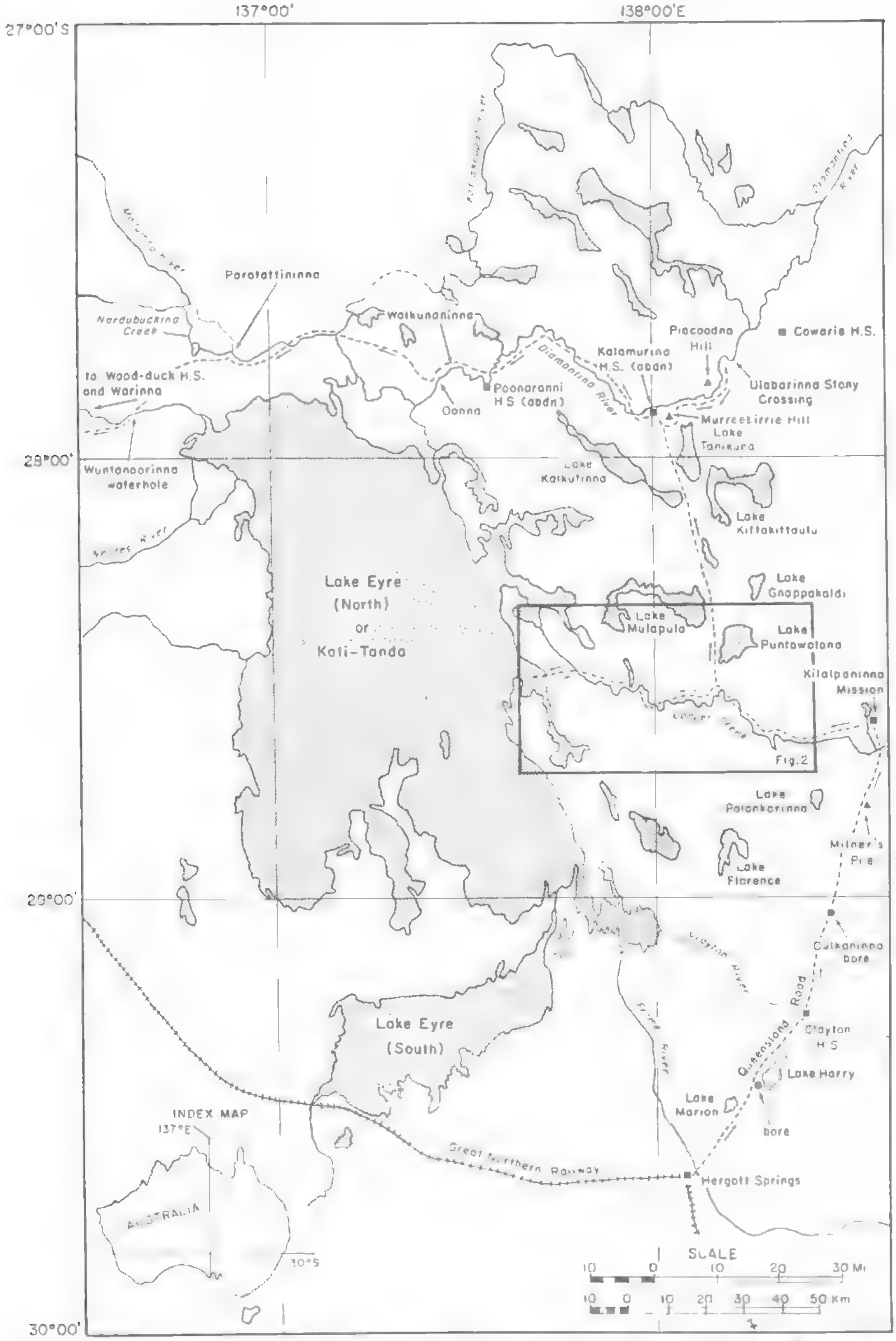

FIG. 1. Index map of part northeastern South Australia showing the position of Figure 2. The 1906 Gregory Expedition (route) and landmarks are given their contemporary orthography.

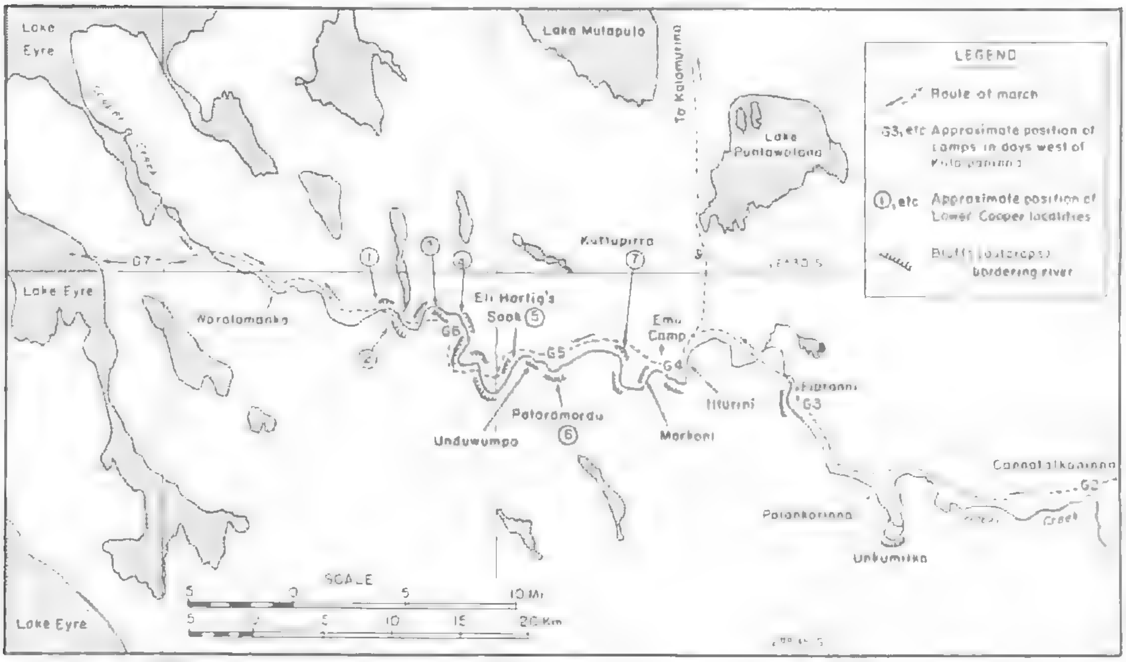

FIG. 2. Map of the lower Cooper Creek showing details of route and camps of the Gregory Expedition (deduced from Gregory 1906), and the approximate position of his localities (see Table 1).

prominent outcrops on the north bank of the river from just north of the homestead downstream nearly to Toolapinna Soak. Part of Brown's Coll. was also obtained near Kalamurina. Two views of outcrops at the western end of this stretch of river are shown by Gregory (1906, photographs opposite pp. 110 and 116) and can be identified as the "Lookout Locality", UCMP locality V5756 (Fig. 4), of the Stirton party. Realizing that only ten days remained to get from Kalamurina to the railway at Warinna, W of Lake Eyre, the Gregory party set off on a direct march. Gregory noted the occurrences of *Diprotodon* bones high in the bluff just N of Poonaranni (1906, p. 125) and at river level nearer Ouana (ibid., p. 126) on the W side of the river below Poonaranni (Poonarunna of the LDSA Pastoral Plan 165, 1897). The HM catalogue records sites as "Poonaranni", "near Poonaranni", "E. of Poonaranni", "SW Poonaranni", a total of 13 specimens collected while the party was camped at this abandoned "horse-station" (Gregory 1906, p. 122).

The Cooper and Warburton sites mentioned above can be located closely, and most have been visited in subsequent work. Present stratigraphic knowledge allows the placement of the fossil remains in geological context. There are two Gregory sites that yielded important collections, particularly bird remains described by de Vis (1905), but the position of which, even relative to the major drainages, is uncertain: "Wurdulumankula" produced 26 (HM), and 15 (QM) bird specimens. There is no similar place-name on Gregory's (1906) map, but the Reuter map (ms. 1901) has a phonetically related "Mudlamarukupa" on the Cooper at the approximate location of Gregory's "Lower Cooper Locality 2", the second most prolific site on the lower Cooper (81 specimens). A second possibility is "Warremandoona" Waterhole (LDSA Pastoral Plan 165, 1879; "Warimardu" of Reuter ms., 1901), a little north of "Ilturini" ("Ilturunna" waterhole of the LDSA Pastoral Plan 165, 1879) where the Gregory party left the Cooper to cross the Tirari Desert to Kalamurina. The second site is "Wankamamina" (with "Wankamurina" as a synonym, Swinton ms., p. 9) which produced 26 (HM) specimens, and two (QM) birds. The related "Waikunaninna" is shown on Gregory's (1906) map downstream from Poonarunna at about the point he referred to on pp. 125-126, but the party was moving rapidly at this time. It seems more likely that a collection of this size would originate from one of the sites between Kalamurina and Ulabarinna where the site "Wadlakanninna" (Gregory, 1906, p. 112) or

"Wadlarkaninna" Waterhole of the 1897 LDSA Pastoral Plan 16S seems phonetically related ("Wadlajerkina" Reuter ms. 1901, map).

SUBSEQUENT INVESTIGATIONS

Stirton (1954) described the initial attempt in 1953 to reinvestigate the Gregory sites; a narrative of the Stirton expeditions E of Lake Eyre to 1963 is given by Tedford (1985). By the early 1960s those workers had retraced nearly the entire Gregory expedition route and obtained new collections from the same localities, some *in situ*, thus establishing provenance. At that time the Pleistocene fluviatile deposits were all grouped as a single stratigraphic unit, the Katipiri Sand; this was typified by cross-stratified, fine white sand that fills channels incised into red mudstones correlated with the Tirari Formation of Pliocene age at Katipiri Waterhole (Reuter ms. 1901, map orthography; Cuttupirra of LDSA Pastoral Plan 16S, 1897 and later maps) on Cooper Creek (Fig. 2). All the channel-filling sands lying above the Tirari Formation and beneath the sandridges that dominate the modern topography were correlated with the Katipiri Sands. These were the deposits that produced most of the Gregory fossils and subsequent collections. Stirton, Tedford and Miller (1961) recognized that their collections included at least two different assemblages. The younger included abundant material from the Katipiri Sands at Malkuni Waterhole (also called "Markoni" by Gregory 1906, p. 80; "Malcoona" on LDSA Pastoral Plan 16S, 1897; and "Malgoona" on the recent Kooperamanna 1:250,000 sheet), the "Emu Camp" site of Gregory, about 1.6 km E of Katipiri. This assemblage, dominated by remains of *Diprotodon* and large kangaroos, was used to typify the Malkuni Fauna of Stirton *et al* (1961). A second, and presumed older fauna, in which *Diprotodon* was a very minor element (although confirmed to be present in later collections), was obtained from correlated Katipiri Sands at Lake Kanunka, 29 km NE of Malkuni Waterhole in the central Tirari Desert. The Kanunka Fauna includes a suite of macropodid genera similar to that of the Malkuni, but the species are different and more closely related to Pliocene taxa elsewhere. Subsequent work at Lake Kanunka has shown that the fossiliferous channel is a part of the Tirari Formation sequence.

Work conducted in 1980 and 1983 focused on the latest Cenozoic deposits. More comprehensive stratigraphic studies were carried out, magnetostratigraphic investigations of the Tirari Formation were conducted, and further searches for fossils proved especially fruitful in the aftermath of the mid-century floods on the Cooper and Warburton. The remainder of this paper details some of the lithostratigraphic and biostratigraphic results of this work and, in combination with previously gathered facts, presents a synthesis of the geological history of the Quaternary deposits of the Tirari Desert E of Lake Eyre in South Australia.

PLEISTOCENE DEPOSITS, TIRARI DESERT

The term Tirari Desert was first used by Gregory (1906, p. 100) for that region between the lower Cooper and Warburton roughly coinciding with Tirari tribal territory. Stirton *et al* (1961) expanded the term to include sandridge country from the Clayton River, SW of Lake Eyre North, to the Kallakoopah at the southern margin of the Simpson Desert. This region is bounded to the W by Lake Eyre North and to the E by the anticlinal uplifts that locally rim the late Cenozoic Lake Eyre Basin. The Cenozoic history of this region was summarized in Wells and Callen (1986), and the late Cenozoic deposits of the Tirari Desert have been discussed by Tedford, Wells and Williams (1986).

The regional depositional framework for the Pleistocene deposits is dramatically revealed by air photos, especially Landsat imagery, obtained during the 1980s flooded intervals in the Lake Eyre Basin (Tedford, Wells & Williams, 1986). Beneath the sandridges are preserved meander-belts of the ancestral Cooper Creek and Warburton River, partly followed by their entrenched present-day descendants (Fig. 3). The ancestral Cooper divided into two distributaries near present-day Unkumilka Waterhole, the southern branch extending southwestward beneath the Tirari dune field turning NW near Madigan Gulf of Lake Eyre North where a long inlet marks its probable course (Fig. 4). The northern branch took a westerly course leaving the present channel near Lake Kutjitara and striking directly toward the opening of the same inlet of the lake into which the southern ancestral branch seems to head. The northern branch, followed by the present river, was deflected to its present course probably as a result of the development of the strandline dunes accompanying the recession of Lake Eyre in late

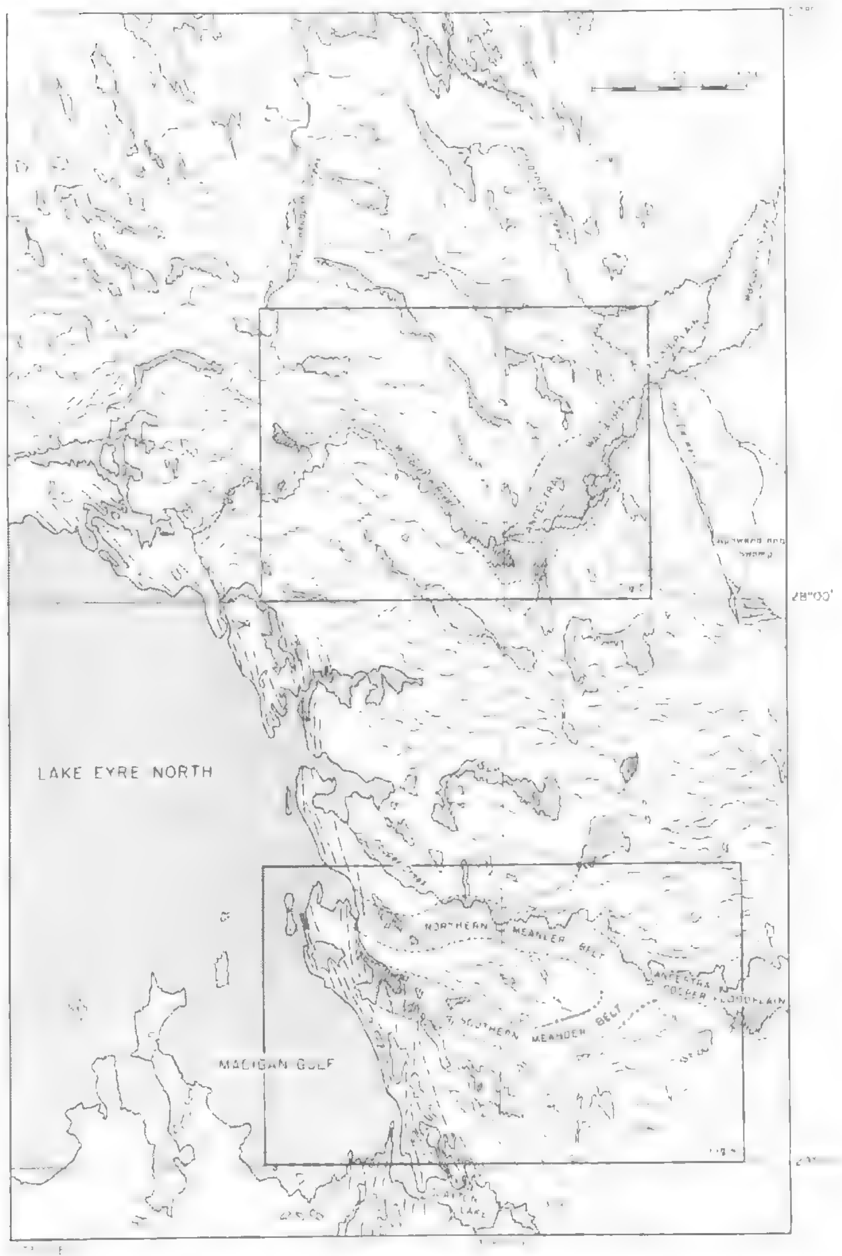

FIG. 3. Geomorphic map of Tirari Desert east and north of Lake Eyre in South Australia (traced from Landsat images 99–79, 80 and 98–80, January 1984, courtesy Bureau of Mineral Resources, Canberra). Position of Figs 4 and 5 shown. Prior streams of the Kutjitara Formation depositional system indicated by low sinuosity distributaries visible on 1984 Landsat images as chains of waterfilled pans. The salina prior-stream relationship in the northern part of the area, postulated by Krieg and Callen (1980), shown by the concordance in orientation of both features. The prior streams emanate from the flanks of pre-Quaternary uplifts just east of the map; and some can be traced to surviving drainage across these uplifts, such as at Apawandinna Swamp where such drainage is impounded on the edge of the last-glacial maximum Tirari dunefield and redirected into the Derwent, skirting the dunefield margin. Outlines of the meander belt of the ancestral Cooper and Warburton rivers are indicated. The narrow northwest limb of the lower Warburton is entrenched in late Tertiary rocks and probably occupies a prior stream valley in this part of its reach. Bold dashes indicate the trends of the gypcreted strandline dunefield of last glacial age along the eastern shore of Lake Eyre North (deduced from Landsat images and airphotos and checked by field observations in the Madigan Gulf region).

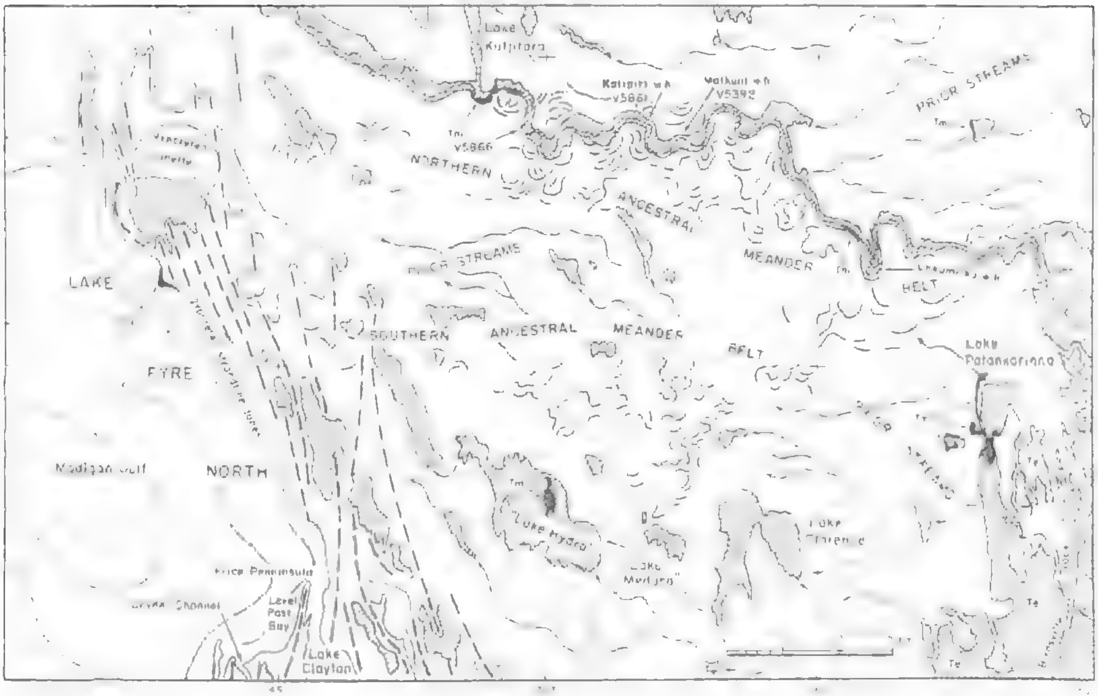

FIG. 4. Map of part of the lower Cooper Creek region (see Fig. 3). Salinas and modern floodplain — left oblique ruling; outcrops of Paleogene Eyre Formation (Te) — right oblique ruling; and medial Miocene Etadunna Formation (Tm) in black. Prior-stream channels visible on Landsat images shown with arrowed lines. Pointbars of two branches of the ancestral Cooper Creek visible on airphotos are also indicated. Trends of gypcreted, last glacial, strandline dunes — bold dashes. Topography of Madigan Gulf floor in meters below sealevel shown. Numbers prefixed by "V" — UCMP localities; "w.h." — waterhole.

Pleistocene time. The shift in course of the southern branch may also be attributed to this recession.

The course of the ancestral Warburton is closely followed by the present river: both trend southwesterly to Kalamurina, where they turn abruptly NW following a trench cut in the Tirari Formation that forms bold outcrops on the western bank. At Keekalanna Soak the river again resumes a southwesterly course ultimately to the northern end of the Lake Eyre (Fig. 5).

These ancestral river tracts cross an earlier drainage field that consists of a low-sinuosity distributary system of westerly to northwesterly trend extending from the margins of the uplifted terrain forming the eastern rim of the Lake Eyre depositional basin (Figs 3, 4, 5). These prior streams and their floodplain represent a broad alluvial apron formed by local drainage, parts of which are preserved as elongate salinas or as chains of claypans which when waterfilled, as during episodes of present day flooding, indicate the courses and extent of this major geomorphic element. The course of these prior streams gives no evidence of drainage having a catchment beyond the uplifted terrain in northeastern South Australia - indicating that the ancestral rivers represent the earliest evidence that Lake Eyre formed the focus of drainage comparable to that of the present-day. The prior streams trend W and NW, presumably focusing on a depocentre in the northern part of Lake Eyre North and NW of the lake in the southernmost Simpson Desert. Limited drilling there (Krieg & Callen, 1980) suggests a thick late Caenozoic section.

Outcrops exposed by entrenchment of the Cooper and Warburton, and those bordering the salinas within the Tirari Desert, illustrate the stratigraphic relationships of the two episodes of sedimentation indicated by geomorphology. The Katipiri Sands (Stirton, Tedford & Miller, 1961) are now recognized as part of the ancestral river deposits; the prior stream deposits are included in the Kutjitara Formation discussed below. The stratigraphic relationship between the deposits, developed from the Cooper Creek outcrops, will be discussed first, followed by consideration of correlative deposits on the Warburton.

Cooper Creek

Favourable outcrops showing the Quaternary fluviatile deposits beneath the Tirari dunefield occur at Katipiri Waterhole and downstream. Particularly instructive are those at Gregory's Lower Cooper Locality 4 where the friable and still active dunes rest on a plinth of older sandplain deposits indurated by a pedocal of calcareous nodules and rhizoconcretions, including carbonate casts of tree trunks (Fig. 6B). Such carbonate soils are widely distributed over the ancestral river deposits and correlative strandline facies near Lake Eyre. Fossil ratite eggshell associated with these deposits produce C14 dates near the limit of the radiocarbon method (Tedford, Wells & Williams, 1986, table 4). The deposits also yield remains of *Diprotodon*, *Macropus* cf. *M. titan*, wombat, and emu and *Genyornis* eggshell. These deposits pre-date the glacial maximum and offer a minimum date for the youngest fluviatile deposits of the ancestral Cooper.

Beneath this calcreted sandsheet, the Katipiri Sands have a gypcrete caprock, not as well-developed near the present Cooper Creek as in adjacent terrain. This is the youngest of three gypsum-cemented caprocks that indurate the tops of the major depositional phases. They are related to saline groundwater levels that remained high in the basin during the waning phases of aggradation.

Entrenchment of the present Cooper Creek through the Katapiri Sands is first seen between Malkuni and Katipiri waterholes. At Malkuni the river floor exposes the basal Katipiri ancestral river deposits and their locally-rich accumulations of

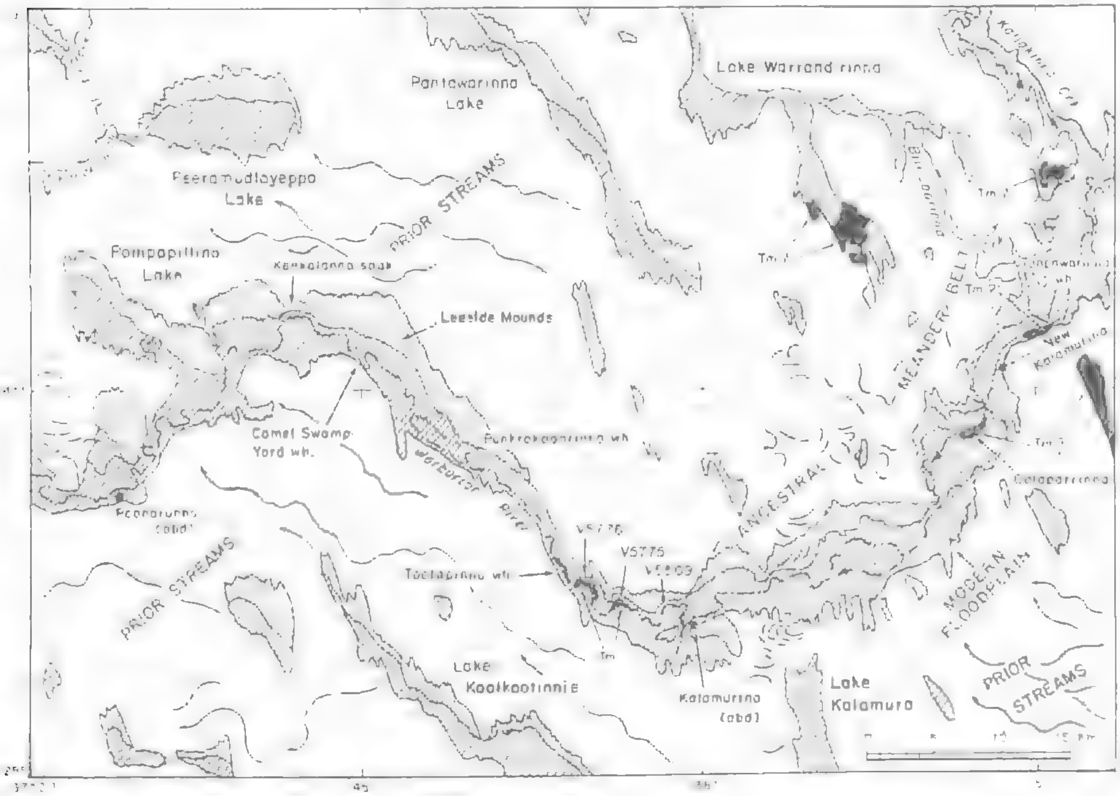

FIG. 5. Map of part of the lower Warburton River region (see Fig. 3). Salinas and modern floodplain — left oblique ruling. Silcreted younger Tertiary rocks questionably assigned to the Etadunna Formation (Tm?) and unsilicified claystones more typical of the Etadunna Formation (Tm) shown in black. Prior-stream courses visible on Landsat images — arrowed lines. Pointbars of an ancestral meander belt of the Warburton River plotted from air photos. Leeside mounds (stippled) playas and salinas taken from airphotos and Landsat imagery. Numbers prefixed by "V" — UCMP sites.

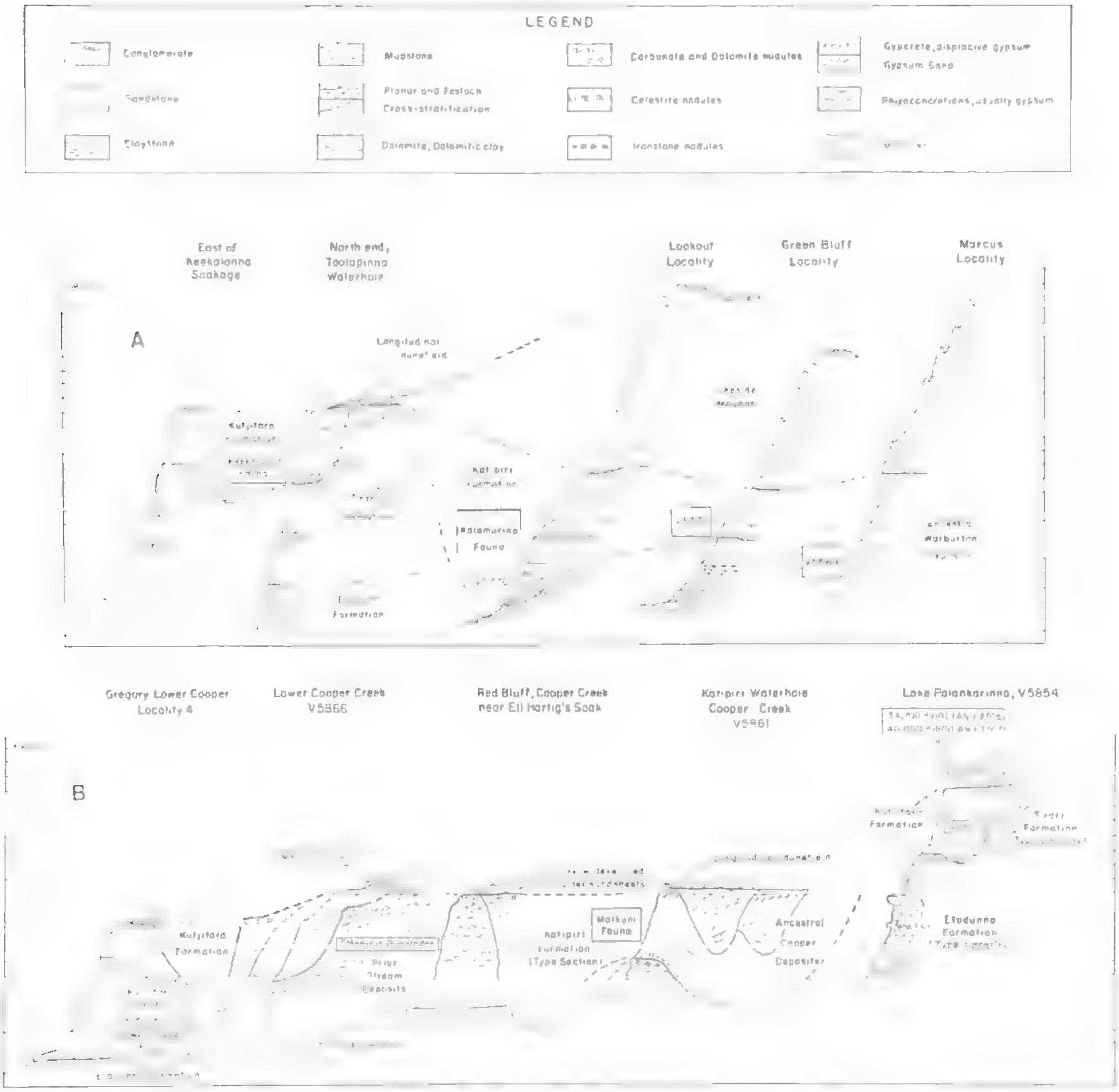

FIG. 6. A, columnar sections showing the relationships between exposed lithostratigraphic units along part of the lower reach of the Warburton River (see Fig. 5). Neogene strata assigned to the Miocene Etadunna and Plio-Pleistocene Tirari Formations form the substrate for the Quaternary Kutjitara prior stream and floodplain and succeeding ancestral river deposits of the Katipiri Formation and capping aeolian sediments. Stratigraphic relationships of the penultimate glacial Keekalanna Fauna and last-glacial Kalamurina Fauna (UCMP sites V5776, V5775, V5569) shown by boxes. B, columnar sections showing the relationships between exposed lithostratigraphic units along part of the lower reach of Cooper Creek and Lake Palankarinna (see Fig. 4). Stratigraphic relationships of the penultimate glacial Lower Cooper Fauna and isolated *in situ Diprotodon* and *Sthenurus* of UCMP V5866 (lower Cooper) and V5854 (Lake Palankarinna) in the Kutjitara Formation and the Malkuni Fauna last-glacial assemblage in the Katipiri Formation are shown. Calcreted sandsheets overlying these fluviatile deposits also yield extinct taxa as indicated and are within the range of C14 dating.

bones amongst the suite of intra- and extraformational clasts that formed the lag at the base of the Katipiri channels. At Katipiri Waterhole the red mudstones of the Tirari Formation are exposed and the deeply-pocketed disconformity surface is packed with rolled selenite, gypsum-cemented rhizonodules, some of large size, flat celestite pebbles and red and green clayballs along with limonite pseudomorphs of wood and fragmentary bones. Rarer pebbles of quartz, quartzite (including silcrete) and limestone from older Tertiary terrain are also present. This suite of clasts was derived from the older terrain on the margin of the Quaternary basin, from the Tirari Formation (mudstone, celestite and selenite) and from the newly-recognized Kutjitara Formation (rhizonodules and some selenite) within the basin. The basal Katipiri Sands are fine to medium-grained with lenses of medium to coarse grains, predominantly cross-stratified, limonite-stained at the base, but finer-grained and white above. A younger suite of channel fills has been incised into the Katipiri Sands. The fills carry a larger suspended-load component. They are well-displayed at Malkuni and Katipiri waterholes and elsewhere on the lower Cooper, where cross-cutting relationships show that green and gray clays form an increasing proportion of the fill in successive channels as the suspended-load gained in importance with time. These younger channels are regarded as an aspect of the Katipiri ancestral river system which shows evolution from higher to lower discharge through time. They can be traced downstream into the delta at the mouth of the ancestral Cooper (Fig. 4) where they make up a larger part of the exposed section and yield the Madigan Gulf Fauna (Tedford, Wells & Williams, 1986), which is taxonomically similar to the Malkuni and indicates the temporal association of the deltaic and fluviatile deposits. Exposures of these younger channel fills at the western end of Malkuni Waterhole contain unionid clams, but no vertebrate fossils. Here we adopt the term Katipiri Formation to include all the facies of this depositional cycle.

From the prominent red bluff near Eli Hartig's soak to Lake Kutjitara (Fig. 6B) the entrenched Cooper intersects a brightly coloured sequence of horizontally-bedded, red and green mudstones and fine sandstones interbedded with shallow channel-fills of fine to medium sand and lenses of red and green clays. Within these fluviatile deposits are thin lacustrine lenses of laminated green clay and fine sand composed of reworked discoidal (displacive) gypsum crystals with charophytes and ostracods. The sandier units in this sequence are packed with gypsum-cemented rhizoconcretions of the type reworked into the basal Katipiri channels. These deposits comprise the Kutjitara Formation, named from the lake which lies adjacent to the Cooper just downstream from the type section (Gregory's lower Cooper localities 3 and 4, Fig. 4). In this part of its reach the modern Cooper trench is incised into the top of the Miocene Etadunna Formation on which the Kutjitara Formation rests, the Tirari Formation having been removed from this area before the Quaternary rocks were laid down (Fig. 6B). At the mouth of the Cooper ancestral river the Katipiri deltaic facies rests directly on the Etadunna Formation, having stripped away the Kutjitara along its lower reach. To the S a saline lacustrine facies has been correlated with the Kutjitara (Tedford, Wells & Williams, 1986), giving evidence of an earlier lake into which subsequent deposits are incised. At the base of the Kutjitara Formation fine sands contain nodules of gypsum-cemented sand and bone fragments but no other clasts. The rare occurrence of bones in the talus of the Kutjitara outcrop suggests that this formation, particularly the basal unit, is the source of the large vertebrate remains. The concentration of bones in the bars at the locality is presumably due to the proximity of their source, a situation similar to that found upstream at the base of the Katipiri Formation outcrop. Thus Gregory's lower Cooper localities yield a fauna derived mainly from the Kutjitara Formation.

Warburton River

An outstanding feature of the N side of the lower Warburton Valley is the dissected remnants of large source-bordering dunes or "Leeside mounds" (Twidale, 1972), intersected by the modern river (Figs. 5 and 6A). These transverse dunes have a pedocal at the top, although more weakly-developed than that on the sandsheets of the Cooper. These dunes rest on gypsites developed at the top of the ancestral river deposits. Internally they show gentle northeasterly dipping, large-scale cross-laminations, each set being several metres in thickness. The dune sands include discoidal gypsum grains and clay pellets. The longitudinal dunes of the Tirari Desert overlie or seem to originate from these sand piles. No C14 dates have been obtained for these deposits, but on the basis of stratigraphy they seem to be contemporaneous with the calcreted sand sheets on the Cooper. The dunes reflect continued high groundwater levels at the close of a major period of aggradation.

At Ulabarinna the floor of the Warburton exposes nodular silcrete (the "stony crossing") developed in Tertiary siltstones. The Katipiri Formation overlies the silcrete, infilling a deeply-pocketed terrain with clasts derived from the Tertiary as well as gypsum-cemented clasts derived from the Quaternary. Locally rich accumulations of fossil vertebrate remains occur in these erosional pockets. They are also redeposited in the older sand bars adjacent to the channel where the river has scoured its floor. Downstream the entrenched modern channel lies within the larger meander belt of the ancestral river, so that the walls of the present river expose only the Katipiri Formation beneath the leeside mounds. There are few fossil vertebrate accumulations until the sector between Kalamurina and Toolapinna, where the Warburton has cut through the Katipiri to expose underlying Miocene clays and dolomites of the Etadunna Formation. Gregory's major Warburton coll. comes from this area, all labelled "Kalamurina". There are several individual sites where fossils can be obtained *in situ*, all of them near the contact with the older rocks.

From Toolapinna Waterhole to Keekalanna Soakage the western bank of the ancestral Warburton is approximated by the long escarpment supported by the Tirari Formation and its massive gypcrete caprock. Its linear nature and the absence of the Tirari Formation upstream suggests that the escarpment represents a fault-line scarp. From place to place along the Tirari escarpment cross-sections of stream channel-fills cut into the top of the Tirari Formation (Fig. 6A). These are regarded as Kutjitara Formation channels because they are truncated by the ancestral river (Katipiri) trench and do not penetrate the base of the Tirari Formation. These channels are filled with cross-bedded, limonite-stained, fine sand with green clay lenses, and they bear a weaker gypcrete caprock, more like that developed on the Katipiri. In the Warburton region the Kutjitara Formation is sparingly fossiliferous, but it does contain some taxa (Keekalanna Fauna, q.v. p. 000) that are important in establishing the nature of its fauna. Downstream from Keekalanna, at Pompapillina Waterhole, the ancestral river cut through the Tirari escarpment and again established a southwesterly course to Poonarunna and finally Lake Eyre. This sector shows brown floodplain mudstones into which are incised deep channels filled with white sand with greenish clay lenses. The whole is capped by gypcrete and overlain by leeside mounds. These poorly fossiliferous rocks are thought to be the Katipiri Formation deposited in a wide palaeovalley or deltaic system. This kind of stratigraphic sequence occurs widely in the lower Warburton and lower Kallakoopah. Gregory's "Poonaranni" collections would have come from these deposits.

PLEISTOCENE VERTEBRATES, TIRARI DESERT

In 1961 Stirton, Tedford and Miller gave annotated faunal lists for the collections made by the University of California parties along Cooper Creek and in the adjacent Tirari Desert. Two suites of stratigraphically associated taxa were labelled "faunas": the Kanunka Fauna from Lake Kanunka, north of the Cooper (since shown to be associated with the Tirari Formation of late Pliocene or possibly earliest Pleistocene age), and the Malkuni Fauna from the type section of the Katipiri Sands and closely associated sites in the ancestral Cooper deposits. In 1963, Stirton figured and described a *Protemnodon* jaw ramus from Malkuni Waterhole; Miller described Malkuni flamingos (1963), pelicans (1966) and anhingas (1966). Rich (1979) reviewed the dromornithids including material from the Katipiri Formation of the Cooper and Warburton. Rich, McEvey and Walkley (1978) recorded a masked owl from Malkuni Waterhole. Rich and Van Tets (1981) reviewed the pelicans, and Rich, Van Tets and McEvey (1982) discussed falcon remains studied by de Vis. Rich *et al* (1987) reviewed the record of flamingos. Hecht (1975) reviewed *Megalania* remains, including Lake Eyre Basin material. New faunal lists from various Cooper and Warburton sites were prepared from the UCMP collections by Williams (1980). The geochronological significance of Australian Caenozoic mammals, including those from the Lake Eyre Basin, was discussed by Woodburne *et al* (1985).

In the following annotated faunal lists we have grouped material into "faunas" from single lithostratigraphic units at one or a few clearly-correlative localities. In this way strati- graphic association, and hence contemporaneity of taxa, are controlled as far as possible.

KUTJITARA FORMATION

Lower Cooper Fauna

Localities — Gregory's Lower Cooper localities 2, 3, and 4; correlative UCMP Cooper Creek 14 (UCMP V5866) and FUAM sites. Most material collected from the bed of Cooper. All material has a distinctive yellowish-grey, dark grey, black or grey-mottled coloration. A ramus of *Sthenurus* cf. *S. andersoni* (UCMP 56472) and diprotodontid bones were collected from Kutjitara outcrop talus or attached to concretions similar to those in the basal sands of that unit.

PISCES

Neoceratodus (*N. eyerensis* and *N. gregoryi*) White (1925) came from the 'Lower Cooper'. Both type specimens are dark grey to black in colour. Teleost fin-rays and skull elements are also present; Swinton (ms.) identified catfish and perch remains among these.

REPTILIA

Chelidae — Turtle shell fragments are present. Swinton (ms.) recorded no fossil turtles in the Gregory collection.

Varanidae — *Megalania prisca* vertebrae are well represented in the Gregory and UCMP collections.

Crocodylidae — Bones and teeth are common at these sites. Swinton (ms.) identified all Gregory material as *Crocodylus porosus*.

AVES

Dromornithidae — Swinton (ms.) identified *Geryornis newtoni* and *Dromornis australis* from limb bone fragments and vertebrae from Lower Cooper localities 4 and 2 respectively. Rich (1979) allocated this material to "Dromornithidae gen. et. sp. indet".

Casuariidae — Swinton (ms.) also noted the presence of emus (referred to *Dromaius patricius* de Vis, 1888, a taxon synonomous with the living *D. novaehollandiae*, *fide* Rich & Van Tets, 1982) at localities 3 and 4. Additional material in the FUAM collection confirms this view; a smaller form (SAM P25218) is also present.

Other birds — de Vis (1905) described eleven taxa of aquatic birds from the "Lower Cooper" without locality number these may belong to any of the sites below "Emu Camp" (Malkuni waterhole) so are not listed here. The UCMP and FUAM collections are under study by P.V. Rich and R. Baird (Monash University). Rich *et al.* (1987) reported the presence of the extinct flamingo *Xenorhynchopsis minor* de Vis, 1905, at UCMP locality V5866. Other flamingo remains were collected by FUAM in 1980 from a nearby site. Baird (pers. comm., 1987) also reports the presence of the flamingo-like Palaeolodidae, previously known only from the Miocene (Rich & Van Tets, 1982, p. 319). Other taxa based on UCMP collections from locality V5866, and listed by Rich and Van Tets (1982, Table 3), include grebes (Podicipedidae), a darter (Anhingidae, *Anhinga novaehollandiae*), a pelican (Pelecanidae, *Pelecanus conspicillatus*), cormorants (Phalacrocoracidae, *Phalacocorax* sp.), herons (Ardeidae) and ducks (Anatidae).

MAMMALIA

The mammalian remains exhibit two types of preservation, either deeply stained in black, yellowish-grey or grey, permineralized and often waterworn, or mottled grey, not permineralized and usually rather complete. The larger remains, mostly extinct forms, comprise the first type, smaller remains, usually extant taxa (including dingo), the second. The following list is based only the first type of material.

Dasyuridae — A jaw fragment with alveoli for M_{4-5} (FUAM coll.) appears to represent a large *Sarcophilus*.

Diprotodontidae —Fragments of upper incisors, two rami and postcranial bones represent *Diprotodon* (Gregory coll.). Additional material (UCMP and FUAM coll.) indicates the presence of this important Pleistocene taxon. Smaller diprotodontids are represented by postcranial remains; a lower molar fragment (SAM P20872) is identified as a smaller diprotodontine, cf. *Nototherium*, and a fragment of an upper central incistor (also SAM P20872) represents a form near *Euryzygoma*.

Macropodidae — Kangaroo remains are the most abundant elements, and the Sthenurinae are particularly well represented. Small potoroine and macropodine remains are usually little permineralized and lightly stained; these taxa are not considered part of the mid-Pleistocene Lower Cooper Fauna.

Protemnodon is represented by jaw and maxillary fragments and the distinctive metatarsals IV-V. Two taxa are present, one similar in size to *P. anak*, and a larger form similar in size to *P. brehus* or *P. roechus*.

Troposodon cf. *T. minor* is indicated by an isolated left M_4 (SAM P25175), while a smaller species, comparable to *T. bowensis*, is indicated by a narrow, elongate right lower incisor whose crown is completely encircled by enamel (SAM P25181).

Sthenurus is well represented by jaw and limb bone fragments (UCMP and FUAM coll.). At least two taxa are present: *S.* cf. *S. andersoni*, a right ramus with M_{1-4} (UCMP 56472) and a larger form, *S.* cf. *S. tindalei*, (UCMP 56473), an edentulous right ramus with roots, unerupted P_3; SAM P25172, fragment of a right ramus with hypolophid of M_3, M_4, and unerupted M_5; HM S69, fragment of a right ramus with M_{1-3}.

Procoptodon is represented by cranial fragments, tooth fragments and edentulous jaw fragments. A right maxillary fragment with unerupted P^3, M^{2-3} (HM S19) and edentulous jaw fragments (SAM P25184 and HM S62) represent a form close to *P. rapha*.

Macropus remains are remarkably few; a few postcranial fragments may represent larger macropodine kangaroos.

KEEKALANNA FAUNA

This name was proposed by Tedford, Wells and Williams (1986) for remains obtained from the correlated Kutjitara Formation outcrops on the lower Warburton River between Toolapinna Waterhole and Keekalanna Soakage. The principal sites for mammalian remains are outcrops at the northern end of Toolapinna Waterhole, near Camel Swamp Yard, downstream from Keekalanna Soakage and at the latter site itself. All material was collected *in situ* or in the outcrop talus (FUAM collection).

REPTILIA

Crocodylidae — A partial skull and mandible of a large crocodilian, probably *Crocodylus porosus*, was collected *in situ* in outcrops south of Camel Swamp Yard.

MAMMALIA

Diprotodontidae — A mandible of *Nototherium* sp. was collected *in situ* west of Camel Swamp Yard. This individual is the size of *N. inerme*, *sensu* Woods, 1968. *Diprotodon* is also present in these deposits. A fragmentary ramus and a calcaneum of *D. optatum* were collected at Toolapinna.

Thylacoleonidae — The distal end of a fibula from Keekalanna appears to represent *Thylacoleo*.

Macropodidae — A fragment of a lower molar of *Troposodon* was obtained at Keelakanna. Fragmentary macropodid remains of indeterminate taxa were collected at Toolapinna.

KATIPIRI FORMATION

MALKUNI FAUNA

Localities — Katipiri and Malkuni waterholes (UCMP localities, V5861, and V5382, the "Emu Camp" and "Malkuni" locality of Gregory, respectively) and the river bed between these waterholes, Cooper Creek (UCMP locality V5860). At these sites sufficient material was obtained *in situ* to identify the collection with the type "Katipiri Sand" unit. The *in situ* material is light in color, often limonite-stained (yellow and red hues) and permineralized. Smaller vertebrate material from the river bed that is mottled-grey and not permineralized is not considered part of the Pleistocene Malkuni Fauna.

PISCES

Lungfish dental plates are present in the UCMP collection, and teleost remains are present in all collections from these sites. Swinton (ms.) recorded percid opercula from Emu Camp.

REPTILIA

Chelidae — Turtle remains occur at these sites.

Varanidae — Vertebrae of *Megalania prisca* are present in the Gregory, UCMP and FUAM collections.

Crocodylidae — Crocodile teeth and scutes are common at these sites. A few vertebrae were also found.

AVES

Dromornithidae and *Casuariidae* — Rich (1979) recorded fragmentary ratite limbs and vertebrae from these sites as "Dromornithidae gen. et sp. indet". *Genyornis* is represented in the FUAM collection. Emus also occur; *Dromaius* sp. was identified by Rich and Van Tets (1982), and further remains were found by the FUAM expedition.

Other birds — Miller's identifications (in Stirton, Tedford & Miller, 1961; UCMP coll.) were revised by Rich and Van Tets (1982). These latter recorded a grebe (*Podiceps* sp.), a pelican (*Pelecanus conspicillatus*, Rich & Van Tets, 1981), two species of cormorant (*Phalacocorax* sp., including the types of *P. gregorii* de Vis, 1905, and *P. vetustus* de Vis, 1905, probably synonymous with living *P. varius* and *P. carbo* respectively, Rich & Van Tets, 1982, table 5), ducks and swans (Anatidae: including *Biziura exhumata* De Vis, 1905, now identified as the living *B. lobata* by Olson, 1977; *Archaeocycnus lacustris* De Vis, 1905; *Chenopsis nanus* De Vis, 1905; and cf. *Cygnus atratus*, Rich & Van Tets, 1982), a heron (Ardeidae), an extinct flamingo (*Xenorhynchopsis tibialis* De Vis, 1905), hawks and eagles (Accipitridae: including the eagle *Uroatus*, Miller in Stirton, Tedford & Miller, 1961), and an owl (*Tyto* cf. *T. novaehollandiae*, Rich, McEvey & Walkley, 1978)

MAMMALIA

Dasyuridae — A right maxillary fragment with M^{3-5} (UCMP 60678) of *Sarcophilus* cf. *S. laniarius*, a large Tasmanian Devil.

Peramelidae — A left ramus fragment of *Macrotis lagotis* with well-worn M_{2-4} and M_5 alveolus (SAM P25134) is stained and permineralized similar to other remains from Katipiri Waterhole and is accepted here as a Pleistocene record of the Rabbit Bandicoot.

Vombatidae — A jaw fragment (FUAM) and teeth (UCMP) of the giant wombat, *Phascolonus gigas*, were obtained.

Diprotodontidae — *Diprotodon optatum* remains are the most conspicuous fossils. Jaw and maxillary fragments, teeth and postcranial remains are abundant. A smaller diprotodontine is indicated by an edentulous maxillary fragment with a relatively small, double-rooted P^3 (UCMP); this may represent *Nototherium* sp. or *Diprotodon minor*. Smaller limb bone fragments could belong to those taxa or *Zygomaturus*.

Potoroidae — A well-preserved left ramus (UCMP 56452) with characteristic preservation represents *Bettongia* cf. *B. lesueuri*.

Macropodidae — A variety of larger macropodids are present, of which *Protemnodon* and sthenurines is more common than *Macropus*. Smaller taxa include *Onychogalea*.

Protemnodon is represented by jaw and maxillary fragments and post-cranial remains. Two size-groups are evident: the more abundant smaller form is identified as *P. anak*, an example of which was figured by Stirton (1963, fig. 8), whereas the larger is *P. brehus* or *P. roechus*.

Various sthenurine kangaroos are found, and several taxa can be identified from teeth. *Sthenurus* cf. *S. atlas* is represented by an edentulous jaw fragment with an unerupted P_3 (UCMP 56470). *S. tindalei* is indicated by a left maxillary fragment with M^{3-4} (SAM 25058) and a right ramus with complete dentition (UCMP 56471) a little smaller than the type and the referred material from Lake Callabonna.

A new, large sthenurine taxon is represented by a left maxillary fragment with P_3 M_{2-5} (SAM P25059). This new genus, to be described elsewhere, combines features of *Sthenurus* and *Procoptodon*.

Simosthenurus is represented by three specimens: a right ramus with M_{2-5} (UCMP 56470), a left maxillary fragment with M^{3-5} (UCMP 60669), and a right maxillary fragment with the metaloph of M^4 and unworn M^5 (UCMP 60674). These specimens indicate a taxon about the size of *S. brownei* or *S. occidentalis*.

Procoptodon cf. *P. rapha* is represented by a right ramus with unerupted P_3, M_{1-2} and unerupted M_{3-4} (SAM P11543), which was part of the small collection (presented to SAM in 1900) made by J. Hillier (Gregory, 1906, pp. 59, 77 and 80) at "Cuttapirra" waterhole, and by an unworn M_3 (UCMP 60670). *Procoptodon* cf. *P. goliah* is indicated by an edentulous left maxillary fragment (UCMP 56454), a broken lower molar (UCMP 60672), and among the larger sthenurine limb bones.

Macropus cf. *M. titan* is present in all collections from the area, but it is not common. Smaller macropodine remains with characteristic staining and permineralization are also present. Stirton, Tedford and Miller (1961) referred parts of two rami to "?*Wallabia*" (UCMP 56443 and 56447). These apparently represent the same taxon as SAM P25069, a fragment of a left ramus with M_{2-3} and unerupted M_4, namely *Macropus (Notamacropus) agilis siva*. From "Emu Camp" there is a fragment of a right ramus with complete cheek-tooth dentition (Gregory coll., HM S46) that corresponds in size and morphology with "*Macropus*" *rama* — previously known only from the eastern Darling Downs. A fragment of a right ramus with P_3, M_{2-5} (SAM P25071) appears to represent the tiny Nail-Tail Wallaby, *Onychogalea lunata*.

We have not been able to relocate the 'part of a right mandible of a medium-sized macropodid, with the protolophid of M/4, M/3 complete and part of the hypolophid of M/2', referred by Stirton, Tedford and Miller (1961, p. 49) to "?subfamily" of macropodids. The description given suggests *Troposodon minor*, a taxon not represented in Malkuni faunal collections.

Phalangeridae — A right ramus with incisor and complete cheek tooth dentition (UCMP 56451) represents *Trichosurus* cf. *T. vulpecula*.

KALAMURINA FAUNA

Localities — Three sites N and W of old Kalamurina Station homestead (corresponds with "Kalamurina" locality of Gregory, 1906): V5569 ("Marcus Locality"), V5775 ("Green Bluff Locality") and V5776 ("Lookout Locality"). Material was collected *in situ* or on the outcrop talus from strata correlated with the Katipiri Formation. Limited screen-washing in 1980 yielded *in situ* small vertebrate remains. Field parties after 1980 made collections upstream, at the silcrete bars at Toopawarinna (vicinity of New Kalamurina Station homestead, UCMP V72058) and Ulabarrinna (UCMP V5776, Cassidy Locality), and from intermediate sites (as had Brown and Gregory). The fauna from these latter sites is derived from correlative strata and seems equivalent to that from the Kalamurina sites.

PISCES

White (1925) referred Kalamurina material to the lungfishes *Neoceratodus eyrensis* and *N. gregoryi*. Catfish spines and percid opercula are among the abundant teleost fish remains from Kalamurina (Swinton, ms.).

REPTILIA

Chelidae — Fragmentary turtle remains are present.

Varanidae — *Megalania prisca* vertebrae are present and a smaller varanid is also indicated.

Pythonidae — Swinton (ms.) reported a vertebra of "*Python* sp." (HM B809), that "agreed very closely with the vertebrae of the modern *P. spilotes*, but is twice the size of those of that species''. This specimen should be compared with the extinct giant python *Wonambi* Smith, 1976.

Crocodylidae — teeth, scutes and postcranial elements are reasonably common. Material includes the partial skull (UCMP 47936) of a large *Crocodylus porosus* (R. Molnar, pers. comm.).

AVES

Dromornithidae and Casuariidae — Rich and Van Tets (1982, table 3) record both unidentified dromornithids and the emu *Dromaius novaehollandiae* from the Kalamurina sites.

Other birds — de Vis (1905) identified a number of smaller bird taxa (all described as new) from ''Kalamurina''. Rich and Van Tets (1982, table 5) allocated these as follows: duck or swan-like forms, Anatidae, *Anas gracilipes* de Vis, 1905 (synonymous with *A. castanea*, fide Olson, 1977), and *Archaeocycnus lacustris* de Vis, 1905; cormorants, *Phalacrocorax gregorii* de Vis, 1905 (probably *P. carbo); P. vetustus* de Vis, 1905, (the assigned material probably *Leucocarbo fuscesens* and *P. carbo)* and possibly a vulture, *Taphaetus lacertosus* de Vis, 1905 (Accipitridae, questionably Gypaetinae). In addition Rich and Van Tets (1982, Table 3) recorded darters (Anhingidae, *Anhinga* sp.), pelicans (Pelecanidae, *Pelecanus conspicillatus),* herons (Ardeidae) and unidentified songbirds.

MARSUPIALIA

Dasyuridae — A nearly complete right ramus of *Sarcophilus* cf. *S. laniarius* (UCMP 46193, Marcus Locality) was mentioned by Stirton (1957, p. 131) from 'the Pliocene at Kalamurina'); measurements were also given (ibid., table, p. 132).

Vombatidae — Remains of *Phascolonus gigas* include cheek teeth and a right ramus with P_3 M_{2-4} (UCMP 56832, Lookout Locality).

Diprotodontidae — *Diprotodon* remains are the most conspicuous fossils along the Warburton. A partial skull, jaw, and limb fragments have been obtained *in situ*. Most represent the large morph *D. optatum*. Fragmentary remains indicate the rarer occurrence of a small *Zygomaturus*, (UCMP 56796, left M_3; UCMP 56834, left I^3). Another small diprotodontine, possibly *Nototherium*, is represented by a maxillary fragment with roots of P^3 and M^2 and a lower incisor from Kalamurina (presented by E.A. King to SAM, 1906).

Thylacoleonidae — E.A. King also presented a left P^3 of *Thylacoleo carnifex* (Kalamurina, SAM P103). An I^3 (Marcus locality, UCMP 56834) and medial phalanx of the manus are also referable to the marsupial lion.

Phascolarctidae — A fragment of a left ramus of a large koala, *Phascolarctos* sp., with P_3 M_{2-4} (FUAM 204) was obtained at the Lookout Locality.

Macropodidae — Most of the mandibular and skull fragments pertain to extinct genera. As on the Cooper, species of *Macropus* are relatively rare at these Warburton sites.

Protemnodon is represented by *P.* cf. *P. anak*, (left maxillary fragment with broken M^{2-3} and complete M^{4-5}; UCMP 56745), and a larger form by limb bone fragments.

Sthenurine kangaroos are represented by *Sthenurus, Simosthenurus* and *Procoptodon. Tropodoson* may also be present if a small, slender and elongate metatarsal IV (SAM P20978) and a correspondingly slender and elongate proximal phalanx of this metatarsal with sthenurine ligament scars, can be referred to this taxon.

Sthenurus andersoni is represented by a left P^3 (UCMP 60867) and a number of rami (FUAM), and *S. tindalei* by jaw fragments (UCMP 56808, 56809) that show most of the lower dentition. A large *Sthenurus*, comparable to the undescribed large species from Lake Callabonna, is indicated by a unworn right M_4 (King coll., SAM).

Simosthenurus is also present and represented by two forms, *S.* cf. *S. orientalis* (left M^{4-5}; UCMP 56901), and *S.* cf. *S. pales* (left ramus fragment with unerupted M_{4-5}; UCMP 56807).

Procoptodon is represented by juvenile jaw fragments of *P. rapha* (UCMP 56831) and *P.* cf. *P. goliah* (UCMP 56810) and two adult rami (SAM P20917 and P20958). Measurements of the cheek teeth of these specimens agree better with the eastern Darling Downs sample of *P. goliah* than with the larger individuals from Lake Menindee.

An euro, *Macropus (Osphranter)* sp., is indicated by upper teeth (UCMP 56835) and by a right maxillary fragment with broken M^2 and complete M^{3-4} (UCMP 60866). *Macropus* cf. *M. titan*, a left M_{4-5} (unerupted), is present (King coll., SAM) and a smaller macropodine of wallaby-size is represented by a jaw fragment with well-worn teeth (UCMP). A fragment of left ramus with M_{2-3} (SAM P20927) appears to represent *Lagorchestes*. Limb bone fragments indicate the presence of large and small macropodines, showing that their diversity is under-represented by dental remains.

EUTHERIA

Muridae — A few rodent jaw fragments and teeth were obtained by screen-washing sand lenses at Lookout Locality. The more useful material includes at least two taxa of conilurine mice, one near *Conilurus* (SAM P20944), the other a smaller form (SAM P20930) of *Pseudomys* or *Notomys* size.

CONCLUSIONS

Geological History — The oldest recognized Quaternary deposits, the Kutjitara Formation, represent a broad alluvial apron which descended from bordering Tertiary uplifts on the eastern side of the Lake Eyre basin towards a depositional centre now buried beneath younger deposits NW of Lake Eyre North. These interior basin deposits were laid down at a time of higher groundwater level than at present, one that supported lacustrine bodies lying SE of, and possibly beneath, the present Lake Eyre salina and extending northward to the depocentre. These waters were saline for lengthy intervals, indicating a negative water balance for the basin, especially for the waning phases of deposition. The postulated aeolian facies corresponding to more arid environments at the close of Kutjitara deposition have not been found, but the upper part of the unit was indurated with groundwater gypsum to form a regional gypcrete surface.

A significant change in basin geometry took place during the hiatus between deposition of the Kutjitara and Katipiri Formations. This was initiated by tectonic subsidence of the southern part of Lake Eyre, the consequent entrenchment and southward shift of drainage, and the integration of the Lake Eyre Basin with the catchments for the Diamantina and Cooper systems in Queensland. Aggradation in this fluviatile system probably began on maintenance of Lake Eyre as a perennial lake. The abundance of freshwater vertebrates in the Katipiri Formation indicates a low salinity environment at least for protracted periods within the trunk streams, if not in the lake itself. The close of Katipiri deposition was marked by waning discharge (shift from bed to suspended loads), a shrinking lake bordered by recessional strandline dunes, and slowing of deposition under an increasingly negative water balance with the formation of a gypsum-indurated horizon at the top of the lowering regional water table. Aeolian deposits overlie this gypcrete. Sandsheets indurated by calcrete occur in the Cooper area and large transverse dunes or leeside mounds adjacent to the valley of the Warburton are also capped by calcrete. These evidences of regional aridity occur at the limit of conventional radiocarbon dating.

Most of the Quaternary depositional record occurs beyond 40 Ka with both lithostratigraphic units recording a shift from positive to negative water budgets in the Lake Eyre Basin, despite differences in depositional geometry. This supports the idea that these units are related to the same extrabasinal control (i.e. climate) and, further, that the climatic cycling is associated with the glacial cycles from evidence in surrounding regions (Bowler, 1976, 1978). Accordingly the Katipiri Formation is regarded as last glacial, the fluviatile sedimentation taking place in the early phases, the aeolian facies forming before 40 Ka, first as transverse dunes associated with lake recession, and in riverine tracts, and, finally, at the peak of aridity, as the longitudinal dune system representing the glacial maximum. The Kutjitara is taken to represent the previous glacial cycle, the penultimate, about 200 Ka, and, despite the absence of an aeolian facies, the saline lake facies are evidence of arid climates. There is a considerable hiatus between the Kutjitara Formation and the underlying terrain, the youngest deposits of which are the Tirari Formation. The Tirari is predominantly reversely magnetized, and represents the Matuyama Chron (period of magnetic pole reversal) whose latest limit is about 700 Ka. The interval between 700 and 200 Ka remains unrepresented by deposits in the Lake Eyre Basin. The initiation of local sedimentation (Kutjitara Formation) in mid-Pleistocene time must be traced to tectonic events, perhaps major subsidence in the northern part of the Lake Eyre Basin. Tectonic control is implicated in the subsequent history of the basin.

Vertebrate History — Any assessment of Pleistocene vertebrate history is the Lake Eyre Basin must take into account any bias in the fossil record, which is drawn almost entirely from fluviatile facies.

Aqatic lower vertebrates and water birds dominate the fauna; terrestrial mammals are relatively rare. In addition, collections from the two lithostratigraphic units are unequal in size: those from the Kutjitara Formation are about half as big as those from the younger Katipiri Formation.

Pleistocene faunas in the Tirari Desert were entombed during vigorous fluviatile and high water-table regimes. These episodes, we believe, are correlative with lacustrine phases of the earlier half of glacial cycles that, at minimum, represent the last two glacials. In Australian terms, these would correspond to paleoclimatic phases IV and VI at Lake George, New South Wales, the longest continuous Pleistocene record presently available in Australia (Singh, Opdyke & Bowler, 1981).

Median ages for these phases are estimated at about 70 Ka and 160 Ka respectively. Following this reasoning the Quaternary depositional record preserved in the Tirari Desert would cover parts of the last third of the Pleistocene.

The rich fauna of aquatic vertebrates includes many forms that presently reside in the Lake Eyre region whenever permanent soakage-fed deep billabongs prevail. Similarly, many of the large raptorial birds still occupy the region. Most of the de Vis' (1905) bird taxa were found to represent living forms when adequate comparative osteological collections were available (Rich & Van Tets, 1982). The ephemeral rivers, saline groundwater and consequent reduction of food supply of the present interglacial, can account for the extinction of lungfish and crocodiles. More enigmatic, given their present adaptation to saline environments, is the loss of the diverse flamingo population that was once a prominent element in the aquatic bird fauna. Rich *et al* (1987) record two extinct genera and the living *Phoenicopterus ruber* in these Pleistocene deposits.

Terrestrial reptiles, the giant goanna and python, were the largest carnivores in evidence in these deposits. These were many times larger than contemporary mammalian carnivores, the Tasmanian Devil and Marsupial Lion, which must be counted among the prey of these reptiles. The record supports the conclusion that the lower vertebrate component of the later Pleistocene biota of the Lake Eyre Basin persisted from the Kutjitara to Katipiri formations. Although much of this fauna persists in the area today, there was notable extinction of some characteristic elements in post-Katipiri time.

Much the same conclusions apply to the larger marsupials except that this fauna was more markedly reduced before post-glacial time. Conspecific or closely related taxa in the following genera are common to both the faunas of the Kutjitara and Katipiri formations: *Sarcophilus, Thylacoleo, Diprotodon, Protemnodon, Sthenurus,* and *Procoptodon.* Given the unequal size of collections from these formations, absences and differences in abundance are difficult to interpret, but *Diprotodon* is not so conspicuous in the Kutjitara faunas. Other diprotodontines (especially *Nototherium)* are more in evidence in the Kutjitara Formation, and the macropodid fauna includes *Troposodon* but not *Simosthenurus.* On the other hand the faunas of the Katipiri Formation have abundant large *Diprotodon optatum* whereas smaller diprotodontids, including *Zygomaturus*, are rare. Giant wombats, *Phascolonus*, are well-represented, and at least two species of *Simosthenurus* are present, as is *Sthenurus atlas*. Further collecting may alter the significance of these differences. For the moment we suspect that the greater diversity of the Katipiri Formation faunas must be partly due to the greater size of collections available. We cannot, on present evidence, detect significant faunal change, at least on the generic level, in the larger marsupials during the later third of the Pleistocene in the Lake Eyre Basin.

Much the same conclusion is reached from examination of the later Pleistocene sequences in two nearby basins SW of Lake Eyre. In the Pleistocene Lake Frome Basin, South Australia, the Millyera, Coomb Spring and Euranilla Formations, in ascending order, record Pleistocene climatic cycles (Callen, 1984) correlative with those from the Lake Eyre Basin. At Lake Callabonna the lacustrine facies of the Millyera Formation contains entrapped large-bodied terrestrial vertebrates (Lake Callabonna Fauna, older references in Williams, 1980). These deposits are correlative with the Kutjitara Formation, and the similar fauna contains *Diprotodon optatum, Protemnodon brehus* or *P. roechus, Sthenurus andersoni*, and *S. tindalei*. In addition, *Phascolonus gigas*, and a new large *Sthenurus* species are shared with the younger Katipiri faunas. The fluviatile Eurinilla Formation overlies the Millyera and Coomb Spring units and has a fragmentary assemblage (Billeroo Creek Fauna) closely comparable in occurrence, stratigraphic position and taxonomic composition with the Katipiri Formation assemblages. Williams (1980) listed in addition to taxa of the older Millyera Formation, *Thylacoleo carnifex, Macropus* cf. *M. ferragus, M. (Osphranter)* sp., the large "*Sthenurus*" sp. nov." and *Procoptodon goliah* in the Billeroo Creek Fauna. Again the evidence indicates little taxonomic change in the large marsupial assemblage over the 700-100 Ka span estimated from local geochronological evidence (Callen, 1984).

At Lake Victoria in the central Murray Basin, southwestern New South Wales, Gill (1973) defined two later Pleistocene lithostratigraphic units lying above the late Pliocene-early Pleistocene Blanchetown Clay and its facies, the Bungunnia Limestone. Subsequent paleomagnetic work (An *et al.*, 1986) has established that the top of the Blanchetown Clay includes the Matuyama-Brunhes boundary, so that the overlying units represent a later part of the Brunhes

Chron. The Rufus Formation fluviatile deposits form the more superficial fill of the Murray paleovalley following incision of the Blanchetown Clay and draining of early Pleistocene Lake Bungunnia. The Rufus Formation contains the Frenchman's Creek Fauna of Marshall (1973) which includes the same large marsupial taxa as obtained from the Kutjitara and Katipiri formations in the Lake Eyre Basin, namely *Sarcophilus*, *Phascolonus*, *Procoptodon goliah* and *Macropus titan*, along with smaller taxa still extant (*Lasiorhinus*, *Bettongia*, *Onychogalea*) and *M. agilis siva*. The lunette of Lake Victoria overlies the Rufus Formation and these aeolian deposits, termed the Lake Victoria Sands by Gill (1973), were divided into two members: the Nulla Nulla Sands of late Pleistocene age (greater than 15 Ka) and the overlying Talgarry sand of Holocene age. These deposits produced the "Lake Victoria Local Fauna" of Marshall (1973), a composite assemblage of Late Pleistocene and Holocene age, considered together because of difficulties of determining provenance. The large marsupial fauna is very diverse and includes the following taxa in common with the Lake Eyre and Lake Frome basins: *Sarcophilus laniarius*, *Thylacoleo carnifex*, *Phascolonus gigas*, *Sthenurus andersoni*, *S. atlas*, *S. tindalei*, *Procoptodon goliah*, *Protemnodon anak*, *P. brehus*, *Macropus titan*, and *Diprotodon optatum*. The Frenchman's Creek Fauna is reconstructed from a smaller collection than the Lake Victoria Fauna, but as we have demonstrated in the more interior basins, there is a significant similarity of the large mammal faunas. The evidence from the Murray Basin does not permit closer estimate of the age range of these assemblages than from less than 700 Ka to greater than 15 Ka, which includes the span interpreted for the Pleistocene sequences in the Lake Eyre and Lake Frome basins.

Elsewhere in Australia faunas now thought to be later Pleistocene, but older than 100 Ka, e.g. the Victoria Cave assemblage, southeastern South Australia (Wells, Moriarty & Williams, 1984) and the Wellington Caves assemblage, New South Wales (Dawson, 1985), although much more diverse taxonomically than the fluviatile sites discussed here, contain the same genera. Major faunal changes in later Pleistocene time seem to be associated with the latest part of the last glacial, probably coincident with the glacial maximum (see Horton, 1984, for summary).

Only the recently-discovered Nelson Bay Local Fauna of coastal southwestern Victoria has been accurately dated as early Pleistocene. The local magnetostratigraphy for the site, coupled with constraints from foraminiferal biochronology and radioisotopic dating of the underlying basalts, indicate a span of 1700-700 Ka within the late Matuyama Chron for the Nelson Bay Local Fauna (MacFadden *et al.*, 1987). This local fauna contains *Diprotodon* sp., *Zygomaturus trilobus*, *Palorchestes parvus* and *Protemnodon* sp. shared with later Pleistocene assemblages. Unique taxa, such as the macropodid *Baringa* and a giant pseudocheirine, suggest that Early Pleistocene faunas, when they are better known, may show important differences at the generic and specific level from those of the later Pleistocene.

Important summaries of Quaternary large marsupial distribution have been compiled by Hope (1982) and Horton (1984) whilst examining the question of late Pleistocene extinction. The new data presented here indicate that during later Pleistocene glacial phases most larger marsupial genera had species ranging into central Australia. An analysis of genera shows little taxonomic difference between the centre and contemporary faunas of the southeastern periphery, at least during parts of late Quaternary time. Habitat diversity during these times was such that "disharmonious" (*sensu* Lundelius, 1983) associations of still-living taxa occur in these last glacial deposits in central Australia comparable to those of the periphery. In the Malkuni and equivalent Kalamurina faunas, representatives of the living *Phascolarctos* sp., and *Macropus agilis*, now restricted to eastern and northern woodlands and savannas of Australia (Fig. 7) coexisted with the southwestern arid land Nail-Tail Wallaby (*Onychogalea lunata*) and the Tasmanian Devil. Other arid-adapted species, such as *Bettongia lesueur*, *Macrotis lagotis* and *Trichosurus vulpecula*, present in these faunas still inhabited the Lake Eyre Basin at the time of European occupation. The implications from such associations for the interpretation of the environment during the early phases of the last glacial cycle are summarized by Lundelius (1983). His study of fossil vertebrates from similar-age Pleistocene sites scattered around the periphery of the continent revealed many "disharmonious" pairs of taxa, implying a more equable climate than at present. The extension of the data into the Lake Eyre Basin in the present arid core of the continent suggests that much lower climatic gradients existed across Australia during those times than during glacial maxima or interglacials. Penultimate glacial events recorded in the Kutjitara Formation similarly include a shift from freshwater lacustrine

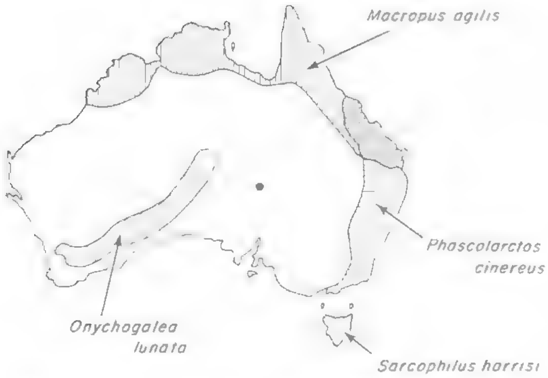

FIG. 7. Geographic ranges of four living species that occur sympatrically in the last-glacial Malkuni Fauna of central Australia (black dot) illustrating the concept of "disharmonious" glacial faunas of Lundelius (1983).

to saline and thus arid conditions, but without evidence of extensive dune building. The Lower Cooper and equivalent Keekalana faunas are like their later counterparts, and thus indicate survival of much of the large vertebrate faunas through the postulated shift from broadly equable to zonal climate in passage from glacial to interglacial times. Unfortunately the older collections are not large enough to detect disharmonious taxa, but the persistence of the large mammals suggests no radical depletion of niches at the close of the penultimate glacial. This is in contrast to the striking evidence Lundelius (1983) presented for ecological reorganization toward the end of the last glacial. Either there was a quantitative difference in environmental impact of the last two glacial cycles (as suggested by the absence of penultimate glacial dune fields) or other factors, including human predation, are involved in terminal Pleistocene extinction.

ACKNOWLEDGEMENTS

We wish to acknowledge our indebtedness to our field companions of the 1980 expedition: Drs John Bye and David Catcheside, Flinders University, Mr Paul Lawson, Adelaide and the late Dr Dominic Williams (a tribute to whom appears in Wells and Callen, 1986) and the 1983 expedition: Mr Ed Bailey and Ms Sandi Tartowski, Flinders University, Dr Steven Barghoorn, American Museum of Natural History, Mr Paul Lawson, Adelaide. The success of our field work is due in great measure to their hard work and companionship. In 1980 Dr Roly Byron-Scott, Flinders University, piloted a light aircraft on our first aerial reconnaissance and in 1983 Mr Peter Dunn provided further aerial reconnaissance and support for ground visits to remote sites on the lower Kallakoopah. The Dunn family of New Kalamurina Station, Jim and Joan Dunn (1980) and their children, Peter and Jenny Dunn (1983), offered traditional bush hospitality and aided us in many ways. Brian and Cath Oldfield (Etadunna) and Kevin Oldfield (Clayton) also made us welcome in work on their stations.

LITERATURE CITED

AN, Z-S., BOWLER, J.M., OPDYKE, N.D., MACUMBER, P.G., AND FIRMAN, J.R. 1986. Paleomagnetic stratigraphy of Lake Bungunnia: Plio-Pleistocene precursor of aridity in the Murrary Basin, Southeastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **54**: 219–39.

ARCHER, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of the Queensland Museum* **18**: 157–64.

BOWLER, J.M. 1976. Aridity in Australia: age, origins and expression in aeolian landforms and sediments. *Earth-Science Reviews* **12**: 279–310.

1978. Glacial age aeolian events at high and low latitudes: a southern Hemisphere perspective. p. 149–71 *In*, E.M. Van Zinderen Bakker (Ed.), 'Antarctic glacial history and world palaeoenvironments'. (A.A. Balkema: Rotterdam).

BROWN, H.Y.L. 1892. Government geologists report on country in the neighbourhood of Lake Eyre. *South Australian Geological Survey*, 1892, 5pp.

CALLEN, R.A. 1984. Quaternary climatic cycles, Lake Millyera region, Southern Strzelecki Desert. *Transactions of the Royal Society of South Australia* **108**: 163–73.

DAWSON, L. 1985. Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney. *Records of the Australian Museum* **37**: 55–69.

DEBNEY, G.L. 1881a. Notes on the physical and geological features about Lake Eyre. *Transactions of the Royal Society of South Australia* **4**: 145–6.

1881b. Sections of strata traversed in boring for water in the country between Cooper Creek and Warburton River. *Transactions of the Royal Society of South Australia* **4**: 147–8.

DE VIS, C.W. 1905. A contribution to the knowledge of the extinct arid fauna of Australia. *Annals of the Queensland Museum* **6**: 3–25.

ETHERIDGE, R., JR. 1894. Official contributions to the palaeontology of South Australia. No. 6-Vertebrate remains from the Warburton or Diamantina River. *Annual Report of the Government Geologist, South Australia* 1894, p. 19–22.

FLANNERY, T.F. AND HANN, L. 1984. A new macropodine genus and species (*Marsupialia: Macropodidae*) from the early Pleistocene of Southwestern Victoria. *Australian Mammalogy* 7: 193–204.

GAFFNEY, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates* 2720: 1–38.

GILL, E.D. 1973. Geology and geomorphology of the Murray River region between Mildura and Renmark, Australia. *Memoirs of the National Museum of Victoria* 34: 1–97.

GREGORY, J.W. 1906. 'The dead heart of Australia'. (John Murray: London).

HECHT, M.K. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proceedings of the Royal Society of Victoria* 87: 239–52.

HOPE, J. 1982. Late Cainozoic vertebrate faunas and the development of aridity in Australia. p. 85-100 *In* Barker, W.R. and Greenslade, P.J.M. (Eds). *'Evolution of the Flora and Fauna of Arid Australia'*. (Peacock Publications, Frewville, South Australia).

HORTON, D.R. 1984. Red Kangaroos: last of the Australian megafauna. p. 639-80 *In* Martin, P.S. and Klein, R.G. (Eds), *'Quaternary Extinctions'*. (University of Arizona Press: Tucson).

KRIEG, G.W. AND CALLEN, R.A. 1980. Geological observations in the playa region of the Simpson Desert, South Australia. *Department of Mines and Energy, South Australia, Geological Survey Report*, 80/68, 24p.

LUNDELIUS, E.L., JR. 1983. Climatic implications of late Pleistocene and Holocene faunal associations in Australia. *Alcheringa* 7: 125–49.

MACFADDEN, B.J., WHITELAW, M.J., MCFADDEN, P. AND RICH, T.H.V. 1987. Magnetic polarity stratigraphy of the Pleistocene section at Portland (Victoria), Australia. *Quaternary Research* 28(3): 364–73.

MARSHALL, L.G. 1973. Fossil vertebrate faunas from the Lake Victoria region, S.W. New South Wales, Australia. *Memoirs of the National Museum of Victoria* 34: 151–72.

MILLER, A.H. 1963. The fossil flamingos of Australia. Condor 65: 289–99.

1966a. The fossil pelicans of Australia. *Memoirs of the Queensland Museum* 14: 181–90.

1966b. An evaluation of the fossil anhingas of Australia. *Condor* 68: 315–20.

OLSON, S.L. 1977. The identity of the fossil ducks described from Australia by C.W. de Vis. *Emu* 77: 127–31.

REUTHER, J.G. 1981. The Dieri (translated from Reuther ms 1901 by P.A. Scherer) *Australian Institute of Aboriginal Studies, Canberra*, Microfiche No. 2.

RICH, P.V. 1979. The Dromornithidae. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 184: 1–196.

MCEVERY, A.R. AND WALKLEY, R. 1978. A probable masked owl, *Tyto novaehollandiae*, from Pleistocene deposits of Cooper Creek, South Australia. Emu 78: 88–90.

AND VAN TETS, G.F. 1981. The fossil pelicans of Australia. *Records of the South Australian Museum* 18: 235–64.

AND VAN TETS, G.F. 1982. Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. p. 236–84 *In* Rich, P.V. and Thompson, E.M. (Eds), *'The Fossil Vertebrate Record of Australasia'*. (Monash University Offset Printing Unit: Clayton, Victoria).

VAN TETS, G.F. AND MCEVERY, A.K. 1982. Pleistocene records of *Falco berigora* from Australia and the identity of *Asturaetus furcillatus* De Vis (Aves: Falconidae). *Memoirs of the Queensland Museum* 20: 687–93.

VAN TETS, G.F., RICH, T.H.V. AND MCEVERY, A.R. 1987. The Pliocene and Quaternary flamingos of Australia. *Memoirs of the Queensland Museum* 25(1): 207–25.

SING, G., OPDYKE, N.D. AND BOWLER, J.M. 1981. Late Cainozoic stratigraphic, paleomagnetic chronology and vegetational history from Lake George, N.S.W. *Journal of the Geological Society of Australia* 28: 435–52.

STIRTON, R.A. 1954. Digging Down Under. *Pacific Discovery* 7: 2–13.

1957. Tertiary marsupials from Victoria, Australia. *Memoirs of the National Museum of Victoria* 2: 121–34.

1963. A review of the macropodid genus *Protemnodon*. *University of California, Publications in Geological Sciences* 44: 97–162.

TEDFORD, R.H. AND MILLER, A.H. 1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Records of the South Australian Museum* 14: 19–61.

SWINTON, W.E., ms (c. 1924). Description of the vertebrate remains collected by Professor J.W. Gregory, D. Sc., PRS, in the Lake Eyre district of South Australia. Hunterian Museum, University of Glasgow, 33p.

TATE, R. 1886. Post-Miocene climates in South Australia. *Transactions, Proceedings and Reports of the Royal Society of South Australia* 8(for 1884-5): 49–59.

TEDFORD, R.H. 1985. The Stirton years 1953-1966, a search for Tertiary mammals in Australia. p. 38-57 *In* Rich, P.V. and Van Tets, G.F. (Eds), 'Kadimakara, extinct vertebrates of Australia'. (Pioneer Design Studio: Lilydale, Victoria).

WELLS, R.T. AND WILLIAMS, D.L.G. 1986. Late Cainozoic sediments and fossil vertebrates. p. 42-72 *In* Wells, R.T. and Callen, R.A. (Eds), 'The Lake Eyre Basin-Cainozoic sediments, fossil vertebrates and plants, landforms, silcretes and climatic implications'. *Australasian Sedimentologists Group Field Guide Series, No. 4*. (Geological Society of Australia: Sydney).

TWIDALE, C.R. 1972. Evolution of sand dunes in the Simpson Desert, central Australia. *Institute of British Geographers, Transactions*, 56: 77–109.

WELLS, R.T. AND CALLEN, R.A. (Eds). 1986. 'The Lake Eyre Basin-Cainozoic sediments, fossil vertebrates and plants, landforms, silcretes and climatic implications'. *Australasian Sedimentologists Group Field Guide Series No. 4*. (Geological Society of Australia: Sydney) 176 pp.

MORIARITY, K. AND WILLIAMS, D.L.G. 1984. The fossil vertebrate deposit of Victoria Fossil Cave Naracoorte: an introduction to the geology and fauna. *Australian Zoologist* **21**: 30-33.

WHITE, E.I. 1925. Two new fossil species of *Epiceratodus* from South Australia. *Annals and Magazine of Natural History* **16**: 139-46.

WILLIAMS, D.L.G. 1980. Catalogue of Pleistocene vertebrate fossils and sites in South Australia. *Transactions of the Royal Society of South Australia* **104**: 101-15.

WOODBURNE, M.O., TEDFORD, R.H., ARCHER, M., TURNBULL, W.D., PLANE, M.D. AND LUNDELIUS, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publications, South Australian Department of Mines and Energy* **5**: 347-63.

THE WYANDOTTE LOCAL FAUNA: A NEW, DATED, PLEISTOCENE VERTEBRATE FAUNA FROM NORTHERN QUEENSLAND

G.C. McNamara

McNamara, G.C. 1990 3 31: The Wyandotte local fauna: a new, dated, Pleistocene vertebrate fauna from northern Queensland. *Mem. Qd Mus.* **28**(1): 285–297. Brisbane. ISSN 0079–8835.

A new Pleistocene, fluvio-lacustrine vertebrate-bearing deposit for northeastern Queensland, the Wyandotte Formation, is reported. Two fossiliferous units occur within the formation. Unit A is basal and consists of lacustrine clays and minor gravels. Its base is beyond the range of conventional ^{14}C(>45,000ybp) dating. On geomorphological grounds the base of the unit cannot be older than a nearby basalt dated at 410,000 ybp and its age is considered to be less than 200,000 ybp. Unit B is a sequence of fluvial gravels and sands with a basal ^{14}C date of 30,400 ybp. A relatively rich and diverse terrestrial vertebrate fauna is represented by disarticulated and fragmentary bones and teeth. The Wyandotte local fauna is typically Pleistocene in composition but is notable for the occurrence of *Megalania prisca* and *Meiolania* cf. *M. platyceps*, which occur in dated context, and *Wonambi* cf. *W. naracoortensis*.

☐ *Pleistocene, Queensland, Wyandotte Formation, vertebrates, Megalania, Wonambi, Meiolania, teleost, crocodile, birds, marsupials, mammals.*

G.C. McNamara, Geology Department, James Cook University of North Queensland, Townsville, Queensland 4811, Australia; 30 November, 1988.

Fossil bones were collected and brought to the attention of the author in 1983 by Messrs Gary Ferguson and Glenn Smith, then of Noranda Australia Ltd. A preliminary investigation revealed a moderately abundant and diverse fauna of Pleistocene aspect deposited in close proximity to a dated basalt. Further investigation was warranted because of the rarity of datable vertebrate deposits of any age in northern Queensland.

THE WYANDOTTE FORMATION

The Wyandotte Formation is a fossil-bearing sequence that outcrops in ribbon-like aspect along the banks of Wyandotte Creek, a tributary of the Dry River, N Queensland. Eleven sites yielding fossils have been located within the mapped area (Fig. 1). Isolated fossils have been found *in situ* in many other localities.

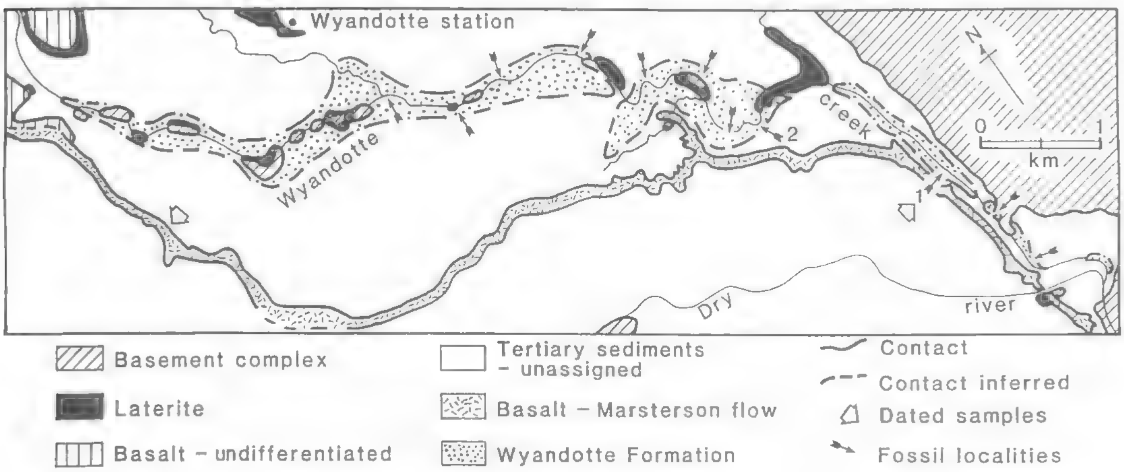

FIG. 1. Mapped extent of the Wyandotte Formation and position of the known fossil localities. Localities labelled 1 and 2 produced the bulk of the fauna. K/Ar dating was performed on a basalt sample taken in the west of the mapped area.

FIG. 2. Idealized cross-section through site 1 normal to the line of the basalt flow and modern creek trends as indicated by the site 1 "fossil locality" arrow in Fig. 1.

GEOCHRONOLOGY AND STRATIGRAPHY

The Wyandotte Formation overlies Precambrian and Palaeozoic basement, weathered and lateritized basement, lateritized early Tertiary sediments and unlateritized, unassigned, Tertiary sediments. Lateritization of basement and early Tertiary sediments occurred during the Oligocene to early Miocene (Grimes, 1980), and this provides a maximum date for any overlying fossiliferous sediments in the region. The age of the unassigned Tertiary sediments is unknown, but within the study area they are indurated and show features reminiscent of the late Pliocene Campaspe Beds further to the south (Nind, 1988; Wyatt & Webb, 1970). A basalt flow (informally named the Marsterson flow) from the McBride Basalt Province, dated at 410,000 ybp (Griffin & McDougall, 1976), fills a palaeodrainage incision in these indurated sediments (Fig. 1). Fossils have not been recorded from these undated sediments.

There is no outcrop relationship between the dated basalt flow and the Wyandotte Formation. To the north of the flow, unassigned Tertiary sediments form a contemporary surface which is nearly level with the weathered surface of the flow. To the south, on the Wyandotte Creek side of the flow, a bluff of blocky basalt up to several metres high, drops away to a contemporary surface of black soil. The Wyandotte Formation overlies the unassigned Tertiary sediments and thins towards the basalt. Auger drill holes taken close to the basalt indicate only unassigned Tertiary sediments under the black soil, confirming that the Wyandotte Formation does not underlie the basalt (Fig. 2). This is consistent with the basalt flow occupying a higher topographic position than the younger Wyandotte Formation sediments, topographic inversion of this kind being common in basalt terrains (Coventry *et al.*, 1985).

The probable explanation of the observed differences north and south of the basalt flow is that after the infill of the palaeodrainage by the basalt, the drainage switched to the south side of the flow and cut a new channel in unassigned Tertiary sediment. A new valley formed, and fossil-bearing Wyandotte Formation sediments and black soil cover accumulated. A new erosive phase is now reworking these fossiliferous sediments.

The Wyandotte Formation consists of two lithofacies associations, Units A and B. Unit A is basal and is comprised of two distinct lithofacies: a granule gravel with clay matrix, and a blue-grey, carbon-flecked clay. The granule gravel forms a definite basal horizon, together with lenses and stringers higher in the section, but the blue-grey clay dominates the unit. Minor diatomaceous clays occur elsewhere as part of Unit A. Unit B also consists of two lithofacies: a gravel with clean sand matrix, and a medium to fine-grained, cross-laminated sand. Together they form an upwards-fining sequence typical of lateral accretion fluvial facies. Minor laminated mud lenses and drape horizons occur within the unit.

The base of the Wyandotte Formation is beyond conventional ^{14}C range (>45,000 ybp — University of Waikato Radiocarbon Dating Laboratory results; test carried out on carbonized wood taken *in situ* from site 1). The rate of downcutting to form the valley is not known, but since 410,000 ybp a substantial valley has been cut. Between 4 to 10 metres of Unit A were deposited prior to Unit B, which has a basal date of 30,400 ybp (+750/-700 yrs — UWRDL results; test carried out on bivalve shells taken *in situ* from site 1). It is reasonable to suppose that the erosive phase might easily have taken half of the available interval, a corollary of which is that the base of the Wyandotte Formation may not be much older than 200,000 ybp. The cause of the onset of sedimentation is not known, but may well be related to Pleistocene climatic changes as the Unit A facies are typical of meander cutoff vertical accretion facies which are suggestive of high runoff and frequent flooding. Elsewhere on the southern margin of the McBride Province flows younger than 100,000 ybp disrupted drainage (Griffin & McDougall, 1976), perhaps contributing to damming of the Wyandotte valley region.

The duration of the hiatus between final deposition of Unit A and the onset of Unit B deposition is unknown. Contacts between Units A and B range from planar horizontal to overhanging. Outcrops indicate that local scouring prior to deposition of Unit B extended to a minimum of one metre. Load casting is not evident even where boulders half a metre in diameter rest directly on the contact. This indicates significant compaction and dewatering of Unit A clays prior to the onset of erosion and Unit B deposition, implying that the upper horizons of Unit A are considerably older than the base of Unit B. Black soil is the youngest sediment in the region and mantles only those regions within flood range of the modern watercourses draining the basalt terrains to the north.

WYANDOTTE LOCAL FAUNA

The Wyandotte local fauna is summarized below. As this paper represents the first appraisal of the Wyandotte Local Fauna, no attempt has been made to describe all taxa in detail, but where good material exists and where I had access to comparative material, diagnostic descriptions have been included. It is hoped that the Wyandotte Fauna will be thoroughly investigated as part of a long-overdue review of the Pleistocene of north Queensland. Dental terminology follows Archer (1974, 1975), and the informal term "Local Fauna" is adopted from Tedford (1970). Catalogue numbers refer to specimens catalogued and held in the Museum of Victoria. The letters A & B indicate which formation units yielded identified specimens. F indicates the specimen was not *in situ*.

MOLLUSCA	
Bivalvia	
Sphaerium sp.	A & B
Velesunio sp.	A & B
Gastropoda	
Plotiopsis sp.	A & B
OSTEICHTHYS	
Teleostei	
Spines, vertebrae and other bones	A
REPTILIA	
Meiolanidae	
Meiolania cf *M. platyceps*	A
Chelidae	A & B
Crocodilidae	
Pallimnarchus sp.	A & B
ziphodont crocodilian	A
Varanidae	
Megalania prisca	A & B
Boidae	
Wonambi cf *W. naracoortensis*	F
?Elapidae	
two small, unidentified vertebrae	A
AVES	
Anhingidae	
Anhinga melanogaster	B
Anatidae	
Anseranas semipalmata	A
Anas ?superciliosa	A
Anas ?castanea	A
MAMMALIA	
Marsupialia	
Dasyuridae	
Dasyurus sp.	F
Antechinus sp.	A
Peramelidae	
Isoodon macrourus	A
Vombatidae	
Phascolonus sp.	F
Macropodidae	
Unidentified macropodids	A & B
Palorchestidae	
Unidentified palorchestid	A
Diprotodontidae	
?*Euowenia* sp.	F
Diprotodon optatum	F
Unidentified diprotodontid	A
Eutheria	
Muridae	
Rattus sp.	A & B
?*Pseudomys* sp.	A

DESCRIPTIONS

MOLLUSCA

Mollusc shells form a significant clastic component in some lithofacies in Unit B, but are relatively uncommon in Unit A. Where they are concentrated in Unit A they form a chalky hash, indicating both destruction in the clastic environment and dissolution in the diagenetic environment. Two bivalves (*Sphaerium* sp. and *Velesunio* sp., Figs 3A, B) and a gastropod (*Plotopsis* sp., Fig. 3C) are identified (pers. comm., L. Benson, James Cook University Tropical Freshwater Research Unit). Specific identifications are not possible because freshwater mollusc taxonomy relies on soft tissues for diagnostic features.

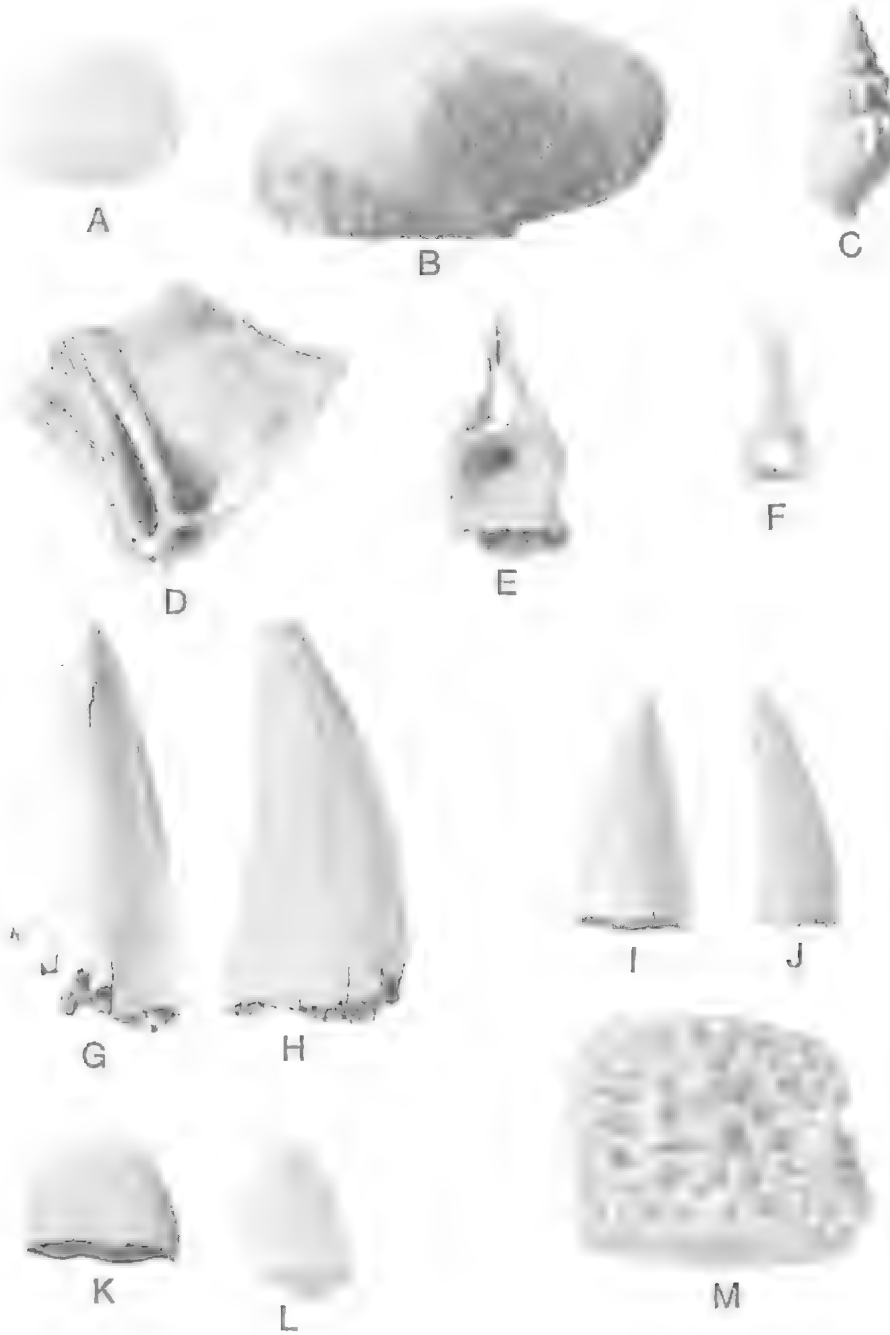

FIG. 3. A. Bivalve, *Sphaerium* sp., X 1.0. B. Bivalve, *Velesunio* sp. with some cemented matrix attached, X 0.75. C. Gastropod, *Plotiopsis* sp., X 1.5. D. Teleost operculum, X 2.0. E. Teleost vertebra, X 2.0. F. Teleost spine, X 2.0. G, H. Conical crocodile tooth (P184006), representative of tooth types i) and ii) in shape but showing the posterior — anterior keel of type ii) specimens, in lateral (G) and anterior — posterior (H) aspects. X 1.0. I, J. Laterally compressed, pointed crocodile tooth ovoid in section (P184010), representative of tooth type iii), in lateral (I) and anterior — posterior (J) aspects. X 1.0. K, L. Laterally compressed, blunt, crocodile tooth ovoid in section (P186638), representative of tooth type iv), in lateral (K) and anterior — posterior (L) aspects. X 2.0. M. Dorsal crocodile scute (P184004) in dorsal aspect, X 0.5.

OSTEICHTHYES

TELEOSTEI

Fish spines, vertebrae and opercula are relatively uncommon in Unit A, although small lenses have yielded large amounts of fish material (Figs 3D, E, F). A small lens of diatomaceous clay in Unit A contained a series of articulated fish vertebrae (P186596). This is the only articulated material known from the deposit. Some spines (e.g. P184046) have ornamentation suggestive of affinities with modern catfish eels but no other diagnostic bones have been discovered.

REPTILIA

CHELIDAE

Turtle carapace and plastron fragments are the most common fossils in both Units A and B. Gaffney (1981) indicates that ornamentation and suture features are not diagnostic even to a generic level and hence no identifications can be made except to say that many of the bones are most probably from chelids (E. Gaffney, pers. comm.).

MEIOLANIDAE

Meiolania cf. M. platyceps

Three horn cores (P183195, P183196, P183197) and a caudal vertebra (P183198), all unusually large, were retrieved from the basal gravel of Unit A. Two of the horn cores were found in close association and could well be from the same individual. Details of these remarkable fossils are discussed elsewhere (Gaffney & McNamara, this volume).

CROCODYLIDAE

Fragments from crocodiles are the most common fossils, next to those of turtles. Forty-seven teeth, four vertebrae and seven dermal scutes are recorded. Four distinct tooth types are recognised:
i) Conical and pointed, with no anterior-posterior keel and no serrations; fluting variable (e.g. P184034).
ii) Conical and pointed with noticeable anterior-posterior keels, both of which are serrated along their length; fluting variable (e.g. P184006, Figs 3G, H).
iii) Laterally compressed, pointed and ovoid in section, with entirely serrate anterior and posterior keels and variable curvature within the plane of compression (e.g. P184010, Fig. 3 I,J).
iv) Laterally compressed, blunt and ovoid in section, with serrate ridge from most anterior to most posterior position in the plane of compression; ridge sometimes with flexure near crown (e.g. P186638, Figs 3K, L).

All four types have been reported previously in Australian literature (see below).

The four procoelous vertebrae (e.g. P184061) are all large, as are six of the seven dermal scutes (e.g. P184004, Fig. 3M). All are typically crocodilian but not enough comparative material is available to allow closer identification.

Pallimnarchus sp.

Within Australia only the fossil genera *Pallimnarchus* and *Crocodylus* are known to have teeth of the conical form described as i) and ii) above. Molnar (1981) noted that the main distinction between these genera is the serrations, but added that this distribution is dubious as insufficient *Pallimnarchus* cranial material exists and dental documentation for *Crocodylus* is inadequate. Consequently the conical teeth from Wyandotte Creek might belong to either or both; they are ascribed to *Pallimnarchus* only on the basis that this is the form more commonly described from inland Queensland deposits.

Ziphodont crocodilian(s)

The laterally compressed condition, or ziphodonty, in serrate crocodilian teeth is known in both eusuchians and sebosuchians and both are reported from Australia (Molnar, 1981; Hecht & Archer, 1977, respectively), thereby making inferences, even about the ordinal status of these fossils, difficult. Hecht and Archer (1977) argued that markedly blade-like, partially recurved crowns distinguish sebosuchian ziphoid teeth, but the degree of compression and recurvature within the Wyandotte sample is highly variable. Some specimens are remarkably similar to *Megalania* teeth except that, unlike the limited serrations on the anterior edge of *Megalania* teeth, the ziphoid teeth serrations are continuous. The basal fluting of *Megalania* teeth is also far more pronounced than fluting on ziphoid teeth. Langston (1956) considered that isolated ziphoid teeth are not diagnostic. Given this uncertainty, no attempt has been made to classify them further. The distinctly

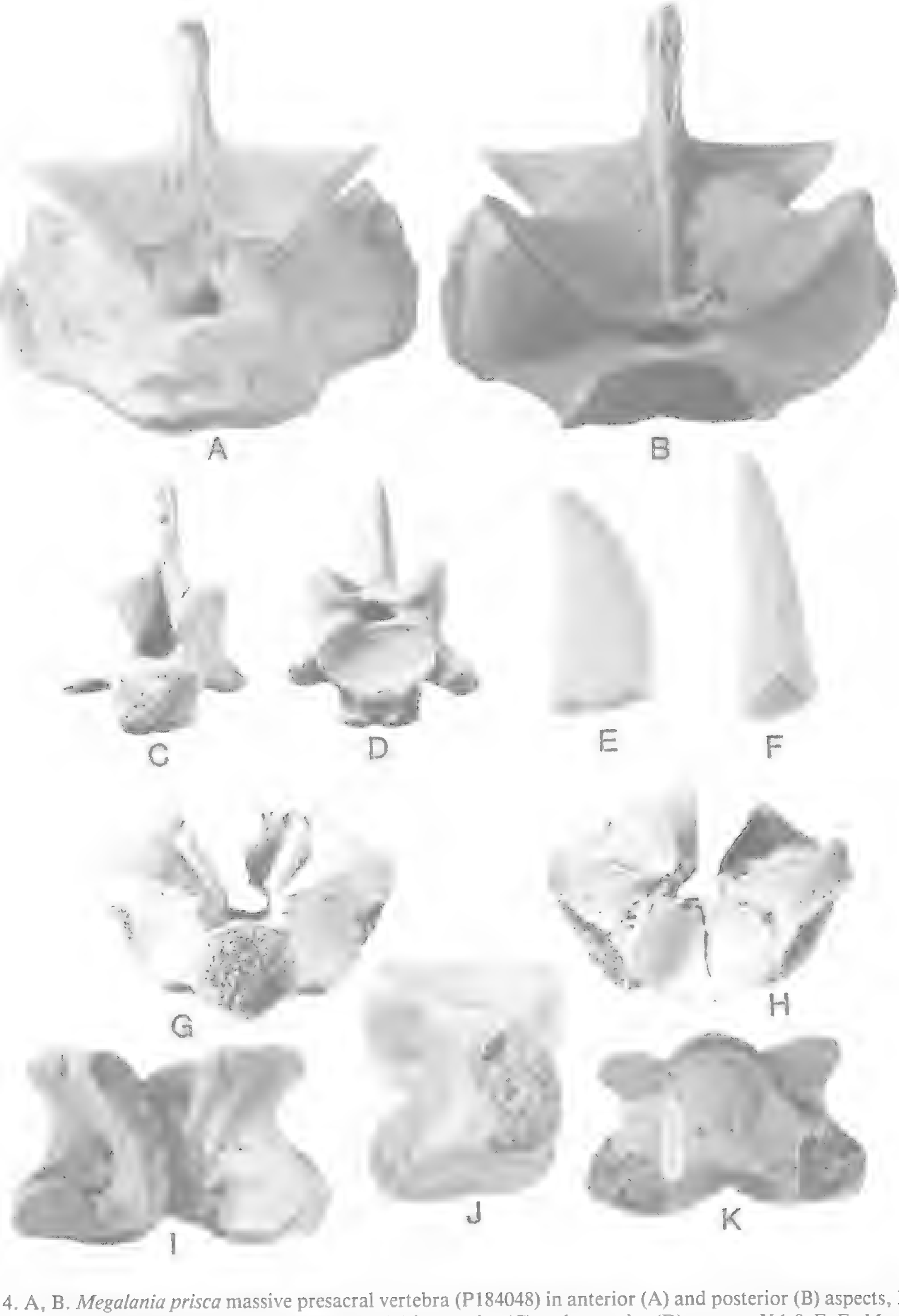

FIG. 4. A, B. *Megalania prisca* massive presacral vertebra (P184048) in anterior (A) and posterior (B) aspects, X 0.5. C, D. Large varanid postsacral vertebra (P186587) in anterior (C) and posterior (D) aspects, X 1.0. E, F. *Megalania prisca* tooth (P186591) in lateral (E) and posterior (F) aspects, X 2.0. G, H, I, J, K. *Wonambi* cf *W. naracoortensis* vertebra (P186652) in anterior (G), posterior (H), dorsal (I), lateral (J) and ventral (K) aspects, X 1.0.

different pointed and blunt types of ziphoid teeth also raise the question of whether they represent a single heterodont crocodilian or several homodont crocodilian species. These questions will be resolved only when more complete material is found.

VARANIDAE

Nine vertebrae (six large, three small) are typically varanid; they are procoelous, with centra constricted anterior to the condyles, weakly-developed zygosphenes on thoracic vertebrae, and postero-ventral pedicles for the haemal arches on the caudal vertebrae.

Megalania prisca

Six of the nine varanid vertebrae are massive presacrals (e.g. P184048, Figs 4A, B), and possess weakly-developed zygosphenes and small, depressed neural canals. These features typify *Megalania*, and all six specimens fall into the known size-range (Hecht, 1975). One of the three postsacrals (P184056) falls within the recorded size-range for *Megalania* while the other two are probably *Megalania* given their massive appearance and relatively large size (e.g. P186587, Figs 4C, D).

Seven large varanid teeth (e.g. P186591, Figs 4E, F) are attributed to *Megalania*. They are distinctive among varanids in having a recurved inclination distally, a rounded anterior cutting edge, serrated only distally, and a thin posterior cutting edge, blade-like and serrated along its entire length. All are of a size consistent with known *Megalania* specimens (Hecht, 1975).

OPHIDIA

Three procoelous vertebrae with zygosphene-zygantrum articulations are attributed to snakes.

BOIDAE

P186652 is recognised as a boid due to its lack of distinct parapophysial processes.

Wonambi cf. W. naracoortensis

P186652 displays the following features: a pair of paracotylar foramina, zygosphenal facets approximately 70° to horizontal, zygosphenes upturned at approximately 20°, absence of horizontal accessory processes, large paradiapophyses, depressed cotyle and condyle tilted approximately 75° anteriorly, parazygantral foramina, ventrally smooth and rounded centrum with no subcentral ridges, and subcentral foramina located near mid-centrum. These features and overall size are matched in *Wonambi* as described by Smith (1976); abrasion of the paradiapophyses, and other damage, precludes detailed comparison of measurements. Therefore, while there are no observable features to distinguish P186652 from *W. naracoortensis*, an identification as cf *Wonambi naracoortensis* is preferred to emphasize the lack of unequivocal data.

ELAPIDAE

Two smaller vertebrae (P184096 & P186597, Figs 5A, B, C) compare favourably with elapid vertebrae, but insufficient comparative material of northern Australian genera (colubrid and elapid) precludes detailed identification. They are sufficiently different to probably represent two separate elapid types.

AVES

ANHINGIDAE

A right ulna (P184058: distal end plus shaft; Figs 5D, E) is the only bird material from Unit B. The distal articular area is characterised by a shallow intercondylar sulcus. This is created by a depressed dorsal condyle and an indistinct ventral condyle that rises to a blunt protuberance in line with an equally blunt carpal tuberculum. Papillae are spaced regularly along the shaft. Only the Anhingidae and the closely allied Phalacrocoracidae possess all these points of morphological detail. The shape and position of the blunt protuberance indicates placement within the Anhingidae.

Anhinga melanogaster

The features used to separate P184058 from the Phalacrocoracidae are matched in *A. melanogaster*, a modern species, the Darter, still to be found on the waterways of the region.

ANATIDAE

Three damaged humeri and eight coracoids from Unit A are all attributed to anatids. The humeral

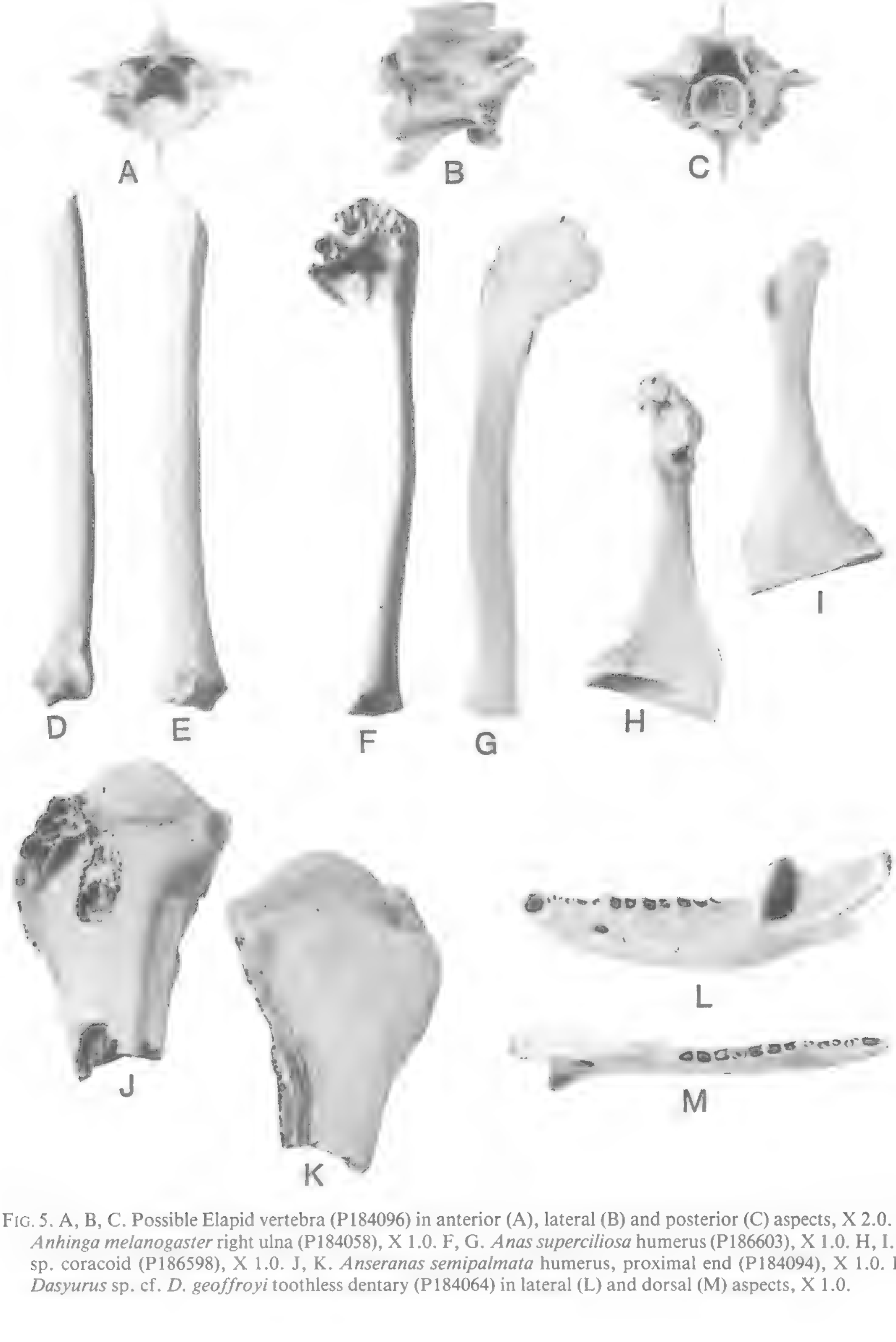

FIG. 5. A, B, C. Possible Elapid vertebra (P184096) in anterior (A), lateral (B) and posterior (C) aspects, X 2.0. D, E. *Anhinga melanogaster* right ulna (P184058), X 1.0. F, G. *Anas superciliosa* humerus (P186603), X 1.0. H, I. *Anas* sp. coracoid (P186598), X 1.0. J, K. *Anseranas semipalmata* humerus, proximal end (P184094), X 1.0. L, M. *Dasyurus* sp. cf. *D. geoffroyi* toothless dentary (P184064) in lateral (L) and dorsal (M) aspects, X 1.0.

fragments share no features that are absolutely diagnostic of the Anatidae in general, though most of the coracoids are sufficiently complete to assign them to the Anatidae on the basis of: i) a reduced procoracoid and brachial tuberosity, resulting in an indistinct triosseal canal; ii) the shape of the internal distal angle; iii) a groove situated antero-ventrally to the furcular facet on the distal "head" of the coracoid; and iv) the enlarged "keel" on the antero-ventral surface of the glenoid facet. The distinctive sternocoracoidal process, typical of anatids, has been lost through breakage in all cases.

Anseranas semipalmata

The largest of the three humeral fragments (P184094: proximal end only, Figs 5J, K) is abraded but exhibits enough characters for positive identification. The orientation of the deltoid crest, the reduced pneumatic fossa and the shape and position of the internal tuberosity are distinctive and allow P184094 to be identified confidently as *Anseranas semipalmata*, the Magpie Goose, a modern species that still ranges over the region. The size also matches that of modern adults.

Anas superciliosa

Specimen P186603 (proximal end and shaft, Figs 5F, G) is morphologically identical to the humerus of *A. superciliosa*, the Black Duck. The position of the deltoid crest and its associated tuberosities are the most obvious correspondences. This species is still common in the region. Coracoid P186598 (Figs 5F, G) may also correspond to *A. superciliosa*, but due to wear, and the close similarity of all *Anas* coracoids, this can only be a tentative identification.

Anas sp.

Coracoids of *Anas* are distinguished from those of other genera within the Anatidae by the shape of the internal distal angle and the bilobate furcular facet but they are difficult to assign to species, especially when they are abraded, because of their structural uniformity. P186598 may correspond with *A. superciliosa* (as above), and P186654 and P186601 may correspond to *A. castanea* (G. Van Tets, pers. comm.). They are clearly distinct from each other and yet too worn to be identified specifically.

MAMMALIA

MARSUPIALIA

DASYURIDAE

Dasyurus sp. cf. **D. geoffroyi**

P184064 is a well-preserved but toothless dentary lacking the anterior portion of the ramus (Figs 5L, M). It is identical, both in morphology and size, to dentaries of adult *D. geoffroyi*. The specimen undoubtedly represents an adult *Dasyurus* but without dentition further identification is not possible.

Antechinus sp.

P183209 is the only fossil located *in situ* from the gravel stringers within the blue-grey clay of Unit A. This right dentary contains M_2 to M_5 but is incomplete more anteriorly (Figs 6A, B). It is about the same size as the jaw of an adult *A. flavipes*, but shows a slightly different arrangement of cusps on the trigonid. As insufficient comparative material was available no attempt has been made to identify this specimen more closely.

PERAMELIDAE

Isoodon macrourus

P183212 is a left M^5 which has a triangular outing in plan view, with a distinct anterior cingulum leading to a well developed protocone (Figs 6C, D). This morphology is typical of peramelid molars. The specimen has a large paracone, a pronounced parastyle and a slightly smaller mesostyle. It has no hypocone, but a posterior cingulum terminates at the base of the distinct posterior cusp. The distinct posterior cusp and the anterior cingulum rising below the parastyle are indicative of *Isoodon* rather than *Perameles* (where the anterior cingulum rises between the parastyle and paracone). The posterior cusp is twice the width of the posterior cingulum where the cingulum terminates against the cusp, a condition unique to *I. macrourus* amongst *Isoodon* species.

VOMBATIDAE

Phascolonus sp.

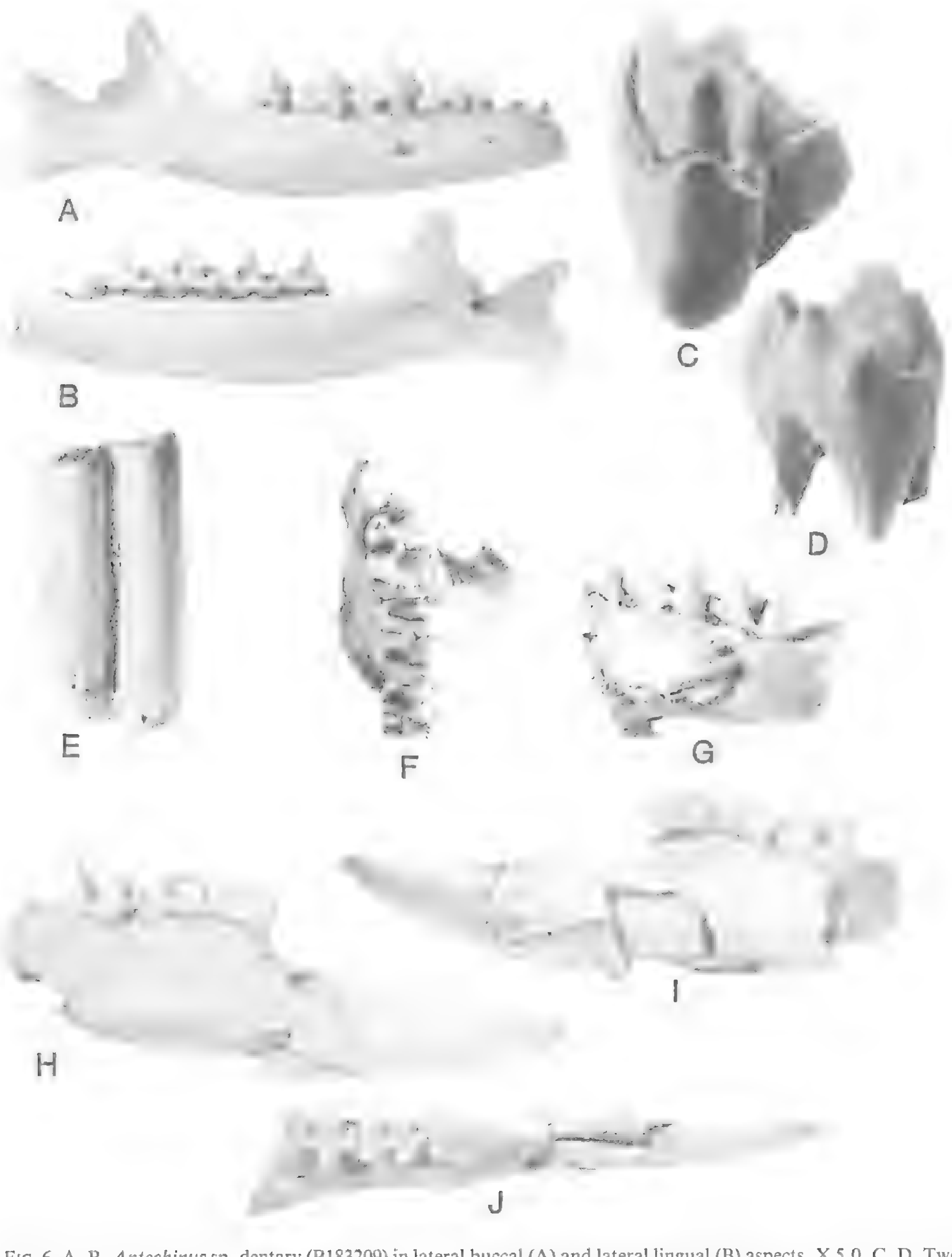

FIG. 6. A, B. *Antechinus* sp. dentary (P183209) in lateral buccal (A) and lateral lingual (B) aspects, X 5.0. C, D. Two oblique views of *Isoodon macrourus* left upper M^5 (P183212), X 10.0. E. *Phascolonus* sp. molar fragment (P186855) in lateral aspect, X 1.0. F, G. Maxilla fragment from unidentified macropodid (P184042) in occlusal (F) and lateral (G) aspects, X 1.0. H, I, J. Unidentified juvenile macropodid dentary (P184052) in lateral buccal (H), lateral lingual (I) and dorsal (J) aspects, X 1.0.

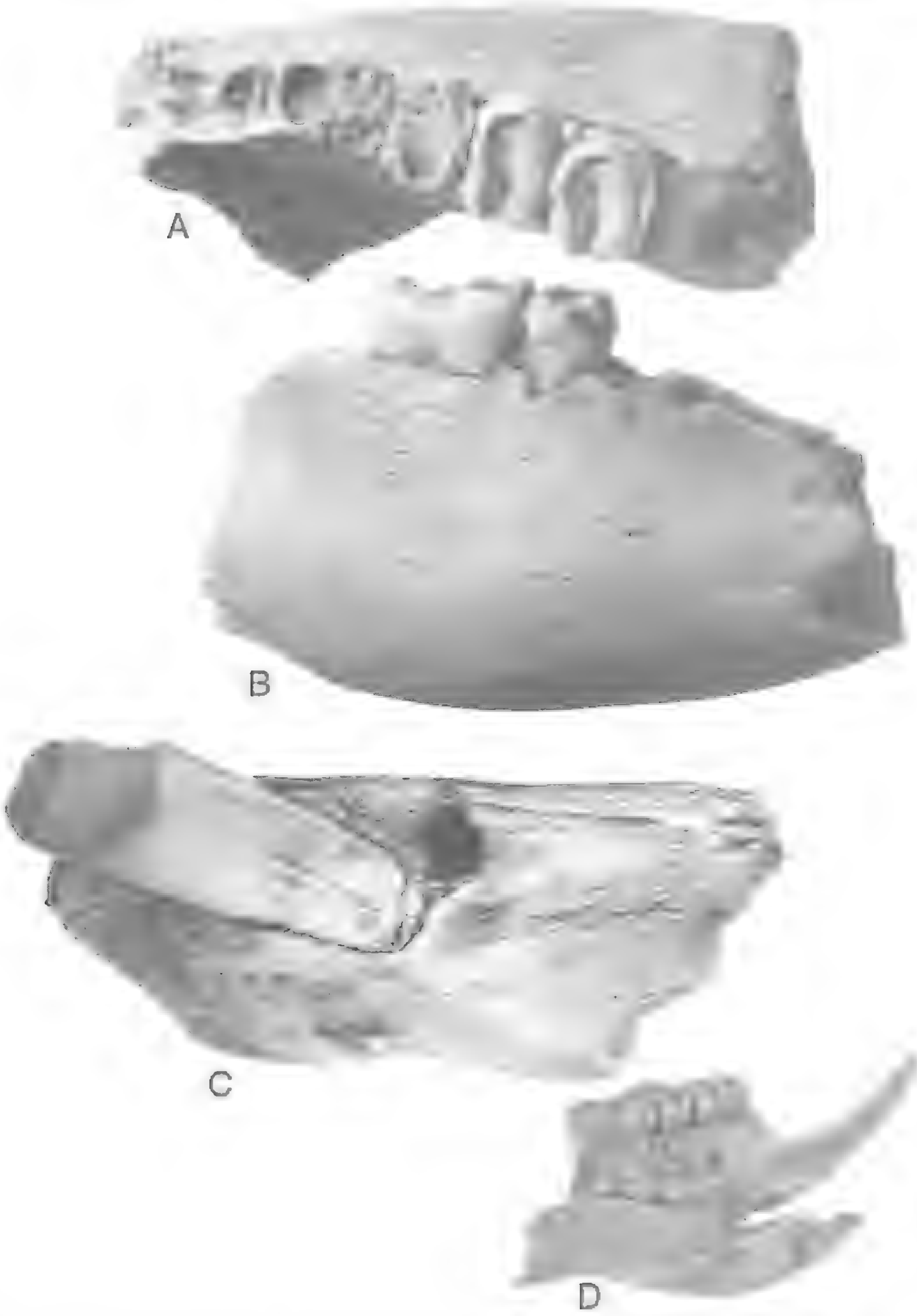

FIG. 7. A, B. Unidentified (?*Euowenia* sp.) diprotodontid dentary (P183996) in lateral (A) and dorsal (B) aspects, X 0.5. C. *Diprotodon optatum* premaxilla fragment (P186656) in occlusal aspect, X 0.5. D. *Rattus* sp. cf. *R. sordidus* dentary pair (P184047) in oblique dorsal aspect, X 2.6.

P186655 consists of a single large molar fragment (Fig. 6E). It is hypsodont and is markedly divided into two columns, subequal in width (12.1 mm & 11.6 mm), with a maximum anterior-posterior distance of 22.3 mm. Evidently this specimen represents a very large wombat, within the size range of *Phascolonus* (Dawson, 1981), but no closer identification is possible.

MACROPODIDAE

Unidentified macropodids

Many fragmentary macropodid remains have been found, including maxilla fragments (e.g. Figs 6F, G), dentaries (e.g. Figs 6H, I, J), isolated molars and premolars, and fragmentary postcranial material. More precise identifications should emerge from current investigation.

PALORCHESTIDAE

Unidentified palorchestid(s)

P186593, P186594 and P186595 represent probable palorchestid molar, incisor, and premolar respectively. All three specimens clearly have palorchestid affinities but they are sufficiently different from known palorchestid forms to warrant further research. The Palorchestidae is currently under revision and these specimens will be examined in that work (M. Archer, pers. comm.).

DIPROTODONTIDAE

?**Euowenia** sp.

A diprotodontid dentary fragment with worn M_3 and M_4 intact (P183996) is tentatively identified as *Euowenia*. This identification rests only on the shape of the molars in occlusal view, as typified by *E. robusta* (Figs 7A, B). The molars are extremely worn, but their outline is clearly not matched in *Diprotodon optatum*, where the molars are far less ovoid in plan view.

Diprotodon optatum

A premaxillary fragment of a large diprotodontid with I^2 intact and containing alveoli I^1 and I^3 (P186656) is identified as *Diprotodon optatum* on the basis of the distinctive outline of the I^1 and the shape and relative position of I^2 (Fig. 7C).

Unidentified diprotodontid

P186657 is a diprotodontid humerus. Its outstanding feature is a broad flattening of the distal articular area, similar to that seen in *Zygomaturus*. No other features seem sufficiently diagnostic to allow further identification.

EUTHERIA

MURIDAE

Rattus sp. cf. **R. sordidus**

A large number of murid maxillary fragments (e.g. P183238, P184075) and isolated upper and lower teeth (e.g. P184078, P184082) were obtained from a single lens in Unit A. A single pair of dentaries plus incisors was isolated from Unit B (P184047; Fig. 7D). All may be referrable to *R. sordidus* (H. Godthelp, pers. comm.).

?**Pseudomys** sp.

A single dentary fragment from Unit A (P184074) is tentatively attributed to *Pseudomys* (H. Godthelp, pers. comm.), but is too incomplete to allow closer identification.

DISCUSSION

The Wyandotte Local Fauna comprises disarticulated and fluvially transported, but nonetheless well-preserved, elements of Pleistocene age and merits further detailed description. The purpose of this paper is to document the existence of the fauna and to put on record its dated context. There are few dated Quaternary vertebrate fossil sites in Australia and even the Pleistocene is not so well served in that regard as it might be. The depositional setting of the Wyandotte Formation is clear, and the dated horizons are well-defined. The dates obtained are unambiguous but indicate the need to utilize techniques other than conventional ^{14}C to place the stratigraphic context of the fossil-bearing horizons within the Pleistocene. The fauna has already proved of interest, even at this preliminary stage, in that:

i) the temporal and geographic ranges of *Megalania prisca, Wonambi*, and *Meiolania* have been greatly extended;

ii) much of the described fauna has been tied to reliable dates within the Pleistocene for the first time; and

iii) there is tantalizing evidence for the existence of previously undescribed taxa (e.g. palorchestids) in concert with extended ranges for known faunal elements. The Wyandotte fauna confirms that the Pleistocene of northern Australia is as yet far from well-known and worthy of much more detailed investigation.

ACKNOWLEDGEMENTS

Work on this fauna would not have been possible without the co-operation of Joy and Eddie Marsterson of Wyandotte Station, who kindly allowed access to the mapped area and generously provided other assistance. Sue and Peter Burger of Greenvale also generously provided assistance and accommodation. Peter Staunton is thanked for his sieving efforts back in Townsville, and Neil Mockett for his efforts entailing the near loss of his thumb. Peter, Sue, Alexander, Ben, Michelle and Lara Burger; Peter and Jill Staunton; Kerry Williamson; Lindsay Williams, Rosemary and Andrew O'Hearn; Neil, Richard, Justin and Santana Mockett; Jim, Margaret and Martin Darley; Roger, Peter and Judy Quick; Mark Audley; Doug Haywick; Bob Henderson; Alister Stephens; Danny Spence; Trevor Beardsmore; Jane Dye; Eleanor Adkins; Tom Rich; Gene Gaffney and Daniel and Hilary McNamara all assisted in the excavation of fossil material at one time or another and are greatly thanked. Financial support was received from James Cook University special research grants. A donation from the Fossil Collectors Association of Australasia gave initial help for which special thanks is given.

LITERATURE CITED

ARCHER, M. 1974. The development of cheek-teeth in *Antechinus flavipes* (Marsupialia, Dasyuridae). *Journal of the Royal Society of Western Australia* **57**: 54–63.

1975. The development of premolar and molar crowns of *Antechinus flavipes* (Marsupialia, Dasyuridae) and the significance of cusp ontogeny in mammalian teeth. *Journal of the Royal Society of Western Australia* **57**: 118–25.

COVENTRY, R.J., STEPHENSON, P.J. AND WEBB, A.W. 1985. Chronology of landscape evolution and soil development in the upper Flinders River area, Queensland, based on isotopic dating of Cainozoic basalts. *Australian Journal of Earth Science* **32**: 433–47.

DAWSON, L. 1981. The status of the taxa of extinct giant wombats(Vombatidae: Marsupialia), and a consideration of vombatid phylogeny. *Australian Mammalogy* **4**: 65–79.

GAFFNEY, E.S. 1981. A review of the fossil turtles of Australia. *American Museum Novitates*, no. 2720, pp. 1–38.

AND McNAMARA, G.C. 1990. A Meiolaniid turtle from the Pleistocene of northern Queensland. This volume.

GRIFFIN, T.J. AND McDOUGALL, I. 1976. Geochronology of the Cainozoic McBride Volcanic Province, northern Queensland. *Journal of the Geological Society of Australia* **22**: 387–96.

GRIMES, K.G. 1980. The Tertiary geology of north Queensland. p. 329–47. *In* Henderson, R.A. and Stephenson, P.J., (Eds) 'The Geology and Geophysics of Northeastern Australia', (Geol. Soc. Aust., Qd Division: Brisbane).

HECHT, M. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proceedings of the Royal Society of Victoria* **87**: 239–50.

AND ARCHER, M. 1977. Presence of xiphodont crocodilians in the Tertiary and Pleistocene of Australia. *Alcheringa* **1**: 383–5.

LANGSTON, W. 1956. The Sebecosuchia: cosmopolitan crocodiles? *American Journal of Science* **254**: 605–14.

MOLNAR, R.E. 1981. Pleistocene ziphodont crocodilians of Queensland. *Records of the Australian Museum* **33**: 803–34.

NIND, M. 1988. Age of the Campaspe Formation, north Queensland. *Search* **19**: 30–2.

SMITH, M.J. 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. IV. Reptiles. *Transactions of the Royal Society of South Australia* **100**: 39–51.

TEDFORD, R.H. 1970. Principles and practices of mammalian geochronology in North America. *Proceedings of the American Palaeontological Convention* **1969**: 666–703.

WYATT, D.H. AND WEBB, A.W. 1970. Potassium-argon ages of some northern Queensland basalts and an interpretation of late Cainozoic history. *Journal of the Geological Society of Australia* **17**: 39–51.

DEVILS ON THE DARLING DOWNS — THE TOOTH MARK RECORD

Ian H. Sobbe

Sobbe, Ian H. 1990 00 00: Devils on the Darling Downs — the Tooth Mark Record. *Mem. Qd Mus.* 27(2): 299-322. Brisbane. ISSN 0079-8835.

Fossil bones collected from Pleistocene deposits of the eastern Darling Downs show a variety of marks, many of which are considered to be the tooth marks of carnivores. A feeding trial was conducted to identify those tooth marks that might have been produced by the Tasmanian Devil (*Sarcophilus harrisii*), the largest extant marsupial carnivore known to have inhabited the Darling Downs. Fifteen categories of tooth marks are described: ten from the fossil sample and five from the feeding trial. A clear overlap exists between some categories of fossil tooth marks and those produced in the feeding trial. From the existing fossil evidence, *Sarcophilus* appears to have been a major carnivore on the eastern Darling Downs in the late Pleistocene.
☐ *Darling Downs, Pleistocene, taphonomy, tooth marks, Sarcophilus, Thylacoleo.*

Ian H. Sobbe, M/S 422, Clifton, Queensland, 4361, Australia;

Recent collecting on the Darling Downs, southeastern Queensland, has yielded a large number of fossil bones which may record the feeding activities of Pleistocene predators and scavengers.

In times of diminished food supply, all carcasses would be consumed by predators and the remnant bones consumed by scavengers such as *Sarcophilus* and most likely *Megalania*. However, in periods of abundant food supply, some carcass remnants will remain unconsumed. Some of these unconsumed bones will bear the tooth marks of the predatory and scavenging animals and will then survive to be preserved as fossils.

Marks on Australian fossil marsupial bones have been recorded by many other workers including de Vis (1900), Spencer and Walcott (1911), Douglas *et al*. (1966), Archer *et al*. (1980), Horton and Wright (1981) and Runnegar (1983). Many of these descriptions placed little emphasis on microscopic examination of the marks or on comparison with marks known to have been made by specific predators or scavengers. One of the problems encountered in this area of research is that some of the animals potentially responsible for tooth marks are extinct and have left no direct descendants that might furnish comparative data.

The major predators and scavengers recorded from Pleistocene sites of southeastern Queensland are: Muridae, (*Rattus* sp.); Thylacinidae, (*Thylacinus* sp.); Dasyuridae, (*Dasyurus* sp., *Sarcophilus* sp.); Thylacoleonidae, (*Thylacoleo* sp.); Varanidae, (*Varanus* sp., *Megalania* sp.); and Crocodylidae, (*Crocodylus* sp.) (Bartholomai, 1976; Molnar, 1982; Archer *et al*., 1984).

The largest extant marsupial carnivore in this list is the Tasmanian Devil (*Sarcophilus harrisii*). In this study I have concentrated on *Sarcophilus* in an attempt to recognise marks left on bone during its feeding activity. *Sarcophilus* is known to eat bone as part of its normal diet and has the potential to produce a range of tooth marks on the bones of its prey. Captive devils are common in zoological gardens and are good subjects for a feeding trial. A feeding trial was conducted at Lone Pine Koala Sanctuary, Brisbane, to determine the nature and extent of tooth marks on bones chewed by *Sarcophilus*. The resulting tooth marks were then

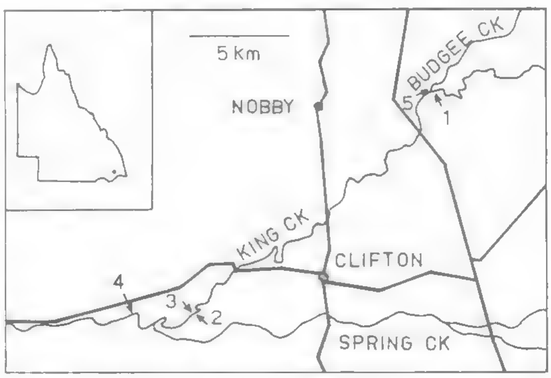

FIG. 1. Map of the King Creek area showing collecting sites.

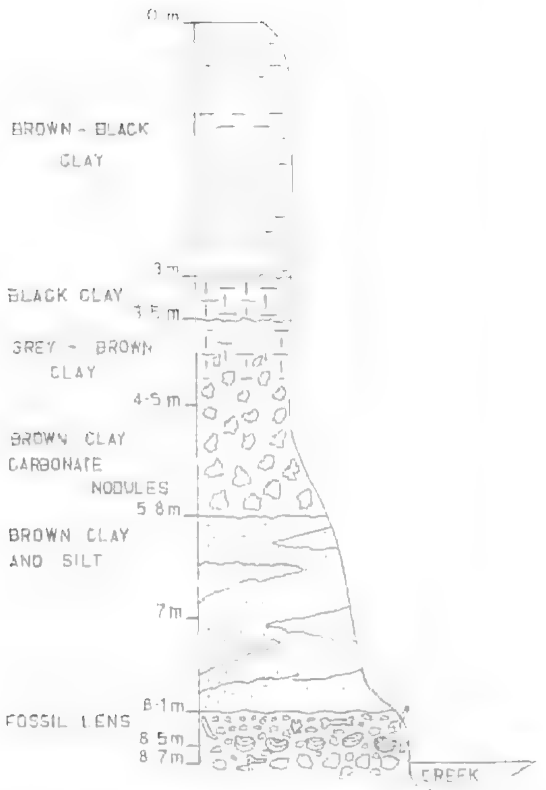

FIG. 2. Stratigraphic section of south bank of King Creek at GR 858079 (Locality 2 of this study).

compared with those on fossil bones of Pleistocene age.

REPOSITORIES

All figured specimens have been placed in the collection of the Queensland Museum. These are identified by the prefix QM. Additional bulk specimens are housed in the collection of the author.

LOCALITIES AND AGE

Fossil specimens used in this study were all derived from Pleistocene fluviatile deposits at various localities along King Creek and Budgee Creek, Darling Downs, SE Queensland (Fig. 1). Grid references for these localities are: (1) King Creek, S bank, between 976193 and 979193; (2) King Creek, S bank, 858079; (3) King Creek, N bank, 856080; (4) King Creek, N bank, 828080; and (5) Budgee Creek, W bank, 975194 (Royal Australian Survey Corps, 1:100,000 Series Map, Toowoomba, Sheet No. 9242). These deposits are exposed by flood-water erosion in the lower portion of the creek bank. In the case of the measured section described below, fossils are accessible to a depth of 8.7 m (Fig. 2). This does not represent the base of the fossil deposits but simply water level as at August, 1988, and thus the approximate limit of available *in situ* collecting.

Associated charcoal and carbonate nodules from site (2) were dated by Gill and MacIntosh and recorded in Gill (1978) and Baird (1985). Dates are: Charcoal 23,600 ± 600 B.P. (N.Z. 612), 28,400 ± 1,400 B.P. (JAK 1394), 41,500 ± 6,100 B.P. (N.Z. 613); and Carbonate 24,000 ± 600 B.P. (N.Z. 641), 30,800 ± 3,000 B.P. (N.Z. 640). These C14 dates were obtained during the late 1960's. They were used by Baird (1985) and would appear to be the only dates available for these particular beds. Further datings for the whole King Creek stratigraphic sequence would be desirable and would further refine our knowledge of the age of fossil beds in this area.

Subsequent to the dating of locality (2), erosion has lowered the water level by approximately 0.5 m — 1 m. This has allowed collecting from slightly deeper in the fluviatile lenses. The stratigraphy and major faunal elements of the various sites appear to be rather uniform, and the specimens in this study should, therefore, be of an age roughly consistent with the dates cited above.

STRATIGRAPHY

Woods (1960) and Gill (1978) have documented some aspects of the stratigraphy of the King Creek area, but their accounts show some variance from the stratigraphy at some localities considered in this paper.

The measured section (Fig. 2) of locality (2) is as follows:

0-3 m — Brown to black clay — Ellinthorpe Clay (Gill, 1978). Occasional small shelly lenses (*Plotiopsis* sp., *Corbiculina* sp.) present in some areas.

3-3.5 m — Deep black clay. Yellow nodules (? iron) present at the lower limit of this soil unit.

3.5-4.5 m — A transitional unit grading from grey clay above through to brown clay with occasional carbonate nodules below.

4.5-5.8 m — Brown clay with extensive carbonate in the form of irregular nodules and crack infillings. — Talgai Pedoderm (Gill, 1978).

5.8-8.1 m — Brown clay with silt lenses containing numerous shells (*Plotiopsis* sp., *Corbiculina* sp.) and some fossil bones — Toolburra Silt (Gill, 1978). The bones are often heavily encrusted with carbonate. In some areas adjacent to the measured section these fossil lenses are continuous up to a level of 7 m. In other parts of King Creek (locality (1) of this study) numerous fossil bones are found throughout this unit

8.1-8.5 m — Nodular lens containing fossil bones. Silt matrix containing numerous waterworn calcareous nodules (maximum size 4 cm). Some well-rounded stones (size up to 1.25 cm, and occasionally to 2.5 cm) and numerous shells. (*Plotiopsis* sp., *Corbiculina* sp., *Velesunio* sp.).

8.5 m — Layer within nodular lens with abundant *Velesunio* sp. shells.

8.5-8.7 m — Continuation of nodular lens containing fossil bones. Similar to the upper portion of the lens except that calcareous nodules (maximum size 7.5 cm) and stones (maximum size 4-5 cm) are generally of larger size.

8.7 m — Creek water level (August, 1988). The nodular lens continues below this level; maximum depth not known.

The stratigraphy of other parts of King Creek differs in some details from the described section. Localities closer to the headwaters of King Creek (e.g. locality (1) of this study) have some stones of larger size (up to approximately 10 cm) in the lower beds. Fossils are rarer and generally fragmentary in these stony beds.

METHODS

More than 100 tooth-marked bones have been collected in the last three years. These range from complete, or near-complete, elements through to unidentifiable fragments with a diameter of 1 cm. Two methods of collection were employed, viz.: systematic collecting of all fossil bones exposed in the creek bank after heavy rainfall and/or flooding; and digging and collection of all fossil bones from selected areas of the creek bank. Most specimens were recovered by the former method.

As all but the most obvious marks are difficult to see, careful cleaning of the specimens is required. First the bones were soaked in water to soften adhering clays, then lightly brushed with a soft nylon bristle brush. Cleaned specimens were checked for marks under sunlight or an incandescent bulb as fluorescent and other diffuse light sources do not produce shadows to highlight the contour of individual marks.

Marks on fossil bones and those from the feeding trial were examined using low magnification microscopy, 35 mm S.L.R. photography, and scanning electron microscopy. Most bones were too big to be examined directly, thus areas of interest were replicated in clear resin for close examination. Rose (1983) provides details of this technique.

DESCRIPTION OF FOSSIL MARKS

Many bones show various degrees of damage due to fluvial, geophysical and chemical factors:

— exfoliation and cracking of the bone surface due to exposure before fossilization (see Behrensmeyer, 1978);
— breakage, abrasion and rounding of the bone surface due to rolling in stream sediments (see Shipman & Rose, 1983);
— breakage due to shrinkage and swelling of the enclosing clays (see Wood & Johnson, 1978);
— pitting of the surface by the action of acidic ground waters and possibly corrosion by plant roots (see Archer *et al.*, 1980);
— breakage and marks accidentally inflicted during excavation. These areas show a distinctly different colour to the remainder of the specimen, and, therefore, are readily identifiable.

Some bones have a series of marks which are not attributable to any of the aforementioned factors. These are interpreted as tooth marks of scavengers or predators, because they take the form of pits, scratches, punctures and blade-like incisions in the bone surface. Such marks have been identified as typical of the damage inflicted to bone by a variety of carnivores (see Haynes, 1983). In addition, the marks often occur as pairs on the opposite sides of single bones; these paired markings presumably correspond to teeth in the opposing jaws of carnivores.

Gill (pers. comm., 1986) suggested that many of the marks, particularly those described here as blade-like impressions, could be the result of aboriginal butchering of carcasses using stone tools. Such butchery would presumably involve separation of the carcass into portions small enough for easy transportation, cooking or eating. The easiest way to dismember a carcass is to separate it at the major joints by severing the attaching flesh and tendons. This process would tend to mark the bones mainly in the area of the major joint tendons, close to the ends of long bones.

In fact, marks are widely distributed on the fossil bones and are not concentrated around the joints. Several paired marks are recorded on a macropod distal phalanx. This, however, would be an unlikely site for butchery marks. Moreover, butchery would be expected to produce a random orientation of marks and not consistent pairing.

Recognition and definition of Man-made marks on bone are discussed by Potts and Shipman (1981) and by Shipman and Rose (1983a, b). The marks include those produced by slicing, chopping and scraping. Slicing marks are "elongate grooves, containing within its edges, multiple fine parallel striations orientated longitudinally" (Shipman & Rose, 1983a). Such fine parallel striations have not been observed in this study. Chopping marks are V-shaped in cross section, as are the marks produced by the sectorial premolars of *Thylacoleo* sp. (Horton & Wright, 1981). The fact that the marks seen on the Darling Downs specimens generally occur as opposed pairs would seem to implicate *Thylacoleo;* examples are described below.

Fossils have been collected from eastern Darling Downs for more than 140 years (Bartholomai, 1976), and in that time not one artifact has been found in the beds containing fossil marsupial bones. By contrast, numerous artifacts are found in surface or near-surface deposits. Thus, it would appear that aboriginal butchery is unlikely to be the cause of the marks in this study.

The tooth marks are divided into ten categories (designated A-J) discussed below. Referred specimens are described in Appendix 1. Some specimens show two or more categories of tooth marks. These associations might result from the different teeth (e.g. incisors and carnassials) of a single carnivore, from juvenile and adult animals chewing on a single bone, or from more than one species of carnivore.

Exact counts of marked bones in individual collections have yet to be compiled. However, washed bones were sorted into marked and nonmarked groups which showed frequencies of marked bones in the range of 10-50%.

Some marks are rare whereas others are present on a large number of specimens, some of which show moderate to severe weathering and breakage. The following descriptions of tooth marks are based on those specimens which show least weathering and breakage.

CATEGORIES

(A) ROUND-BOTTOMED SCRATCHES WITH ANCHOR POINTS

A series of shallow, closely-spaced, near-parallel scratches that taper slightly present on one surface of several specimens (Fig. 3). Length 3-7 mm; Width 0.3 — 0.6 mm; Depth approximately 0.25-0.5 mm. Immediately above the broader end of the scratches is a series of shallow, near-circular pits, 0.4-0.6 mm in diameter, which appear to be tooth anchor points (Fig. 3A, C). In some areas the scratches are so frequent and closely-spaced as to remove complete areas of the bone surface (Fig. 3B).

Rodents chew by anchoring their upper incisors and drawing the lower incisors upwards. At times only one lower incisor is in contact with the surface being chewed, thus producing a single tooth mark (Archer *et al.*, 1980). This action would produce marks similar to those described from the fossil specimens, which also resemble the murid gnawings described by Archer *et al.* (1980) and by Shipman and Rose (1983).

(B) BLADE-LIKE IMPRESSIONS

Long blade-like impressions on opposing bone surfaces are present on a considerable number of specimens. The marks are V-shaped in cross section, and about 1 mm deep. One side of the "V" is quite flat, terminating sharply at the base, whereas the other side is rather chipped (Fig. 4). In the case of paired marks, the flat sides of the marks oppose each other (Fig. 5). The maximum length is not known since the marks extend fully across many specimens. The longest recorded mark is approximately 27 mm, present on the edge of a fragment of macropod pelvis, apparently sheared in two by a bite at the level of the acetabulum (Fig. 4C). These pairs of opposing marks subtend an angle in the range of 18°-28°. They appear to be formed by a pair of large blade-like teeth, probably *Thylacoleo* premolars. Similar marks have been attributed to *Thylacoleo* by other workers including de Vis (1900) and Horton and Wright (1981).

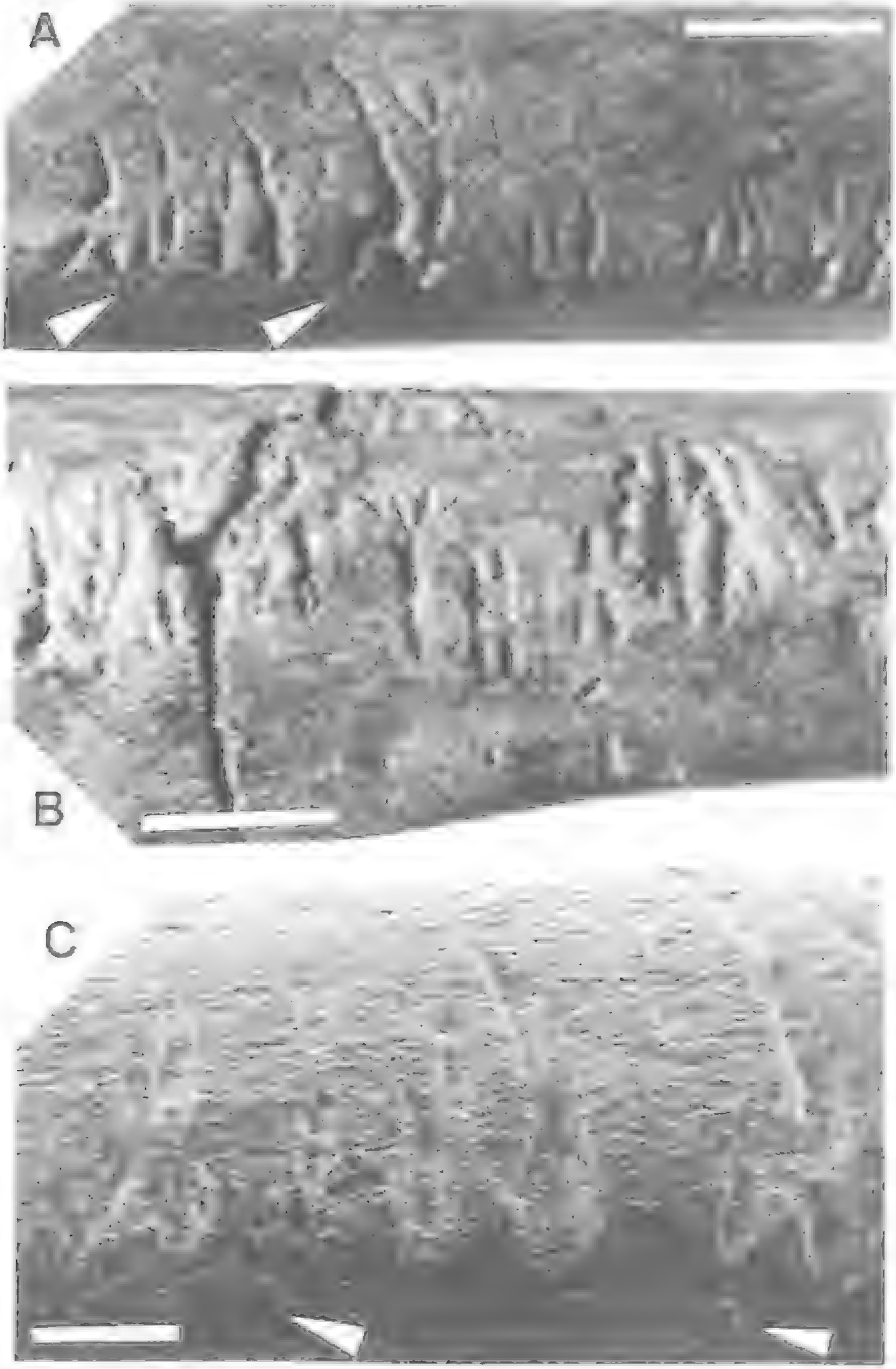

FIG. 3. CATEGORY A — Round Bottomed Scratches with Anchor Points
A Macropod rib (QM F14504) showing shallow, closely spaced, tapering scratches with anchor points (Arrowed).
B Closely spaced scratches resulting in complete removal of bone surface (QM F14504).
C Scanning Electron Micrograph showing detailed shape of marks (QM F14504).
Scale: A and B Scale Bar = 5 mm, C Scale Bar = 1 mm

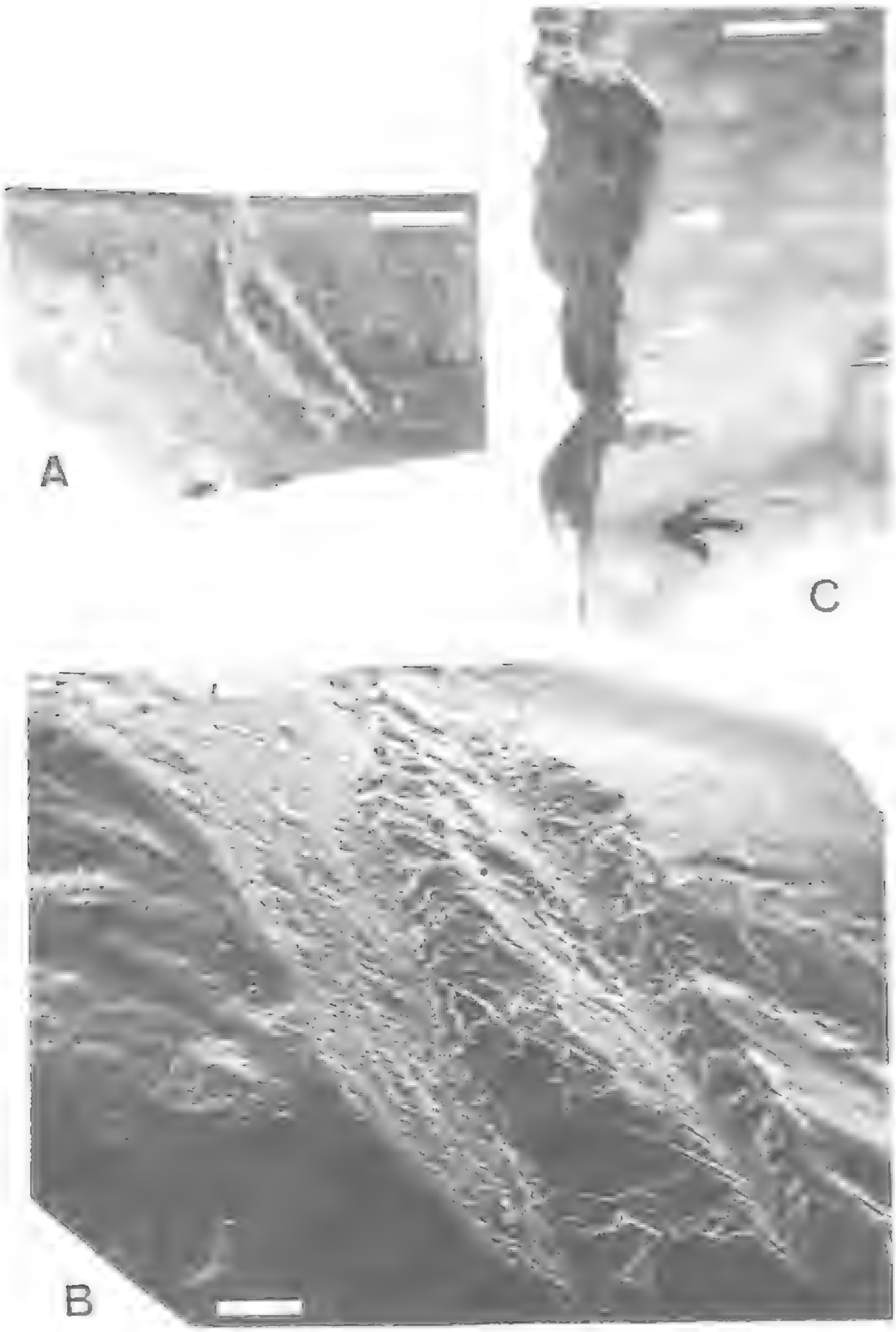

FIG. 4. CATEGORY B — Blade-Like Impressions
A Macropod rib (QM F14505) showing blade like impressions with V shaped cross section.
B Scanning Electron Micrograph of QM F14505 showing details of flat and chipped sides of V shaped mark. The dark spheres in this and subsequent SEM's are air bubbles trapped during casting procedures.
C Macropod pelvis (QM F14506) apparently sheared in two by a single bite — Note bite facet (arrowed).
Scale: A and C Scale Bar = 5 mm. B Scale Bar = 1 mm.

If these marks are sufficiently deep to break through the compact bone (3 mm on one specimen), they assume a different round-bottomed shape in the spongy bone (Fig. 6A). It is only possible to see that these are an extension of the V-shaped marks on specimens where a complete gradation of marks exists.

(C) CRESCENT-SHAPED MARKS
One specimen shows three crescent shaped marks 4-5 mm wide and about 1 mm deep. The bone surface has been displaced at right angles to the long axis of the mark to leave a ridge of semi-detached bone at the concave edge (Fig. 6B).

Other marks on the same specimen are so poorly defined that they cannot be assigned to a particular category.

(D) PITS AND SCRATCHES
Many specimens bear small pits and scratches, either singly or combined in large groups, giving the bone surface a rough appearance (Fig. 7). The pits are round to oval with a diameter of up to 2 mm and depth up to 1 mm (Fig. 8). The round-bottomed scratches have parallel or slightly convergent walls and distinct basal corrugations at right angles to the long axis of the mark (Fig. 7). These corrugations, which are generally visible without magnification, show where a tooth cusp has broken through successive layers of

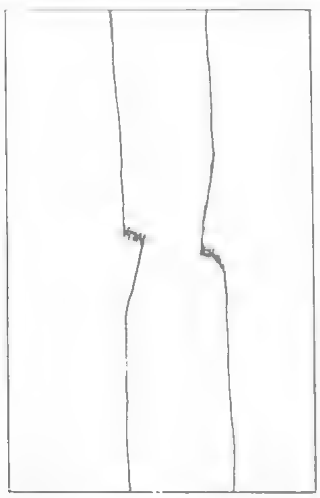

FIG. 5. Side view of paired blade like marks showing relationship to each other.

bone tissue. Length is up to 20 mm, with most being 4-7 mm, and width up to 2 mm, with most specimens approximately 1 mm.

These marks are among the most numerous so far observed. Two specimens, QM F14512 and QM F14514, show boomerang-shaped marks; a shape which Horton and Wright (1981) attribute to *Thylacoleo* (Fig. 8). While such marks might well have been produced by the sectorial premolars of *Thylacoleo*, the differences in cross-sectional and basal shape indicate a different origin for QM F14512 and QM F14514.

(E) LARGE DEEP SCRATCHES

Specimen QM F14515 is a vertebra which shows a scratch mark of exceptional size. Length 27 mm; Width 5 mm; Depth approximately 2 mm. This mark shows a tapering lead into the point of greatest depth and width. From there it continues near that size for 15 mm where it strikes a large depression in the vertebra (Fig. 9A, B). A round impact point 2 mm in diameter is formed from which the mark continues at much shallower depth (approximately 0.25 mm). The initial lead in, point of greatest depth, and secondary impact suggest formation by a conical tooth under great pressure.

Three blade-like marks (Category B) and other smaller pits and scratches (Category D) are also present on the specimen.

(F) FINE SCRATCHES TAPERED AT BOTH ENDS
Several fine, round-bottomed scratches, having their widest point near the middle, and tapering markedly towards both ends, are present on specimen QM F14516. Length is 13 mm and width 0.25-0.75 mm (Fig. 9C). Transverse basal corrugations are visible under low magnification. Superficially these marks resemble those in Category (D), but sufficient differences exist to warrant separation, at least initially. Other parts of the specimen show marks assigned to Categories (D) and (J).

(G) ROUND PUNCTURES
Three round punctures of 3-3.5 mm diameter and 3-5 mm depth penetrate the compact bone

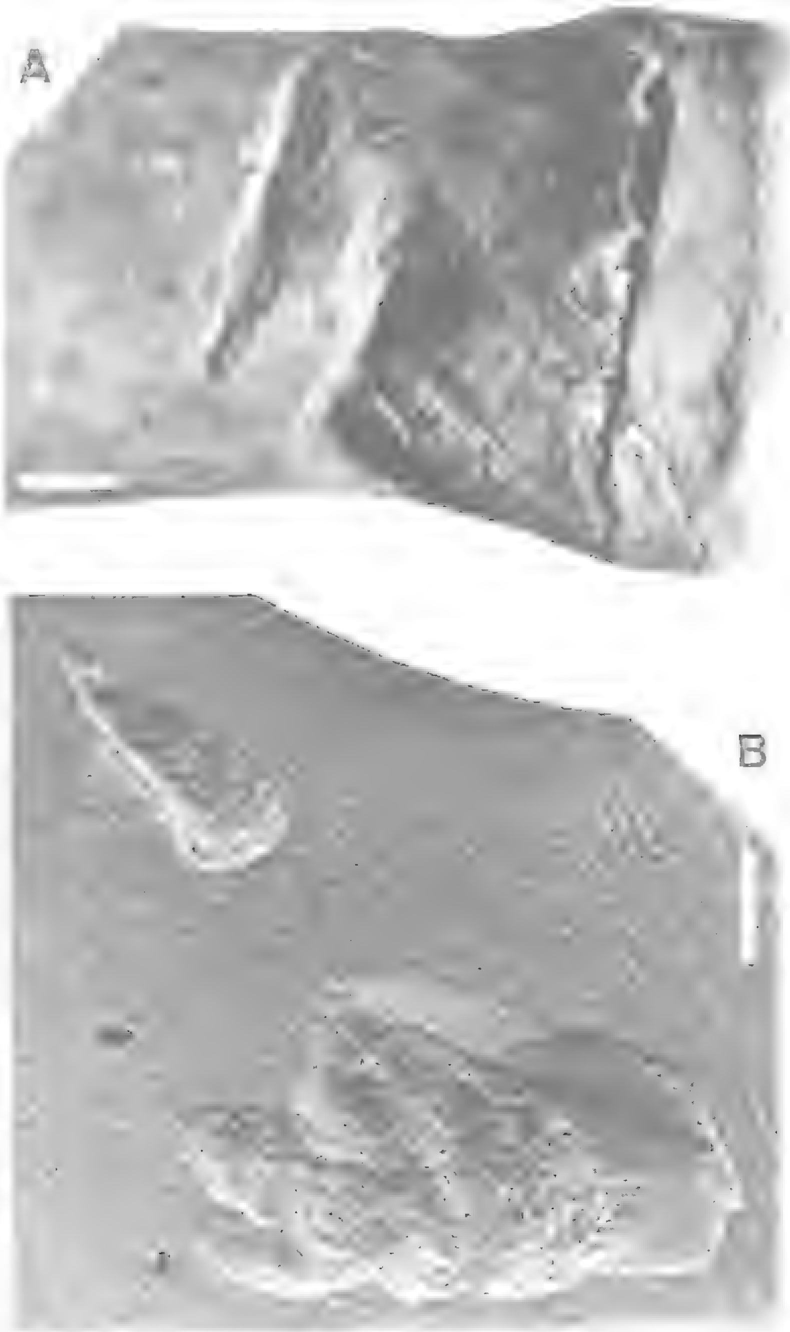

FIG. 6. CATEGORY B — Blade-Like Impressions
A Macropod radius (QM F14507) showing a gradation of marks from shallow V-shaped marks through t o deep round bottomed marks.
CATEGORY C — Crescent Shaped Marks
B Bone fragment with 3 crescent shaped marks. Note the ridge of semi-detached bone at the concave edge of the single mark.
Scale: A Scale Bar = 5 mm. B Scale Bar = 1 mm.

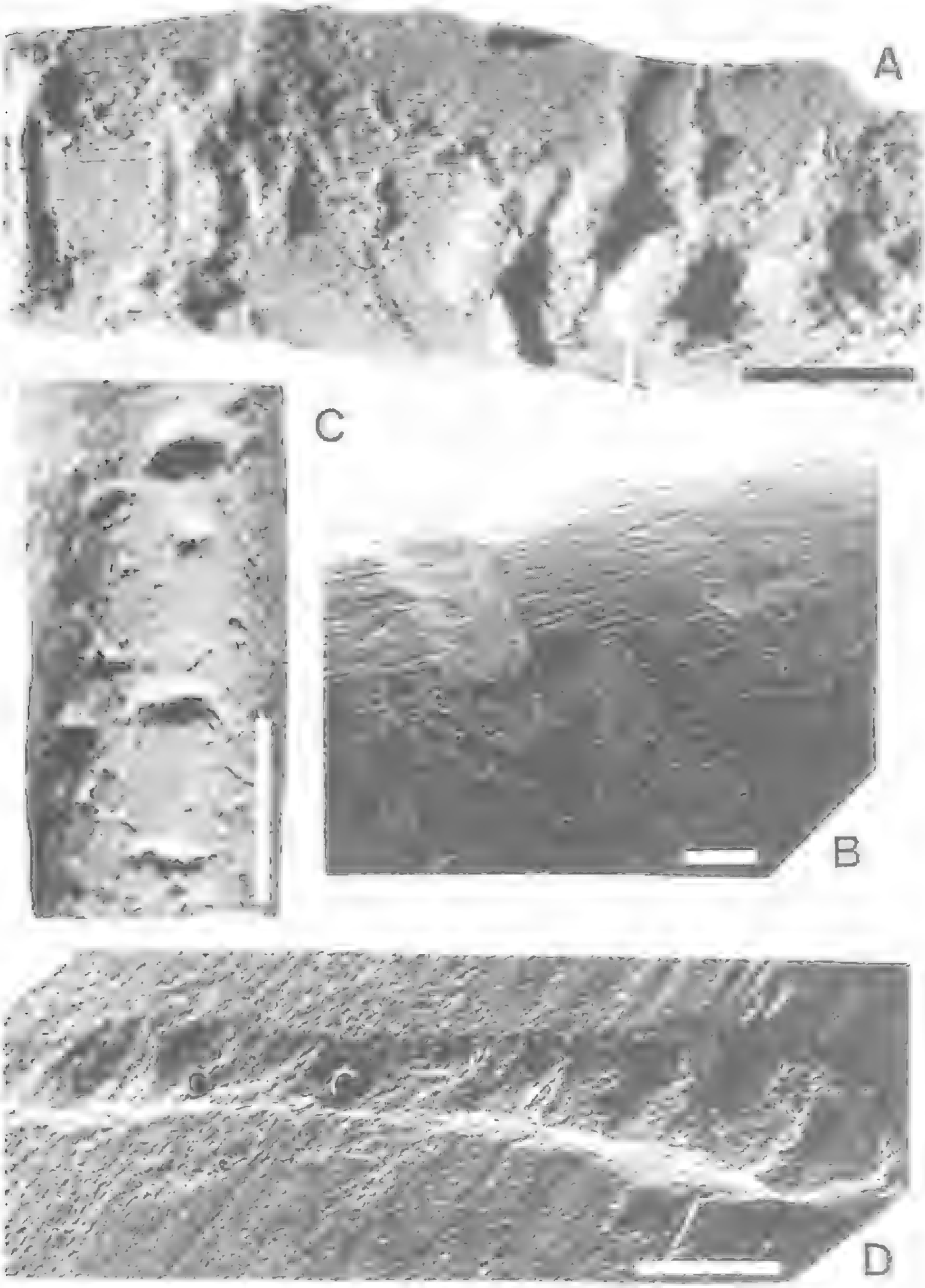

FIG. 7. CATEGORY D — Pits and Scratches

A Bone fragment (QM F14510) with numerous pits and scratches resulting in a very rough surface. Specimen coated with magnesium oxide.

B Scanning Electron Micrograph showing detail of scratches on QM F14510.

C Fifth metatarsal (QM F14509) of a small macropod showing pits and scratches. Specimen coated with magnesium oxide.

D Scanning Electron Micrograph of scratch mark showing distinct transverse basal corrugations (QM F14513).

Scale: A and C Scale Bar = 5 mm. B and D Scale Bar = 1 mm.

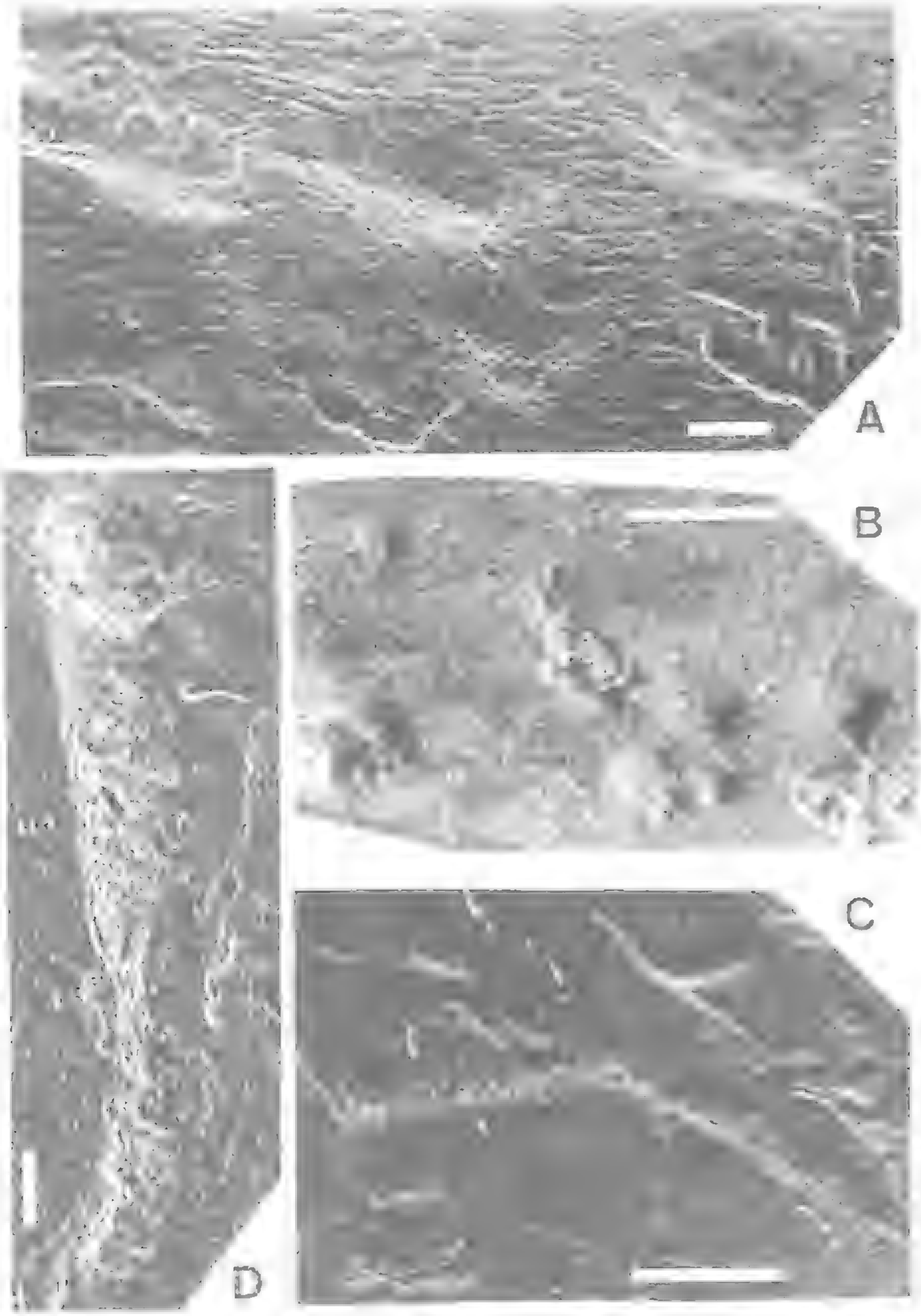

FIG. 8. CATEGORY D — Pits and Scratches
A Scanning Electron Micrograph of bone fragment (QM F14511) showing pit marks. The rough base in the pit at upper left is caused by an encrustation of calcium carbonate. This is also visible in the centre of photograph 8B.
B Bone fragment (QM F14511) showing pit marks.
C Bone fragment (QM F14514) with a boomerang shaped scratch mark. Note the round tooth impact point at the broad end of mark.
D Scanning Electron Micrograph showing initial portion of the boomerang shaped mark in 8C (QM F14514).
Scale: B and C Scale Bar = 5 mm. A and D Scale Bar = 1 mm.

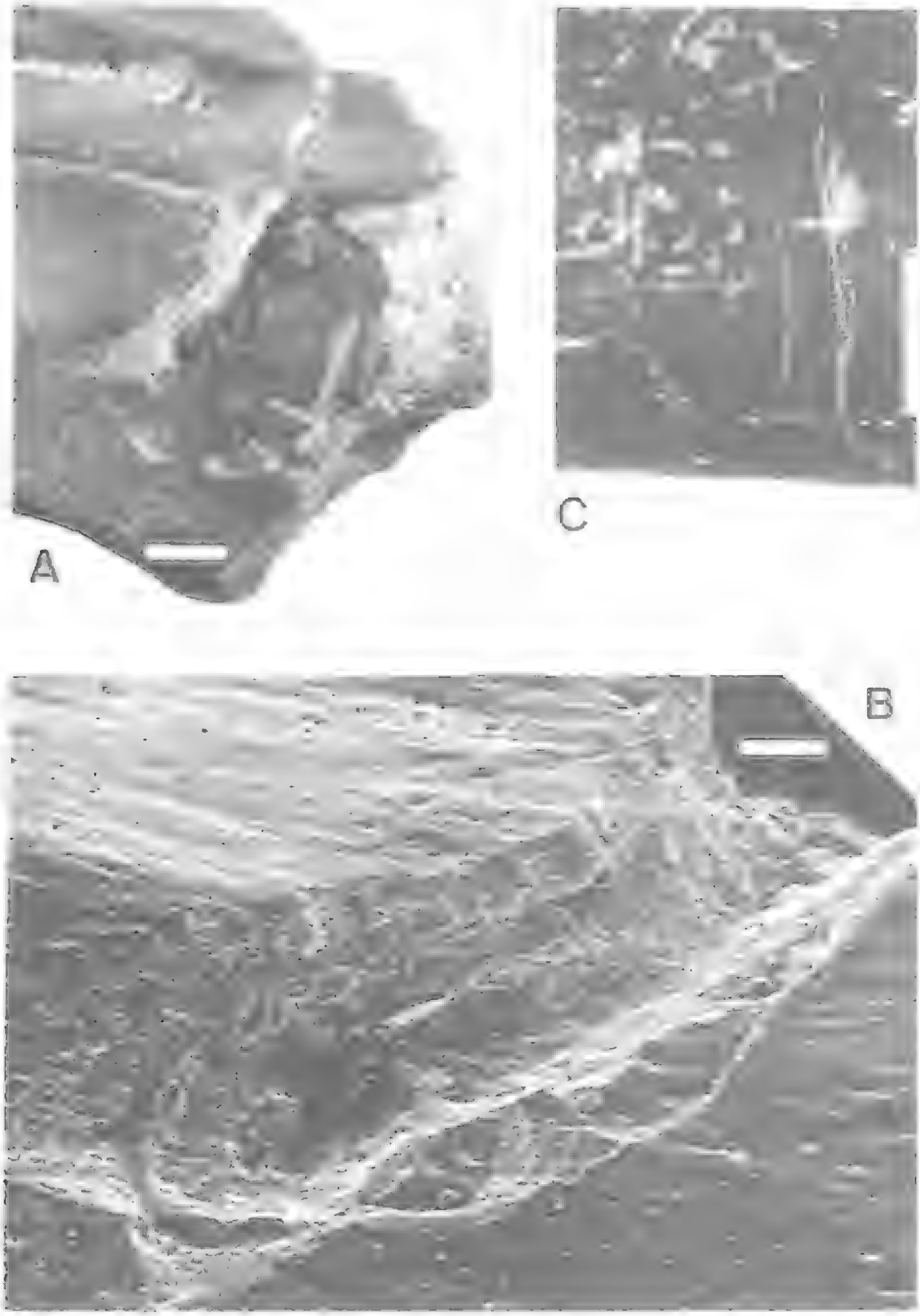

FIG. 9. CATEGORY E — Large Deep Scratches

A Caudal vertebra (QM F14515) of a large macropod with one end removed by carnivores. Note the scratch of exceptional size and depth.

B Scanning Electron Micrograph of the large deep scratch on QM F14515.

CATEGORY F — Fine Scratches Tapering to Each End

C Three scratches tapering to each end on tibia shaft (QM F14516). Distinct basal corrugations are visible.

Scale: A and C Scale Bar = 5 mm. B Scale Bar = 1 mm.

into the underlying spongy bone on specimen QM F14517. The surrounding compact bone is fractured and partially depressed (Fig. 10A); a fourth mark has depressed, but not fully punctured, the compact bone. These punctures appear to be similar to punctures assigned to a carnivore about the size of *Sarcophilus* by Archer *et al.* (1980, fig. 6). Several pits and scratches assignable to Category (D) are also present.

(H) LARGE OVAL PUNCTURES
Large oval punctures 14 mm long X 7 mm wide are present on three specimens. The compact bone has been depressed into the underlying cancellous bone and is still visible at the base of the tooth mark. Depth is in the range 5-9 mm (Fig. 10B). In all cases the long axis of the mark runs parallel to the long axis of the bone in which it is imprinted.

One specimen, QM F14519, shows small pits on the reverse side partially obscured by carbonate encrustation. Numerous marks assignable to Category (B) are visible on other parts of this specimen.

(I) SPONGY BONE REMOVAL WITH DEPRESSED PUNCTURES: FURROWING
The distal portion of a femur, QM F14520, has large areas of the articular surfaces removed. Included in these areas are the remnants of at least five depressed punctures 5-8 mm in diameter (Fig. 11). The remaining articular surface has one depressed puncture 3.5 mm diameter and 1.5 mm deep. A large, compressed oval fracture 10 mm X 6 mm is present at the base of the articular surface; depth is approximately 1 mm. This specimen is partly weathered, but the damage noted is undoubtedly primarily due to carnivores. Similar damage was referred to as furrowing by Haynes (1983).

(J) RAGGED EDGES AND HOLLOW-BACKED FLAKES
Many specimens have ragged edges which show small (4-5 mm) concave depressions where carnivore or scavenger gnawing has systematically removed the bone edge (Fig. 12A,B). Each concave depression represents the impact point of a tooth cusp. Some specimens also show depressions on bone edges in which the bite has removed a large flake from the back of the specimen (Fig. 12C,D). This category of tooth marks is unlikely to be assignable to any particular carnivore or scavenger.

The noted specimens also show tooth marks assignable to Categories (B), (D) and (F), which superficially resemble each other, especially in specimens that are partially weathered. It is only when non-weathered specimens are examined under magnification that the differences in profile can be fully appreciated.

FEEDING TRIAL

A *Sarcophilus* feeding trial was undertaken at the Lone Pine Koala Sanctuary, Brisbane. The animal selected for the feeding trial was a healthy mature male with an estimated age of six years. It was housed in a 6 by 6 m concrete and rock walled pen with a natural earth floor and shade trees. The captive animal's normal diet was rotationally selected from raw beef, commercial greyhound pellets, dead rats and chickens (P. Douglas, pers. comm.).

Because macropods form part of the natural diet of Tasmanian devils, and because a large percentage of bones found in the fossil sites under study are from medium (*Macropus siva*) and large (*Macropus titan* and *Protemnodon anak*) macropods, two articulated hind legs of a red-necked wallaby (*Macropus rufogriseus*) were used in this feeding trial. Test bones were largely stripped of meat and hide at the request of sanctuary staff to reduce the risk of introducing internal parasites. Care was taken not to mark the bones in this process. Phalanges were removed with the hide and were not presented for feeding.

Bones were placed in the pen at approximately 5 pm and removed at about 7.30 am the following day. The retrieved bones were boiled in enzyme detergent solution (Bio-Ad^{TM}) to remove all remaining flesh and tendons, and then dried and examined for tooth marks.

Three bones (a femur and two metatarsals) had been consumed; others had some areas consumed and showed evidence of tooth marks. A detailed summary of damage is presented in Appendix 2.

DESCRIPTION OF TOOTH MARKS

The marks produced by *Sarcophilus harrisii* on the wallaby bones fall into five distinct categories.

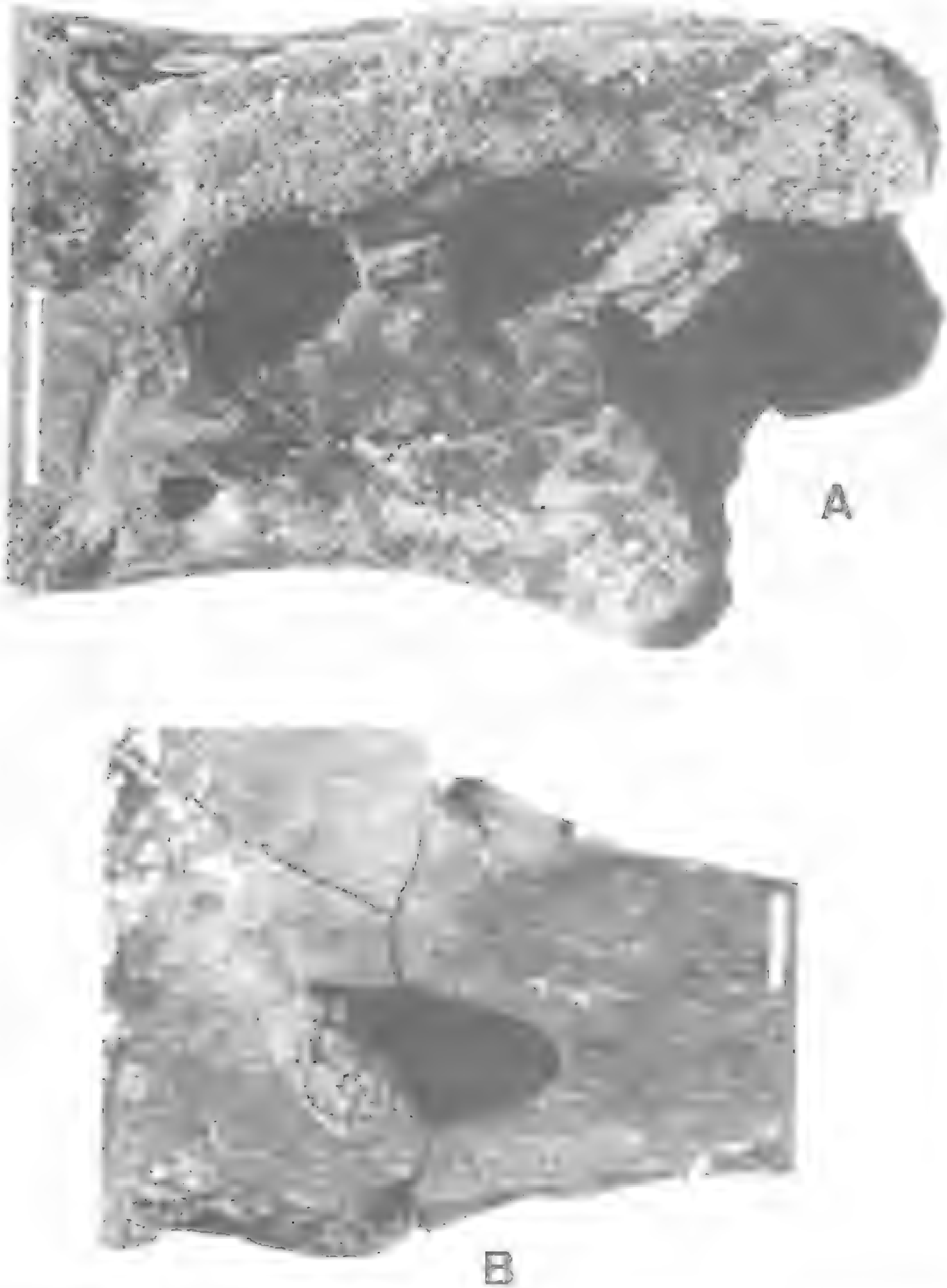

FIG. 10. CATEGORY G — Round Punctures
A Bone section (QM F14517) showing small round punctures. The small hole at lower left is a foramen.
CATEGORY H — Large Oval Punctures
B Partial macropod pelvis (QM F14519) showing a large oval puncture in the pubis.
Scale: A and B Scale Bar = 5 mm.

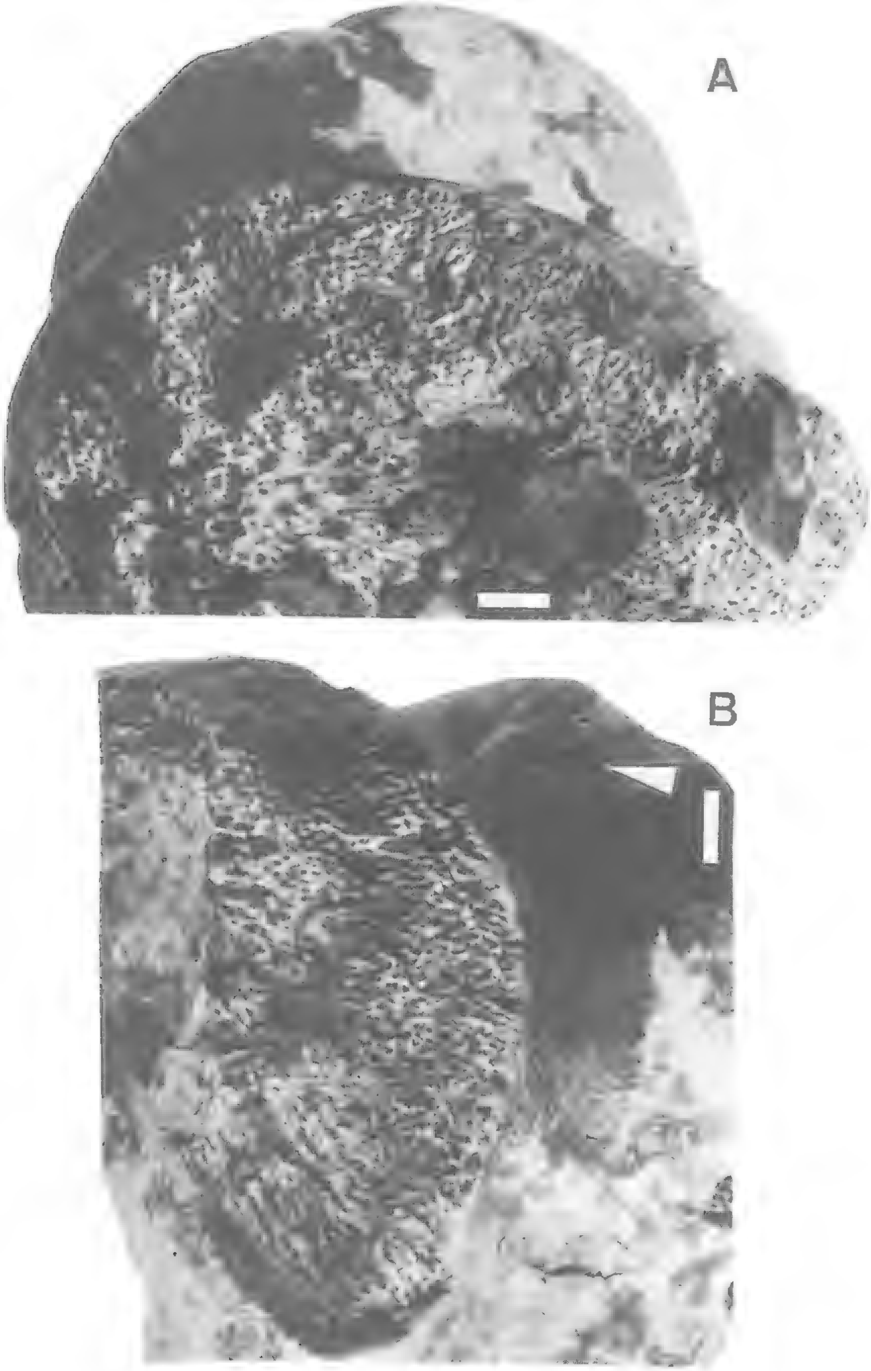

FIG. 11. CATEGORY I — Spongy Bone Removal with Depressed Punctures
A Distal femur (QM F14520) showing removal of articular surfaces and several depressed punctures.
B Another view of QM F14520 showing similar damage plus a compressed fracture at lower right and small round puncture at upper right (Arrowed).
Scale: A and B Scale Bar = 5 mm.

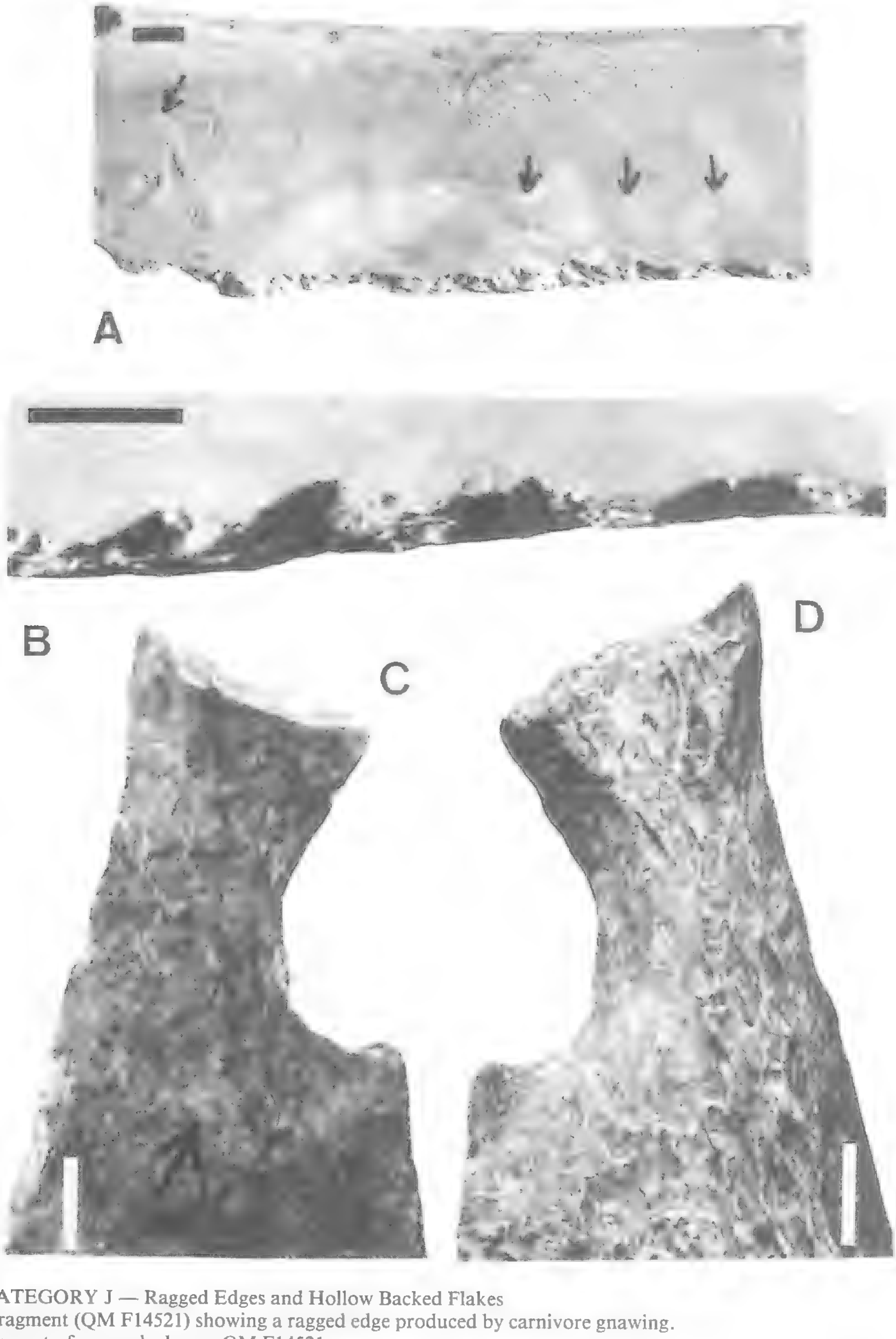

FIG. 12. CATEGORY J — Ragged Edges and Hollow Backed Flakes
A Tibia fragment (QM F14521) showing a ragged edge produced by carnivore gnawing.
B Enlargement of gnawed edge on QM F14521.
C Obverse view of bone fragment (QM F14523) with a concave edge where a bite has removed a flake of bone.
D Reverse view of QM F14523 showing the hollow back produced by the bite.
Scale: All Scale Bars = 5 mm.

(1) VERY SHALLOW SCRATCHES: These are particularly noticeable on the proximal end of the tibia, adjacent to areas of heavier tooth marks; some are also present on the distal end of the femur. These scratches commence at a maximum width of 0.3-1 mm and taper to disappear entirely. Length varies between 3 mm and 20 mm, but only occasionally do they exceed 10 mm (Fig.13). They are extremely shallow, barely breaking the surface of the compact bone. These marks may be caused by incisor teeth in removing small areas of muscle and tendon, although some may be claw marks produced when the bones are held in the front paws during feeding. Solomon (pers. comm., 1987) has observed this type of feeding behaviour by devils. It is doubtful that such shallow marks would survive to be visible in fossil specimens, particularly those from fluviatile deposits.

(2) PITS AND SCRATCHES: Deeper pits and scratches are present on all chewed bones and are particularly noticeable on opposing surfaces of the femur and metatarsals. Pits are round to oval with a maximum diameter of 2 mm; most are 1 mm — 1.5 mm. Depth ranges up to a maximum of 1 mm (Fig. 14). Occasional pits show a concentric double crater effect (Fig. 15A; see Solomon, 1985). Scratches are elongated round bottomed marks with a maximum length of 5 mm and maximum width of 1.5 mm. Smaller and more shallow scratches are nearly parallel while larger and deeper scratches taper slightly and become more shallow along their length (Figs 14, 15). Scratches often show basal corrugations at right angles to the long axis of the mark where a tooth has broken through successive layers of bone tissue (Fig. 15). These pits and scratches are often associated in large numbers on opposing bone surfaces (femur and metatarsals) producing a very rough appearance (Fig. 14). Both pits and scratches appear to be produced by carnassial teeth as these were used to break the bone into pieces small enough to be swallowed. These marks should be easily visible in fossil material, with the exception of specimens which are severely weathered or abraded.

(3) LARGE PUNCTURES WITH SPONGY BONE REMOVAL: FURROWING. Part of the articular surface and underlying spongy bone have been removed from the distal end of the femur. Impressed in this region are large punctures of oval or triangular outline with maximum width of 8 mm and maximum depth of 5 mm (Fig. 16A). These marks appear to be from carnassial and possibly canine teeth. They appear larger and deeper simply because of the lesser resistance offered by the spongy bone. Damage of this type was referred to as furrowing by Haynes (1983), and it should be easily visible in well-preserved fossil material.

(4) SEMICIRCULAR MARK: The broken end of one fibula shows a semi-circular mark perpendicular to the long axis of the bone; here a round tooth or tooth cusp has broken through the bone, severing it into two pieces (Fig. 16B). Despite being clearly recorded, this mark is unlikely to be diagnostic.

(5) DEEP LONGITUDINAL "V". A deep "V" parallel to the long axis of the bone is impressed in the chewed proximal end of the tibia (Figs 16C, D). The end of the "V" has the compact bone depressed downwards into the underlying spongy bone. The reverse side of the bone shows remnants of two similar marks, one being the counterpart of the mark described above. These depressed areas, which have a width of 5 mm — 6 mm, appear to be made by canine teeth and should easily be preserved in fossil material.

DISCUSSION

It is conceivable that the tooth marks and amount of damage observed may not be entirely representative for *Sarcophilus*. Additional feedings and field studies need to be conducted, using other portions of carcasses and whole carcasses. As much of the fossil material found in southeastern Queensland Pleistocene sites is from larger macropods, trials using larger macropods would be desirable.

Feeding competition by numbers of animals may change the intensity of marks and damage. Guiler (1983) noted up to twelve animals feeding on and squabbling over a carcass. This may result in complete consumption of the carcass. The effects of such behaviour could not be investigated here because too few animals were available.

The marked bones discussed in this paper are all derived from fluviatile deposits. Fluvial action will undoubtedly have an affect on any bones that find their way into such an environment. The nature and extent of that damage and, more importantly, its

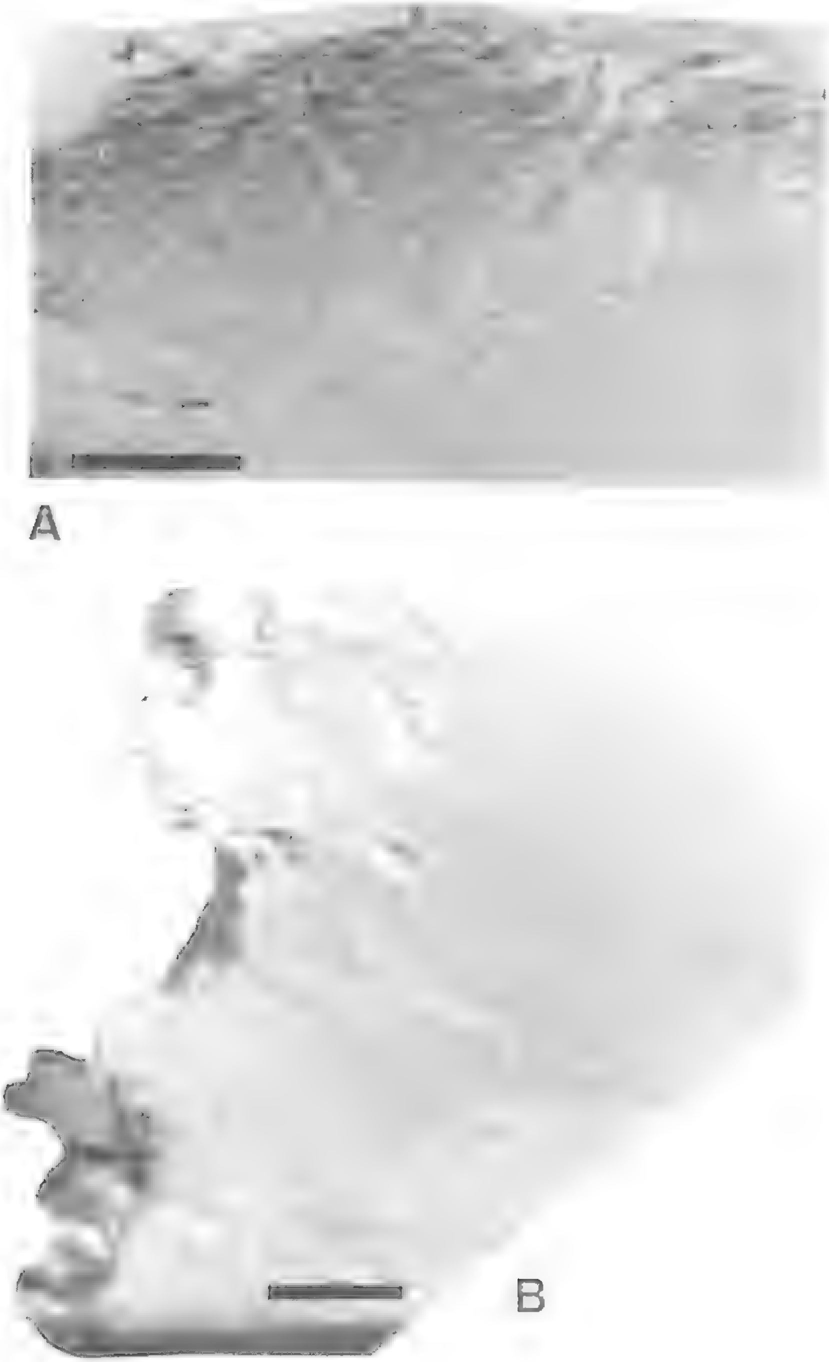

FIG. 13. CATEGORY I — Very Shallow Scratches (Feeding Trial)
A Wallaby proximal tibia (QM JM6533) showing very shallow scratches; one being of extreme length.
B Wallaby tibia (QM JM6527) with proximal end consumed. Some very shallow scratches are prsent along with much deeper pits and scratches.
Scale: A and B Scale Bar = 5 mm.

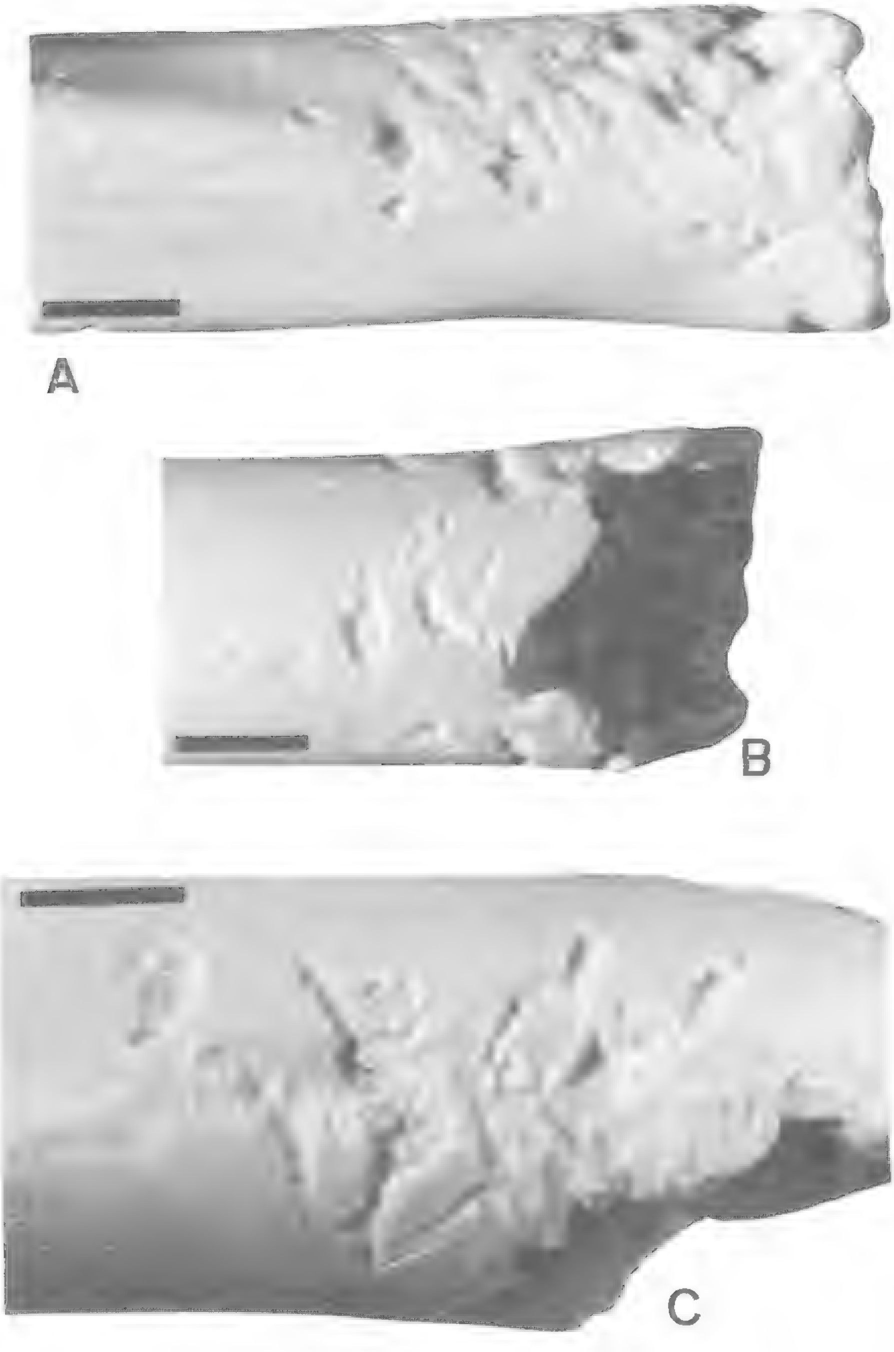

FIG. 14. CATEGORY II — Pits and Scratches (Feeding Trial)
A Wallaby fourth metartarsal (QM JM6530) with distal end removed by chewing. Adjacent areas show numerous pits and scratches producing a very rough surface.
B Reverse side of metatarsal (QM JM6530) shown in 14A.
C Shaft of wallaby femur (QM JM6532) with proximal end removed by chewing. Numerous pits and scratches producing a very rough surface.
Scale: A, B and C Scale bar = 5 mm.

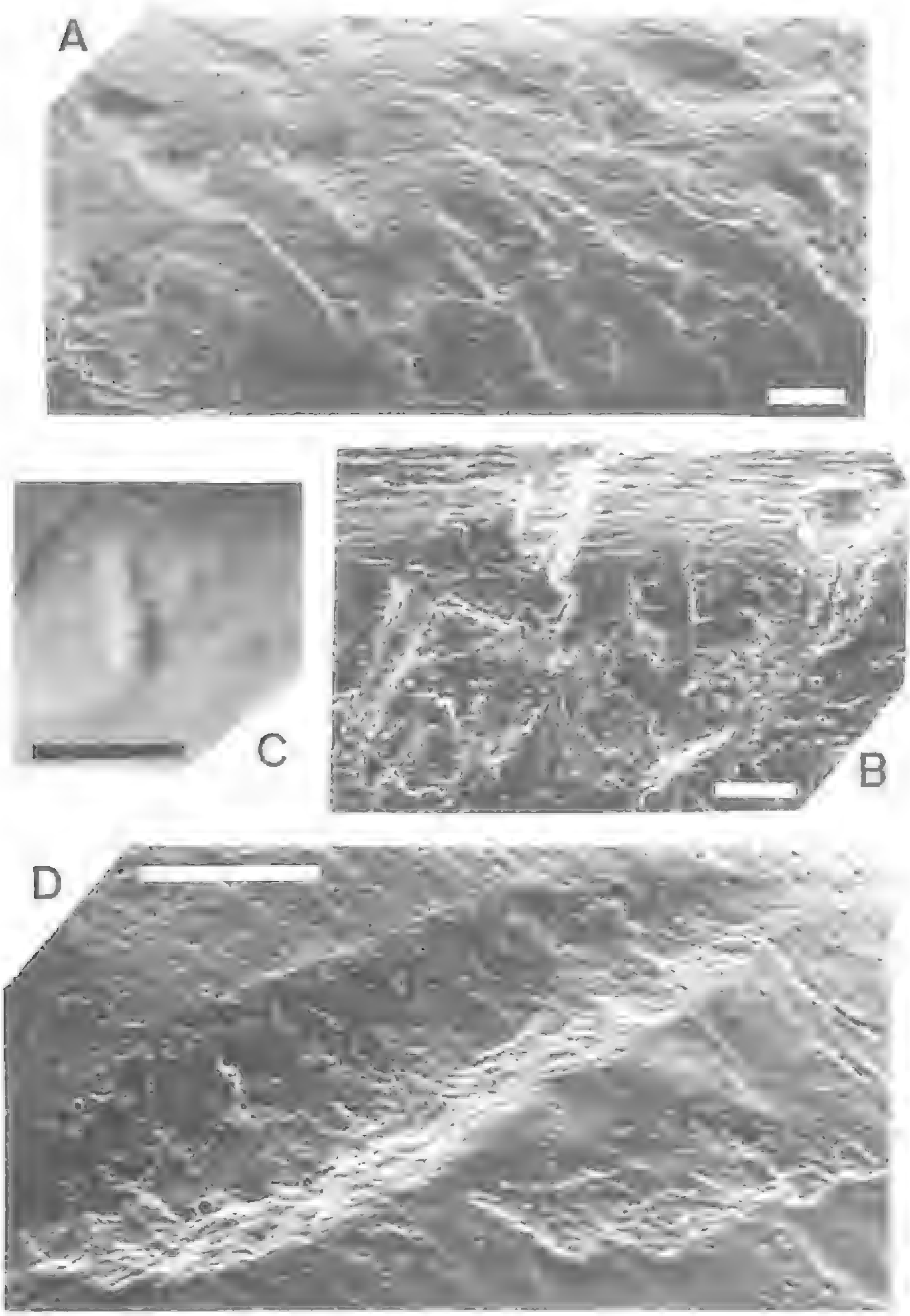

FIG. 15. CATEGORY II — Pits and Scratches (Feeding Trial)
A Scanning Electron Micrograph of distal fourth metatarsal (QM JM6530) shown in Fig. 14A. Note concentric double crater at top right.
B Scanning Electron Micrograph of proximal femur (QM JM6532) shown in Fig. 14C.
C Large scratch mark on wallaby femur (QM JM6532) showing distinct transverse basal corrugations.
D Scanning Electron Micrograph of large scratch mark on wallaby femur (QM JM6532) shown in Fig. 15C to show detail of the transverse corrugations.
Scale: A, B and D Scale Bar = 1 mm. C Scale Bar = 5 mm.

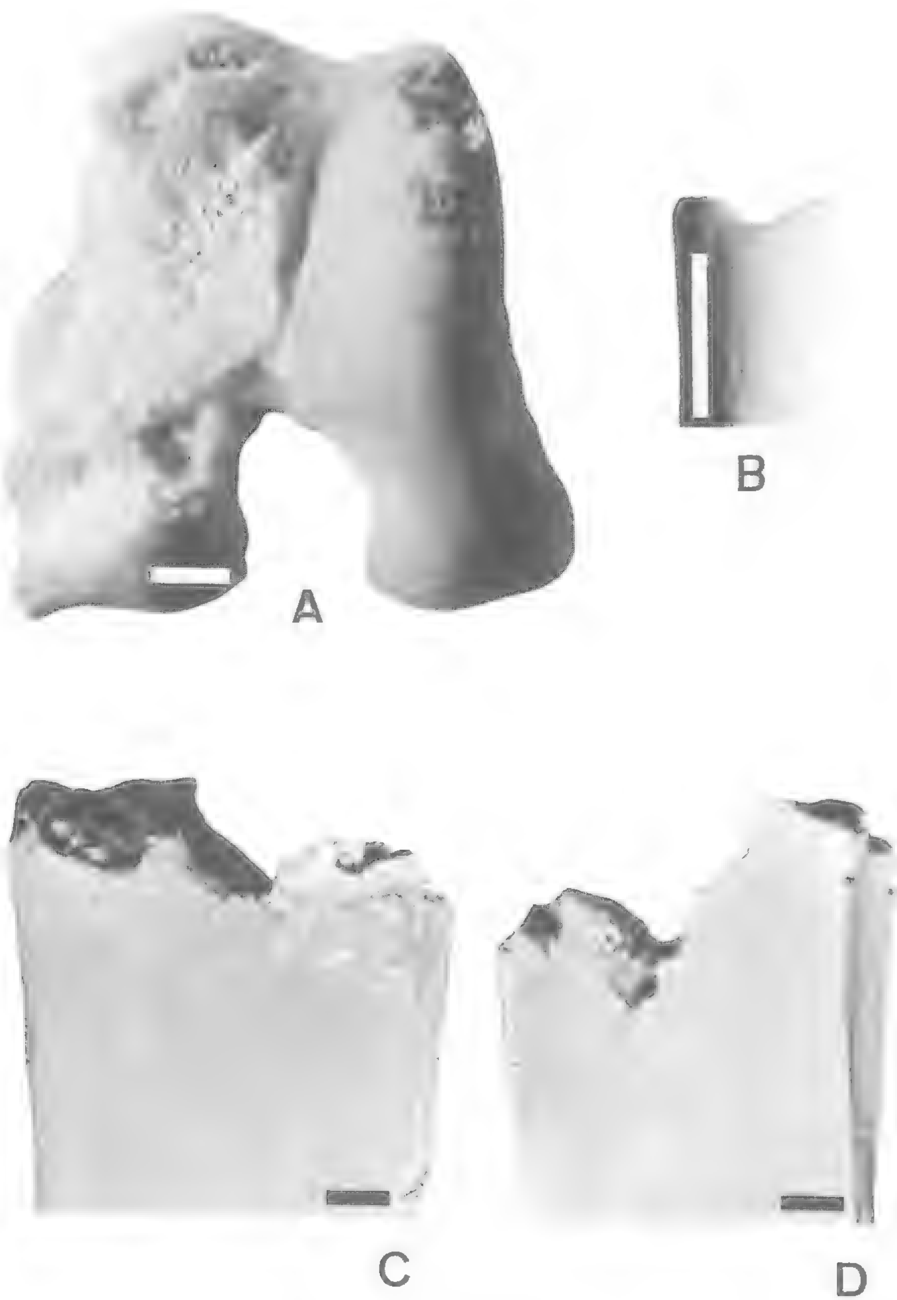

FIG. 16. CATEGORY III — Large punctures with Spongy Bone Removal (Feeding Trial)
A Distal femur (QM JM6532) showing where the articular surface and underlying spongy bone have been removed. Several large punctures are visible.
CATEGORY IV
B Proximal fibula (QM JM6528) showing semicircular tooth mark where the bone was bitten into two pieces.
CATEGORY V — Deep Longitudinal "V" (Feeding Trial)
C Reverse view of proximal tibia (QM JM6527) showing remnants of two deep "V" shaped marks.
D Obverse view of proximal tibia (QM JM6527) showing deep "V" shaped mark.
Scale: A, B, C and D Scale bars = 5 mm.

ability to mimic tooth marks is of importance to this paper. Shipman and Rose (1983a) have shown that sedimentary abrasion tends to obliterate marks on bone and only occasionally produces marks that mimic carnivore tooth scratches.

Marks produced by contact with rocks need to be considered. The biggest rocks in the measured section are 5-7 cm in diameter, and, these occur only in the lowest exposed level. Most of these large pieces are calcareous and well-rounded, with few sharp projections. Some hard, well-rounded rocks occur in the very lowest levels of locality 1, but only a small number of bones was recovered from this level. The remainder of the matrix is composed of fine sandy alluvium with patches of small pebbles. In localities (2) and (3), marked bones are found both in the finer sediments and in the underlying nodular areas. A very high proportion of the marks derived from the nodular areas are abraded to a point where many of the features of the marks are obliterated and are often not able to be assigned to a particular category with confidence. Specimens with this degree of abrasion are much rarer in the finer sediments.

If these marks were produced by contact with stones during transport and deposition, the greatest concentration of unabraded marks would be expected to occur on bones in the stony areas. However, the reverse is true, with these bones having most marks heavily abraded. It would appear, therefore, that fluvial action is obliterating rather than producing the marks considered here.

The object of the feeding trial was to establish the appearance of a normal range of tooth marks on bone fed to *Sarcophilus harrisii*. These marks were then compared with a collection of tooth marks on fossil bones to see if *Sarcophilus* damage could be recognised in the fossil sample. Five categories (named and numbered 1-5) of tooth marks were recognised on bones fed to *Sarcophilus* at Lone Pine Koala Sanctuary, whilst ten categories (named and designated A-J) were recognised in the fossil material.

A distinct overlap is present within the modern and fossil tooth marks. The most numerous tooth marks in the feeding trial are pits and scratches (Category 2). Similar pits and scratches (Category D) are among the most common tooth marks in the fossil material. The two categories are clearly similar in the size and shape of the marks. In both cases the tooth marks tend to be so densely grouped as to give the bone a very roughened surface, particularly near the extremities. This is especially noticeable in both fossil and trial metatarsals.

Specimens are present from both the fossils and feeding trial where areas of articular surface and the underlying spongy bone have been removed (Categories 3 and I). Both show large punctures up to 8 mm diameter where teeth have penetrated the spongy bone. Both specimens are distal portions of femora, a fact which may be coincidental or may show a preferential feeding habit. Although the fossil specimen is partly weathered there is clear overlap between these two classes of marks.

The round punctures (Category G) are clearly similar to those attributed to a carnivore about the size of *Sarcophilus* by Archer *et al.* (1980). They are not exactly duplicated in the feeding trial but might easily be produced by the teeth of *Sarcophilus*. These marks are not considered to be of diagnostic value.

There is great similarity between the tooth marks produced by *Sarcophilus harrisii* in feeding trials and some categories of tooth marks found on fossil bones from Pleistocene sites in southeastern Queensland. *Sarcophilus* is well represented by dental elements in these sites. Thus it seems likely that *Sarcophilus* was one of the principal carnivores present during the Pleistocene in southeastern Queensland and that its presence may be detected by the examination of tooth marked bones.

Some tooth marks in the fossil sample are clearly not the work of *Sarcophilus*. Of these, some may be attributed to rodents and *Thylacoleo*, whilst others are of uncertain origin. Dingos have not been considered as a possible source of tooth marks because their skeletal remains are unknown from the fossil beds considered here. Moreover the earliest skeletal remains of a dingo come from Madura Cave, Western Australia, and are dated at 3450 ± 95 B.P (ANU807) (Solomon & David, 1987); the King Creek beds are at least 20,000 years older (minimum age 23,600 ± 600 B.P.)

Looking at faunal lists we would expect to find tooth mark evidence of other major Pleistocene predators like thylacines, crocodiles and *Megalania*. However, because of the voracious feeding habits of crocodiles and Komodo Dragons (the closest comparable varanid to *Megalania*), along with the ability to substantially digest bone, tooth mark evidence for these carnivores may be difficult to locate (see Auffenberg (1972) for a discussion of the feeding habits of Komodo Dragons).

These unidentified tooth marks are to be the basis of further studies.

ACKNOWLEDGEMENTS

Many people have helped during the course of this project. Firstly, thanks go to my wife Diane for her patience and for typing the various drafts of this manuscript. Scanning electron microscopy was carried out by Rob Jupp and Bill Young (Department of Oral Biology and Oral Surgery, University of Queensland) with the cooperation of the Electron Microscope Centre, University of Queensland. Su Solomon, Andrew Rozefelds Mary Wade, Peter Hiscock and Susan Turner made valued comment on various drafts of the manuscript. Alan Bartholomai, Ralph Molnar, Steve van Dyck, Rod Wells, David Horton, Mike Archer, Bruce Runnegar and the late Edmund Gill commented on various specimens. The *Sarcophilus* feeding trial was carried out at Lone Pine Koala Sanctuary, Brisbane with the kind co-operation and help of Mr Peter Douglas. Mr Peter Pearce (Soil and Water Conservation Branch, Department of Primary Industries, Clifton) helped measure the stratigraphic section of King Creek. Photography was undertaken by Bruce Cowell, Queensland Museum, and the final manuscript was typed by Peta Woodgate. This work was supported by an honorary research fellowship of the Queensland Museum.

LITERATURE CITED

ARCHER, M., CRAWFORD, I. AND MERRILEES, D. 1980. Incisons, breakages and charring, some probably man made, in fossil bones from Mammoth Cave, Western Australia. *Alcheringa* 4: 115–31.

CLAYTON, G. AND HAND, S. 1984. A checklist of Australian Fossil Mammals. p. 1027–87 *In* Archer, M. and Clayton, G. (Eds) 'Vertebrate Zoogeography and Evolution in Australia'. (Hesperian Press: Perth).

AUFFENBERG, W. 1972. Komodo Dragons. *Natural History* 81(4): 52–9.

BAIRD, R. 1985. Tasmanian Native Hen *Gallinula mortierii*. The first late Pleistocene record from Queensland. *The Emu* 86(2): 121–2.

BARTHOLOMAI, A., 1976. Notes on the Fossiliferous Pleistocene Fluviatile Deposits of the Eastern Darling Downs. *Bureau of Mineral Resources, Bulletin* 166: 153–4.

BEHRENSMEYER, A.K. 1978. Taphonomic and Ecologic information from Bone Weathering. *Paleobiology* 4(2): 150–62.

DE VIS, C.W. 1900. Bones and Diet of *Thylacoleo*. *Annals of the Queensland Museum* 5: 7–11.

DOUGLAS, A.M., KENDRICK, G.W. AND MERRILEES, D. 1966. A fossil bone deposit near Perth, Western Australia, interpreted as a carnivore's den after feeding tests on living *Sarcophilus* (Marsupialia, Dasyuridae). *Journal and Proceedings of the Royal Society of Western Australia* 49: 88–90.

GILL, E.D. 1978. Geology of the Late Pleistocene Talgai Cranium from S.E. Queensland, Australia. *Archaeology and Physical Anthropology in Oceania* 13: 177–97.

GUILER, E.R., 1983. Tasmanian Devil. p. 27-8 *In* Strahan, R. (Ed) 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson Publishers: Sydney).

HANSON, C.B. 1980. Fluvial Taphonomic Processes: Models and Experiments. P. 156-81 *In* Behrensmeyer, A. and Hill, A. (Eds.) 'Fossils in the Making'. (University of Chicago Press: Chicago).

HAYNES, G., 1980. Evidence of Carnivore Gnawing on Pleistocene and Recent Mammalian Bones. *Paleobiology* 6(3): 341–51.

1983. A guide to differentiating Mammalian Carnivore taxa, responsible for gnaw damage to herbivore limb bones. *Paleobiology* 9(2): 164–72.

HORTON, D.R. and WRIGHT, R.V.S. 1981. Cuts on Lancefield Bones:Carnivorous *Thylacoleo*, not Humans, the cause. *Archaeology in Oceania* 16: 73–80.

MOLNAR, R.E. 1982. A Catalogue of Fossil Amphibians and Reptiles in Australia. *Mem. Qd Mus.* 20(3): 613–33.

POTTS, R. AND SHIPMAN, P. 1981. Cuts made by Stone Tools on Bones from Olduvai Gorge, Tanzania. *Nature* 291: 577–80.

ROSE, J. 1983. A Replication Technique for Scanning Electron Microscopy: Applications for Anthropologists. *American Journal of Physical Anthropology* 66: 255–61.

RUNNEGAR, B. 1983. A *Diprotodon* ulna chewed by the Marsupial Lion, *Thylacoleo carnifex*. *Alcheringa* 7: 23–5.

SHIPMAN, P. AND ROSE, J. 1983(a). Early Homonid hunting, butchering and carcass processing behaviour: approaches to the fossil record. *Journal of Anthropology and Archaeology* 2: 57-98.

AND ROSE, J. 1983(b). Evidence of butchering and homonid activities at Torralba and Ambrona: an evaluation using microscopic techniques. *Journal of Archaeological Sciences* 10: 465–74.

AND ROSE, J. 1984. Cutmark mimics on modern and fossil bovid bones. *Current Anthropology* 25: 116–7.

SOLOMON, S., 1985. People and other Aggravations. Taphonomic research in Australia. Bachelor of Arts thesis, Department of Prehistory and Archaeology, University of New England, Armidale, New South Wales (Unpublished).

AND DAVID, B. (in press). Middle range theory and actualistic studies: Bones and dingoes in Australian Archaeology. "Taphonomy of Bones Conference", University of New England, Armidale, 21-22 February, 1987.

SPENCER, B. AND WALCOTT, F.O.S., 1911. The origin of cuts on Bones of Australian Extinct Marsupials. *Proceedings of the Royal Society of Victoria* 24(1): 92–123.

WOOD, W.R. AND JOHNSON, D.L. 1978. A Survey of Disturbance Processes in Archaeological Site Formation. P. 539-605 *In* Schiffen, M.A. (Ed.) 'Advances in Archaeological Method and Theory', vol. 1. (Academic Press: New York).

WOODS, J.T., 1960. Fossiliferous fluviatile and cave deposits. *Journal of the Geological Society of Australia* 7: 393–403.

APPENDIX 1

REFERRED FOSSIL SPECIMENS

(A) ROUND BOTTOMED SCRATCHES WITH ANCHOR POINTS
QM F14504: from locality (1) (King Creek). Central fragment of a rib of a large macropod which measures 165 mm in length X 12 mm average diameter.

(B) BLADE LIKE IMPRESSIONS
QM F14505: from locality (5) (Budgee Creek). Proximal portion of a rib of a large macropod? showing six bite marks. Length 165 mm; Average Diameter 12 mm.
QM F14506: from locality (2) (King Creek). Central fragment of large macropod pelvis showing three bite marks. Length 85 mm; Width 55 mm.
QM F14507: from locality (3) (King Creek). Unidentified large radius missing distal end (chewed off). Length 365 mm; Average Diameter 25 mm. Numerous bite marks each end.

(C) CRESCENT SHAPED MARKS
QM F14508: from locality (1) (King Creek). Fragment of a long bone showing three crescent shaped marks. Length 113 mm; Width 23 mm.

(D) PITS AND SCRATCHES
QM F14509: from locality (3) (King Creek). Fifth metatarsal of a small macropod, missing distal extremity. Numerous pits and scratches over much of bone. Length 77 mm; Width 10 mm.
QM F14510: from locality (1) (King Creek). Bone fragment with numerous pits and scratches. Length 51 mm; Width 10 mm.
QM F14511: from locality (1) (King Creek). Long bone fragment with six pit marks. Length 187 mm; Width 28 mm.
QM F14512: from locality (1) (King Creek). Long bone fragment with six scratch marks, with corrugated bases, arranged in boomerang shape. Length 63 mm; Width 19 mm.
QM F14513: from locality (3) (King Creek). Bone fragment with transverse scratches with distinctly corrugated bases. Length 208 mm; Width 15 mm.
QM F14514: from locality (1) (King Creek). Bone fragment with numerous scratches. One boomerang shaped mark shows distinct round impact point. Length 40 mm; Width 30 mm.

(E) LARGE DEEP SCRATCHES
QM F14515: from locality (1) (King Creek). Caudal vertebra of a large macropod with one end missing due to carnivores. Length 75 mm; Diameter 54 mm.

(F) FINE SCRATCHES TAPERED AT BOTH ENDS
QM F14516: from locality (1) (King Creek). Shaft of tibia from large macropod, both ends showing tooth marks. Length 345 mm; Width 48 mm.

(G) ROUND PUNCTURES
QM F14517: from locality (3) (King Creek). Bone section with small round punctures. Length 31 mm; Width 17mm.

(H) LARGE OVAL PUNCTURES
QM F14518: from locality (1) (King Creek). Bone fragment with one large oval puncture. Length 110 mm; Width 32 mm.
QM F14519: from locality (1) (King Creek). Central portion of the pelvis of a very large macropod with one large oval puncture on the pubis. Length 350 mm.

(I) SPONGY BONE REMOVAL WITH DEPRESSED PUNCTURES: FURROWING
QM F14520: from locality (3) (King Creek). Distal portion of femur (?macropod). Length 70 mm; Width 65 mm.

(J) RAGGED EDGES AND HOLLOW BACKED FLAKES
QM F14521: from locality (1) (King Creek). Fragment of shaft of large tibia (?macropod). Length 243 mm; Width 30 mm.
QM F14522: from locality (1) (King Creek). Shaft of tibia from large macropod. Length 345 mm; Width 48 mm.
QM F14523: from locality (1) (King Creek). Bone fragment with semicircular flake removed leaving a hollow back. Length 115 mm; Width 38 mm.

APPENDIX 2

SUMMARY OF DAMAGE TO BONES FROM FEEDING TRIAL

LEG 1

Femur: This was apparently consumed as no portion of the bone was returned.

Tibia (QM JM6527): 2.5 cm of the proximal end was consumed leaving a rather jagged edge on the remainder. The adjacent 4 cm showed tooth marks ranging from very shallow scratches to more deeply impressed pits and scratches. A large depressed fracture is present at the edge of the proximal end.

Fibula (QM JM6528): 2.5 cm of the proximal end was consumed. The fractured end retains a single furrow perpendicular to the long axis of the bone where a bite has severed the consumed end. The adjacent 5 cm of the bone show occasional small pits and scratches.

Calcaneum (QM JM6529): Returned intact, but with several small pits and scratches present.

Metatarsals: Metatarsals 2 and 3 were not returned. The distal 2 cm of metatarsal 4 (QM JM6530) and distal 1.5 cm of metatarsal 5 (QM JM6531) were consumed leaving jagged edges. The adjacent 1-2 cm show extensive areas of tooth marks made up of a series of pits and scratches. These are very closely spaced and leave the bone surface with an extremely rough texture.

LEG 2

Femur (QM JM6532): One third of the proximal end was consumed, leaving the end with a jagged outline. The adjacent 2 cm have areas of closely spaced pits and scratches leaving the bone with a very rough surface. Approximately one third of the distal articular surface and underlying spongy bone were consumed. Large depressed tooth marks are present in the remaining spongy bone. These appear to be from carnassial teeth.

Tibia (QM JM6533): Damage is slight and restricted to the proximal 5 cm of the bone. Small areas of spongy bone have been removed. Three large pits are present on the edge of the epiphysis. Adjacent areas of the shaft show long but very shallow scratches.

Fibula (QM JM6534): Several shallow scratches are present 3-4 cm from the distal end. Calcaneum (QM JM6535): No damage was evident. Metatarsals (QM JM6536): No damage was evident.

DATING THE GREAT NEW GUINEA-AUSTRALIA VICARIANCE EVENT: NEW EVIDENCE FOR THE AGE OF AUSTRALIA'S TERTIARY MAMMAL FAUNAS

ABSTRACT

T.F. FLANNERY

Flannery, T.F. 1990 3 31: Dating the Great New Guinea-Australia vicariance event: new evidence for the age of Australia's Tertiary Mammal Faunas. *Mem. Qd Mus.* **28**(1): 323. Brisbane. ISSN 0079-8835.

Recent geological evidence suggests that there were only two periods during the Tertiary when Australia and New Guinea were united — the Eocene-Oligocene, and the Pleistocene. The ancestors of most of New Guinea's rainforest-dwelling marsupial/monotreme fauna were likely to have been isolated on New Guinea by the Early Miocene. Pleistocene interchanges were mainly of savannah/woodland species, though some rainforest species did cross.

There are numerous conflicts between this zoogeographic scenario based on systematics, geology and palaeoclimate, and our current interpretation of the age of many Australian "Miocene" mammal faunas. A primary one is that the oldest well-known faunas, currently dated to the Middle Miocene, bear no resemblance to the New Guinean fauna, even at the familial and subfamilial level, but seem to be much more archaic. Australian fossil faunas showing the gr eatest similarity to the New Guinean fauna are those from some of the Riversleigh sites, and those from Alcoota and Bullock Creek. The latest assessments date these sites to the later part of the Mio cene, or at least slightly younger than the Pinpa and Etadunna faunas. In the light of the geological history of Australasia, I suggest that the Riversleigh site may date to earliest Miocene, while the Etadunna and Pinpa faunas are probably late Palaeogene (Oligocene) in age. These revised dates corroborate the zoogeographic scenario proposed above.

! *Mammalia, Tertiary, Palaeobiogeography, Australasia.*

T.F. Flannery, The Australian Museum, 6-8 College Street, Sydney, NSW 2000; 1 August, 1988.

QUATERNARY PALAEONTOLOGY IN MELANESIA: RECENT ADVANCES

ABSTRACT

T.F. FLANNERY

Flannery, T.F. 1990 3 31: Quaternary palaeontology in Melanesia: recent advances. *Mem. Qd Mus.* 28(1): 324. Brisbane. ISSN 0079-8835.

The existence of a Pleistocene marsupial megafaunal assemblage in New Guinea was announced in 1983 (Flannery, Mountain and Aplin, 1983). Since then a total of three macropodid and two diprotodontid species have been described from Pleistocene sediments in New Guinea. These taxa shed some light on the zoogeography and palaeoecology of New Guinea during the Pleistocene.

Two marsupials (*Thylacinus cynocephalus* and *Thylogale christenseni*) have become extinct in New Guinea during the Holocene, and a chiropteran (*Aproteles bulmerae*) has suffered a massive reduction in its range. It seems likely that both climatic and human factors have been responsible for these events.

Recent discoveries of fossil mammals associated with archaeological material on some of the smaller Melanesian islands (New Ireland, Buka, Nissan, Tikopia and Erromanga) have added greatly to knowledge of the region's zoogeography. It is now apparent that the entire marsupial fauna of New Ireland (a wallaby, *Thylogale brunii*, and two cuscuses, *Phalanger orientalis* and *Spilocuscus maculatus*) was introduced, probably by human agency, during the Holocene. All of the extant terrestrial mammal fauna, except one murid (*Melomys rufescens*), is also introduced. However, a native *Rattus* species that was present in Pleistocene times became extinct by the late Holocene, probably as a result of competition with the introduced *R. praetor*. This work, in conjunction with that of Glover (1971) markedly alters thought about the marsupial biogeography of the Moluccas and the Bismarck/Solomon Island groups.
☐ *Mammalia, Quaternary, Zoogeography, Melanesia.*

LITERATURE CITED

FLANNERY, T., MOUNTAIN, M.-J., AND APLIN, K. 1982. Quaternary kangaroos (Macropodidae: Marsupialia) from Nombe Rock Shelter, Papua New Guinea, with comments on the nature of megafaunal extinction in the New Guinea highlands. *Proceedings of the Linnean Society of New South Wales* **107**: 77-99.

GLOVER, I. 1971. Prehistoric researches in Timor. p. 158-81. *In* Mulvaney, D.J. and Golson, J. (Eds), 'Aboriginal Man and Environment in Australia'. (Australian National University Press: Canberra).

THE CENTRIFUGAL PATTERN OF SPECIATION IN MEGANESIAN RAINFOREST MAMMALS

COLIN P. GROVES

Groves, C.P. 1990 3 31. The centrifugal pattern of speciation in Meganesian Rainforest Mammals. *Mem. Qd Mus.* 28(1):325–328, Brisbane. ISSN 0079–8835.

The usual model of speciation adopted for mammals is the peripheral population model, a mode of allopatric speciation. Analysis of some patterns of taxonomy in rainforest mammals in the Meganesian ("Greater Australia") region shows, on the contrary, that the more derived taxa — both species and subspecies — tend to occur in the central parts of the distributional area, the more primitive ones at the periphery. This finding seems to support the Centrifugal Speciation model of W.L. Brown, a sympatric mode. An example from Africa is also given, to demonstrate that the centrifugal model is not a local nor a habitat-specific one, but has more general applicability.
☐ *Biogeography, Dendrolagus, Meganesia, New Guinea, centrifugal speciation, sympatric speciation, colour pattern.*

C.P. Groves, Department of Prehistory and Anthropology, Australian National University, Canberra, ACT, Australia; 1 July 1988.

The taxonomist is often accused of working haphazardly, revising a group that happens to be of current interest, without a philosophical aim: mere stamp-collecting, it has been called, and if so then the charge is true, for philately will get us nowhere. This is not to say that essential basic information does not emerge from a taxonomic study, and certainly biology could not progress without taxonomy.

The other side of the coin is the search for patterns. A reviser who is awake is bound to wonder whether his or her new information is forming part of a pattern, and taxonomists make some of the best biogeographers.

This paper will describe a pattern which one taxonomist has found, and discuss whether it has any significance. Crucial to the study were the tree-kangaroos, genus *Dendrolagus*, of which one extant species, *D. bennettianus*, was first described by C.W. de Vis (1886), whom this symposium honours. Other examples are drawn largely from the mammals of Meganesia (for this term, see Filewood, 1984).

SPECIES AND SUBSPECIES IN MEGANESIAN RAINFOREST MAMMALS

The Tree-Kangaroos (*Dendrolagus*) are typical Meganesian rainforest mammals, ranging over most of the New Guinea mainland (with a gap in Irian Jaya, perhaps resulting from a lack of collecting and observation rather than from a lack of tree-kangaroos), into at least one offshore island, and the Tablelands rainforests of northern Queensland. In a recent revision (Groves, 1982) it was found that the various taxa can be sorted, using mainly characters of the feet and the teeth, into three grades from most primitive to most derived, distributed as follows:

— the primitive long-footed species, namely *D. inustus*, recorded from the whole of Cenderawasih, the Bird's Head peninsula, Yapen Island, and a strip of the northern New Guinea coast; and the two

FIG. 1. Distribution of species-groups in *Dendrolagus*.

☐ Primitive long-footed group (*inustus*; + *lumholtzi* and *bennettianus* in Australia)

▥ Short-footed, narrow-toothed (*matschiei* group)

☐ Short-footed, broad-toothed (*D. dorianus*)

FIG. 2. Distribution of taxa of the *Dendrolagus matschiei* group.

Primitive taxa with no golden markings (*ursinus, spadix*)

Taxa with slightly developed golden markings (*goodfellowi, buergersi*)

Taxa with extensive golden markings (*shawmayeri, matschiei*)

FIG. 3. Distribution of subspecies of *Dendrolagus dorianus*.

Primitively dull-coloured subspecies (*dorianus, mayri*)

Brightly coloured subspecies (*notatus*)

Queensland species, *D. lumholtzi* and *D. bennettianus*.

— intermediate short-footed species, with little-modified, narrow teeth (especially the secator, P); these are *D. ursinus*, known only from the eastern side of Cenderawasih, and the *D. matschiei* group (including so-called *D. goodfellowi*, as well as *D. spadix* which may be a distinct species), found over most of mainland Papua New Guinea.

— a highly derived, extremely short-footed species, with broad and complex P^3, *D. dorianus*, which seems to be found only in the highlands, from far southeastern Papua westwards into Irian Jaya, with an isolated(?) population in the Wondiwoi peninsula. It does not extend into the Huon peninsula, nor into the hilly regions of the south coast.

FIG. 4. Distribution of species-groups in *Dorcopsulus*.

Primitive taxa, with long feet and long secator (*vanheurni* group)

Derived taxa with short feet and shortened secator (*macleayi* group)

FIG. 5. Distribution of taxa in *Microperoryctes*.

Primitive taxa: duller colour without strong contrasts (*longicauda, dorsalis, murina, papuensis*)

Derived taxa: brightly coloured with strong contrasts (*ornata, magna*)

Looking at the ranges of these three species-groups (Fig. 1), it is evident that the primitive group occurs on the western, northern and southern extremities of the distribution of the genus (and is the only one on an offshore island; *D. matschiei*, on Umboi I., is probably introduced). The highly derived *D. dorianus* has the most central distribution; the intermediate group has an intermediate range.

The subspecies/species within at least two of these groups show a similar pattern. In the *D. matschiei* group, the most strikingly marked taxa occupy the central portion of the group's range

(Fig. 2). In *D. dorianus* it is again the most brightly coloured, most metachromatically advanced, subspecies which is centrally distributed (Fig. 3).

In collaboration with T.F. Flannery (Australian Museum), I am working on revisions of certain other rainforest marsupials; a progress report on two genera is given here. *Dorcopsulus* — the dwarf, montane forest wallabies — can probably be divided into several species, constituting a primitive and a relatively derived group. The more primitive taxa, with long feet and long narrow P^3, occur from the Idenburg River region east to the Huon peninsula, and recur in southeastern Papua. Between these two ranges — and, as far as we know, allopatric to either — is found the highly derived *D. macleayi* group (Fig. 4).

For the New Guinea Striped Bandicoots, genus *Microperoryctes* (which includes some taxa transferred from *Peroryctes* — see Groves & Flannery, in press), we have again incomplete distributional data. Even so, we again appear to have a highly derived group — bright yellow with well-marked black dorsal, face and rump stripes — occurring between the ranges of duller, less disruptively marked (metachromatically more primitive) taxa (Fig. 5).

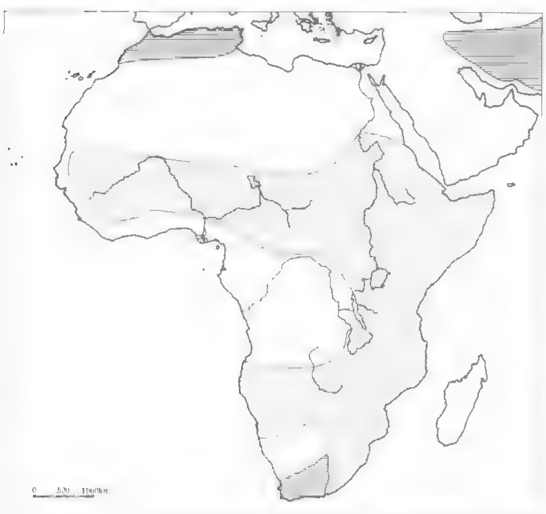

FIG. 6. Distribution of subspecies-groups in *Panthera leo*.

Primitive, small-brained subspecies (*leo, persica, melanochaita*)

Derived, large-brained subspecies (*senegalensis, nubica,* etc.)

ANALOGOUS PATTERNS OUTSIDE MEGANESIA

The immediate question must be: is this pattern coincidental, or is it a more widespread phenomenon? Does it occur only in Meganesia? Or is it something to do with a rainforest habitat?

It turns out that the pattern is neither specific to this particular region, nor is it limited to the rainforest environment. On the contrary, it is a common distributional pattern, which has sometimes been noticed and commented upon by taxonomic revisers who have worked on groups which exhibit it. Thus Hemmer (1974) found that the Lion (*Panthera leo*) can be divided into two subspecies-groups: a primitive one with relatively small cranial capacity, and a more evolved one in which cranial capacity is greater, the male's mane is more heavily concentrated around the head-pole, and social organisation is more complex. The derived group is common to most of Subsaharan Africa, while the primitive group is dotted around the periphery — the Cape of Good Hope, the Maghreb, and southwestern Asia (Fig. 6).

THE CENTRIFUGAL MODEL

Brown (1957) named this pattern 'centrifugal speciation'. According to his model, genetic novelties are generated in the centre of a species' range, and subsequent climatic changes break up the range, providing the opportunity for allopatric speciation to occur, leaving primitive taxa around the edges while a new, more derived species has evolved in the centre.

Brown's model remained little appreciated, but was briefly discussed by White (1978), who, however, rejected it. It seems to me that, in modified form, centrifugal speciation explains patterns of taxonomic differentiation such as I have described above. Moreover, from a population genetic point of view, it would seem so obvious as to be almost the expected mode of taxonomic advance.

As demonstrated by the above examples, the centrifugal pattern applies to subspecies as well as to species, and, indeed, to polymorphisms as well (Groves, 1989). Lewontin (1974) emphasises that the sorts of characters that differentiate species are the same as those subject to polymorphism or polytypism within a species, indeed they are often the same characters. *Contra* the ideas of the proponents of rectangular speciation (Stanley, 1979), there is no fundamental difference between the kinds of variation distinguishing species, subspecies, and even sub-taxonomic degrees of variation: only in species the differentiation is accompanied, due to whatever mechanism, by reduction or loss of interfertility.

Brown's appeal to range changes, to create opportunities for allopatric speciation, may be unnecessarily cumbersome. As long ago as 1966, Maynard Smith proposed a viable mechanism for sympatric speciation; to which White added the stasipatric mode, where there is a chromosomal rearrangement leading in effect to a high degree of inbreeding. I cannot insist on sympatric speciation as part of the revived centrifugal model, but I will point out that, viewed as a package, the two concepts make sense together:

1) the package is geographically parsimonious;
2) breeding systems regularly promote the wide dissemination of mutations and recombinations;
3) only a "minute fraction" (White, 1978) of all individuals of a species, and so a minute fraction of the genetic diversity, is geographically peripheral; and
4) central environments are likely to be more diverse than peripheral, so a new species or morph generated there is more likely to be successful.

HOW COMMON IS CENTRIFUGAL DIFFERENTIATION?

I have elsewhere (Groves, 1989) surveyed patterns of taxonomic differentiation among Primates, and have found 34 instances of clearly expressed centrifugal patterns. Of these, 26 cases involve full speciation, where the generation of new characters has involved the generation of reproductive isolation as well. On the other hand there are only 14 clear cases (plus four more probable) of allopatric speciation.

Of the 26 cases of evident centrifugal speciation, only eight are clearly stasipatric, i.e. involving chromosomal changes. Moreover, breeding systems with inbreeding potential are involved in only two of the eight stasipatric cases, contrary to the arguments of Bush *et al.* (1977).

Those cases where an allopatric mode best explains the speciation pattern concern genera ranging over two or more major biome-types, whereas in the centrifugal list there are no such cases. The implication would seem to be that if there are habitat differences then adaptation (or exaptation?) will occur; if not, then evolution will proceed just the same, non-adaptively, by centrifugal processes.

LITERATURE CITED

Brown, W.L., Jr. 1957. Centrifugal speciation. *Quarterly Review of Biology* 32: 247–77.

Bush, G.L., S.M. Case, A.C. Wilson and J.L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. *Proceedings of the United States National Academy of Sciences* 74: 3942–6.

De Vis, C.W. 1886. Notice of an apparently new species of *Dendrolagus*. *Proceedings of the Royal Society of Queensland*, 3: 11–4.

Filewood, W. 1984. The Torres connection - zoogeography of New Guinea. p. 1121-31. *In* Archer, M. and Clayton, G. (Eds), 'Vertebrate Zoogeography and Evolution in Australasia'. (Hesperian Press: Carlisle, W.A.).

Groves, C.P. 1982. The Systematics of Tree Kangaroos (Dendrolagus). *Australian Mammalogy* 5: 157–86.

1989. 'A Theory of Human and Primate Evolution'. (Oxford University Press: Oxford).

and Flannery, T.F. (in press). A revision of the families and genera of bandicoots. *In* Brown, P. and Sebeck, J. (Eds), 'Bandicoots'. (Surrey Beatty and Sons: Sydney).

Hemmer, H. 1974. Zue Artgeschichte des Löwen *Panthera leo* (Linnaeus 1758). *Ver. Zool. Staatssammlung*, München, 17: 167–280.

Lewontin, R. 1974. 'The genetic basis of evolutionary change'. (Columbia University Press: New York).

Smith, J.M. 1966. Sympatric speciation. *American Naturalist* 100: 637–50.

Stanley, S.M. 1979. 'Macroevolution Pattern and Process'. (W.H. Freeman: San Francisco).

White, M.J. 1978. 'Modes of Speciation'. (W.H. Freeman: San Francisco).

BELIDEUS GRACILIS — SOARING PROBLEMS FOR AN OLD DE VIS GLIDER

STEPHEN VAN DYCK

Van Dyck, S. 1990 3 31: *Belideus gracilis* — soaring problems for an old de Vis glider. *Mem. Qd Mus.* 28(1): 329–336. Brisbane. ISSN 0079-8835.

The taxonomic status of *Belideus gracilis* de Vis 1883 is reviewed in the light of the discovery of 3 large glider skins and their skulls, from Mt Echo, NE Queensland, during the Queensland Museum's 1986 move to new premises. De Vis' poor record in extant mammalian taxonomy is discussed in terms of his rash descriptions of *Dromicia frontalis* and *Pseudocheirus mongan*. Skull and tail morphology of the Mt Echo specimens differ from typical *Petaurus norfolcensis*, but it is concluded that at present *gracilis* should remain a junior synonym of *norfolcensis* and that caution should be exercised in applying the subspecific title *gracilis* to gliders from outside the Mt Echo area.
□ *Petauridae, Possum, Belideus gracilis, Petaurus norfolcensis, Mt Echo.*

Stephen Van Dyck, Queensland Museum, PO Box 300, South Brisbane, Queensland, 4101, Australia; 21 September 1988.

Charles de Vis was a late starter in the field of extant mammal taxonomy. He was 54 when he described his first marsupial type, and at the age of 78, two years after his retirement, he published, albeit 'reluctantly', the description of what was to be his last new mammal, a giant rat from New Guinea: '. . . I hardly feel justified in running the risk of perpetuating a synonym, otherwise I should propose for it the name *Dendrosminthus aroaensis*' (de Vis 1907, p. 11).

Of his 15 extant mammals from Australia and New Guinea, Bennett's tree-kangaroo, *Dendrolagus bennettianus* and a fruit-bat *Dobsonia pannietensis* are still regarded as specifically distinct (Groves, 1982; Bergmans, 1979), while the status of *Dendrosminthus aroaensis* is currently being reassessed (T. Flannery, pers. comm.). All others have slipped into junior synonymy.

The contribution of de Vis to modern mammalogy must be regarded with some suspicion, not only for his equivocal approach to species descriptions (see *D. aroaensis* quote above) but more particularly for his worst mistake, which was a description in 1886 of the Feathertail Glider *Acrobates pygmaeus* — a distinctive and ubiquitous species already described 93 years earlier (Shaw 1793) — as a 'new' pigmy possum, *Dromicia frontalis*. This he based on three well-preserved spirit specimens collected for him by Kendall Broadbent in north Queensland. In his description, de Vis recognized that each of the three was sub-adult, each possessed a 'distinct patagial fold' (p. 1134) and that the hair of the tail had 'a distinct tendency to form a fringe on either side' (p. 1135). Yet he failed to recognise that the specimens represented *Acrobates pygmaeus*.

However, de Vis' first mammalian description, published in 1883 of the gliding possum *Belideus gracilis* and treated merely as synonymous with *Petaurus norfolcensis* as early as 1888 by Thomas, may yet prove to be correct. The significance of this description and its enigmatic connection to three very old museum glider skins is now discussed.

THE *B. GRACILIS* DESCRIPTION AND ITS BACKGROUND

On March 18, 1882, in 'The Naturalist' column of the 'Queenslander' newspaper, de Vis, in his unique and charming style, introduced his readers to Australia's gliding possums:

'Many who with senses impressible by the objects around them, have long been dwellers in the wilderness are acquainted with the prettiest of its aborigines — the flying possum — more suggestively, flying squirrel, more correctly petaurist. With its soft-piled delicately tinted mantle of silky fur, calm demeanor, and admirable temper, the petaurists are the gentles of the race, and would make charming pets but like many gentles of another race, they display their dress and pursue their pleasures only at night'.

This was a fitting tribute to the group of marsupials from which de Vis' first mammalian type description would come early in 1883, the beginning of his second calendar year as the curator of the Queensland Museum. The new glider, which de Vis chose to name *Belideus gracilis*, had been sent to him by Kendall Broadbent from the Cardwell area of northern Queensland. First mention of it was made in the Minutes of the Board Meeting published in the 'Brisbane Courier' 9 November 1882 p. 5. 'A cursory examination of the specimens shows that two new birds, a new flying squirrel and two or more new fish have been acquired. It is very desirable that Mr Broadbent should be sent into the interior to collect on the Diamantina and Georgina rivers'.

The formal description which was published in April 1883 drew attention to the following features which de Vis considered unique to *gracilis*: its large size ('between *B. australis* and *B. sciureus* [*norfolcensis*] . . . its markings and in having shorter ears and a rather more slender and less hairy tail') (de Vis 1883c, p. 620).

However, in anticipation of this description, its abstract was read to the December 27 (1882) meeting of the Linnean Society of New South Wales and was subsequently published in January 1883 (de Vis 1883a). This January announcement of the new species *Belideus gracilis*, accompanied by those diagnostic features considered significant by de Vis, therefore pre-empted the formal April (1883c) account as the original description of *B. gracilis*.

An identical copy of this original Linnean Society abstract appeared in print a few weeks later (Jan. 1883) in the *Southern Science Record* (de Vis 1883b).

The annual report of the Trustees of the Queensland Museum for the year 1882, tabled in Parliament on 26 June 1883, notes *B. gracilis* in Appendix VII ('List of species of which types have been placed in museum'). However, it is not known if a single type specimen was ever formally nominated and marked as such, or if the holotype was mounted and put on public display in keeping with the museum's habit of displaying every specimen and dispensing with duplicates (see Ingram 1986, p. 161).

As early as 1888, Thomas treated *Belideus gracilis* as synonymous with *Petaurus norfolcensis* (then as *Petaurus sciureus*) and subsequent references to *B. gracilis* deal with it as a northern subspecies of *norfolcensis* (Iredale and Troughton, 1934; Marlow, 1962; Troughton, 1973; Suckling, 1983). None of these authors records having made a personal examination of a *B. gracilis* holotype or topotype.

THE THREE GLIDER SKINS AND MT ECHO

During the Queensland Museum's move to new premises in 1986, three faded study skins representing large gliding possums were found in a drawer containing old gallery mounts. None of the gliders bore registration numbers, though each carried two tags. One was printed on paper stating the date '1886', the initials of the collector 'K.B.' (Kendall Broadbent), the locality "Mt. Echu, Herbert River" (= Mt Echo, Herbert River) and a 'cabinet name' which alluded to the agile nature of the gliders. (Cabinet names were unpublished convenient titles which de Vis used to differentiate forms which he considered distinct). This label was not written in de Vis' own hand. The second tag attached to each skin was a wooden sliver, commonly used by de Vis with spirit specimens, on which de Vis had written in pencil the name '*P. sciureus*' and a letter 'a', 'f' or 'g'. The letters corresponded with de Vis' own hand-written catalogue cards which are still held in the Museum. These cards confirm the collection locality and sex of the three glider skins which are accessed under the specific title of '*sciureus* Shaw', but with a further note in parentheses, mentioning again the cabinet name. The unwieldy and confusing nature of de Vis' cataloguing system is discussed by Ingram (1986, p. 162).

The outstanding size of the three glider skins, their extremely long, thin, sparsely-haired tails and the pattern of fur coloration agree closely with de Vis' description of *B. gracilis* from 'North of Cardwell' (de Vis, 1883c, p. 620). In particular the vital measurements included by de Vis in his formal description are matched in the skins (Figs 1 and 2).

The coincidence of the *gracilis* description matching these skins is too significant to be overlooked, yet the evidence to identify them as possible syntypes is too open-ended to provide a convincing explanation. Three possible explanations are as follows:

(a) The gliders may represent the original specimens sent from Broadbent in 1882 and the species described by de Vis early the next year.

This suggestion considers as most significant the corroboration of the large measurements and fur patterns presented by de Vis in his description with the three large skins. The collection locality as stated by de Vis was 'North of Cardwell'. Mt Echo is 18 km SW of Cardwell, being part of the southwestern slopes of the Cardwell Range overlooking the Herbert River valley, and approached from Ingham. 'North of

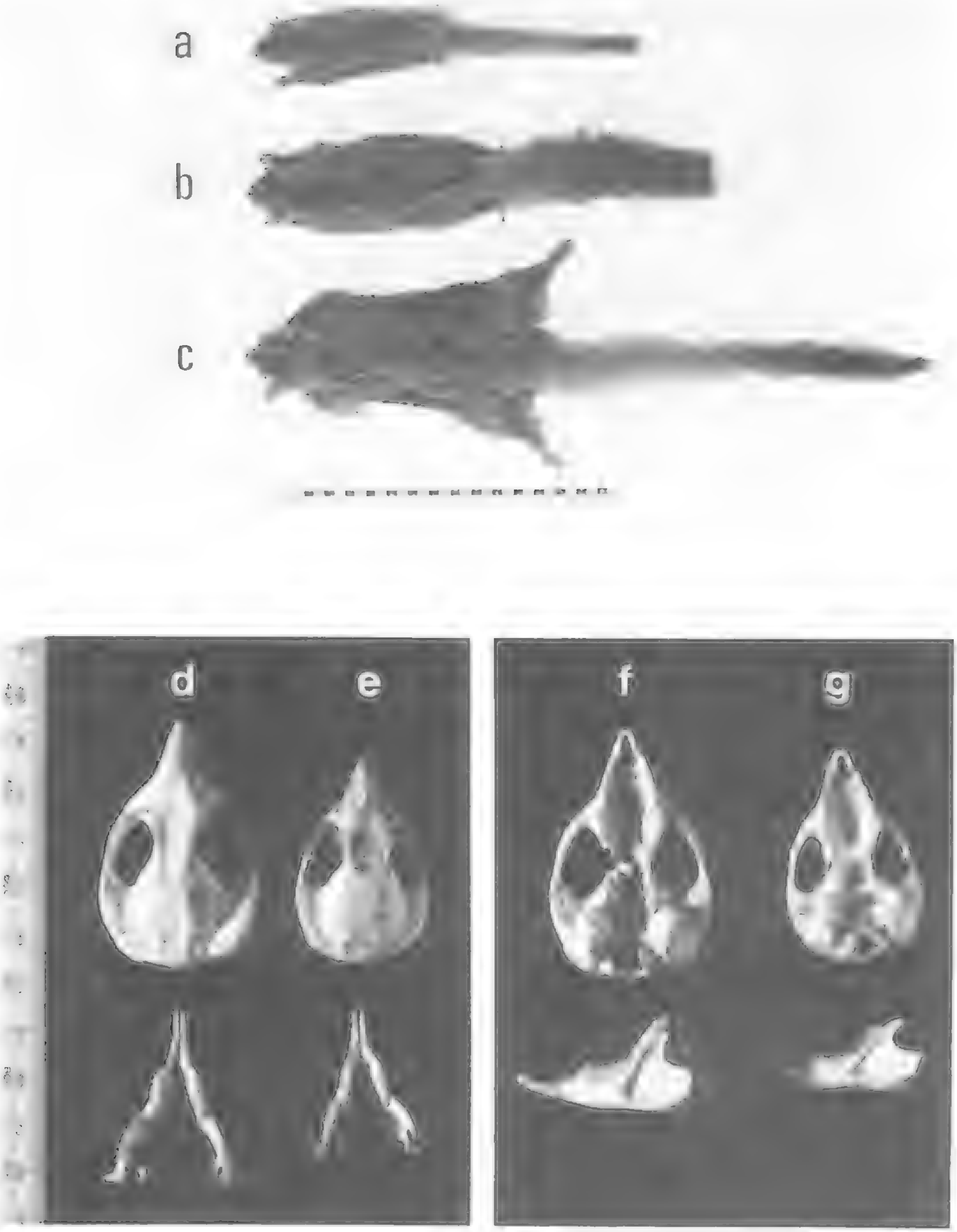

FIG. 1. Comparison of the Mt Echo *Petaurus norfolcensis* (c) JM5521 with average-sized specimens of *P. breviceps* (a) J10466 from Gordonvale NEQ and *P. norfolcensis* (b) J11514 from Warwick SEQ. d and f, skull and dentary of the Mt Echo *P. norfolcensis* JM5523. e and g, skull and dentary of an average-sized *P. norfolcensis* J4270 from Brisbane SEQ. (J and JM registrations represent specimens housed in the Queensland Museum).

FIG. 2. Comparison of skin size in the Mt Echo *Petaurus norfolcensis* (c) JM5521 (Queensland Museum) with: (a) *P. australis*, CM 207 (CSIRO, Wildlife Canberra) from Bonalbo N. N.S.W. (b) *P. norfolcensis*, CM 25 (CSIRO, Wildlife Canberra) from Albury N.S.W. (largest *P. norfolcensis* skin available). (d) *P. abidi* (paratype) PNGMR 23215 (National Museum and Art Gallery, Papua New Guinea, Boroko) from Mt Somoro, Papua New Guinea.

Cardwell' would have put Broadbent to the northeast and other side of the Cardwell Range. It is possible that de Vis' presented locality data were inaccurate.

This suggestion also assumes that de Vis did not label a holotype as such, and that the 1886 date shown on the labels and accession card is either incorrect as a collection date, or is an accession date.

No other reference can be found to the cabinet name on specimen tags and accession cards. If the three specimens represent the original 1882 Broadbent specimens, the cabinet name may have been an early de Vis choice later to be discarded in favour of *gracilis*.

(b) The gliders represent the form *gracilis*, but were collected four years later by Broadbent at or close to the type locality (near Cardwell). This possibility raises the puzzling question of why they should be labelled with the cabinet name after the published description of the virtually identical *gracilis*.

(c) The gliders represent a form collected in 1886 by Broadbent, which de Vis considered distinct enough to warrant a cabinet name, but which was never described by him. In this case the similarity of the three study skins to the formal description of *gracilis* is coincidental.

Unfortunately, de Vis freely interchanged references to the collection locality, 'Herbert River' with 'Herberton' (17°23'S. 145°23'E) a town 145 km NW of Mt Echo and formally gazetted in 1880. His indexing card for the three gliders notes their collection locality as 'Mt Echo, Herberton'. His description of 'New and rare vertebrates from the Herbert River North Queensland' (de Vis 1886) frequently makes reference to the 'Herberton Petaurist' or the 'Herberton Mountains' (p. 1134) for the area of the Main Range, north of the Herbert River.

The collection area for the three Broadbent gliders, Mt Echo (18°54'S 145°48'E) is now part of Yamanie National Park and is situated approximately 50 km NW of Ingham, northeast Queensland. A short but unsuccessful attempt was made by me in June 1986 to locate living representatives of the old glider skins on Mt Echo and adjacent areas. The vegetation types in the area varied through floodplains of the Herbert River to the vine forest summit of Mt Echo (c.700 m above sea-level). On the floodplains, open and tall woodland species consisted of *Eucalyptus tereticornis*, *E. pellita*, *E. intermedia* and *Melaleuca dealbata*, with small patches of mesophyll vine forest and open forest and woodland species such as *Melaleuca quinquenervia*, *M. viridiflora* and *E. alba*. This changed on the steep foothills to medium-low woodland dominated by *E. alba*, *E. intermedia* and *Tristania suaveolans* 15-18 metres in height. A dense ground layer of *Imperata cylindrica*, *Heteropogon contortus* and *Themeda australis* made climbing the mountain difficult. The moist uplands and sheltered gullies were characterized by vine forest of which the major species were *E. intermedia*, *Syncarpia glomulifera*, *T. conferta*, *Casuarina torulosa* and *Banksia compar*, 20-30 metres in height. These vegetation types correspond roughly with types 2a, 16g, 16p, 13f and 19 of Tracey (1982).

The vegetation of Mt Echo has probably altered little since Broadbent's day. In his diary entry for Saturday, July 3 1886, he describes the Mt Echo terrain in the following manner: 'I have 15 miles to go to get Yabbies from here, on top of the main range and travelling is a terror in this country, the grass in the open places in the mountains is 6 feet high broad blady grass cuts like a knife, all the mountain creeks are nearly a swim and then to climb those mountains is a caution rocks and precipices thrown together in beautiful confusion and covered with dense jungle, great masses of lawyer palms tear flesh and clothes to pieces'.

It is possible, therefore, that the glider still exists somewhere on the rugged slopes of Mt Echo or in its vicinity.

A REASSESSMENT OF THE MT ECHO MATERIAL

Unlike many other Australian mammals, large body size in *Petaurus norfolcensis* is not restricted to specimens from the southern limits of the species' range, and in that respect does not conform with Bergmann's rule (see Yom-Tov and Nix, 1986). Large specimens, approaching the size of the Mt Echo gliders, have been recorded from Albury, NSW (36°05'S, 146°51'E, e.g. CM 25), Fraser Island, SE Qld (25°33'S, 152°59'E, e.g. J11237) and Cape River, NE Qld (20°50'S, 146°15'E, e.g. JM5058). Russell (1980) comments on a large female from Watsonville, NE Qld (17°23'S, 145°19'E). None of these larger than average specimens, however, displayed the slender, sparsely-haired tails of the Mt Echo skins, the caudal morphology of which most closely resembles *Petaurus abidi* from Papua New Guinea rainforest.

TABLE 1. Measurements for *Petaurus norfolcensis* from Queensland compared with large specimens JM5521-3 (Queensland Museum) from Mt Echo; CM 25 (CSIRO Canberra) from Albury, N.S.W.; JM5058 (Queensland Museum) from Cape River, Qld; BM 41.1227 (British Museum, Natural History) from Liverpool Plains, N.S.W. and *P. abidi* BBM-NG 101818 (Bishop Museum, Hawaii) from Papua New Guinea. The method of mensuration is demonstrated in Fig. 1.

Petaurus norfolcensis Queensland							JM 5521	JM 5522	JM 5523	CM 25	JM 5058	BM 41.1227	BBM-NG 101818
Measurement (mm)		N	$\bar{x} \pm R$	OR	SD	CV							
1	M^{1-4} (crown)	41	8.03±0.06	7.14–8.93	0.36	4.48	9.10	8.55	8.84	—	8.42	8.37	9.70
2	P^4-M^4 (crown)	41	9.82±0.06	9.02–10.80	0.41	4.17	11.23	10.68	10.77	—	10.60	10.40	11.73
3	I-P	40	8.37±0.11	7.42–9.30	0.67	8.00	9.55	9.16	9.78	8.90	8.69	8.71	9.28
4	I-P	40	14.37±0.13	12.40–16.30	0.81	5.64	16.71	16.12	16.53	15.92	15.51	16.03	17.40
5	I-M	40	21.63±0.14	20.21–23.60	0.86	3.98	24.71	23.97	24.54	—	23.22	23.68	25.56
6	nasal width	38	4.32±0.11	3.24–6.21	0.67	15.51	6.69	5.54	5.29	4.81	3.82	4.28	5.57
7	rostral height	38	12.48±0.12	10.79–13.73	0.75	6.01	12.96	13.85	13.41	13.63	11.25	—	14.25
8	lachrymal width	38	13.49±0.11	12.10–15.20	0.69	5.11	15.05	16.95	15.32	15.29	12.82	14.97	15.15
9	ramal width	41	11.07±0.10	10.01–12.32	0.67	6.05	13.28	13.61	13.07	11.73	12.08	11.46	12.60
10	zygomatic width	38	30.03±0.19	27.93–32.40	1.16	3.86	—	—	34.19	32.00	30.79	-	34.61
11	interorbital width	40	9.01±0.09	7.26–9.84	0.56	6.22	8.73	10.73	7.62	9.21	9.04	8.07	10.06
12	I_1-M_4	41	13.02±0.09	11.74–14.22	0.61	4.69	14.93	14.37	14.49	—	13.88	14.24	—
13	M^{1-4} (crown)	41	8.67±0.05	7.99–9.24	0.32	3.69	9.79	9.25	9.15	—	9.12	9.27	—
14	M width	41	1.80±0.01	1.67–1.99	0.08	4.44	2.03	2.07	1.95		1.87	2.04	—

Fortunately the collector, Broadbent, had left one complete skull inside one skin, JM5523, and partial skulls inside the skins of JM5521 and JM5522. These skulls have never before been examined. They have been extracted and their dental and cranial morphology compared against other known gliders. The tooth row is massive and the skull is larger than in any known specimen of *P. norfolcensis*, or as de Vis put it 'intermediate between *B. australis [Petaurus australis]* and *B. sciureus [P. norfolcensis]*' (de Vis 1883c, p. 620) (Table 1, Fig. 3, Fig. 1).

While the Mt Echo specimens approach *P. abidi* in skull and tooth size, their dental and cranial affinities lie not with *P. abidi* (whose affinities are with *P. australis*) but with *P. norfolcensis*.

At this stage there seems little justification in advocating full specific status for the three Mt Echo gliders JM5521-3 despite their consistently large size and long, slender tails. In addition it would seem inappropriate to continue the use of the subspecific reference *P. norfolcensis gracilis* in respect of all northeastern and mideastern Queensland examples of *P. norfolcensis*, which are indistinguishable from their more southern conspecifics.

DISCUSSION

The publication of Oldfield Thomas' 'Catalogue of the Marsupialia' (1888) must have done little to boost de Vis' self-confidence as a mammalian taxonomist. In the catalogue, Thomas synonymised all the extant mammals which de Vis had described up to its publication in 1888 (*Belideus gracilis, Halmaturus jardinii, H. gazella, H. temporalis, Onychogalea annulicauda*).

It is difficult to explain de Vis' poor record in extant marsupial taxonomy. It is insufficient to suggest that he lacked the necessary literature with which to test his thoughts. De Vis had been the librarian at the Rockhampton School of Arts immediately prior to assuming his curatorial position in the Queensland Museum. While he may not have had all the relevant literature available to him then, he would have been familiar with those

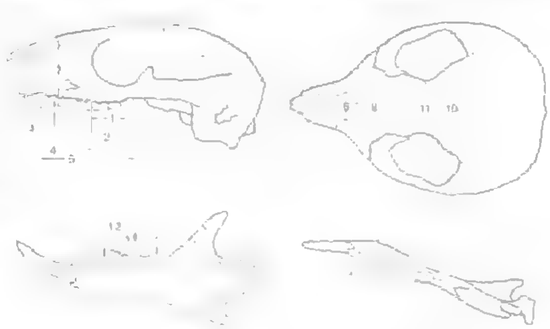

FIG. 3. Method of mensuration used in association with all *Petaurus* skulls measured. Numbers correspond with numerical sequence of measurements in Table 1.

procedures associated with literature searches and the acquisition of relevant mammalian works. When he took office in the Queensland Museum in 1882 the library was already well stocked and growing (Wixted, 1986) and Gould's 'Mammals of Australia' had been purchased by W.A. Haswell from Williams and Norgate, Covent Garden, London in 1880. In the light of Gould's substantial treatment of the Feathertail glider *Acrobates pygmaeus,* it is hard to excuse de Vis' unwarranted description of *Dromicia frontalis.*

De Vis may have been facing serious competition from southern and overseas institutions, which were employing collectors during the late 1800's to provide them with material from north Queensland, many of which were previously unknown to science. A note of professional rivalry with Collett can be detected in de Vis' rash description of *Pseudocheirus mongan* (*P. herbertensis*). 'There is reason to fear that the describer of *Phalangista (Pseudochirus) Herbertensis* has been led into a mistake in his determination of the sexes of that *Phalanger*. It would appear that in the mountain-top scrubs of the Herbert Gorge there are two associated species of *Pseudochirus,* and that these are, curiously enough, not distinguished from each other by the natives of the locality, who give to them the common name 'Mongan'. From such community of name has probably resulted an idea that they are identical, and this, communicated to Mr Collett, has no doubt misguided him in his determination' (de Vis, 1886, p. 1130).

Collett's (1884) creditable description was based on material collected by Lumholtz from the Herbert River district at almost the same time as Broadbent was collecting there. De Vis' description of *P. mongan* might be interpreted as a dyspeptic attempt to save face in the light of four new marsupial species (*P. archeri, Hemibelideus lemuroides, P. herbertensis* and *Dendrolagus lumholtzi*) being described from under his nose. De Vis' failure to appreciate the natural range of colour variation found in *P. herbertensis* (Van Dyck, 1980), which led to his description of *P. mongan,* demonstrates one of the inherent dangers of being a 'closet naturalist' (Ingram, 1986, p. 157).

It could also be argued that there were probably high expectations of new mammals, as well as new species of birds, in the barrage of material being forwarded by Broadbent from north Queensland. Moreover, the case before the Museum's Board for Broadbent's future employment as a collector could be strengthened if more new species were described as a direct result of his efforts.

The multiple problems associated with matching the de Vis description of *B. gracilis* with the three Mt Echo specimens may never be resolved. However, it is still possible that living specimens may be rediscovered on or near the mountain. Until then, in the words of de Vis (1907) '. . . I feel hardly justified in running the risk of perpetuating a synonym . . .' and defer to the judgement of Thomas (1888) who treated *gracilis* simply as a junior synonym of *Petaurus nofolcensis.*

ACKNOWLEDGEMENTS

The advice and criticism of Drs J.W. Winter, R.A. Thulborn, G. Ingram and Mr N.W. Longmore is especially acknowledged. Mrs L. Crevola-Gillespie assisted with the production of the table and figures. Mr J. Menzies (National Museum and Art Gallery, Papua New Guinea) Dr A. Allison (Bernice Bishop Museum, Hawaii), Dr P. Jenkins (British Museum (Natural History)) and Dr J. Calaby (CSIRO, Canberra) generously made specimens in their care available to me. The hospitality and assistance of Mr and Mrs A. Mackee of Longpocket, Ingham, is also gratefully acknowledged.

LITERATURE CITED

BERGMANS, W. 1979. Taxonomy and zoogeography of *Dobsonia* Palmer, 1898 from the Louisiade Archipelago, the D'Entrecasteaux Group, Trobriand Island and Woodlark Island (Mammalia, Megachiroptera) *Beaufortia* 29(355): 199–214.

COLLETT, R. 1884. On some apparently new marsupials from Queensland. *Proceedings of the Zoological Society of London* 381–9.

DE VIS, C.W. 1883a. Description of a new *Belideus* from northern Queensland [in Anon]. *Abstracts of Proceedings of the Linnean Society of New South Wales* for 27 December, 1882, p.ii.

1883b. Description of a new *Belideus* from northern Queensland [in Anon]. *Southern Science Record* (1)3(1): 27 (Jan).

1883c. Description of a new *Belideus* from northern Queensland. *Proceedings of the Linnean Society of New South Wales* (1)7(4):619–20.

1886. On new or rare vertebrates from the Herbert River, north Queensland. *Proceedings of the Linnean Society of New South Wales* 1(2): 1129–37.

1907. A New Guinean tree rat. *Annals of the Queensland Museum* 7: 10–1.

GROVES, C.P. 1982. The systematics of tree kangaroos (*Dendrolagus*; Marsupialia, Macropodidae). *Australian Mammalogy* 5: 157–86.

INGRAM, G.J. 1986. Scales, feathers and fur, p. 142-171 *In* Mather, P. (Ed.) 'A time for a museum : The history of the Queensland Museum'. *Memoirs of the Queensland Museum* **24**.

IREDALE, T. AND TROUGHTON, E. Le G. 1934. A check-list of the mammals recorded from Australia. *Memoirs of the Australian Museum* **6**: 1–122.

MARLOW, B.J. 1962. 'Marsupials of Australia'. (Jacaranda Press: Brisbane).

RUSSELL, R. 1980. 'Spotlight on Possums'. (Queensland University Press: Brisbane).

SHAW, G. 1793. 'Zoology and Botany of New Holland and the Isles Adjacent' (i): 5. (J. Sowerby: London).

SUCKLING, G.C., 1983. Squirrel glider *Petaurus norfolcensis,* p. 140–1 *In* Strahan, R. (Ed) 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson: Sydney).

THOMAS, O. 1888. 'Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History)'. (British Museum of Natural History: London).

TRACEY, J.G. 1982. 'The vegetation of the humid tropical region of north Queensland'. (CSIRO: Melbourne).

TROUGHTON, E. Le G. 1973. 'Furred Animals of Australia'. (Angus and Robertson: Sydney).

VAN DYCK, S., 1980. A colour aberration in the Herbert River Ringtail, *Pseudocheirus herbertensis* (Petauridae : Marsupialia). *Australian Mammalogy* **3**: 53–4.

WIXTED, E.P. 1986. The need for scientific works, p.253–73 *In* Mather, P. (Ed) 'A time for a museum: The history of the Queensland Museum'. *Mem. Qd Mus.* **24**.

YOM-TOV, Y. AND NIX, H. 1986. Climatological correlates for body size of five species of Australian mammals. *Biological Journal of the Linnean Society* **29**: 245–62.

NOTE ADDED IN PROOF: At 12:32AM, 6 Dec. 1989, living representatives of *B. gracilis* were located at Barrett's Lagoon, 18°02'S, 146°58'E, 14 km SE of Tully. To pay one's devoirs to de Vis, Barrett's Lagoon is 24 km N of Cardwell, precisely the vicinity referred to in his original description.

TOOTH WEAR AND ENAMEL STRUCTURE IN THE MANDIBULAR INCISORS OF SIX SPECIES OF KANGAROO (MARSUPIALIA: MACROPODINAE)

WILLIAM G. YOUNG, MICHAEL STEVENS AND ROBERT JUPP

Young, W.G., Stevens, M. and Jupp, M. 1990 3 31: Tooth wear and enamel structure in the mandibular incisors of six species of Kangaroo (Marsupialia: Macropodinae). *Mem. Qd Mus.* 28(1): 337–347. Brisbane. ISSN 0079-8835.

Tooth wear and enamel ultrastructure of the mandibular incisors of six macropod species were investigated using plain and polarized light microscopy and scanning electron microscopy. Three modes of wear occurred on these teeth; (i) abrasive wear on the incisal edge; (ii) attritional wear on the medial edge; and (iii) occlusal wear on parts of the incisal edge. The first two modes of wear relate to the known mastication of the macropods. Possible causes of the third are discussed. The enamel structure of the teeth is complex and shows several distinct features: zones within the enamel, a distinct bend in the prisms which overall are oriented antero-laterally; prism decussations and whorls. These features are interpreted as either wear retardants or possible adaptations to minimize damage on fracture. The latter interpretation is based on the loading experienced by these teeth and the known physical properties of enamel and dentine in relation to the behaviour of anisotropic materials and crack propagation theory.

☐ *Tooth wear, enamel ultrastructure, Wallabia, Macropodinae, Macropus, Protemnodon.*

William G. Young, Michael Stevens and Robert Jupp, Department of Oral Biology and Oral Surgery, University of Queensland, St. Lucia, Qld 4076, Australia; 30 November, 1988.

The procumbent mandibular incisor is the hallmark of diprotodont marsupials. Its form and function are distinctive in the Macropodinae. The lateral margin of the crown forms an incisal edge that occludes with the three maxillary incisors, for a relatively greater length than in the closely related possums (Phalangerinae). Much of the medial edge abuts its counterpart over a ventral, interproximal contact area.

Using cinematographic and cineradiographic techniques, Ride (1959) found that the medial edges of the mandibular incisors of Bennett's Wallaby, *Macropus rufogriseus fruticus*, abut in the resting position, lying within the maxillary incisal arcade. The movable mandibular symphysis, and mandibular protraction allow a slight separation of the mandibular incisors to bring them simultaneously into occlusion with the premaxillary ones. Food, such as grass, is gripped and detached with a jerk of the head; it is apparently not incised. Harder objects such as carrot, cause greater separation. A scissoring action, employing the medial edges (Murie & Bartlett, 1866), has not been observed. It is possible that this variation of mandibular incisor position permits full occlusion during incision or allows the mandibular incisors to clear their maxillary counterparts during lateral, anisognathous molar chewing movements (Ride, 1959).

Tooth wear, be it abrasion (food to tooth) or attrition (tooth to tooth), has been used to determine the relative direction of jaw movements and the nature of occlusion in a number of mammalian species. The diagnostic wear and microwear features are facet location, polish, striation orientation, pitting and the asymmetry of the enamel to dentine interfaces of the leading and trailing dentine profiles (Greaves, 1973; Rensberger, 1973; Gordon, 1984; Walker, 1984; Young & Marty, 1986; Young & Robson, 1987).

Microwear features often reveal how the underlying enamel ultrastructure has been adapted, by selection, to resist various forms of wear (Rensberger, 1978; von Koenigswald, 1980; Fortelius, 1985; Boyde & Fortelius, 1986; Young, McGowan & Daley, 1987). Variations in the course of enamel prisms from the enamel-dentine junction (EDJ) to the surface are probably adaptations to resist wear and fracture (Rensberger & von Koenigswald, 1980; Boyde & Fortelius, 1986).

The complexity of the mandibular incisor enamel of macropods has long been recognized (Owen, 1840-1845; Tomes, 1849; Carter, 1920; Williams, 1923; Beier, 1983). Principally, the prism orientation undergoes a marked change a short distance from the EDJ. Schmidt and Keil (1971), using polarized light microscopy, noted three zones in macropod mandibular incisors, evidently the result of changes in hydroxyapatite crystal orientation. Zone 1 extends from the EDJ to a prominent directional change; Zone 2 from that directional change to a colour interdigitation; and Zone 3 from the interdigitation to the outer surface. A scanning electron microscopic (SEM) study of the enamel of 14 macropod species found that vertical decussations (Hunter-Schreger bands) occur at locations subject to excessive wear, such as incisal edges, shearing premolar blades and the occluding surfaces of molar lophs. The presence, extent, or absence of decussations seems to be related to the degree of enamel attrition (Beier, 1983). Lester *et al.* (1987), also using SEM, found that within the lateral and medial enamel of the mandibular incisors of *Macropus eugenii* there is, in addition to the prominent change in prism direction, a region of gnarled enamel. These ultra-structural features could be, to some extent at least, adaptations to resist wear and perhaps to prevent fracturing under load (Rensberger & von Koenigswald, 1980). This study examined the microwear and ultrastructure of the incisal and medial edges of mandibular incisors from several macropod species to (a) determine the mode of wear, and (b) further document the enamel ultrastructure and its variability. Where possible the wear and microwear on the matching maxillary incisors was also examined.

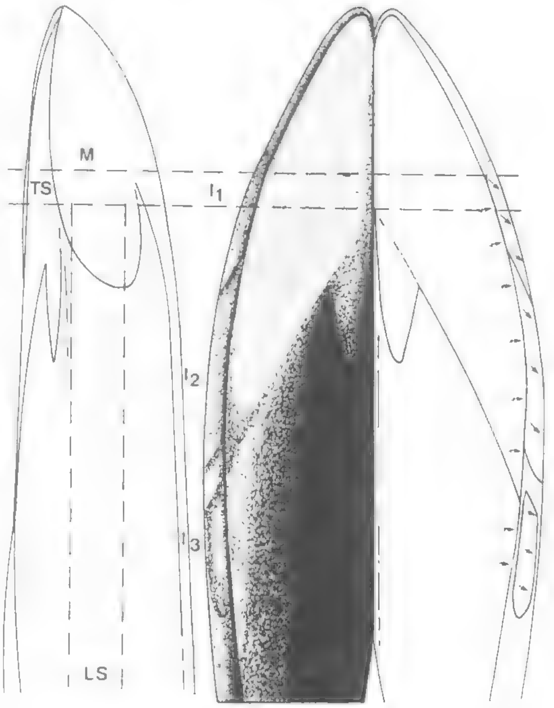

FIG. 1. Left: Medial aspect of left mandibular incisor. Right: dorsal aspect of both left and right mandibular incisors of a macropod (in this case, *Macropus rufogriseus*) illustrating where the various sections were taken, and the location of facets and striations. TS, transverse section; LS, longitudinal section; M, interproximal attrition facet; I1, I2, I3, the facets caused by occlusion with maxillary incisors; Bent arrow, direction of abrasion striations on dentine and incisal enamel; Straight arrows, attrition striations on occlusal facets.

MATERIALS AND METHODS

Mandibular incisors of the following species (with status and number of teeth in brackets) were used in this study: *Wallabia bicolor* (extant — 2); *Macropus rufogriseus* (extant — 4); *Macropus giganteus* (extant — 1); *Macropus siva* (extinct — 1); *Macropus titan* (extinct — 1); *Protemnodon* sp. (extinct — 1).

Scanning Electron Microscopy

Epoxy resin replicas of each tooth were produced by the method of Waters and Savage (1971) and Grundy (1971). These were cut longitudinally with a wheel on a microlathe to separate lateral and medial surfaces, then mounted uppermost on stubs and gold sputtercoated for SEM examination. Where possible the maxillary incisors were also prepared for SEM. Microwear features were recorded with a Phillips 505 SEM at 15-300X magnification and are described using the terminology of Rensberger (1978). The actual teeth were sectioned for light microscopy (see below). The remaining portions of the incisors were embedded in an acrylic based resin (L.R. White), polymerized in an argon atmosphere for 48 hours at 55°C. These were then mounted, ground, polished, etched in 3% phosphoric acid for 90s and finally gold-coated for examination at 15-1000X magnification. Surface-parallel windows were similarly prepared to view the unworn enamel underlying the incisal and medial edges.

Transmitted Light Microscopy

Each tooth was sectioned transversely, midway along the enamel crown and perpendicular to the unworn posterior incisal edge. A longitudinal section, normal to the first, was then taken parallel to the medial edge and midway between it and the

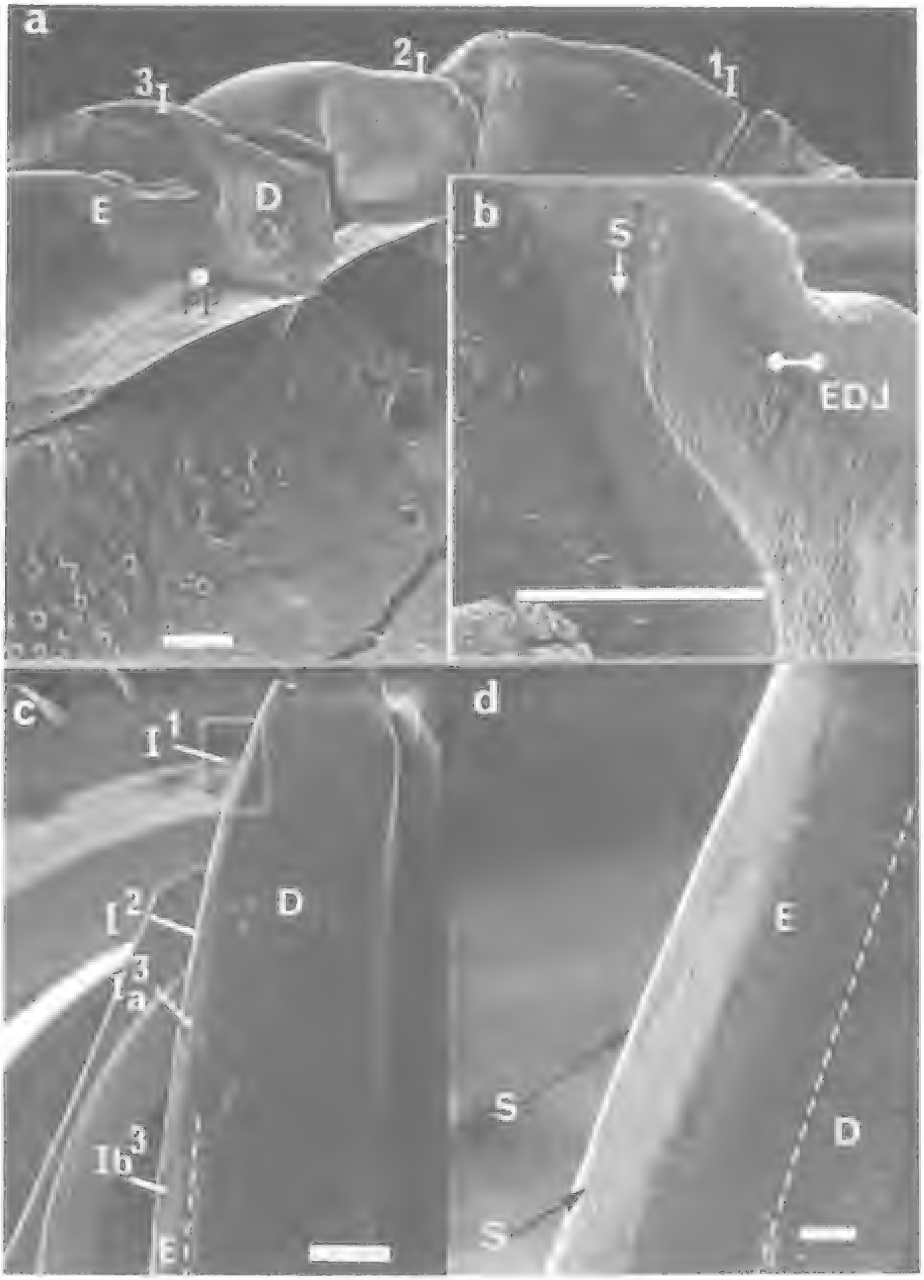

FIG. 2. (a) Scanning electron micrograph (SEM) of a replica of the three right maxillary incisors of *Macropus rufogriseus* showing the occlusal surfaces. E, attrition wear on enamel edges; D, abrasive cavitation of exposed dentine; PP, flaked pits on lingual aspect of the enamel edge; ^{1}I, central maxillary incisor; ^{2}I, second maxillary incisor; and ^{3}I, third maxillary incisor. Note the exaggerated labial groove on ^{3}I. Scale bar = 1 mm. (b) Enlargement of ^{3}I. S, parallel striations orientated antero-medially on enamel incisal edge; EDJ, enamel-dentine junction showing the gentle transition on labial side. Scale bar = 0.5 mm. (c) SEM of a replica of the incisal edge of the mandibular left incisor of *Macropus rufogriseus*. D, exposed dentine; E, enamel edge; ^{1}I, ^{2}I, ^{3}Ia and ^{3}Ib indicate rhomboidal attrition facets due to occlusion with the central, second, anterior aspect of the third, and posterior aspect of the third maxillary incisors respectively. Scale bar = 1 mm. (d) Enlargement of 2c. E, the convex, abraded enamel edge; D, exposed dentine; S, anteromedial, parallel striations on the attrition facet (^{1}I); dotted line represents EDJ. Scale bar = 0.1 mm.

incisal edge (Fig. 1). These sections were mounted on glass slides with cyano-acrylate adhesive and ground to a thickness of 70 to 100 microns (μm) with progressively finer silica and alumina grits on a Buehler polisher. After cleaning and drying, the sections had a cover slip attached with a polystyrene mounting medium. Plain and polarized light microscopy was conducted using a Leitz Orthomat microscope equipped with a polarizing objective and a quarter wave plate. Linear dimensions, where applicable, were determined with a calibrated eyepiece micrometer, accurate to one μm. Tubule and prism angles in relation to the EDJ were measured with an eyepiece protractor accurate to one degree. Wear and microwear features were recorded from SEM micrographs of the replicas. The three-dimensional organization of the enamel ultrastructure was determined using a combination of transmitted plain and polarized light microscopy and SEM microscopy of the polished and etched sections.

RESULTS

Tooth Wear

All maxillary incisors available for study, have broad incisal facets on their incisal surfaces (Fig. 2). Parallel striations, orientated antero-medially, traverse the labial enamel, whereas flaked pits are found on the lingual enamel (Figs 2a & b). The profile between enamel and dentine surfaces is relatively gentle labially but dentine is hollowed out in front of the lingual enamel (Fig. 2).

The enamel on the labial incisal edge of the mandibular incisors is smoothly convex and traversed by fine striations directed more or less laterally. This rounded edge is interrupted by several well defined, relatively flat facets which correspond to the upper incisors (Figs 1 and 2). These facets are traversed by parallel, antero-medially oriented striations (Fig. 2). In the case of *Wallabia bicolor* and *M. rufogriseus*, a distinct labial groove in the third maxillary incisor effectively divides the occluding surface of that tooth. Thus in these two species, two facets are found on the mandibular incisor which corresponds to this feature on the third maxillary incisor.

The medial edges of the mandibular incisors are flat, well-defined facets (Figs 3a, b & c). The microwear on the enamel comprised many small pits and short striations of random orientation (Fig. 3).

Three modes of wear are, therefore, represented on the mandibular incisors:

(a) well-rounded incisive edges traversed by predominantly parallel, striations oriented in a lateral direction;

(b) well-defined rhomboidal facets along the incisal edge, traversed by parallel, antero-medially aligned striations; and

(c) well-defined interproximal facets with extensive pitting and short striations of variable orientation.

Enamel Structure

In all the species studied, the dorso-lingual surface of relatively unworn mandibular incisors is virtually free of enamel (Fig. 3a). The labial surface enamel is approximately uniform in thickness, whilst the medial surface varies in thickness. The incisal enamel edge is generally convex. The prisms of the mandibular incisor enamel are arranged in closely packed parallel arrays and are separated by distinct interprismatic sheets (Fig. 4). The crystals of the sheets do not intrude between the prisms of an array. In cross-section, the prisms are oval, their greatest and least widths being 5 μm (parallel to the sheets) and 2-3 μm respectively. Sheet widths average 1.7 μm (Figs 4b, c & d). Generally, the prism axis coincides with the long axis of the crystals. In the region of the incisal and medial edges, however, the crystals are aligned at about 25° to the prism axis and are approximately normal to the tooth surfaces. The sheet crystals are aligned at 85-95° with respect to those in the adjacent prisms. Enamel tubules are best seen when they are represented as artificial casts in resin embedded sections. Tubules are present only in the prisms, or immediately adjacent to them, and thus follow the same course (Fig. 3b).

Four additional ultrastructural differentiations are found within the mandibular incisor enamel. Three of these, overall change in prism orientation, zoning, and prism decussation, are present in all the species examined. The fourth, whorled enamel, although present in all six species, differs in its location. Although these differentiations are discussed below separately, they are often interrelated. For example, zoning is largely the consequence of change in prism orientation.

Prism Orientation

The inner labial enamel, viewed in longitudinal section, is composed of a series of parallel prisms and sheets, aligned antero-laterally and departing from the EDJ at 60-100° (Fig. 4). A short distance out from the EDJ there is an abrupt directional

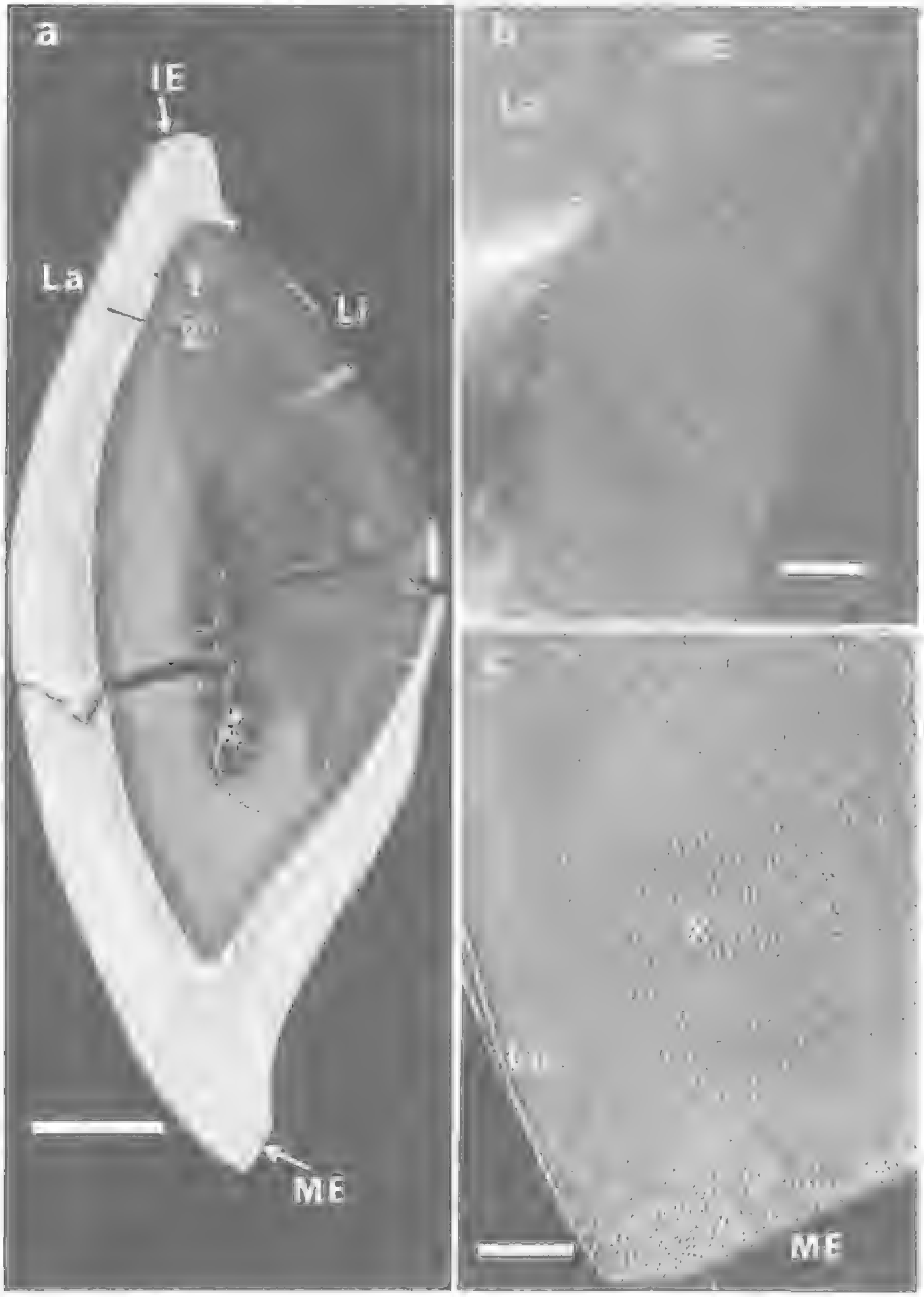

FIG. 3. (a) Light micrograph of transverse section of mandibular incisor of *Macropus giganteus*. IE, relatively unworn incisal edge with convex profile, the "arrowed" portion being an attrition facet due to occlusion with a maxillary incisor; La, labial enamel approximately 700 μm thick (note artefactual crack along the prism interface that changes direction between zones 1 and 2); 1, zone I narrowing towards the incisal edge; 2, zone II of approximately uniform thickness; Li, lingual aspect of tooth devoid of enamel; ME, medial attrition facet. Scale bar = 1 mm. (b) SEM of medial edge enamel. ME, interproximal facet with pitted texture indicating compressive wear; La, labial enamel. Scale bar = 0.2 mm. (c) SEM of an etched section of the most ventral enamel. La, labial surface; ME, medial edge attrition facet; X, extensive prism decussation. A similar pattern of decussation was found in the incisal edge enamel. Scale bar = 0.1mm.

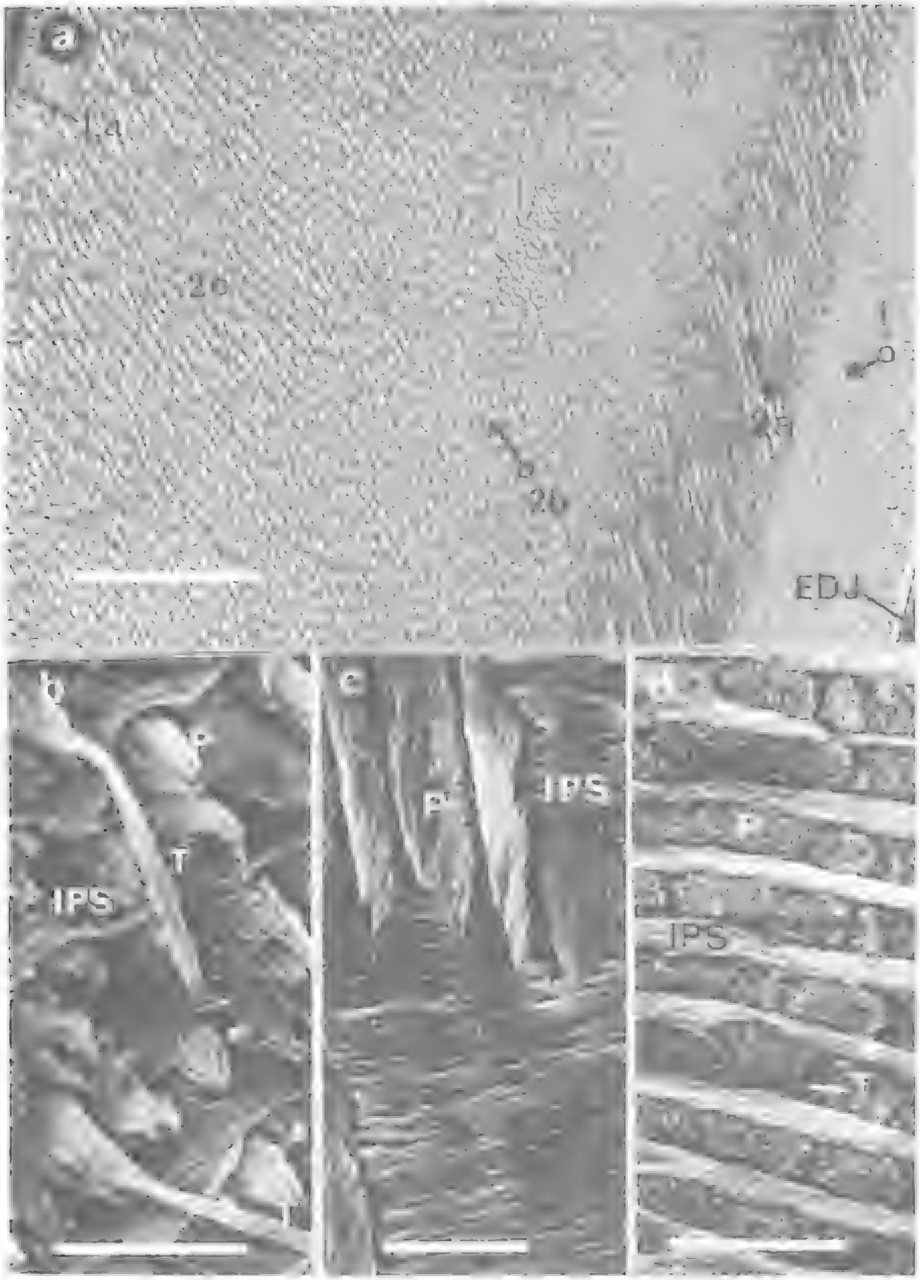

FIG. 4. (a) SEM from an etched transverse section of labial enamel of ¹I of *Macropus giganteus*. EDJ, enamel-dentine junction; La, labial enamel; 1, zone I with prisms cut transversely and aligned posteroventrally (2a). A marked change of direction, a 90° bend occurs between zones I and II. In the inner region of zone II the prisms are aligned dorso-laterally and anteriorly (2b); in the outer region of zone II (2c) the prisms are similarly oriented but now assume a less anterior alignment. Scale bar = 0.1 mm. (b) SEM from an etched transverse section of the enamel of *Macropus rufogriseus*. P, prism; IPS, interprismatic sheets; T, cast of tubule, an artefact of epoxy resin embedding. Scale bar = 10 μm.(c) SEM from an etched longitudinal section of the incisal enamel of *Macropus rufogriseus*. P, prism; IPS, interprismatic sheets. In this orientation the tubules are not readily apparent. Scale bar = 10 μm. (d) SEM of an etched transverse section of the incisal enamel of *Macropus rufogriseus*. P, row of prisms; IPS, interprismatic sheets; T, tubule. Scale bar = 10 μm.

change to a more anterior orientation of 45-60° relative to the EDJ. This change in direction delineates zones I and II (see below and Fig. 5b). In transverse sections, the inner labial prisms are ventro-laterally aligned and at 135-155° to the EDJ. At the point of directional change, the prisms turn, through 90-100°, thus aligning dorso-laterally at 30-55° relative to the EDJ.

Zoning

Zoning, which is primarily a consequence of the overall change in prism orientation, occurs in the labial, and, to a lesser extent, in the medial enamel. Two main zones are evident. Zone I extends from the EDJ to, and is delimited by, the abrupt change in prism direction. Zone II is composed of the remaining outer enamel (Fig. 4a). This zone may be further subdivided into inner and outer regions on the basis of a more subtle ultrastructural differentiation (see below). The ratio of the thickness of zone I to the overall enamel thickness exhibits interspecific variation (Table 1).

On the labial enamel zone I is of approximately uniform thickness. At its more dorsal (incisal) extremity, zone I narrows somewhat, whilst ventrally it broadens and becomes ill-defined (Fig. 3a). Zone II, when viewed with transmitted polarized light, appears to have a distinct inner and outer region. Delineating these two regions is a boundary of interdigitating colors. This boundary is found to correspond to the position of enamel prisms in a whorled arrangement (see below). The inner and outer regions of zone II probably correspond to zones two and three of Schmidt and Keil (1971).

Prism Decussation

Within the incisal and medial edges decussating arrays of prisms (i.e. parazones and diazones), are present and overlap each other at obtuse angles (Figs 3c and 5d). This arrangement probably corresponds to the gnarled enamel of Lester *et al* (1987).

Whorled Enamel

In the smaller kangaroos, (*Wallabia bicolor* and *M. rufogriseus*) mid-labial, subsurface sections reveal regions of whorled enamel (Figs 5a and c), which in oblique transverse section are prisms arranged in spirals. This feature does not manifest itself at the tooth surface. Rather the prisms resume their parallel lateral course towards the incisal edges before terminating in the aprismatic region immediately below the surface. Whorled enamel also occurs in the other species studied but, is found well below the incisal and medial surfaces.

TABLE 1.

Species	Zone I thickness : Total thickness
Macropus rufogrisea	1/6 to 1/5
Wallabia bicolor	1/6 to 1/5
Protemnodon sp.	1/6 to 1/5
Macropus siva	1/5 to 1/4
Macropus titan	1/4 to 1/3

DISCUSSION

Our observations of macropod enamel structure confirm and amplify those of previous workers. This discussion attempts to relate modes of wear to details of enamel structure, and suggests how the main ultrastructural differentiations may be adaptations to the wearing forces.

Tooth Wear

Three modes of wear occur on the mandibular incisors. Two of these are readily explained by recognized functions. The convex contour to, and generally lateral striations on, the incisal enamel edge are almost certainly due to cropping. The lateral striations could result from siliceous grasses or particles being dragged across the outer dentine and enamel edge as the head pulls back to divide the grass. Such attrition can cause considerable wear in cropping (Young & Marty, 1986).

The medial facets with their extensive pitting and short, randomly-aligned striations, appear to be the result of compressive attrition. This occurs when grasses and extraneous materials are trapped between the constantly closing and spreading mandibular incisors. Facet microwear due to attrition of this nature is found in other taxa (Young & Marty, 1986).

The third mode of wear, distinct rhomboidal wear facets with striations aligned antero-medially, is not explicable by the type of cropping observed in cinefluorography by Ride (1959). It is possible that an anisognathous incision is also employed, in addition to the isognathous cropping action of the incisors. The antero-medial orientation of the striations indicates that the action is unilateral. The enamel-dentine transition on the maxillary incisal edges is smooth labially and relatively abrupt lingually. This shows that the direction of this action is a labial to lingual occlusal movement (Greaves 1973). Another explanation could be that the inter-incisal attrition facets occur as an

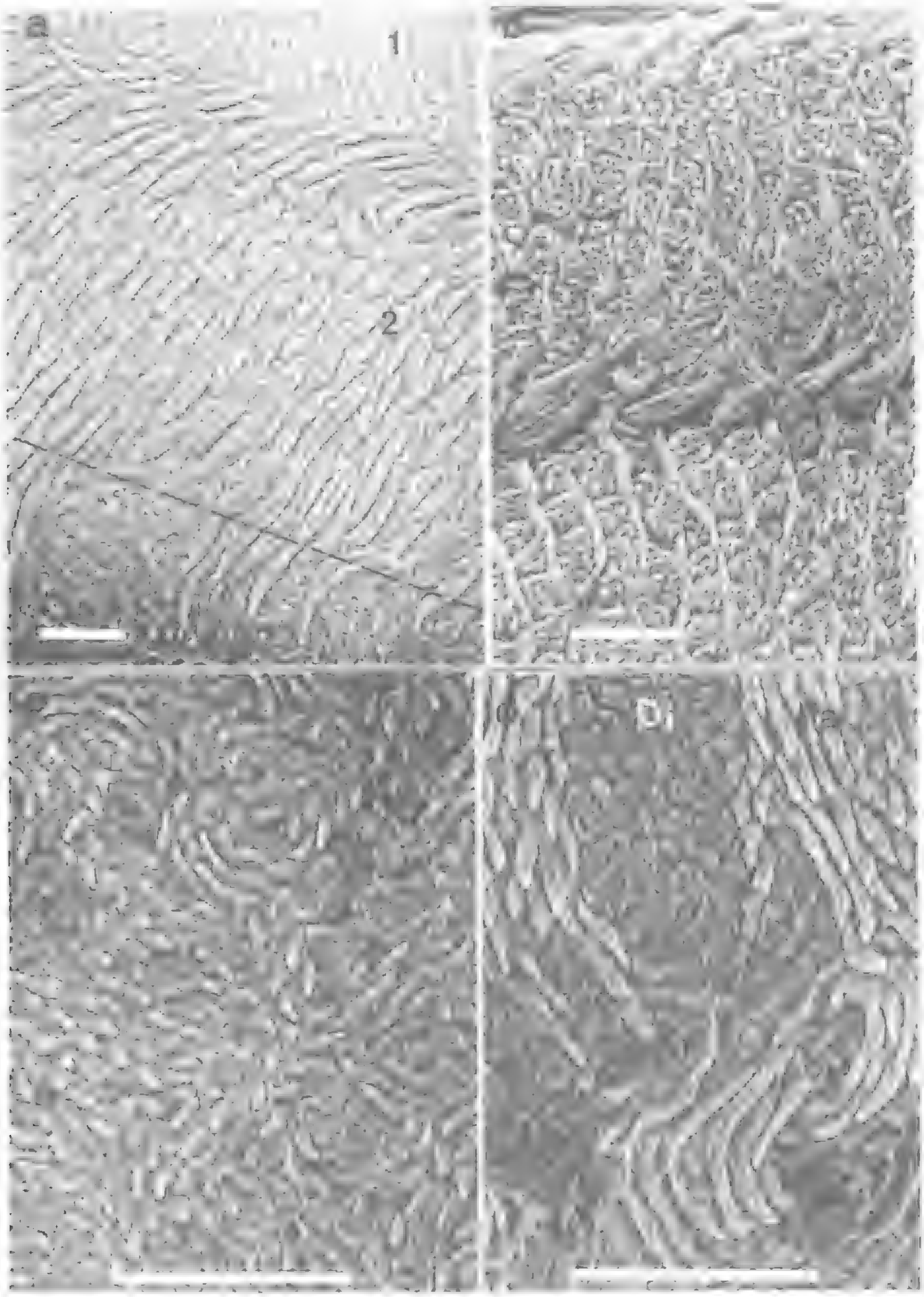

FIG. 5. (a) SEM of an etched longitudinal section of the incisal enamel of *Wallabia bicolor*. 1, zone I enamel prisms cut transversely; 2, zone II enamel prisms cut in oblique longitudinal section. Anterior to left. At the dashed line, a surface parallel window has been cut perpendicular to the longitudinal section, revealing location of the whorled pattern (cf. 4c). Scale bar = 20 μm. (b) SEM of etched longitudinal section of the incisal enamel of *Macropus rufogriseus*. Showing the prism bend. Anterior to left. Scale bar = 10 μm. (c) SEM of an etched, sub-surface section of the lateral incisal enamel of *Wallabia bicolor*. Clearly showing whorled enamel. Scale bar = 10 μm. (d) SEM of an etched, sub-surface section of the incisal edge enamel of *Macropus rufogriseus*, showing prism decussation (Hunter- Schreger bands). Di, diazone; Pa, parazone. Scale bar = 10 μm.

incidental consequence of the antero-medial chewing action of the molars. However, the mandibular incisors appear to be able to clear their maxillary counterparts when approximated (Ride, 1959), and thus this seems an unlikely possibility, despite the observation that chance glancing contacts can be produced by manipulation of dried skull and jaws.

ENAMEL STRUCTURE

One feature which dominates the differentiation of macropod enamel ultrastructure is the abrupt directional change in prism orientation resulting in zoning.

Such distinct zones do not occur in two other diprotodont marsupials which have procumbent mandibular incisors, the Koala *Phascolarctos cinereus*, and the possum *Trichosurus vulpecula* (personal observation). This suggests that the high degree of enamel differentiation found in the macropod incisors is an adaptation to the functional loads imposed on these teeth by the extent of the incisal edge. Consequently a comparison of these differentiations over a wider range of diprotodontians would be instructive.

Although prism decussation occurs in the labial and medial edges, it does not manifest itself at the surface as a series of troughs and ridges as in rhinoceroses (Rensberger & von Koenigswald, 1980). This suggests either that the decussations are not as well-defined in the macropods, or that they suffer multidirectional abrasion that obliterates any protruding.

The following is a tentative explanation of different prism orientations. Assuming that the main loading on the mandibular incisors results from cropping and anisognathous incision forming the facets, then the major force operating will be applied to the anterior portion of the tooth and lateral to its longitudinal axis. This will cause a torsional stress, and tend to bend the tooth ventrally. Young's modulus, is almost certainly lower for dentine than for enamel, even though the values quoted in the literature are highly variable (e.g. ^{E}dentine = 7.6 to 19.0 x 10^9 N.m^{-2} and ^{E}enamel = 9.6 to 84 x 10^9 N.m^{-2}; Rassmussen & Patchin, 1984). So, for a given stress (load per unit area), the dentine, although thicker, is likely to experience a greater strain deflection. This would be expressed as the fractional change in a linear dimension, or as an angular deflection in (unitless) radians. Thus, during cropping, the torsional stress would cause greater deflection of the dentine than the enamel. The enamel prisms will then experience compressive torsional loading. If this is so, then the overall postero-ventral orientation of the labial zone II prisms will redirect such loadings in an oblique, circumferential path through the enamel and away from the point of application. In this manner the antero-lateral tooth loadings are redistributed more evenly along the length of the tooth. This may solve one problem but another is introduced. The prism orientation in zone II, seemingly so favourably arranged to redirect compressive torsional loadings in the posterior portion of the teeth, will now undergo a tensile loading in the more dorso-posterior regions of the enamel. Also, the tension will operate more or less at right angles to the prism alignment. The tension failure (i.e. cracking of brittle, heterogenous, anisotropic materials like enamel) occurs preferentially along interfaces (Gordon, 1968). For example, the "work of fracture" value, — i.e. the energy to create new surfaces (by crack propagation) — within enamel, is 0.13 x 10^2 J.m^{-2} parallel to the prisms and 2.0 × 10^2 J.m^{-2} perpendicular to them (Rassmussen & Patchin, 1984). The artifactual crack in the mandibular incisor of *Macropus giganteus* (Fig. 3a) shows this and demonstrates that the prisms have relatively weak interfaces. This is a necessity for the successful operation of a crack-stopping mechanism (Cook & Gordon, 1964). The existence of prism decussations on the lateral and medial edges and subsurface regions of whorled enamel may represent a solution to this problem. Further, should a crack occur, then upon encountering the whorled enamel, with its multiplicity of non-aligned interfaces, it is likely to be halted by the crack-stopping mechanism. This mechanism simultaneously redirects a crack along an interface approximately normal to the original direction of crack propagation and increases its tip radius by many orders of magnitude. The effect of redirection is that the new alignment is energetically less favourable for opening and thus spreading the crack in terms of the pattern of stress concentrations which spread the original crack. The increased tip radius further lowers stress concentration in the immediate vicinity. This in turn increases the critical Griffith length, beyond which catastrophic failure occurs and which is inversely proportional to the square of the imposed stress (Gordon, 1968). It is also possible that the energy required for the formation of new surfaces (between the separating interfaces) is provided by an equivalent decrease in strain energy and, therefore, in the stress experienced by the system. Either way, the locational differences of whorled enamel in the species studied may indicate differences in the site of these tension loadings.

There may be two explanations also for the bend in the prisms. Either the bend is a crack deflector, or it represents a developmental necessity, given the possible constraints of enamel formation. As illustrated by Figure 3a, cracks readily follow the relatively weak prism interfaces. Just what is achieved by this is not obvious. Once a crack of external origin has reached the bend, much damage has already occurred. However, the crack will encounter the EDJ more dorsally. Perhaps this is a form of damage control in that, having failed, the enamel ventral to the crack (in danger of breaking away) retains a greater area of attachment to the dentine. If such a mechanism is operating, then it is reasonable to ask why the bend is not closer to the outer surface where these possible benefits would be greatest. The other explanation is that the bend has nothing to do with fracture resistance or crack deflection. Given that prisms can neither bifurcate, nor appreciably alter their diameter, ameloblasts (and therefore the prisms) might be constrained in terms of the angle at which they depart the EDJ. Cell packing or the spatial organization of the Tome's processes might require this. Achievement of the final tooth crown morphology and a suitable ultrastructure (i.e. with the prisms in regions of high wear intersecting the crown surface at suitably obtuse angles) may, in some instances, necessitate this drastic directional change by the ameloblasts.

CONCLUSIONS

The pathways of the prisms in macropod incisor enamel are remarkedly regular, three-dimensionally complex, differentiations. A uniform bend in the prisms occurs a short distance from the EDJ on the lateral aspect of the tooth. This may be a device to transmit torsional loads to the dentine. Microwear indicates that the torsional loads probably exist. Further from the EDJ, the prisms spiral in whorls. This may be a device to resist crack propagation along the paths of the prisms. In the lateral incisal edge and on the medial proximal contact edge, the prisms decussate. This may be a device to increase edge strength and to resist compressional loads for the microwear, particularly on the medial facet, where microwear indicates compression. As these differentiations were uniform throughout the macropod species studied, it seems unlikely that differences in the presence or absence of whorls, or in the widths of zones, for example, could be used for taxonomic separation of closely-related macropods. However, if these differentiations have functional significance, they would be expected to scale allometrically in macropods of different size but similar incisor functions. Examination of these differentiations in a wider range of diprotodonts might therefore be instructive regarding taxonomic interrelationships.

ACKNOWLEDGEMENTS

We would like to thank Mr T. Daley for the excellent preparations of material for SEM and Mr Ian Sobbe for the specimens of extinct macropod incisors used in this study. The expertise of the Electron Microscope Centre, University of Queensland is acknowledged. Mr Stevens was supported by an ADREF scholarship.

LITERATURE CITED

BEIER, K. 1983. Hunter-Schreger-Bander in Zahnschmeltz von Kangurulis (Macropodine, Marsupialia). *Zoologischer Anzeiger* **210**: 315–32.

BOYDE, A. AND FORTELIUS, M. 1986. Development, structure and function of rhinoceros enamel. *Zoological Journal of the Linnean Society* **87**: 181–214.

AND LESTER, K.S. 1984. Further SEM studies of marsupial enamel. p. 442–6. *In* Fearnhead, R. and Suga, S. (Eds) 'Tooth Enamel IV'. (Elsevier Science Publishers: Amsterdam).

CARTER, J.T. 1920. The microscopical structure of the enamel of two Sparassodonts, *Cladosictis* and *Pharsophorus*, as evidence of their marsupial character together with a note on the value of the pattern of the enamel as test of affinity. *Journal of Anatomy* **54**: 189–95.

COOK, J. AND GORDON, G.E. 1964. A mechanism for the control of crack propagation in all-brittle systems. *Proceedings of the Royal Society of London* A.**282**: 508–20.

FORTELIUS, M. 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelationships. *Acta Zoologica Fennica* **180** 1–76.

GORDON, J.E. 1968. 'The new science of strong materials or why you don't fall through the floor'. (Penguin Books Ltd.: Harmondsworth).

GORDON, K.D. 1984. The assessment of jaw movement direction from dental microwear. *American Journal of Physical Anthropology* **63**: 77–84.

GREAVES, W.S. 1973. The inference of jaw motion from tooth wear facets. *Journal of Paleontology* **47**: 1000–1.

GRUNDY, J. 1971. An intraoral replica technique for use with the scanning electron microscope. *British Dental Journal* **130**: 113–7.

KOENIGSWALD, von W. 1980. Schmeltzstructur und morphologie in der Arvicolidae (Rodentia). *Abh. Senckenberg. Naturforsch. Ges. Frankfurt. M.* **539**: 1–129.

LESTER, K.S., BOYDE, A., GILKESON, C. AND ARCHER, M. 1987. Marsupial and monotreme enamel structure. *Scanning Microscopy* **1**: 401–20.

MURIE, J. and BARTLETT, A.D. 1866. On the movement of the symphysis of the lower jaw in the kangaroos. *Proceedings of the Zoological Society of London* **1866**: 28–34.

OWEN, R. 1845. 'Odontography'. (London).

RASSMUSSEN, F.T. AND PATCHIN, R.E. 1984. Fracture properties of human enamel and dentin in an aqueous environment. *Journal of Dental Research* **63**(12): 1362–8.

RENSBERGER, J.M. 1973. An occlusion model for mastication and dental wear in herbivorous mammals. *Journal of Paleontology* **47**: 515–28.

1978. Scanning electron microscopy of wear and occlusal events in some small herbivorous mammals p. 414–38. *In* Butler, P. and Joysey, K.A. (Eds). 'Development Function and Evolution of Teeth'. (Academic Press : London).

AND KOENIGSWALD, von M. 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. *Paleobiology* **6**: 477–95.

RIDE, W.D.L. 1959. Mastication and taxonomy in the macropodinae skull. *Publications of the Systematics Association* **3**: 33–59.

SCHMIDT, W. AND KEIL, J. 1971. 'Polarizing microscopy of dental tissues'. (Pergamon Press: Oxford).

TOMES, J. 1849. On the structure of the dental tissues of marsupial animals and especially of the enamel. *Philosophical Transactions of the Royal Society of London* **139**: 403–42.

WALKER, A. 1984. Mechanisms of honing in the male baboon canine. *American Journal of Physical Anthropology* **65**: 47–60.

WATERS, B. AND SAVAGE, D. 1971. Making duplicates of small vertebrate fossils for teaching and research collections. *Curator* **14** 123– 32.

WILLIAMS, B. 1923. Disputed points and unsolved problems in the normal and pathological histology of enamel. *Journal of Dental Research* **5**: 27–116.

YOUNG, W.G. AND MARTY, T.M. 1986. Wear and microwear on the teeth of a moose (*Alces alces*) population in Manitoba, Canada. *Canadian Journal of Zoology* **64**: 2467–79.

AND ROBSON, S. 1987. Jaw movements from microwear on the molar teeth of the koala (*Phascolarctos cinereus*). *Journal of Zoology, London* **213**: 51–61.

MCGOWAN, M. AND DALEY, T. 1987. Tooth enamel structure in the koala, *Phascolarctos cinereus* :some functional interpretations. *Scanning Microscopy* **1**: 1925–34.

CORRELATION OF CRANIAL AND DENTAL VARIABLES WITH DIETARY PREFERENCES IN MAMMALS: A COMPARISON OF MACROPODOIDS AND UNGULATES

CHRISTINE M. JANIS

Janis, C.M. 1990 3 31: Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodoids and ungulates. *Mem. Qd Mus.* 28(1): 349–366. Brisbane. ISSN 0079-8835.

Kangaroos and ungulate placental mammals are compared for correlations of craniodental variables with dietary type. The comparisons aim to identify those diet-related morphological variables that transcend taxonomic categories and thus represent physical constraints on craniodental design in herbivorous mammals. Kangaroos and ungulates are closely similar for most variables examined, although the absolute morphological values tend to be relatively slightly smaller in kangaroos in most cases. In addition kangaroos show a greater tendency for negative allometric scaling of these variables. Differences are mainly in molar widths, occipital height and muzzle width. To a large extent these differences, and profound differences in absolute values for variables, may related to differing modes of incision and occlusion in ungulates and kangaroos.

☐ *Macropods, ungulates, craniodental design, functional anatomy, diets, phylogenetic constraints.*

Christine M. Janis, Program in Ecology and Evolutionary Biology, Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912, U.S.A.; 1 July, 1988.

While it is intuitively obvious that the morphological design of animals reflects their general ecology and mode of life, few studies have attempted to quantify this apparent correlation between skeletal anatomy and behavioural ecology. Most studies of a quantitative nature have focused on carnivores (e.g. Radinsky, 1981a and b, for cranial proportions; van Valkenburgh, 1985, 1987 and 1988, for dental and postcranial proportions), or on primates (e.g. Kay & Couvert, 1984 and numerous references therein). Fewer studies are available for herbivorous mammals. Sanson (1978, 1980, 1982) has published extensively on the relation between dental wear and diet in macropodids, but has mentioned little about craniodental proportions in relation to diet. Boué (1970) noted that the lateral incisors of grazing ungulates are broader and more cup-shaped than those of browsers, and Vrba (1978) discussed the fact that grazing bovids tend to have more hypsodont cheek teeth, a shorter premolar row, a longer diastema and a deeper mandibular ramus than browsers, but neither of these studies provide quantitative evidence. However, some quantitative studies on ungulates do exist: Bell (1970) and Owen-Smith (1982) noted that grazing African bovids have relatively broader muzzles than browsers; Radinsky (1984) discussed changes in equid cranial proportions during the evolution from a browsing to a grazing diet; Scott (1979) showed how bovid postcranial proportions may be correlated with habitat preference; and Janis (1988) demonstrated a quantitative relationship between hypsodonty index and diet in ungulates. Muzzle width and relative incisor width in all ungulates have been the subject of a more extensive quantitative analysis by Janis and Ehrhardt (1988), whose conclusions generally support those of Bell, Owen-Smith and Boue, but also show that phylogenetic history may play a role in the absolute values of these morphological variables.

The present study arose from an interest in establishing the role played by phylogenetic constraints in the design of craniodental morphology in herbivorous mammals. Preliminary studies, on the correlation between craniodental variables and dietary type in ungulates, showed that, while many variables could be correlated with diet, differences existed between ungulates of different phylogenetic lineages (e.g. between ruminant artiodactyls, suoid artiodactyls and perissodactyls — including hyracoids). Sometimes the trend was similar between animals of similar dietary types in the different lineages, but the absolute values were different. (For example, in the correlation of basicranial angle with diet, the angles are generally more acute in artiodactyls than in perissodactyls, but nevertheless within each order grazers have more acute angles than browsers; see Fig. 9). In other cases the trend was totally different in the different lineages (for example, grazing ruminants have relatively shorter premolar rows than browsers, while grazing perissodactyls have relatively longer premolar rows; see Fig. 4).

The correlation of craniodental variables with dietary type in herbivorous mammals will be examined more fully elsewhere. In comparing macropodids with ungulates in this study my aim is to discover which morphological variables were *invariably* correlated with dietary type in herbivores, those variables might then be used to determine the diets of those fossil ungulates that lack living relatives. My rationale was as follows: kangaroos and ungulates had very different evolutionary origins, yet convergently developed into large-bodied terrestrial herbivores spanning the dietary range from omnivore to fibrous grazer. If similar trends in diet-related morphological variables could be shown to hold true for both groups, then (even if the absolute values were somewhat different) it could be assumed that the value of such a variable was somehow determined by physical constraints affecting craniodental design in all herbivores. Such variables might then be applied with confidence to fossil ungulates; by contrast those which showed different trends in living ungulates and kangaroos might be more subject to influence from phylogenetic constraints imposed on the lineages by their past evolutionary history.

MATERIALS AND METHODS

Twenty-four craniodental measurements were made on 136 species of living ungulates. These included 99 ruminant artiodactyls (families Antilocapridae, Bovidae, Cervidae, Giraffidae, Moscidae and Tragulidae), ten suiod artiodactyls (families Hippopotamidae, Suidae and Tayassuidae), five camelid artiodactyls (family Camelidae) 16 perissodactyls (families Equidae, Rhinocerotidae and Tapiridae), and three hyracoids (family Procaviidae). The sample of marsupials included 52 kangaroo species (families Macropodidae and Potoroidae), one koala species (family Phascolarctidae), and three wombat species (family Vombatidae). This list does not include the complete range of living species, but

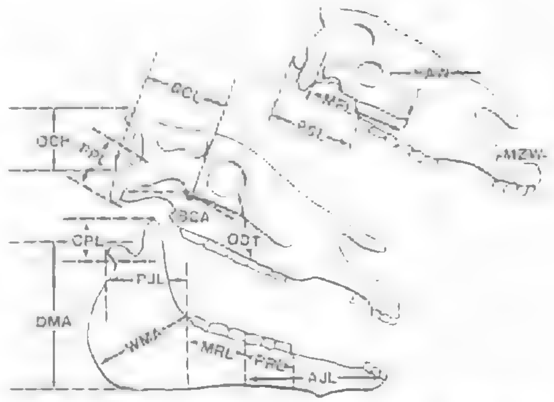

FIG. 1. Craniodental measurements. All dental lengths and widths were measured on the (occlusal) labial surface of the tooth. Other measurements were taken as follows: Lower premolar row length (PRL) and lower molar row length (MRL): along the base of the visible tooth crowns on the lateral side of the jaw. Anterior jaw length (AJL): from the boundary between molar and premolar rows to the base of the first lower incisor. Posterior jaw length (PJL): from the posterior end of the molar row to the level of the posterior border of the jaw condyle. Depth of mandibular angle (DMA): from the top of the jaw condyle to the maximum vertical depth of the angle of the mandible. Width of the mandibular angle (WMA): from the end of the molar row to the maximum linear distance on the angle of the mandible. Length of coronoid process (CPL): from the base of the jaw condyle linearly to the top of the coronoid process. Length of masseteric fossa (MFL): from the postglenoid process to the anterior-most extension of the masseteric fossa. Occipital height (OCH): from the base of the foramen magnum to the apex of the occipital ridge. Posterior skull length (PSL): from the back of the molar row to the posterior border of the occipital condyles. Orbital distance from tooth row (ODT): from the boundary between molar and premolar rows, to the closest point on the ventral border of the orbit. Length of paraoccipital process (PPL): from the top of the occipital condyles linearly to the tip of the paraoccipital process. Muzzle width (MZW): from the outer border of the junction between maxillary and premaxillary bones. Palatal width (PAW): between the protocones of the upper second molars third molars in the case of marsupials). Basicranial length (BCL): from the base of the foramen magnum to the point of angulation of the basicranial region with the face. Basicranial angle (CA): the angle between the basioccipital bone and the palate. Total jaw length = anterior jaw length (AJL) + lower molar row length (MRL) + posterior jaw length (PJL). Total skull length = anterior jaw length (AJL) + lower molar row length (MRL) + posterior skull length (PSL).

does include all living genera. Because of time constraints, and availability of specimens, some species of the very speciose genera (*Bos, Capra, Cephalophus, Cervus, Dendrohyrax, Gazella, Heterohyrax, Ovis* and *Procavia* in the case of the ungulates; *Petrogale* in the case of kangaroos) were excluded from the analyses. Measurements were usually made on at least six individuals of each species, and on considerably more of certain species that were better represented in collections (see Table 1). Each species was classified as a "grazer" (more than 90% of grass in the diet on a year round basis), "browser" (less than 90% of grass in the diet on a year round basis), "intermediate feeder" (10-90% of grass in the diet) or "omnivore" (taking mainly non-fibrous vegetation, including some fungal or animal material). These distinctions follow the definitions of Hofmann and Stewart (1972). Diets and body weights (expressed in kilograms) were obtained from a range of published sources for ungulates (see note following Literature Cited), and from Strahan (1983) and Lee and Cockburn (1985) for marsupials. (I am also indebted to Kathleen Scott for information on ungulate body weights, and to Peter Jarman and Tim Flannery for information on kangaroo diets and body weights).

The measurements taken on ungulates are explained in Figure 1. The way in which these measurements were modified (when necessary) in the case of the kangaroos is discussed below. All measurements, with the exception of the basicranial angle (measured in degrees by means of dividers and a protractor) were taken in centimetres with vernier or dial calipers. Measurements were obtained only from animals of specific age, as indicated by the degree of dental wear. In ungulates, measurements were made on those individuals where the last molar had fully erupted, but in which the molars did not exhibit extreme wear. Relative ages of kangaroos were treated more strictly; many of the ungulate measurements were made using the position of the first or last molar as reference points, but certain kangaroo genera exhibit molar progression, making these reference points somewhat more labile. For such macropodid taxa, care was taken to measure only those individuals that were considered to be "young adults" — i.e. those in which the last molar had fully erupted, but had not shown signs of considerable wear or of forwards progression in the jaw.

Certain variables were calculated as compounded variables. Obviously dental areas and hypsodonty index must be calculated as compounded values, but I also calculated total skull length and total jaw length in this fashion (see legend for Fig. 1). The reason for this was that the measurements taken were originally intended for comparison of fossil mammals with living ones. Complete skulls and jaws are rare in the fossil record, although partial ones are more common. Compounded variables derived in this fashion for living mammals allow for a more direct comparison with fossil taxa, as compounded values for total skull and jaw length may be all that are available in the latter case. Hypsodonty index was calculated as the average width of the last molar (M_3 in ungulates and M_4 in kangaroos) divided by the maximum unworn height (measured on the labial border of the tooth from the base of the crown to the tip of the protoconid). In the case of the hypsodont ungulates, where the base of the unworn crown is concealed within the body of the jaw, the height of the unworn M_3 was derived from X-ray photographs (see Janis, 1988).

Ungulates and kangaroos are not directly comparable for certain variables. My designation of equivalent measurements in kangaroos (see discussion below) came both from theoretical considerations and from extensive handling of comparative material, giving confidence that any differences between the two groups in such "equivalent" variables represent differences in functional morphology. Kangaroos have four molars (or possibly five; see Archer, 1978), while ungulates have three. Rather than compare the equivalent numbered molar in each case (which would have been meaningless in terms of biology), I compared the second molars of ungulates with the third molars of kangaroos. The second molar was chosen for ungulates because this has been shown to the best-correlated with body weight (Janis, in press). Examination of a wide range of kangaroo material led me to conclude that the third molar is the closest analogue with the second molar in ungulates, both in terms of the time of eruption in the development of the individual, and in the relative rate of wear. Both teeth are also analogous in being the "second to last from the back". Thus molar dimensions of the second molar of ungulates were compared with those of the third molar of kangaroos. The length of the lower premolar tooth-row could not be determined very easily in those kangaroo species that exhibit molar progression, (i.e. *Lagorchestes, Onychogalea, Macropus, Peradorcas* and *Petrogale*), since at the "young adult" stage described previously, the premolar had usually been shed. In these taxa, lower premolar row length (calculated as basal P_3

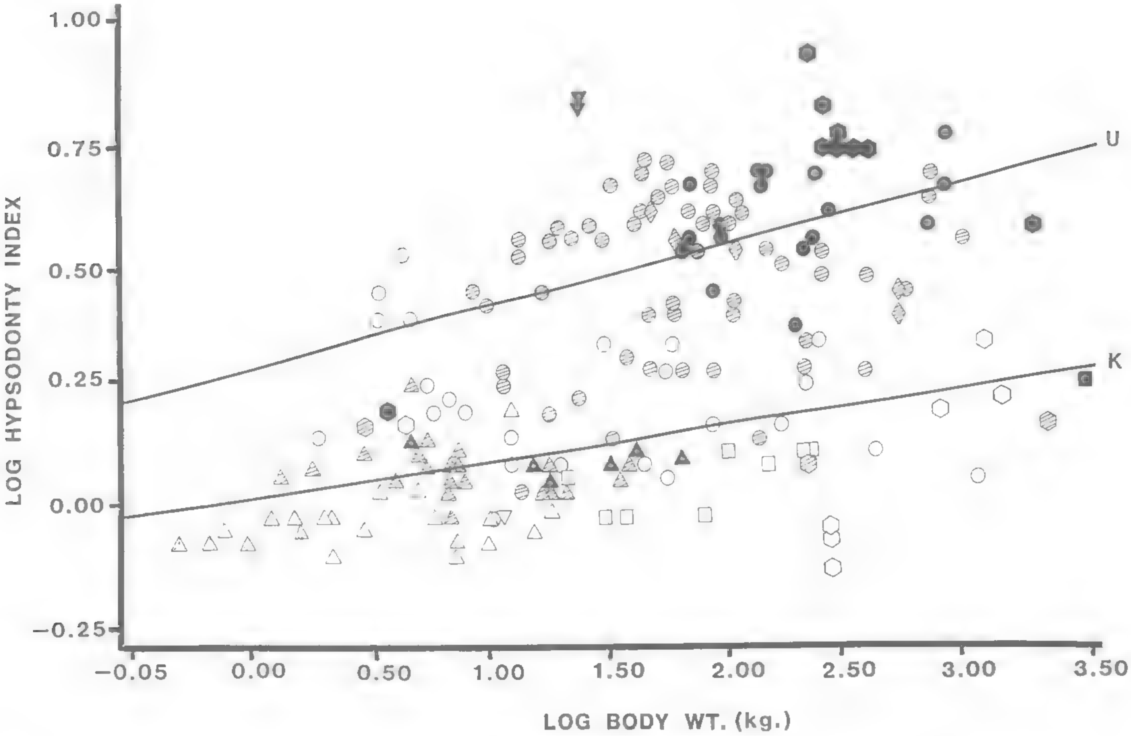

FIG. 2. Relationship of log hypsodonty index to log body weight in ungulates and kangaroos: [U — ungulates, K — kangaroos]: triangles — Macropodoid marsupials (kangaroos and potoroines), inverted triangles — Phascolarctoid marsupials (koala and wombats), circle — Ruminant artiodactyl ungulates, diamonds — Camelid artiodactyl ungulates, squares — Suoid artiodactyl ungulates, hexagons — Perissodactyl or Hyracoid ungulates; open symbols — grazers, hatched symbols — intermediate feeders, closed symbols — browsers, stippled symbols — omnivores].

length) was determined from younger individuals in which the tooth exhibited little or moderate wear.

The mode of incision is very different between ungulates and kangaroos. In ungulates, the upper and lower incisors meet directly, while in kangaroos the diprotodont lower incisors fit inside the upper incisor arcade. The width of the central and lateral incisors was obtained from the lower incisors in ungulates (as ruminant artiodactyls lack upper incisors). (The relative widths of central and lateral incisors are similar for the upper and lower teeth in those ungulates, such as equids and tapirs, that retain a full compliment of upper and lower incisors). For the kangaroos, with their diprotodont lower incisors, these measurements were taken on the upper teeth. The "anterior jaw length" of ungulates was calculated as the distance from the junction of the premolar and molar row to the base of the lower first incisor. In kangaroos the premolars are usually lost in those genera that exhibit molar progression, and the lower incisor forms part of the functional length of the lower jaw, occluding behind the upper incisors (in contrast to the direct occlusion seen in ungulates). Thus in the marsupials "anterior jaw length" was calculated as the distance between the M_1 and the tip of the lower incisor.

Plots were derived of each craniodental variable (as the dependent variable) against the body weight. In the case of sexually dimorphic species, the values and body weights of the males alone were used. All regression lines were calculated by the least squares method, and the distribution of the residuals according to feeding type around the regression line was examined in each case. Significant differences were determined by means of a *t*-test. This type of bivariate analysis, while a relatively simplistic approach, nevertheless allows for a direct comparison between ungulates and kangaroos for each morphological variable. Multivariate techniques will be used in future studies, but it is evident from these results that

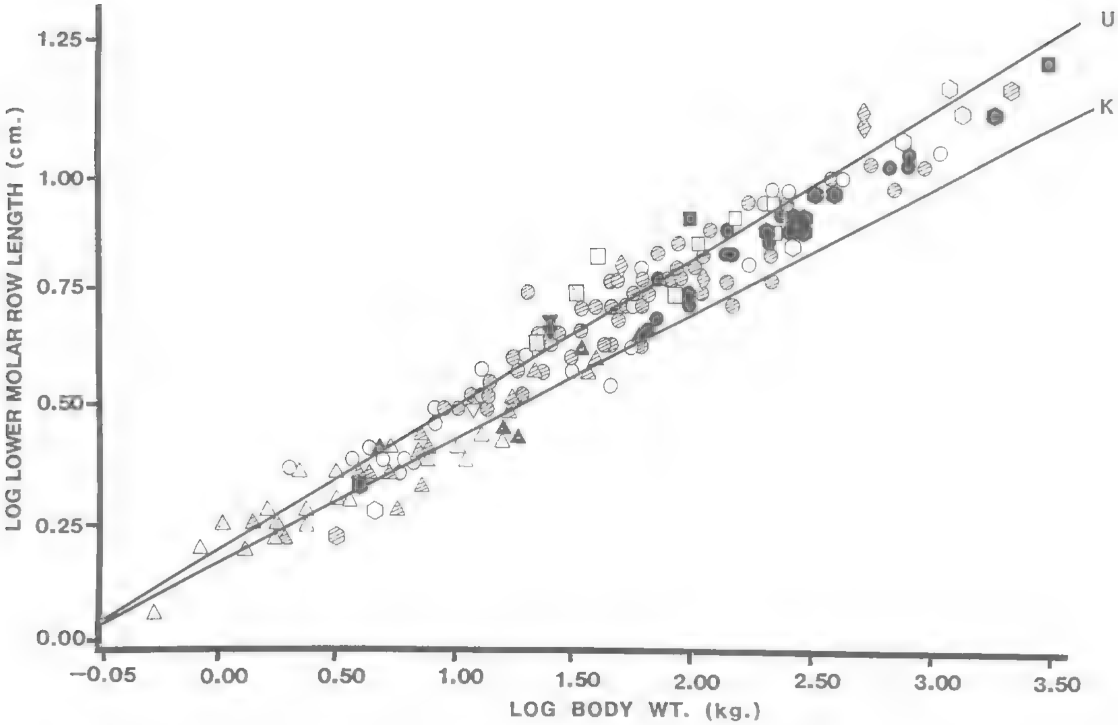

FIG. 3. Relationship of log lower molar row length to log body weight in ungulates and kangaroos (key as for Fig. 2).

many morphological variables covary with dietary type. The koala and wombat species are included on the figured plots for comparison with the kangaroos, but they were not used in the calculation of the kangaroo regression line, nor in the examination of the distribution of the residuals by dietary type around this regression line. The fact that kangaroos show a smaller number of significant differences in the distribution of the residuals is probably due to the smaller data set. The small number of true grazing kangaroos (six species in this study) is probably the reason why the residuals for kangaroos grazers rarely show a significant difference from those of the intermediate feeders.

For each variable regressed against body weight Table 2 shows: the r^2 value, the intercept, the slope, the trend in the distribution of the residuals by feeding type (including significant differences at the $P<0.05$ and 0.01 levels), the percentage standard error (% S.E.) and a test for the allometric value of the line (i.e. whether the regression line exhibits isometry, negative allometry or positive allometry). The % S.E. reflects the extent of the scatter of the residuals around the regression line, and thus differs from the r^2 value which reflects the direct correlation of the dependent variable with the independent variable. It is calculated by adding 2 to the log of the standard error, taking the antilog function, and subtracting 100 (see Smith, 1984). In general, a high r^2 value and a low % S.E. show that the value of the variable is closely correlated with body weight (and is thus less likely to reflect differences in dietary type), although the two functions may show considerable independent variation. The % S.E.s are generally lower for any given variable in kangaroos, which probably reflects the fact that the taxonomic diversity of the kangaroos data set is less than that for the ungulates (two families versus fourteen). In contrast, the correlation coefficients (r^2 values) are usually somewhat lower for the kangaroos, but this is probably due to the fact that the body weights of kangaroos span a smaller absolute range than those of ungulates. The regression lines were tested for allometric relations by checking if they differed significantly ($P<0.01$) from a slope of 0.33 in the case of linear variables, or a slope of 0.66 in the case of area variables. Table 3 shows the actual mean residual values obtained for each dietary type in both ungulates and kangaroos.

RESULTS

Dental Measurements

HYPSODONTY INDEX: This is a dimensionless index of relative tooth crown height, in this case obtained by dividing the unworn crown height of the last molar by the width of the same tooth. Molar crown dimensions scale isometrically with body weight in ungulates (Janis, 1988), indicating that smaller animals are neither relatively more or nor less hypsodont than larger ones. Kangaroos are much less hypsodont than ungulates of similar dietary type (see Fig. 2), even though grazing and intermediate-feeding kangaroos resemble grazing ungulates in possessing a significantly greater hypsodonty index than browsers and omnivores (significance levels for differences in residuals are detailed in Table 2).

MOLAR DIMENSIONS: As explained previously, the third molars of kangaroos were compared with the second molars of ungulates. The absolute molar dimensions are similar in both ungulates and kangaroos, but the molar lengths in kangaroos are somewhat smaller than in ungulates. This reflects the fact that the total length of the lower molar row is almost identical in both groups (see below and Fig. 3). However, in the case of the lower molar widths, browsing ungulates have relatively wider molars than grazers, while the reverse is true (though non-significant) for kangaroos; i.e. grazers have wider molars than browsers. The same is true for the molar areas, which probably reflects the contribution of the width dimension to the calculation of the area.

Grazing and intermediate-feeding kangaroos also have a significantly longer M^3 than other feeding types, and hence have larger M^3 areas. Among ungulates, the omnivores and intermediate-feeders have a longer M^2 than other feeding types. In both ungulates and kangaroos the molar dimensions show negative allometry, in contrast to the usual mammalian isometric scaling (Fortelius, 1985). In fact, the values for the perissodactyls plus hyracoids alone do scale isometrically with body weight, but the large numbers of ruminant artiodactyls in this study have biassed the results for ungulates in general (Janis, in press). Kangaroos exhibit more profound negative allometry than ungulates in the scaling of dental dimensions.

INCISOR DIMENSIONS: Absolute values for the width of the central incisors are similar in both

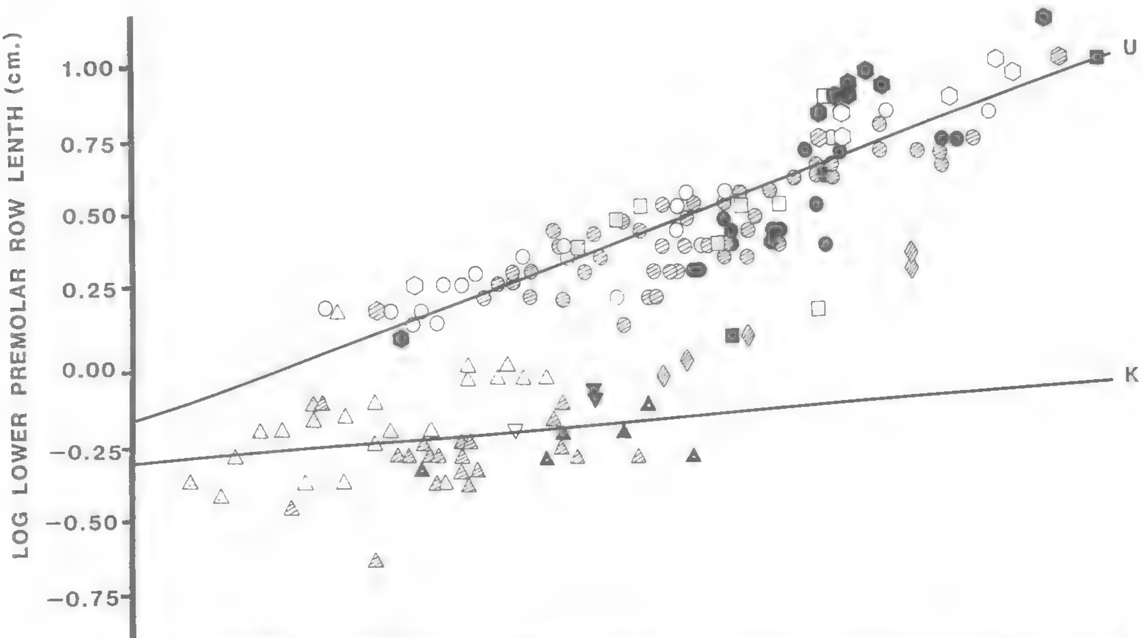

FIG. 4. Relationship of log premolar row length to log body weight in ungulates and kangaroos (key as for Fig. 2).

groups, but the width of the lateral incisor is absolutely greater in kangaroos. Browsing ungulates have relatively narrow central and lateral incisors; among kangaroos, browsers have relatively wide central incisors (although this trend is non-significant), but they resemble browsing ungulates in the significantly narrower lateral incisors. In both groups, omnivores have relatively narrow central incisors and relatively broad lateral ones (this difference being significant in both groups).

Absolute values for length of the lower molar row are similar in both ungulates and kangaroos, despite the difference in the number of molars (Fig. 3). This variable shows little variation with dietary type, and is one of the best correlates with body weight in both groups. Absolute values for length of the lower premolar row in kangaroos are much less than in ungulates, but in both groups browsers have a longer premolar row than grazers and intermediate-feeders (Fig. 4).

JAW MEASUREMENTS: Values of anterior jaw length, posterior jaw length, maximum width of the mandibular angle and total jaw length are similar for both kangaroos and ungulates, although kangaroos usually have slightly lower values. For most of these variables, grazers have relatively larger values than browsers or intermediate-feeders. Omnivorous ungulates have relatively large values, but omnivorous kangaroos do not. The length of the coronoid process has similar absolute values for kangaroos and ungulates; in both, browsers have relatively short processes, but in ungulates intermediate- feeders have the longest processes, while in kangaroos the grazers possess the highest values. Absolute values for the depth of the mandibular angle are considerably lower in kangaroos than in ungulates. In both groups, grazers have relatively larger values than other feeding types (as would be expected to accommodate the greater volume of the masseter muscle), and omnivorous ungulates (but not kangaroos) have relatively large values (Fig. 5).

Anterior jaw length, total jaw length and the length of the coronoid process scale isometrically in ungulates, but with negative allometry in kangaroos. Maximum width of the mandibular angle scales isometrically in both. Posterior jaw length and depth of the mandibular angle scale with positive allometry in ungulates, and isometrically in kangaroos. It might be expected that the depth of the mandibular angle would show positive

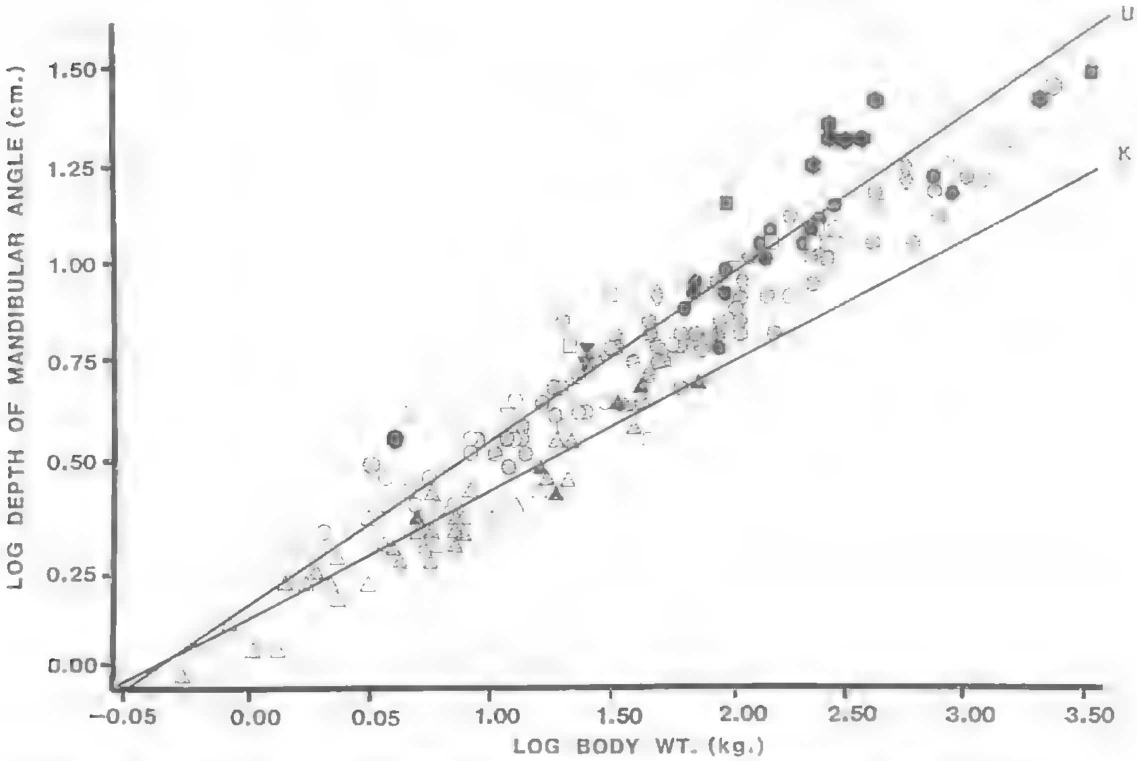

FIG. 5. Relationship of log mandibular depth to log body weight in ungulates and kangaroos (key as for Fig. 2).

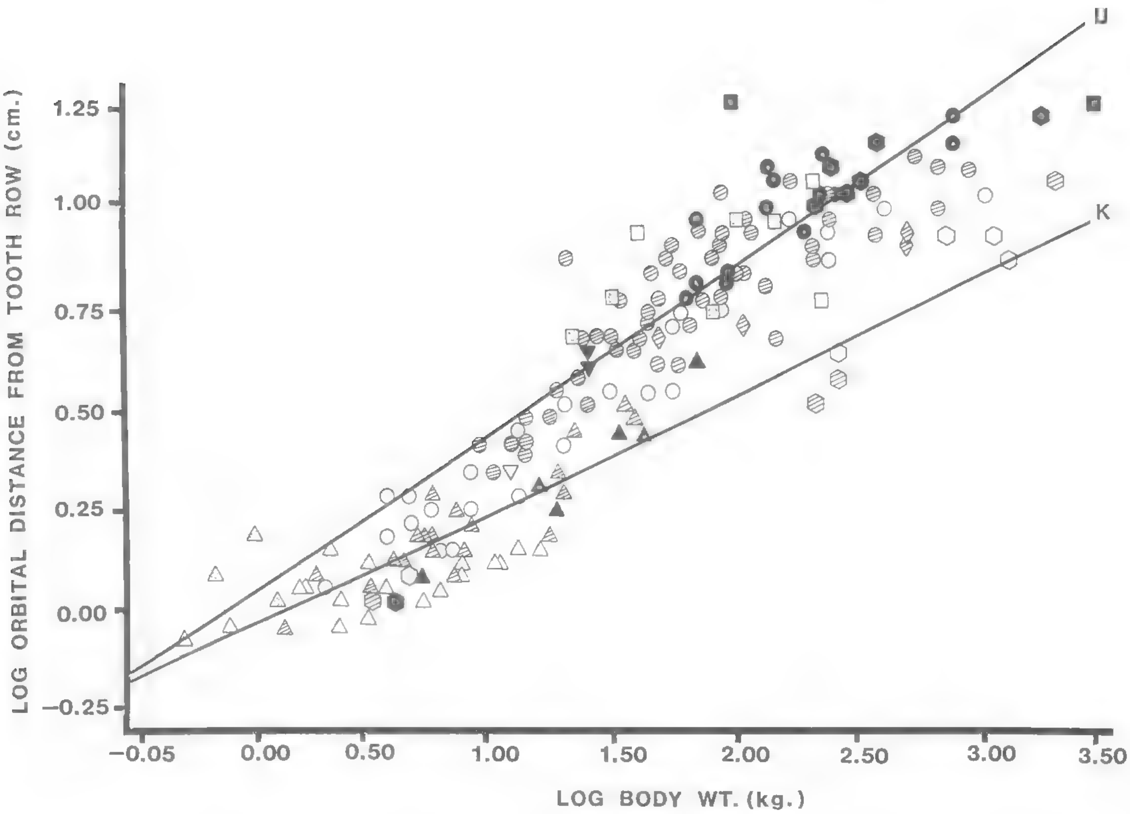

FIG. 6. Relationship of log orbital distance from tooth row to log body weight in ungulates and kangaroos (key as for Fig. 2).

allometry, since it reflects the size of the masseter muscle, which for scaling reasons would need to be relatively bigger in larger animals.

Skull Measurements

LENGTH MEASUREMENTS: Posterior skull length and total skull length show similar absolute values in ungulates and kangaroos (although the values for kangaroos are slightly smaller). In both groups, grazers have relatively larger values than browsers and intermediate-feeders. The absolute values of length for the paroccipital process are greater in kangaroos than for all ungulates except suids, but in both groups the paroccipital process is relatively longer in grazers than in browsers or intermediate-feeders. The occipital height of the skull in kangaroos is matched in all ungulates except suids (where it is considerably larger). However, in ungulates, browsers have larger values than other folivores (significantly larger than intermediate feeders); in kangaroos, grazers have larger values than all other feeding types (significantly larger than browsers). The distance of the orbit from the tooth row is considerably less in kangaroos than in ungulates but, in both groups, browsers have significantly lower values than other dietary types (Fig. 6). Length of the paroccipital process scales with positive allometry in both groups. All the other skull measurements scale isometrically or with positive allometry in ungulates, but with negative allometry in kangaroos.

WIDTH MEASUREMENTS: Kangaroos show slightly lower values of palatal width than most ungulates (Fig. 7), and both groups show negative allometric scaling of this variable. Relative palatal width shows no significant correlation with dietary type in either group, (with the exception of particularly low values for omnivorous ungulates, in fact seen in all suoids). Smaller kangaroos have somewhat broader muzzles than ungulates of comparable size, but the muzzles of the larger kangaroos are relatively narrower (Fig. 8). A striking difference exists in the correlation of relative muzzle width with diet. While in ungulates the muzzles are broad in grazers, and significantly

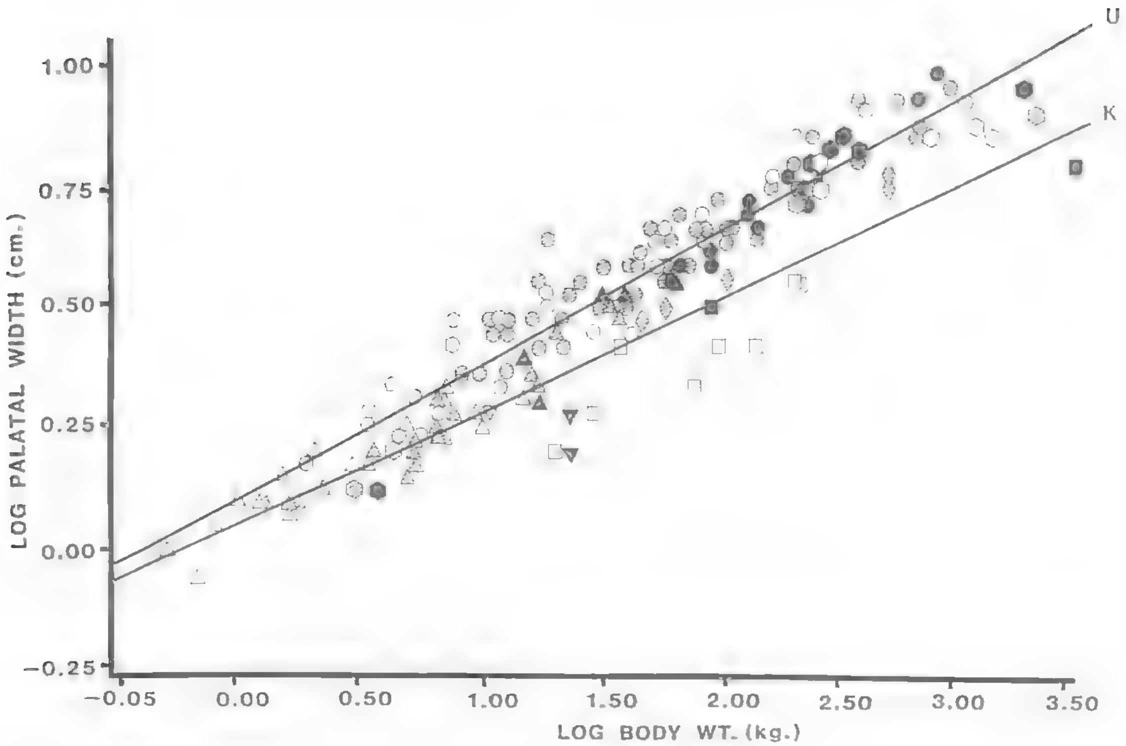

FIG. 7. Relationship of log palatal width to log body weight in ungulates and kangaroos (key as for Fig. 2).

broader than in intermediate-feeders (see also Janis and Ehrhardt, 1988), in kangaroos the muzzles are significantly broader in browsers than in other folivores. However, muzzles are relatively narrow in intermediate-feeders and broad in omnivores within both groups. Palatal width scales with negative allometry in both groups. Muzzle width scales with positive allometry in ungulates, and with negative allometry in kangaroos. However, this may merely reflect the fact that large grazing ungulates have relatively broad muzzles, while large grazing kangaroos have relatively narrow ones, and among kangaroos the broad-muzzled omnivores are the small species.

BASICRANIAL MEASUREMENTS: Kangaroos and ungulates show similar values for basicranial length; in both there is a trend (non-significant for ungulates, but significant for kangaroos) for the basicranial length to be greater in browsers. Basicranial length scales with negative allometry in both groups. Similar values are also seen in both groups for the basicranial angle (Fig. 9). However, while in ungulates intermediate-feeders have the most acute angles, in kangaroos they have the most obtuse ones. Both are similar, however, in the fact that browsers have more obtuse angles than grazers.

DISCUSSION

Kangaroos and ungulates show a number of parallels in their adaptations of craniodental morphology to dietary type, and in many instances, they possess similar absolute values for various craniodental morphological variables. Absolute values are similar for molar widths (especially in the case of the lower molars), total length of the lower molar row, length of coronoid process, maximum width of the mandibular angle, basicranial length, and basicranial angle (although kangaroos do not show the extremes in angulation in either the acute or obtuse direction displayed in certain ungulates).

A number of convergences are seen between kangaroos and ungulates in the correlation of the relative value of craniodental variables with dietary type, irrespective of any differences in absolute values. Grazers are more likely to have the following features, in contrast with other folivorous dietary types: a larger hypsodonty

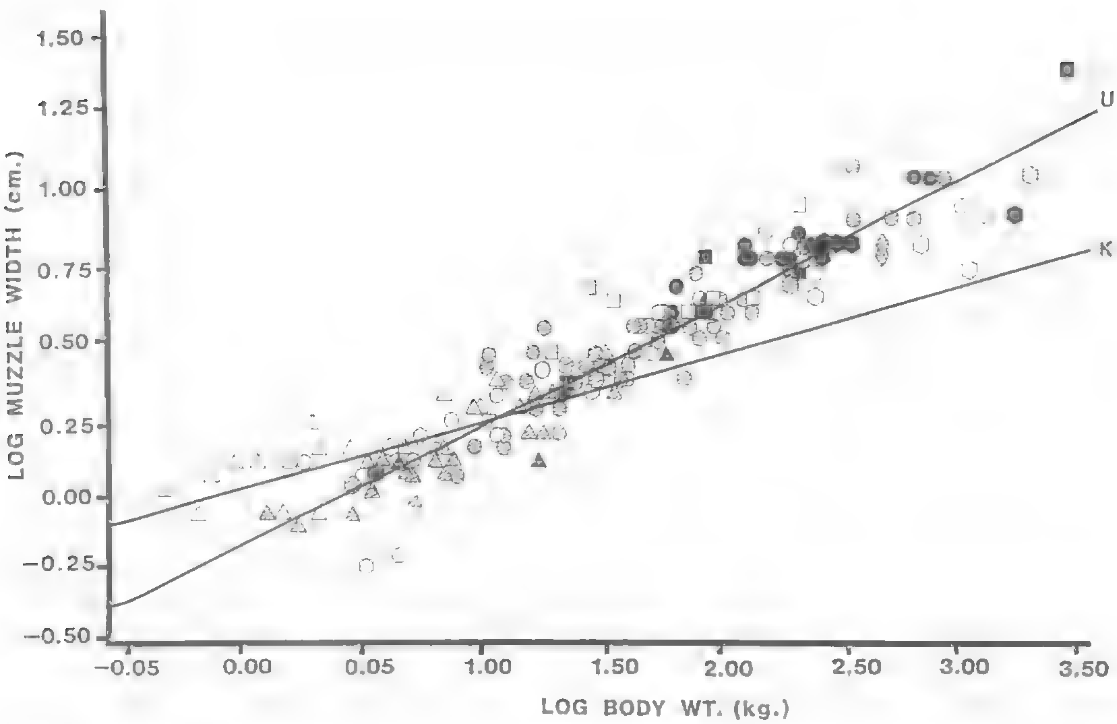

FIG. 8. Relationship of log muzzle width to log body weight in ungulates and kangaroos (key as for Fig. 2).

index; broader lateral incisors; a greater total jaw length (including a longer posterior portion to the lower jaw); a greater total skull length (including a longer posterior portion to the skull); a deeper and wider angle to the mandible; a longer masseteric fossa; an orbit that is more posteriorly displaced from the upper tooth row; a longer paroccipital process; and a fairly acute basicranial angle. In comparison with grazers, browsers are more likely to have: a low hypsodonty index; relatively narrow lateral incisors; a greater premolar row length; a shorter coronoid process; a longer basicranium; and a fairly obtuse basicranial angle. Intermediate feeders are likely to have: a moderate to high hypsodonty index; relatively narrow lateral incisors; a relatively short lower premolar row; a relatively shallow mandibular angle; a relatively short total jaw length (including short anterior and posterior parts of the jaw) and total skull length; a relatively low occiput; a relatively short basicranium; and a relatively narrow muzzle. Omnivores are likely to have: a low hypsodonty index; relatively narrow central incisors, but relatively broad lateral ones; a relatively great total skull length; and a relatively broad muzzle.

Kangaroos and ungulates show a number of absolute differences in relative craniodental proportions. The individual molars are shorter in kangaroos than in ungulates, and consequently the molar areas are smaller, which relates to the fact that kangaroos have four molariform cheek teeth, while ungulates have only three. As previously noted, the total lower molar row length is similar in both groups. The central incisors are slightly narrower in kangaroos than in ungulates, and the lateral incisors are considerably broader, which presumably relates to their diprotodont type of incision. The absolute index of hypsodonty is much less in grazing and intermediate feeding kangaroos than in ungulates of similar dietary types. This may be related to the fact that these kangaroos possess bilophodont cheek teeth, which cannot be modified to the hypsodont condition (Fortelius, 1985; Janis & Fortelius, 1988). Instead, kangaroos render their dentition more durable by means of molar progression (see Sanson, 1980). Grazing kangaroos may also be under less intense selective pressure to render their dentition more durable because of the relatively lower metabolic rate in marsupials, which means that they have to consume less food per day (see Arnold, 1985). However, it should be noted

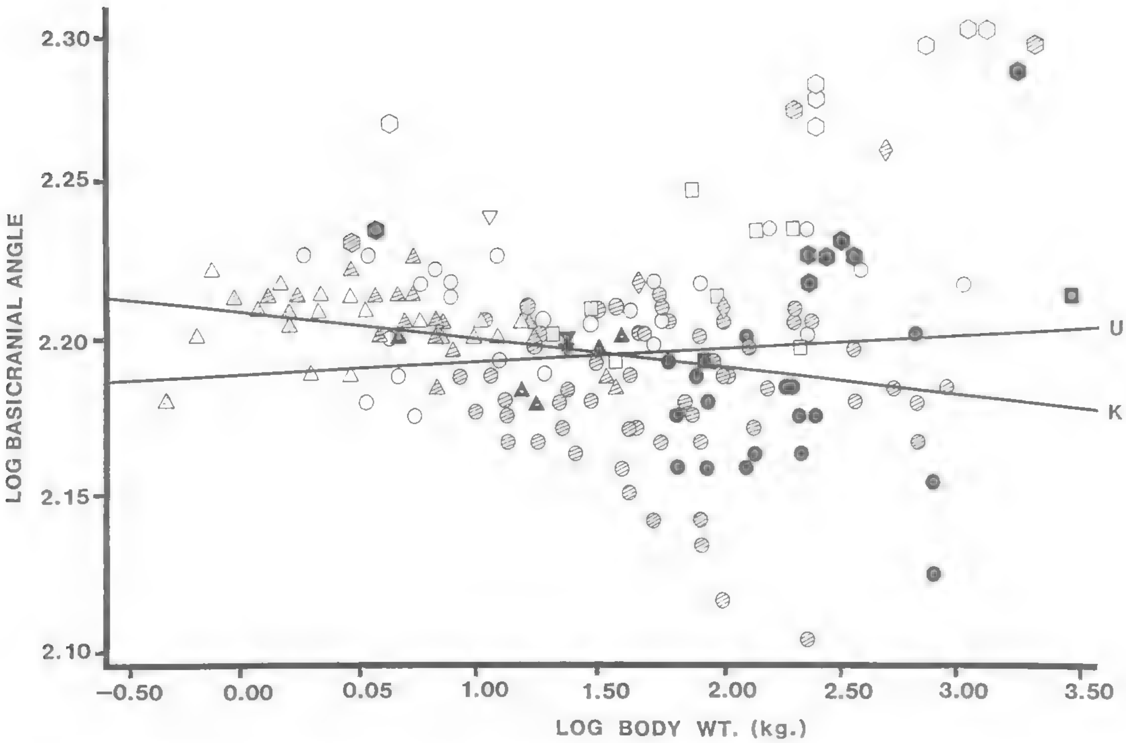

FIG. 9. Relationship of log basicranial angle to log body weight in ungulates and kangaroos (key as for Fig. 2).

that wombats are exceptional in being hypselodont (with evergrowing cheek teeth), and thus have an extremely large hypsodonty index (which should really be an index of infinity; see Fig. 2). The effective maximum height of molar crown was used in calculating hypsodonty index for wombats.

The premolar row is much shorter in kangaroos than in ungulates. This reflects the fact that adult kangaroos have a single lower premolar in contrast to the two to four seen in ungulates. Additionally, kangaroos exhibit virtually no correlation of the lower premolar length with body weight; the functional implications of this are unclear. In both groups, browsers have longer premolar rows than grazers. However, for ungulates this observation masks a difference between foregut fermenters (ruminant and camelid artiodactyls) and hindgut fermenters (perissodactyls and hyracoids). Foregut fermenters show a decrease in length of the premolar row with increasing fibre content of the diet, while hindgut fermenters show an increase (Janis, in press). Although kangaroos do have a type of forestomach fermentation (Hume, 1982), the resemblance to ruminant artiodactyls probably does not reflect a correlation with digestive physiology. A simpler, and more plausible, explanation is that grazing kangaroos exhibit molar progression and shed the premolar at an early stage. Hence, the length of the unworn lower premolar is shorter in grazing kangaroos, as it does not form an important functional component of the cheek tooth row in the adult. (However, it should be noted that the in the hindgut-fermenting phascolarctoid marsupials, the browsing koala has a relatively shorter premolar row than the grazing wombats).

In kangaroos, both total jaw length (including both anterior and posterior jaw length) and total skull length (including the posterior skull length) are slightly shorter than in ungulates. These differences may reflect differences in food handling. Most kangaroos use the forepaws to help in manipulating vegetation, and so have less need of a long skull to probe into vegetational stands. (Folivorous primates and rodents, which also manipulate food with the forepaws, also have short skulls in comparison with ungulates). Occipital height is somewhat less in kangaroos than in ungulates, and the paroccipital process is somewhat longer. Both differences probably relate to differences in the role of head-movements in association with food handling. Ungulates use head-movements to sever vegetation gripped with the incisors (Boué, 1970), while in kangaroos the forepaws may aid in this activity. The occipital area serves as the origin for muscles that elevate the head (splenius, rectus capitus and cleidotrapezius), while the paroccipital process serves as the origin for the sternomastoid muscle, which acts to depress the head. (The large mastoid process in suids among ungulates presumably reflects their rooting behaviour with the snout).

The depth of the mandibular angle is considerably less in kangaroos than in ungulates. This could possibly reflect the lower metabolic rate of marsupials; as less food is consumed per unit time the volume of masticatory musculature does not need to be so relatively great as in ungulates. Alternatively the masseteric fossa on the jaw of kangaroos may provide an expanded area for insertion of the masseter, so that the angle of the mandible need not be as deep to accommodate the same volume of masseter muscle that would be seen in an ungulate of similar body size and dietary type. As the koala and the wombats (which do not possess this masseteric fossa) have values for this variable which are close to those of ungulates (Fig. 5), this may be the preferred explanation (see also Sanson, 1980).

The distance of the orbit from the tooth row is considerably less in kangaroos than in ungulates. This difference might correlate with the fact that kangaroos are less hypsodont than ungulates. Radinsky (1984) noted posterior movement of the orbit with increasing hypsodonty in equid evolution, and concluded that this was related to the need to house the total crown length of exceedingly hypsodont cheek teeth in horses. It is certainly true that posterior displacement of the orbit provides space for the upper molar crowns in both equids and hypsodont bovids. However, the fact that grazing kangaroos (which are not hypsodont in comparison with ungulates) show a similar relation (albeit with lower absolute values) throws doubt upon this causal explanation (as do the high values for the brachydont omnivores in both groups). In fact, some hypsodont mammals, such as rabbits and (to a lesser extent) camelids, show little posterior displacement of the orbit, and house the unerupted upper molar crowns within the anterior border of the orbit. It seems most likely that displacement of the orbit in grazing herbivores is associated with reorganization of skull proportions (such as increased acuteness of the basicranial angle and reduction in basicranial length, seen in grazers in both ungulates and kangaroos). As kangaroos show less extreme variation than ungulates in these cranial proportions (Fig. 9), this may be the preferred explanation for the lower values for the orbital distance from the tooth row.

The palate is somewhat narrower in kangaroos than in ungulates, and the muzzle is relatively broader in small species, but relatively narrower in larger species. This narrower palate may be related to the more orthal mode of occlusion in kangaroos (Sanson, 1980). Extremely narrow palates are seen in both wombats and suines of all dietary types, and both types of mammals possess an isognathous type of dentition, implying a predominantly orthal mode of occlusion (Fortelius, 1985). As noted previously, the differences in muzzle widths with body size are probably related to the difference in size distribution of the broad-muzzled omnivorous species in the two groups.

Kangaroos differ from ungulates in the correlation of craniodental variables with dietary type in a number of ways. The molars tend to be broader in browsing ungulates, but broader in grazing kangaroos. This is probably due to the different mode of jaw occlusion. In ungulates the lower jaw moves with a broad transverse sweep across the uppers. It appears that, the more fibrous the diet, the greater the amount of transverse movement, and the relatively narrower the lower molars (Fortelius, 1985). However, the bilophodont teeth of kangaroos, and the precise fit of the lower incisors into the upper dental arcade, restricts the jaw motion to a more orthal mode. Among kangaroos the relatively wider teeth of grazers may reflect an increase in total tooth surface area for the mastication of more fibrous vegetation (also reflecting a greater total volume of food processed by the teeth per day).

The height of the occiput is greatest in omnivorous ungulates, and large in browsers; among kangaroos it is greatest in grazers and smallest in browsers. This may relate to differences among the feeding types in use of the head for obtaining food (see above). The muzzle width is greatest in grazers among ungulates, but in browsers among kangaroos. This again is probably related to differences in the modes of incision and food selection between the two groups; the implication is that grazing kangaroos are much more selective feeders than are grazing ungulates. Finally, the length of the coronoid process is greatest in intermediate-feeding ungulates, but shortest in intermediate-feeding kangaroos and greatest in grazers. This may relate to differences in use of the temporalis muscle (which inserts on the coronoid process) in kangaroos and ungulates of different feeding types, in association with differences in the mode of occlusion. Omnivorous ungulates have high values for dental, skull and jaw lengths, while omnivorous kangaroos have low values. These differences probably reflect the fact that omnivorous kangaroos are all rather small, while omnivorous ungulates are of medium size. Thus, in addition to any scaling effects, the actual diets of the two types of omnivores are probably rather different.

Dental variables scale with negative allometry in both kangaroos and ungulates, although the negative scaling is more profound in kangaroos. Many cranial variables that scale isometrically or with positive allometry in ungulates scale with negative allometry in kangaroos. The significance of this is not clear, and it may be an artifact resulting from differences in the taxonomic diversity of the two data sets. Alternatively, differences in the ontogeny of the craniodental region between marsupials and placentals may make kangaroos more likely to exhibit negative allometric scaling of these variables (Case, pers. comm.).

CONCLUSION

Most of the craniodental differences between kangaroos and ungulates probably relate to differences in the modes of food handling and tooth occlusion. Ungulates crop vegetation with the lower incisors biting directly against the upper incisors (or a horny pad), and chew the food with transverse jaw movements, involving lophodont or selenodont cheek teeth. Kangaroos employ a precise fit of diprotodont lower incisors within an upper incisor arcade, and chew with a more orthal mode of jaw movement, involving bilophodont cheek teeth. Most kangaroos use the forepaws in handling food, while ungulates rely entirely on movements of the head to sever vegetation. Although some speculations are advanced in this paper, the role of behavioural difference in the divergent evolution of craniodental morphologies in kangaroos and ungulates remains largely unexplored.

ACKNOWLEDGEMENTS

I am indebted to the following persons and institutions for the opportunity to measure specimens in their collections: Dr M. Rutzmoser, Museum of Comparative Zoology, Harvard University, U.S.A.; Dr R. Thorington, Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A.; Dr G. Musser, American Museum of Natural History, New York, U.S.A.; Drs J. Clutton-Brock and K. Bryan, British Museum of National History, London, U.K.; Dr A. Friday, University of Cambridge, Cambridge, U.K.; Dr L. Jacobs, National Museum of Kenya, Nairobi, Kenya; Dr E. Vrba, Transvaal Museum, Pretoria, South Africa; Dr Q. Hendy, South African Museum, Cape Town, South Africa; Dr R. Molnar and S.M. Van Dyck, Queensland Museum, Brisbane, Australia; Dr T. Flannery, Australian Museum, Sydney, Australia; Dr C. Kemper, South Australian Museum, Adelaide, Australia.

Viyada Sarabanchong collected the kangaroo data for the pilot study for this analysis, and Loren Mitchel provided invaluable assistance with data analysis. Useful information on diets and body weights was provided by Drs T. Flannery, P. Jarman and K. Scott. This paper has benefited from discussion with Drs J. Case, J. Damuth, T. Flannery, M. Fortelius, P. Jarman, K. Scott and R. Wells, and greatly benefited by comments on an earlier version from Dr William Young and an anonymous reviewer, and was supported by a National Science Foundation Grant (no. BR 84-18148) and by a Brown University Biomedical Research Grant (no. RR0708-22). Funds from the Phyllis and Eileen Gibbs Travelling Fellowship (Newnham College, University of Cambridge) permitted collection of data from the African museums.

LITERATURE CITED

Archer, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of the Queensland Museum*, **18**: 157–64.

Arnold, G.W. 1985. Regulation of forage intake, p. 81-102. *In* Hudson, R.J. and White, R.G. (Eds), 'Bioenergetics of Wild Herbivores'. (C.R.C. Press Inc.: Boca Raton).

Bell, R.H.V. 1970. 'The use of the herbaceous layer by grazing ungulates in the Serengeti National Park, Tanzania'. Unpublished, Ph.D. thesis, University of Manchester, England.

Boué, C., 1970. Morphologie fonctionelle des dents labials chez les ruminants. *Mammalia*, **34**: 696–771.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica*, **180**: 1–76.

HALTENORTH, T. AND DILLER, H. 1977. 'A Field Guide to African Mammals including Madagascar'. (William Collins Sons and Co: London). [DW]

HANSEN, R.C. AND CLARKE, R.C. 1977. Foods of elk and other ungulates at low elevation in Northwestern Colorado. *Journal of Wildlife Management*, **41**: 76–80.

HOFMANN, R.R. 1985. Digestive physiology of deer: their morphophysiological specialization and adaptation. *Bulletin of the Royal Society of New Zealand*, **22**: 393–407. [D]

AND STEWART, D.R.M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African Ruminants. *Mammalia*, **36**: 226–40. [D]

HUME, I.D. 1982. 'Digestive Physiology and Nutrition of Marsupials'. (Cambridge University Press: Cambridge).

JANIS, C.M. (1988). An estimation of tooth volume and hypsodonty indices in ungulate mammals. *In* Russell, D.E., Santoro, J.P. and Sigogneau-Russell, D. (Eds), 'Teeth Revisited: Proceedings of the VIIth International Congress of Dental Morphology'. *Memoires du Musum d'Histoire naturelle, de Paris*, serie C, **53**: 371–91.

(in press). Correlation of craniodental variables with body weight in ungulates and macropodoid marsupials. *In* Damuth, J. and MacFadden, B.J., 'Body Size Estimation in Mammalian Paleobiology'. (Cambridge University Press: Cambridge).

AND EHRHARDT, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, **92**: 267–84.

AND FORTELIUS, M. (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Review*, **63**: 197–230.

JARMAN, P.J. 1974. The social organization of ungulates in relation to their ecology. *Behaviour* **48**: 213–67. [D]

KAY, R.F. AND COUVERT, H.H. 1984. Anatomy and behaviour of extinct primates. p. 467–508. *In* Chivers, D.J., Wood, B.A. and Bilsborough, A. (Eds), 'Food Aquisition and Processing in Primates'. (Plenum Press: New York).

KINGDON, J. 1979. 'East African Mammals, Vol. IIIB'. (Academic Press: London). [DW]

1982a. 'East African Mammals, Vol. IIIC'. (Academic Press: London). [DW]

1982b. 'East African Mammals, Vol. IIID'. (Academic Press: London). [DW]

LAMPREY, H.F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal*, **1**: 63–92 [D]

LEE, A.K. AND COCKBURN, A. 1985. 'Evolutionary Ecology of Marsupials'. (Cambridge University Press: Cambridge).

MACKIE, R.J. 1970. Range, ecology and relation of mule deer, elk and cattle in the Missouri River Breaks, Montana. *Wildlife Monographs*, **20** [D]

MEDWAY, G.G.-H. 1969. 'The Wild Mammals of Malaya'. (Oxford University Press: Oxford). [DW]

OWEN-SMITH, N. 1982. Factors influencing the consumption of plant products by herbivores. p. 359-404. *In* Huntley, B.J. and Walker, B.H. (Eds), 'The Ecology of Tropical Savannas'. (Springer-Verlag: Berlin).

RADINSKY, L.B. 1981a. Evolution of skull shape in carnivores. 1. Representative modern carnivores. *Biological Journal of the Linnean Society*, **15**: 369–88.

1981b. Evolution of skull shape in carnivores. 2. Additional modern carnivores. *Biological Journal of the Linnean Society* **16**: 337–55.

1984. Ontogeny and phylogeny in horse skull evolution. *Evolution* **38**: 1–15.

SANSON, G.D. 1978. Evolution and significance of mastication in the Macropodidae. *Australian Mammalogy*, **2**: 23–8.

1980. The morphology and occlusion of the molariform cheek teeth in some Macropodinae (Marsupialia: Macropodidae). *Australian Journal of Zoology*, **28**: 341–65.

1982. Evolution of feeding adaptations in fossil and recent macropodids. p. 490-506. *In* Rich, P.V. and Thompson, E.M. (Eds), 'The Fossil Vertebrate Record of Australasia'. (Monash University Offset Printing Unit: Clayton).

SCHALLER, G.E. 1967. 'The Deer and the Tiger'. (University of Chicago Press: Chicago). [DW]

1983. 'Mountain Monarchs'. (University of Chicago Press: Chicago). [DW]

SCOTT, K.M. 1979. 'Adaptation and allometry in bovid postcranial proportions'. Unpublished, Ph.D. thesis, Yale University, New Haven.

1983. Body weight prediction in fossil Artiodactyla. *Zoological Journal of the Linnean Society*, **77**: 197–228. [W]

1985. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History*, **179**: 197–228. [W]

SMITH, R.J. 1984. Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology*, **246**: R152–60.

STEWART, D.R.M. AND STEWART, J. 1970. Food preference data by faecal analysis from African plains ungulates. *Zoologica Africana*, **15**: 115–29. [D]

STRAHAN, R. 1983. 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson Publishers: Sydney).

VAN VALKENBURGH, B. 1985. Locomotor diversity within past and present guilds of large, predatory mammals. *Paleobiology*, **11**: 406–28.

1987. Skeletal indicators of locomotor behaviour in living and extinct carnivores. *Journal of Vertebrate Paleontology*, **7**: 162–82.

1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, **14**: 155–73.

VRBA, E.S. 1978. The significance of bovid remains as indicators of environment and predation patterns. p 247-71. *In* Behrensmeyer, A.K. and Hill, A.P., 'Fossils in the Making: Vertebrate Taphonomy and

Paleoecology'. (University of Chicago Press: Chicago).
WALKER, E.P. 1983. 'Mammals of the World', 4th. ed. (The Johns Hopkins Press: Baltimore). [DW]
WHITEHEAD, G.K. 1972. 'Deer of the World'. (Constable: London).

[DW][D] signifies reference used as source of information on ungulate diets.
[W] signifies reference used as source of information on ungulate body weights.

TABLE 1. Complete list of species measured for craniodental dimensions.

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES			
ORDER ARTIODACTYLA			
Family Antilocapridae			
Antilocapra americana	14	55/45	I
Family Bovidae			
Alcelaphini			
Aepyceros melampus	23	61/45.5	I
Alcelaphus buselaphus	44	136	G
Connochaetes gnou	11	136	G
Connochaetes taurinus	42	239/193	G
Damaliscus dorcas	22	73/66	G
Damaliscus hunteri	10	91/86	I
Damaliscus lunatus	36	155/145	G
Boselaphini			
Boselaphus tragocamelus	6	250/170	I
Tetracerus quadricornis	16	17	I
Bovini			
Anoa depressicornis	8	156/145	I
Bison bison	11	865/450	G
Bison bonasus	4	865/450	G
Bos gaurus	10	1000/510	I
Bos indicus	6	750/450	I
Bos banteng	6	750/450	I
Bubalis bubalis	6	725/400	G
Syncerus caffer	23	400/320	I
Caprini			
Ammotragus lervia	10	113/59	I
Capra ibex	14	87	I
Hemitragus jemlahicus	10	91	I
Ovis canadensis nelsoni	10	73/45	I
Ovis dalli	8	84/59	I
Pseudois nayaur	10	59	I
Cephalophini			
Cephalophus dorsalis	7	20	B
Cephalophus monticola	25	5.5	B
Cephalophus sylvicultor	12	61	B
Cephalophus spadix	8	57	B
Sylvicapra grimmia	12	13	B
Gazellini			
Ammodorcas clarkei	10	31/25	B
Antilope cervicapra	7	45.5/29.5	I
Antidorcas marsupialis	29	34/28	I
Gazella dorcas	10	23/18	I
Gazella granti	10	75/50	I
Gazella thomsoni	29	23/18	I
Litocranius walleri	22	45/41	B
Procapra gutturosa	8	20/16	I
Hippotragini			
Addax nasomaculatus	4	118/104	I
Hippotragus equinus	18	280/260	G
Hippotragus niger	24	235/218	G
Oryx gazella	25	177/164	I
Neotragini			
Dorcatragus megalotis	8	9.0	I

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES			
Madoqua guentheri	8	3.5	B
Madoqua kirki	8	4.5	B
Neotragus pygmaeus	9	3.5	B
Nesotragus moschatus	20	4.5	B
Ourebia ourebi	14	18	I
Oreotragus oreotragus	18	13.5	I
Raphicerus campestris	31	13.5	I
Raphicerus melanotis	26	10	I
Reduncini			
Kobus ellipsiprymnus	28	227/182	G
Kobus kob	8	70/45.5	G
Kobus leche	9	100/73	G
Kobus vardoni	8	100/73	G
Pelea capreolus	14	41/23	I
Redunca arundium	25	68/57	G
Redunca fulvorufula	27	32/29.5	I
Rupicaprini			
Budorcas taxicolor	6	250	I
Capricornis sumatrensis	10	102	I
Nemorhaedus goral	10	27	I
Oreamus americanus	10	114/80	I
Ovibos moschatus	10	425/364	I
Pantholops hodgsoni	2	50	I
Rupicapra rupicapra	8	45/34	I
Saiga tatarica	8	45/40	I
Tragelaphini			
Taurotragus oryx	30	590/432	I
Tragelaphus angasi	15	114/68	I
Tragelaphus buxtoni	10	216/150	I
Tragelaphus euryceros	9	227/182	B
Tragelaphus imberbis	10	91/64	I
Tragelaphus scriptus	37	64/52	I
Tragelaphus spekei	12	91/57	G
Tragelaphus strepsiceros	28	260/170	B
Family Camelidae			
Camelus bactrianus	7	550	I
Camelus dromedarius	8	550	I
Lama guanicoe	10	110/75	I
Lama pacos	6	60	I
Vicugna vicugna	16	50	I
Family Cervidae			
Alces alces	10	450/318	B
Axis porcinus	8	50/35	I
Blastocerus dichotomus	9	140/120	I
Capreolus capreolus	8	35/25	I
Cervus canadensis	14	400/250	I
Cervus elaphus scottius	8	200/125	I
Cervus nippon	10	64/41	I
Cervus unicolor equinus	8	215/162	I
Dama dama	12	67/44	I
Elaphodus cephalophus	7	18	I
Elaphurus devidianus	17	200/150	G
Hippocamelus bisulcus	7	50	I
Hydropotes inermis	8	12/9.5	I

TABLE 1. (Continued)

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES			
Mazama americana	10	20	B
Muntiacus muntjak vaginalis	8	25	I
Muntiacus reevesi	8	14/12	I
Odocoileus hemionus	15	91/57	B
Odocoileus virginianus	16	58/45	B
Ozotoceros bezoarticus	10	40/35	I
Pudu mephistophiles	3	8.0/10	B
Pudu pudu	6	8.0/10	B
Rangifer tarandus	12	145	B
Family Giraffidae			
Giraffa camelopardalis	29	1150/1000	B
Okapia johnstoni	16	250	B
Family Hippopotamidae			
Choeropsis liberiensis	6	240	B
Hippopotamus amphibius	6	3200	G
Family Moschidae			
Moschus moschiferus	8	12	I
Family Suidae			
Babyrousa babyrussa	8	85	B
Hylochoerus meinertzhageni	8	215	B
Phacochoerus aethiopicus	8	80/58	G
Potamochoerus porcus	9	78	O
Sus scrofa cristatus	7	80	O
Family Tayassuidae			
Catagonus wagneri	6	36	B
Tayassu pecari	6	30	O
Tayassu tajacu	8	22	O
Family Tragulidae			
Hyemoschus aquaticus	8	12.5	B
Tragulus javanicus	10	2.0/3.0	B
Tragulus meminna	8	7.0	B
Tragulus napu	6	8.0	B
ORDER PERISSODACTYLA			
Family Equidae			
Equus asinus	4	220	G
Equus burchelli	57	280/235	G
Equus grevyi	8	400	G
Equus hemionus	6	290	G
Equus kiang	6	300	G
Equus przewalski	6	350	G
Equus zebra	19	260	G
Family Rhinocerotidae			
Ceratotherium simum	15	3000	G
Dicerorhinus sumatrensis	7	800	B
Diceros bicornis	23	1800	B
Rhinoceros sondaicus	7	1400	B
Rhinoceros unicornis	7	2500	I

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES			
Family Tapiriidae			
Tapirus bairdii	8	250	B
Tapirus indicus	7	275	B
Tapirus pinchaque	4	250	I
Tapirus terrestris	6	240	
BORDER HYRACOIDEA			
Family Procaviidae			
Dendrohyrax dorsalis	8	4.5	B
Heterohyrax brucei	8	3.0	I
Procavia capensis	8	4.0	G
MARSUPIALS			
FAMILY MACROPODIDAE			
Subfamily Potoroinae			
Aepyprymnus rufescens	9	2.1/2.5	B
Caloprymnus campestris	1	0.8	B
Hypsiprymnodon moschatus	5	0.5	O
Bettongia gaimardi	9	1.7	O
Bettongia lesueur	6	1.7	O
Bettongia penicillata	7	1.3	O
Potorous platyops	1	0.7	O
Potorous tridactylus	7	1.0	O
Subfamily Macropodinae			
Dendrolagus bennettianus	2	13/10	B
Dendrolagus dorianus	9	16.5/10.5	B
Dendrolagus goodfellowi	4	7.5	B
Dendrolagus lumholtzi	8	7.4/5.9	B
Dendrolagus matschiei	2	10	B
Dendrolagus ursinus	2	13/10	B
Dorcopsis hageni	4	8/5.5	B
Dorcopsis veterum	6	11/5	B
Dorcopsulus macleayi	2	3.0	B
Dorcopsulus vanheurni	9	2.3/2	B
Lagorchestes conspicillatus	11	3.0	B
Lagorchestes hirsutus	5	2.3	B
Lagorchestes leporides	1	1.6	B
Lagostrophus fasciatus	5	1.8	I
Macropus agilis	15	19/11	I
Macropus antilopinus	7	37/17.5	I
Macropus bernardus	3	21/13	I
Macropus dorsalis	12	16/6.5	G
Macropus eugenii	7	7.5/5.5	I
Macropus fuliginosus	12	35/23	G
Macropus giganteus	8	43/27	G
Macropus greyi	4	7.0	I
Macropus irma	7	8.0	I
Macropus parma	6	4.9/4	G
Macropus parryi	15	16/11	G
Macropus robustus	18	39/20	I
Macropus rufogriseus	8	19.2/13.8	I
Macropus rufus	16	66/26.5	G
Onychogalea fraenata	6	5.5/4.5	I
Onychogalea lunata	2	4.0/3.0	I
Onychogalea unguifera	7	5.5/4.5	I

TABLE 1. (Continued)

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
MARSUPIALS			
Peradorcas concinna	7	1.4	I
Petrogale brachyotis	3	4.2	I
Petrogale godmani	5	5.0	I
Petrogale inornata	7	4.0	I
Petrogale lateralis	6	5.7	I
Petrogale penicillata	11	7.5	I
Petrogale rothschildi	2	5.25	I
Petrogale xanthopus	8	7.0	I
Setonix brachyurus	7	3.6/2.9	B
Thylogale brunnii	6	6.0/3.6	B
Thylogale billardierii	6	7.0/3.9	I
Thylogale stigmatica	6	5.1/4.2	B
Thylogale thetis	11	7.0/3.8	I
Wallabia bicolor	8	17/13	I
FAMILY PHASCOLARCTIDAE			
Phascolarctos cinereus	6	11.8/7.9	B

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
MARSUPIALS			
FAMILY VOMBATIDAE			
Lasiorhinus krefftii	1	25	G
Lasiorhinus latifrons	7	25	G
Vombatus ursinus	6	26	G

Key to Dietary Symbols
(See text for further explanation)
"B" = browser; "G" = grazer; "I" = intermediate feeder; "O" = omnivore.

Note: Not all individuals of each species provided a complete set of all (37) measurements. (This is especially the case for those species with very large sample sizes.) Some samples include juveniles, but these are excluded from the analyses.

TABLE 2. Values for regression of craniodental morphological variables on body weight.

KEY: Int. = Intercept. % S.E. = % standard error of line. Iso = Allometric value of line (X = isometric scaling; +ve = positive allometry; −ve = negative allometry; NA = not applicable). B = Browser; G = Grazer; I = Intermediate Feeder; O = Omnivore.

A: UNGULATES								
Variable	r^2	Int.	Slope	% S.E.	Iso	Residuals of Feeding Types		
						Trend	P>0.01	P>0.05
Hypsodonty Index	0.027	0.299	0.064	69.8%	NA	G>I>B>O	G>I>B G,I>O	
M_2 Length	0.912	−0.289	0.280	12.9%	−ve	O>B>I>G	O>G,I,B	
M_2 Width	0.853	−0.567	0.288	18.3%	−ve	O>B>I>G	O>G,I B>G	B>I O>B
M_2 Area	0.903	−0.855	0.567	29.7%	−ve	O>B>I>G	O>G,I,B	B>G
M^2 Length	0.895	−0.276	0.280	14.3%	−ve	O>I>B>G	O>G	O>B,I I>G
M^2 Width	0.892	−0.416	0.291	15.3%	−ve	O>B>G>I		O>I
M^2 Area	0.913	−0.692	0.571	27.9%	−ve	O>B>I>G	O>G	O>I,B
Width of Central Incisor	0.616	−0.534	0.259	33.0%	−ve	G>I>B>O	G>B,O I>O	I>B
Width of Lateral Incisor	0.704	−1.258	0.490	56.0%	+ve	O>G>I>B	O>I,B	G,I>B
Lower Premolar Row Length	0.548	−0.003	0.268	40.6%	−ve	O>B>G>I	B>I	O>I
Lower Molar Row Length	0.911	0.221	0.280	13.0%	−ve	O>I>B>G	O>G,I,B	
Anterior Jaw Length	0.918	0.391	0.328	14.6%	X	O>B>G>I		O,G>I
Posterior Jaw Length	0.906	0.047	0.390	19.1%	+ve	O>G>I>B	G>I,B O>B	O>I
Depth of Mandibular Angle	0.852	0.200	0.377	24.7%	+ve	O>G>B>I	G,O>I,B	
Maximum Width of Mandibular Angle	0.900	0.173	0.330	16.7%	X	O>G>B>I	G>I,B O>I	O>B>I
Length of Coronoid Process	0.637	−0.027	0.306	38.4%	X	I>G>B>O	I>B	G>B,O I>O
Total Jaw Length	0.946	0.716	0.332	11.7%	X	O>G>B=I	O>I,B	G>I
Length of Masseteric Fossa	0.927	0.465	0.330	13.8%	X	G>I>B>O	G>B	G>I>O I>B,O
Occipital Height	0.854	0.234	0.315	19.9%	X	O>B>G>I	O>B>I O>G	G>I

TABLE 2. (Continued)

A: UNGULATES								
Variable	r^2	Int.	Slope	% S.E.	Iso	Residuals of Feeding Types		
						Trend	P>0.01	P>0.05
Posterior Skull Length	0.937	0.373	0.354	13.8%	+ve	G>O>I>B	G>I,B	
Orbital Distance from Tooth Row	0.751	0.047	0.388	36.8%	+ve	O>G>I>B	G,I,O>B O>I	O>G>I
Length of Paroccipital Process	0.845	−0.168	0.373	25.0%	+ve	O>G>I>B		
Total Skull Length	0.954	0.811	0.328	10.7%	X	O>G>B>I	O,G>I	O>B
Muzzel Width	0.863	−0.191	0.388	24.2%	+ve	O>G>B>I	O,G>I	O>B
Palatal Width	0.854	0.084	0.290	18.3%	−ve	I>B>G>O	G,I,B>O	
Basicranial Length	0.881	0.407	0.283	15.6%	−ve	B>G=I>O		
Basicranial Angle	0.004	2.191	0.004	9.4%	NA	B>O>G>I	B>G,I	O>I
B: KANGAROOS								
Hypsodonty Index	0.095	0.005	0.054	19.7%	NA	I>G>O>B	G,I>B I>O	G>O
M_3 Length	0.871	−0.369	0.269	11.9%	−ve	G>I>O>B		
M_3 Width	0.815	−0.506	0.220	12.2%	−ve	O>G>I>B		
M_3 Area	0.868	−0.875	0.489	23.3%	−ve	G>O>I>B		
M^3 Length	0.855	−0.351	0.268	12.7%	−ve	G>I>B>O	I>O	I>B G>O
M^3 Width	0.834	−0.476	0.256	13.2%	−ve	B>O>I>G		
M^3 Area	0.888	−0.827	0.524	22.5%	−ve	G>I>B>O		I>O
Width of Central Incisor	0.201	−0.561	0.186	50.0%	-ve	B>G>I>O		G,B,I>O
Width of Lateral Incisor	0.670	−0.647	0.341	29.7%	X	G>O>I>B>	O,I>B	G>B
Lower Premolar Row Length	0.023	−0.239	0.049	41.9%	NA	B>O>G>I	B>I	B>G
Lower Molar Row Length	0.905	0.187	0.246	9.1%	−ve	G>I>B>O		
Anterior Jaw Length	0.860	0.307	0.289	13.5%	−ve	G>O>I>B		G>I,B
Posterior Jaw Length	0.927	0.199	0.311	9.9%	X	G>O>I>B		
Depth of Mandibular Angle	0.868	0.123	0.309	14.0%	X	G>I>B>O		
Maximum Width of Mandibular Angle	0.941	0.215	0.311	8.9%	X	G>I>B>O		
Length of Coronoid Process	0.862	0.004	0.277	12.7%	−ve	G>O>B>I		
Total Jaw Length	0.933	0.713	0.283	8.6%	−ve	G>I>I>B	G>I	
Length of Masseteric Fossa	0.944	0.464	0.249	6.9%	−ve	G>O>I>B		
Occipital Height	0.912	0.248	0.236	8.4%	−ve	G>O>I>B	G>B	
Posterior Skull Length	0.938	0.400	0.271	7.9%	−ve	O>G=B>I	O,B>I	
Orbital Distance from Teeth Row	0.706	−0.035	0.269	20.8%	−ve	O>G>I>B	O,I>B	G>B O>I
Length of Paroccipital Process	0.934	−0.104	0.433	13.2%	+ve	G>I>B>O	I>O	B>O
Total Skull Length	0.935	0.784	0.271	8.1%	−ve	G>O>B>I		
Muzzle Width	0.566	−0.026	0.214	22.5%	-ve	O>B>G>I	O,B>I	O,B>G
Palatal Width	0.919	0.056	0.266	8.9%	ve	G>B>O>I		
Basicranial Length	0.926	0.396	0.271	8.6%	-ve	B>I>G>O	B>I,O	B>G
Basicranial Angle	0.199	2.218	−0.011	2.3%	NA	I>B>G>O		I,B>O

INDEX OF TAXONOMIC NAMES

The index does not include names in bibliographic citations or appendices.

CONTENTS

(Continued inside back cover)