# PROCEEDINGS OF THE CONFERENCE OF AUSTRALASIAN VERTEBRATE EVOLUTION, PALAEONTOLOGY AND SYSTEMATICS

BRISBANE
31 MAY 2005

MEMOIRS OF THE
QUEENSLAND MUSEUM

VOLUME 51
PART 1

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# MEMOIRS

# OF THE

# QUEENSLAND MUSEUM

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PUBLISHED BY ORDER OF THE BOARD 31 MAY 2005

PO Box 3300, South Brisbane 4101, Australia
Phone 61 7 3840 7555
Fax 61 7 3846 1226

National Library of Australia card number
ISSN 0079-8835

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**A Queensland Government Project**
Typeset at the Queensland Museum
Printed by Watson Ferguson & Co.,
35 Hamilton Road, Moorooka, Queensland 4105

# *PLATALEA SUBTENUIS* DE VIS (AVES) IS A WHITE IBIS

WALTER E. BOLES

Boles, W.E. 2005 05 31. *Platalea subtenuis* De Vis (Aves) is a White Ibis. *Memoirs of the Queensland Museum* **51**(1): 1-2. Brisbane. ISSN 0079-8835

*Platalea subtenuis* De Vis 1892, was based on 3 syntypic bones from late Pleistocene deposits along Cooper Creek, South Australia. Two of these were re-identified as belonging to the flightless rail *Gallinula (Tribonyx) mortierii*, leaving QMF1140, a proximal right femur, previously designated as the lectotype. Re-examination of this specimen indicates that it is from an Australian White Ibis *Threskiornis molucca.* ❒ *White Ibis, Pliocene.*

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C.W. De Vis of the Queensland Museum was very active in the late 19th and early 20th Centuries in describing new Australian fossil birds (van Tets & & Vickers-Rich, 1990). Most of these came from the Darling Downs or along Cooper Creek. Re-examination of De Vis' specimens has shown that many of his identifications were incorrect, with a large number of the putative fossil taxa being inseparable from living species, often from different orders than those in which they had been described (van Tets & Vickers-Rich, 1990). One of these fossil species was the spoonbill *Platalea subtenuis* De Vis 1892, named on the basis of 3 syntypic bones (QMF1140, QMF5554, QMF5555) from late Pleistocene deposits along Cooper Creek at what is equivalent to University of California Museum of Paleontology, Berkeley, Site 18 (UCMP V-6147).

These were re-examined by Olson (1975), who found that QMF5554 and QMF5555 belonged to the large flightless rail, *Gallinula (Tribonyx) mortierii*, as did those of several other of De Vis' fossil taxa. This species, now known as the Tasmanian Native-hen, was once widespread in eastern Australia (Olson, 1975; Baird, 1984; Boles, in press).

QMF1140, a proximal right femur with about half of the shaft, was designated lectotype by Olson (1975) but he did not comment on whether the assignment to *Platalea* was valid. Van Tets (1984) included it as incertae sedis in his list of Australasian fossil birds.

Australian fossil *Platalea* is otherwise known only from Weekes Cave, SA (van Tets, 1974) represented by a near complete skeleton of Yellow-billed Spoonbill *P. flavipes*. The only other Tertiary record of Threskiornithidae from Australia is in the Pliocene Allingham Formation, Bluff Downs Local Fauna, Queensland (Boles & Mackness, 1994). This, based on the shoulder end of a coracoid, was cited as *Threskiornis* sp. cf. *T. molucca*.

The lectotype of *P. subtenuis* indicates that it is properly assigned to the ibises, *Threskiornis*, and is probably conspecific with the Australian White Ibis *T. molucca*. Ibises and spoonbills are closely related, and the post-cranial skeletons of these two similar-sized animals are very similar.

## SYSTEMATIC PALAEONTOLOGY

### Family THRESKIORNITHIDAE Richmond, 1917

### **Threskiornis** Gray, 1842

### **Threskiornis molucca** (Cuvier, 1829)
(Fig. 1)

1892 *Platalea subtenuis* DeVis, p.443, pl. 23, fig. 5a,b.

MATERIAL. The lectotype of *Platalea subtenuis* QMF1140, a proximal right femur; proximal width 15.9 mm and proximal depth 10.3 mm. Specimen is abraded on some edges, particularly on the anterior face of the crista trochanterica, thus depth measurement is somewhat reduced.

REMARKS. Assignment to *Threskiornis* rather than *Platalea* is based on having a more curved medial margin (anterior view), shallower proximal end (not as lateromedially elongate) and the caput femoris not undercut as far on anterior and posterior faces. Although not evident on the incomplete specimen, other femoral characters that distinguish *Threskiornis* from *Platalea* are the shorter element (66-76 mm vs 76-83 mm), greater angle between the sulcus intercondylaris and the long axis of shaft (10° vs 5°), and a deeper (posterior border more extensive) and rounder condylus medialis (medial view).

FIG. 1. *Platalea subtenuis* De Vis lectotype (QMF1140) compared with right femora of living species of Threskiornithidae. Left to right, *P. regia, Threskiornis spinicollis, T. molucca, P. subtenuis*. A, anterior view; B, posterior view. Scale =10 mm.

QMF1140 is referred to *T. molucca* rather than the Straw-necked Ibis *T. spinicollis* because the proximal end is proportionally wider and deeper, the crista trochantericus angled more proximomedially-distolaterally (anterior view), the caput femoris larger and the collum femoris more distinct, with the caput femoris not joining the shaft as abruptly (anterior view). A deeper condylus lateralis helps distinguish distal ends.

A substantial proportion of modern specimens of the Australian Threskiornithidae examined are not sexed. These species are known to be sexually size dimorphic, and this appears to be reflected in femoral measurements of specimens for which sex has been recorded (Table 1). Comparison of the fossil with the values for *T. molucca* in (Table 1) suggests that the specimen was a female. The putative fossil spoonbill *P. subtenuis* De Vis, 1892, is therefore placed in synonomy with the living ibis *Threskiornis molucca* (Cuvier, 1829).

TABLE 1. Measurements of proximal femora of *Platalea subtenuis* and extant Australian species of Threskiornithidae (mm)

| | *Platalea subtenuis* | *Platalea regia* | *Threskiornis molucca* | *Threskiornis spinicollis* |
|---|---|---|---|---|
| ♂ proximal width | | 17.2 | 16.3-16.8 | 16.9-17.2 |
| ♂ proximal depth | | 12.1 | 12.1-12.7 | 12.1-12.9 |
| ♀ proximal width | | 16.0-16.2 | 13.9-15.3 | 16.1-16.6 |
| ♀ proximal depth | | 11.5-12.3 | 10.8-11.4 | 11.2-13.2 |
| all birds: proximal width | 15.9 | 15.7-17.9 | 13.9-16.9 | 15.2-17.5 |
| all birds: proximal depth | 10.3 | 11.5-13.2 | 10.8-12.9 | 11.2-13.2 |

## ACKNOWLEDGEMENTS

I thank staff of the Queensland Museum for making fossil and recent specimens available, and P. Ovenden of the Australian Museum Photographic Department for taking the photographs.

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# THE ACANTHODIAN FAUNA OF THE CRAVEN PEAKS BEDS (EARLY TO MIDDLE DEVONIAN), WESTERN QUEENSLAND

CAROLE J. BURROW & GAVIN C. YOUNG

Burrow, C.J. & Young, G.C. 2005 05 31. The acanthodian fauna of the Craven Peaks Beds (Early to Middle Devonian), western Queensland. *Memoirs of the Queensland Museum* **51**(1): 3-25. Brisbane. ISSN 0079-8835.

Two acanthodian faunas of different ages have been identified from calcareous lithologies assigned to the Cravens Peak Beds, Georgina Basin, western Queensland. A sparse fauna comprising scales of *Nostolepis* sp. cf. *N. striata* and *Radioporacanthodes* sp. indicates a Lochkovian or Pragian age for one shot-hole sample south of the Toko Range. A limestone outcrop further south in the Toomba Range yielded a more abundant fauna which includes dissociated remains of two new acanthodians *Teneracanthus toombaensis* gen. et sp. nov. and *Machaeracanthus pectinatus* sp. nov. *Teneracanthus* gen. nov. is an acanthodid acanthodian which is most similar to the early Frasnian *Lodeacanthus* from Latvia. *M. pectinatus* sp. nov. is based on isolated scales. Comparison with acanthodian and thelodontid microremains from well-dated sequences in the Broken River Group indicate a late Emsian to early Eifelian age for the limestone stratum. ❒ *Acanthodian, Mesacanthidae,* Teneracanthus *gen. nov., Machaeracanthidae fam. nov., Machaeracanthus, Cravens Peak Beds, Georgina Basin, Devonian.*

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Devonian fish remains have been known from the Amadeus and Georgina Basins of central Australia for nearly 50 years (Hills, 1959; Gilbert-Tomlinson, 1968; Young, 1985, 1988). Central Australian Devonian rocks are predominantly sandstones and siltstones which, in the absence of marine invertebrate fossils, have been interpreted as fluvial, lacustrine, or aeolian deposits that were laid down at the initial emergence of the central Australian landmass from the ocean. The only known exception is a small limestone outcrop, previously assigned to the basal calcareous unit of the Cravens Peak Beds in the Georgina Basin of western Queensland. This limestone was first sampled for microfossils to confirm its assumed Early Ordovician age, but instead was found to contain an assemblage of Devonian fish remains (Draper, 1976). Various scales of thelodont agnathans and acanthodians, associated with eridostracans and ostracods, were described by Turner et al. (1981) from this limestone, and from five other (seismic shot-point) localities in the Toko Range area, about 40 km to the north (Fig. 1). They assigned the fauna a probable Emsian age, and associated eridostracans and ostracods were used to infer a probable shallow marine environment of deposition. On this evidence, an elongate marine incursion from the south was included on the palaeogeographic map for the Emsian-Eifelian timeslice of the Devonian by Struckmeyer & Totterdell (1990: 34).

Further collecting (GCY, 1977) revealed exceptionally well preserved but extremely fragile vertebrate remains, which could be extracted by acetic acid digestion. Based on this additional material, Young (1984) described some pterichthyodid antiarch placoderm bones, at the time considered to be one of the oldest records of this group. Turner & Young (1987) described enigmatic chondrichthyan teeth of the shark *Mcmurdodus whitei*, which display advanced features and are comparable to those of the living hexanchid sharks. *Mcmurdodus* was erected by White (1968) for a tooth from the Aztec Siltstone of Victoria Land, Antarctica, which was compared with teeth of the hexanchid *Notidanus*. The fossil record of hexanchids otherwise extends back only to the Jurassic, so if correctly assigned, the Devonian *Mcmurdodus* is by far the oldest known neoselachian (Cappetta et al., 1994). Turner (1995) redescribed the thelodontids, erecting *Turinia gavinyoungi*, and listed an associated fauna of shark scales, onychodont teeth, sarcopterygian scales, lepidotrichia, and acanthodian remains including climatiid spines and *Acanthodes*-type and *Machaeracanthus* scales.

Turner (1991) and Young (1993) noted microvertebrate assemblages described by Turner et al.

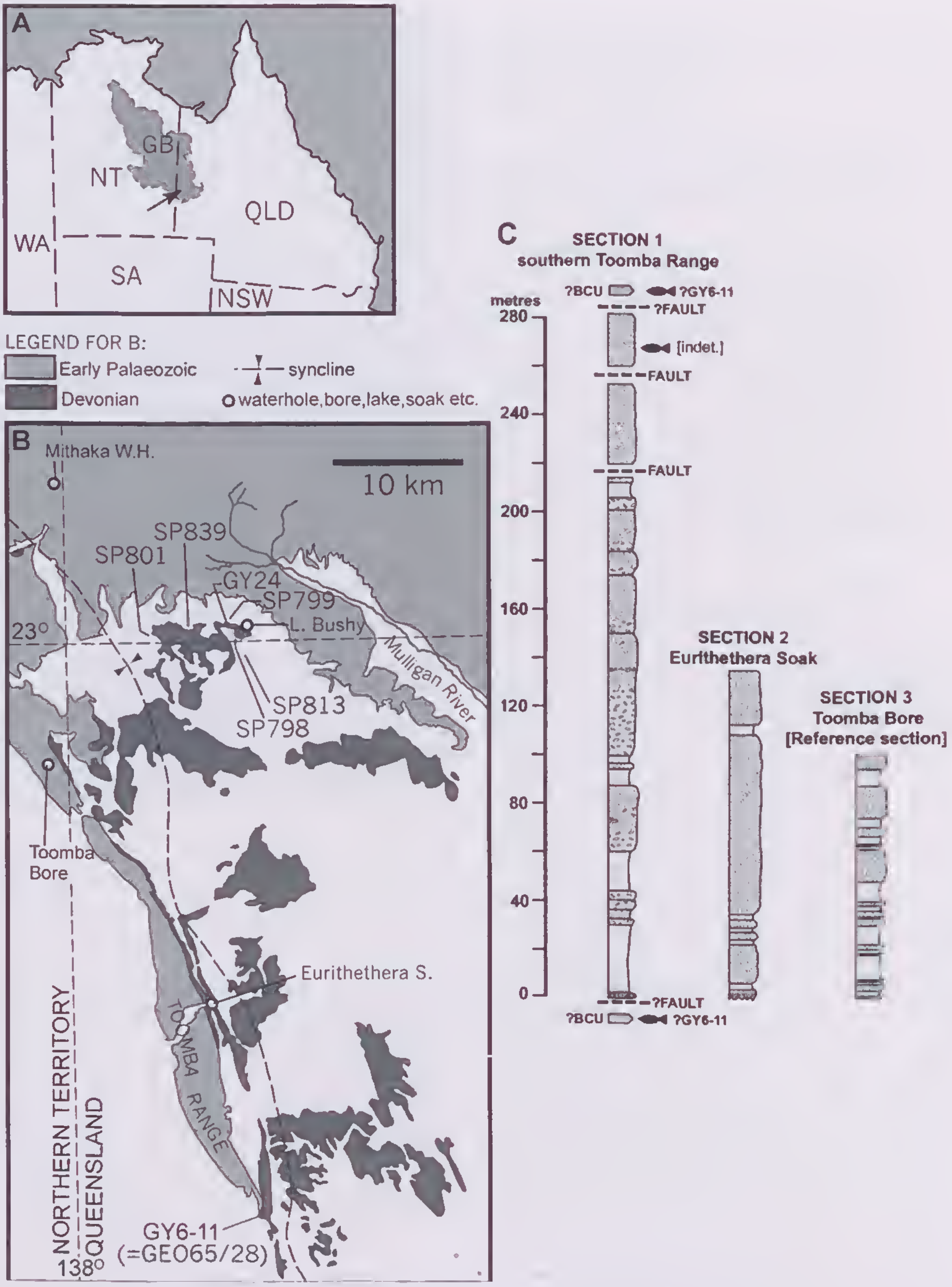

FIG. 1. A, Georgina Basin (GB) northern Australia; location of B indicated by arrow. B, S part of the Toko Syncline, geology from Hay River-Mt Whelan Special 1:250 000 sheet (Shergold, 1985), location of GY fossil localities collected 1977, and approx. localities for shot-point samples (prefix SP). GY24; locality for indeterminate spine (Young & Goujet, 2003). C, 3 measured sections through Cravens Peak Beds, modified from Draper (1976: fig. 4), and Turner et al. (1981: fig. 3): Section 1, S Toomba Range, about 100m S of GY6-11 (Fig. 1B), Section 2, Eurithethera Soak (see text for stratigraphic; Section 3, reference section of Smith (1972) as modified by Draper (1976), about 100m E of Toomba Bore.

(1981) contained conflicting evidence of age, and Young (1995: 20) discussed the possibility that the assemblage could have mixed material from older (shot-point samples) and younger (outcrop) horizons. Young (1996: 103) considered the basal calcareous unit of the Cravens Peak Beds to include a component younger (Eifelian) than the Early Devonian age assigned by Turner et al. (1981). Young & Turner (2000: fig. 4) gave alternative late Pragian-Emsian, or late Emsian-Eifelian, ages for the assemblage. Turner (1995, 1997) compared thelodontids from the outcrop with younger (Middle Devonian) turiniid scales from the Broken River Province, Queensland and the Aztec sequence of Victoria Land, Antarctica.

Turner et al. (1981) originally assigned the acanthodian fish scales to two taxa (*Nostolepis* sp. and *Gomphonchus* sp.), but examination of other remains, including spines and ossified scapulocoracoids, suggested a younger element in the fauna (Burrow, 2002). We suggest that at least some of the samples from west of the Toko Range are of ?late Lochkovian to early Pragian age, and the samples from the Toomba Range might be late Emsian or Eifelian.

## FIELD OCCURRENCE

Turner et al. (1981) dealt with material from five shot-point samples, but only one sample from the limestone outcrop. Shot-point samples, obtained during a 1963 seismic survey of the Toko Range for Phillips Petroleum, and first recorded by Jones (in Reynolds & Pritchard, 1964), were calcareous marl, processed by washing, not acid digestion. They included some Ordovician conodonts (probably reworked, or perhaps due to contamination; Turner et al., 1981: 53). This is circumstantial evidence that the shot-point localities were sampling the basal contact between the Devonian sequence and underlying Early Palaeozoic (P.J. Jones, pers. comm.). In contrast, the limestone is a solid rock, only broken down by normal acid digestion techniques, so there is a lithological difference between the two sources.

According to field data for the Georgina Basin Project held at Geoscience Australia in Canberra, the original limestone sample (74710577), assumed initially to be from the Early Ordovician Coolibah Formation, was collected by J.J. Draper on 8 August 1975 from an outcrop which 'occurs along a fault'. Draper (1976: 3) stated that the outcrop occurred 'at the base of the scarp at the SE end of the Toomba Range; this outcrop has an area of about 5m$^2$ along a spur fault of the Toomba Fault'. He originally considered it to be probably unconformable on the Ordovician Mithaka Formation and to be unconformably overlain by sandstone and conglomerate of the Cravens Peak Beds, but later reinterpreted this to be a conformable contact (Turner et al., 1981). A 280m thick measured section of Cravens Peak Beds situated 100m south of the limestone outcrop begins with a basal pebbly unit (Draper, 1976: fig. 4, section 1), and the limestone occurs in gullies only about 10m from similar strata assumed to be the base of the Cravens Peak Beds (see Young & Turner, 2000: 464). However, an alternative interpretation is that the whole sequence is overturned, i.e. younging to SW, not NE. At least two faults were identified higher up in Draper's measured section (beneath the 220 and 260m levels; Draper, 1976: fig. 4), but these were omitted from the published section (Turner et al., 1981: fig. 3). The faulted contact noted in the original field assessment places uncertainty on the stratigraphic relationship between the two lithologies. Field observations (GCY, 1977) noted a nearby 'basal' conglomerate of the Cravens Peak Beds, but there are conglomeratic beds at many levels within the measured sections, so this evidence is not compelling. In addition, the supposed contact between clastics and limestone is parallel to mapped faults in the vicinity, consistent with it being an unrecognised fault. The (assumed) top of section 1 of Draper (1976) finishes in non-exposure; the only fossils are one poorly preserved fish sample showing a faint impression of tuberculate ornament, and a possible arthropod impression, collected within 20m of the (assumed) highest exposure. However, in the reference section for the Cravens Peak Beds at Toomba Bore (Draper, 1976: fig. 4, section 3), the only fossil (a plate impression from the placoderm *Wuttagoonaspis* sp.) occurs at the base. Many localities yielding a diverse fish assemblage including *Wuttagoonaspis* sp. (Young & Goujet, 2003) also occur in the lower part of the sandstone sequence. Field work is required to re-examine the outcrop relationships between Devonian limestone and sandstone in this area, but the geological information just summarised provides circumstantial evidence consistent with recognition of different acanthodian faunas in the limestone and the shot-point samples. Two alternative stratigraphic positions for the 'basal calcareous unit' (BCU) are indicated in Section 1 of Fig. 1C.

Of eight taxa originally documented from the 'basal calcareous unit', five were listed by Turner et al. (1981: fig. 4) as common to the limestone and shot-point samples, but two thelodont taxa from the former were reassigned to a single new species by Turner (1995). The best preserved ostracods (*Healdianella* and *Bashkirina*?) come from the shot-point samples, and the eridostracan *Cryptophyllus* is best represented only from the limestone sample (Turner et al., 1981: fig. 15). Given the possibility that different levels may have been sampled, the poorly preserved unfigured remains of these crustacean taxa are in need of restudy (P.J. Jones, pers. comm.).

Young & Goujet (2003) concluded that the *Wuttagoonaspis* fauna from the Cravens Peak Beds and lower Dulcie Sandstone in the Georgina Basin was probably no older than Pragian, and no younger than early Eifelian, consistent with the suggested stratigraphic position of the limestone. Whether this *Wuttagoonaspis* fauna is younger or older than the *W. fletcheri* Ritchie, 1973 fauna in the type area in the Darling Basin, NSW (Mulga Downs Group) must await detailed analysis of faunal associations from many known but unstudied fish localities. The *Wuttagoonaspis* assemblage in the Darling Basin is recorded from many sites in the vicinity of the type locality (Wuttagoona Station, about 60km NW of Cobar), plus some 150km to the S (Glen et al., 1987; Young, pers. obs.), and some 360km to the W, in the Barrier Ranges north of Broken Hill (Coco Range Formation; Neef et al., 1995). Correlation of these widespread localities is uncertain without detailed systematic work, but we note a range of undescribed acanthodian material from various localities and cores in the Darling Basin which represent at least several horizons.

## OTHER LOCALITIES

UQL4697 = BRJ103A. Section ~70m west of old road crossing of Digger's Creek; stratigraphically below Fish Hill limestones; Bracteata Formation, ?late Emsian-early Eifelian.

UQL4704 = BRJ104B. Mid-level in section/traverse along limestone outcrop from Digger's Creek Crossing to road; GR 683 489 Burges 1:100000 sheet; Bracteata Formation, late Emsian, probably *serotinus* or *patulus* CZ.

BRJ133K. Jessey Springs; Chinaman Creek Limestone, late Emsian/Eifelian.

*Abbreviations.* ANUV, Gavin Young collection, Australian National University; BMR, Bureau of Mineral Resources, now Geoscience Australia; BRJ, J. Jell Broken River Formation collection; CPC, Commonwealth Palaeontological Collection, Canberra; CZ, Conodont Zone/s; GY, Gavin Young sample localities from 1977 collecting; L, Natural History Museum collection, Prague; SP, shot-point localities; UQL, University of Queensland Earth Sciences locality; UQY, University of Queensland Earth Sciences (Queensland Museum) collection.

## SYSTEMATIC PALAEONTOLOGY

### Class ACANTHODII

REMARKS. Nostolepis has usually been assigned to the Climatiiformes Berg, 1940, now considered to be a paraphyletic group (Janvier, 1996). Also, scales with *Nostolepis*-type histology have been described on articulated fish with dentigerous jaw bones (Valiukevicius, 2003), indicating they should be assigned to the Ischnacanthiformes. These new taxa thus also throw doubt on the familial assignment of *Nostolepis*, which was erected for isolated scales. For these reasons, we have not assigned *Nostolepis* to an order or family.

### **Nostolepis** Pander, 1856

TYPE SPECIES. *Nostolepis striata* Pander, 1856.

### **Nostolepis** sp. cf. **N. striata**
(Fig. 2A,B)

MATERIAL. One scale CPC20088/3 from SP799 (*?pesavis/sulcatus* CZ, ?late Lochkovian/early Pragian).

DESCRIPTION. Light amber coloured, about 1.0mm long, with about four crown ridges rising up from the short, slightly-inclined neck anteriorly. Main central plane of crown horizontal, smooth behind ridges; a narrow, lower ledge is preserved on one side. Scale base bowl-shaped, moderately swollen. Posterior crown and base have been broken off.

REMARKS. The scale is one that Turner et al. (1981: 60) referred to as "scales ... resemble *Nostolepis striata*". Based on morphology, the scale is comparable to nostolepid scales also assigned to *Nostolepis* sp. cf. *N. striata* from the Martins Well Limestone (*?pesavis/sulcatus* CZ) of the Broken River region, north Queensland (Turner et al., 2000; Burrow, 2002).

### Order ISCHNACANTHIFORMES Berg, 1940
### Family PORACANTHODIDAE Vergoossen, 1997

### **Radioporacanthodes** Vergoossen, 1999
### **Radioporacanthodes** sp.
(Fig. 2C,D)

MATERIAL. Two scales CPC20088/1 (Fig. 2C; figured as *Nostolepis* sp. in Turner et al., 1981: fig. 14D) and

CPC20088/2 (Fig. 2D), from SP799 (?*pesavis/sulcatus*, ?late Lochkovian/early Pragian).

DESCRIPTION. Scales amber-coloured; CPC20088/1 1.0mm wide; CPC20088/2 0.7mm wide; crowns flat, horizontal. CPC20088/2 with about eight short weakly-developed ridges along the anterior crown margin; most of this area on CPC20088/1 is broken off. Posterior crowns broken off on both scales. Necks deep, concave and about the same depth all round. Short vertical slits score neck just above the base/neck junction anteriorly and high on the neck posteriorly. Bases strongly convex forward of centre, protruding markedly in front of crown, tapering towards the posterior corner.

REMARKS. Although diagnostically important posterior crown regions have broken off the scales, they compare closely in all other respects with *Radioporacanthodes* sp. from Martins Well Limestone (?*pesavis/sulcatus* CZ; Turner et al., 2000; Burrow, 2002). Some Lochkovian scales of *Gomphonchoporus hoppei* (Gross), 1971 and *R. porosus* (Brotzen), 1934, and scales from the Pridoli and Lochkovian of the East Baltic and Byelorussia which Valiukevicius (1998: pl. 7.4) assigned to "*Gomphonchus sandelensis* or *Poracanthodes punctatus*", are also similar.

### Order ACANTHODIFORMES Berg, 1937

REMARKS. Berg (1940) listed seven orders within the Acanthodii: Climatiiformes, Ischnacanthiformes, Gyracanthiformes, Diplacanthiformes, Acanthodiformes, Cheiracanthiformes, and Mesacanthiformes. Miles (1966) and Novitskaya & Obruchev (1967) demoted the latter three monofamilial groups to families within one order. Presumably to avoid confusion with Berg's groups, Novitskaya & Obruchev (1967) used the '–ida' suffix rather than '–iformes' for acanthodian orders, but present consensus favours reverting to the '-iformes' suffix. Acanthodiformes thus comprises Mesacanthidae, Cheiracanthidae and Acanthodidae. According to Denison (1979), this familial division was based on gradual transition from 'primitive' to specialised states, without clearcut diagnostic characters. Denison placed all relevant species in Acanthodidae, because of this perceived lack of clearcut boundaries between the groups. However, some characters of the families (cf. Miles, 1966) are not transitional. Mesacanthids have one pair of intermediate spines and smooth scales, characters which are plesiomorphic for the order, but also have synapomorphies including blade-like hyoidean gill covers and a mandibular splint (Hanke & Wilson, 2004: app. 1,2). All cheiracanthids have ornamented scales and lack intermediate spines; and all acanthodids have smooth scales, erectile pectoral spines, either unpaired or no pelvic spines and no intermediate spines. Zajíc (1995) redefined Acanthodidae to exclude *Howittacanthus*, and erected Howittacanthidae, diagnosed by paired pelvic spines, smooth scales and lack of intermediate spines. However, paired pelvic spines is a plesiomorphy, and the Acanthodidae also have smooth scales and lack intermediate spines.

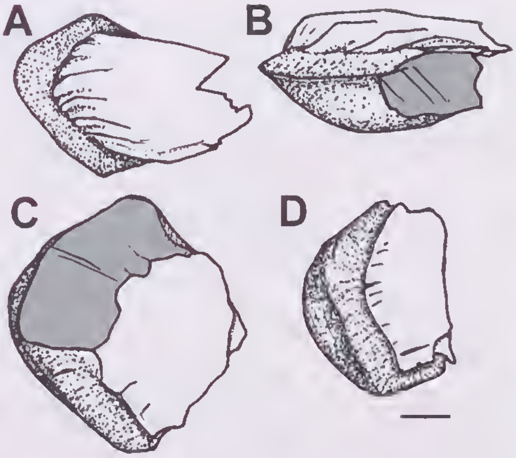

FIG. 2. Acanthodian scales from SP799. A-B. *Nostolepis* sp. cf. *N. striata* scale CPC 20088/3. A, crown view; B, lateral view. C-D. *Radioporacanthodes* sp. scales. C, CPC 20088/2 crown view; D, CPC 20088/3 crown view. Anterior is to left, scale bar = 0.2mm.

### Family MESACANTHIDAE Moy-Thomas, 1939

### **Teneracanthus** gen. nov.

TYPE SPECIES. *Teneracanthus toombaensis* sp. nov.

ETYMOLOGY. Latin: *tener*, delicate; and the common suffix used for acanthodian taxa: *acanthus*, thorn or spine.

DIAGNOSIS. Acanthodiform acanthodian; scapulocoracoid with a long, slender scapular shaft having a circular cross-section, a lateral wide-based, triangular scapular blade which is about one-quarter the height of the scapular shaft, and a medial coracoid blade of similar shape which diverges at ca. 45° to the axis of the shaft; scapulocoracoid articulates with the trailing and lateral sides of the proximal end of the pectoral

TABLE 1. Comparison between five mesacanthid taxa.

| | *Lodeacanthus gaujicus* | *Mesacanthus mitchelli* | *Melanoacanthus minutus* | *Teneracanthus toombaensis* gen. et sp. nov. | *Triazeugacanthus affinis* |
|---|---|---|---|---|---|
| longitudinal ribs on fin spines | deep anterior groove, fine post. grooves | deep anterior groove, fine post. grooves | none | deep anterior groove, some with fin post. grooves | 2-3 shallow grooves |
| denticulations on fin spine | juveniles- distal half of leading edge; adults- none except on intermediate spines | none | none | distal half of leading edge on pectoral spines | none |
| longitudinal cleft, proximal pectoral spine | yes | no | ? | yes | ? |
| fin spine insert base | short | short | short | short | short |
| scapulocoracoid/ pectoral fin spine articulation | scapulocoracoid blades dorsal and lateral to pectoral spine | pectoral spine lateral to coracoid blade | ? | scapulocoracoid blades dorsomedial and lateral to pectoral spine | scapulocoracoid blade ?dorsolateral to pectoral fin spine |
| cross-sectional shape of scapular shaft | juveniles- flat; adults- circular | circular | ? | circular | circular |
| height of expanded scapulocoracoid blade: total scapulocoracoid height | 1:5 | 2:3 | 1:2 | 1:5 | 1:4 |
| shape of scapulocoracoid blade | short-based triangle | ? triangle | short-based triangle | long-based triangle | short-based triangle |
| procoracoid | none | none | none | none | none |
| palatoquadrate | single growth centre; fenestrated | two growth centres; no fenestra | ? | ? | ? |
| branchiostegal rays | mid-sized, curved, outer face with single fine longitud. ridge | long, ornamented | long | ? | short, some forked and some pointed |
| ceratotrichia | none | ?none | ?none | ? | round, forked |
| tectal tesserae | edging infraorbital sensory line | cover head | cover head | ?head and sensory line | cover head |
| size of flank scales | 7/mm | 16/mm | 'small' | 4-5/mm | 5/mm |
| scale crown | smooth | smooth | smooth | smooth | smooth |
| scale base | juveniles – concave; adults - conical | rounded convex | 'tumid' | pyramidal | relatively flat |
| scale histology | ? | pulp canals, orthodentine | *Acanthodes*-type? | *Acanthodes*-type but no interconnecting network | ? |

fin spine, astride its longitudinal cleft; small rounded 'glenoid' process posteromedial to base of scapular shaft; no procoracoid; pectoral fin spines bear fine denticulations on the distal half of the leading edge; fin spines are slightly curved, with one deep longitudinal groove separating the rounded ridge which forms the leading edge from the main body of the spine; the sides of some non-denticulated (?median) spines bear fine longitudinal ridges proximally; some symmetrical fin spines with basal cartilages; fin spines have a relatively wide central pulp cavity, a network of fine dentine tubules leading into vascular canals which run more or less longitudinally; tri-basal pectoral fin; smooth-crowned scales of two types: normal flank scales with a square crown, concave neck and a base shaped like an inverted pyramid, and probable caudal scales with an elongated crown, negligible neck, and a shallow, diamond-shaped base; scales have *Acanthodes*-type histology but lack a fine network of processes between centripetal dentine tubules in the crown.

### **Teneracanthus toombaensis** gen. et sp. nov.
(Figs 3A-E,4A-T,5A-K,6D-F; Table 1)

1981'*Gomphonchus?* sp.' Turner et al.: fig. 14A-C
1981'acanthodian spines' Turner et al.: 60
1987'smooth ischnacanthid scales' Young et al.: 239
1995'climatiid spines' Turner: 683
1995'*Acanthodes*-type scales' Turner: 683
2000'new mesacanthid' Young & Turner: 464
2003'Acanthodian remains', in part Young & Goujet: 9

ETYMOLOGY. For the Toomba Range.

MATERIAL. HOLOTYPE: ANUV2940 (Figs 3A-C,4R-S), pectoral fin spine attached to a scapulocoracoid; Locality GY11, Toomba Range, western flank of Toko Syncline, Georgina Basin, western Queensland (Fig. 1A,B). PARATYPES: left scapulocoracoid ANUV2969.2 (Figs 3D-F,4C-D), pectoral fin spine ANUV2969.1 (Fig. 4L-M), fin spine ANU V2969.5 (Fig. 4K), fin spine ANUV2969.6 (Fig. 4P-Q). ADDITIONALMATERIAL: One right scapulocoracoid articulated with pectoral fin spine, one left pectoral fin spine, 13 fin spine fragments, one ground thin section from fin spine fragment, one left and one right scapulocoracoid, two scapulocoracoid shaft fragments, one ?pharyngobranchial, and 47 scales in samples ANU V2937-41 from GY11; one left and one right scapulocoracoid, fin spines, branchial elements, scales, and a left palatoquadrate in ANUV2969 from GY11; seventeen scales including CPC20087/1 and CPC20087/2 and two ground thin sections, in BMR sample 74710577 from locality GEO 65/28 (Turner et al., 1981); all from the Cravens Peak Beds. One scale in BRJ103A and 16 scales in BRJ104B (Fig. 5K), Bracteata Formation, and ?one scale in BRJ133K, Chinaman Creek Limestone, Broken River Group.

DIAGNOSIS. As for genus.

GEOGRAPHICAL & STRATIGRAPHIC DISTRIBUTION (AUSTRALIA). Cravens Peak Beds (?late Emsian/early Eifelian), Georgina Basin, western Queensland (Fig. 1A-C); Bracteata Formation and possibly Chinaman Creek Limestone (late Emsian/early Eifelian), Broken River Group, north Queensland.

DESCRIPTION. *Scapulocoracoids* (Figs 3D,4A,B). Samples from GY11 include four scapulocoracoids, two left and two right. ANUV2939.5 (Fig. 4A) is an element from the right side, 2.5mm high, with a long thin scapular shaft having a circular cross-section of 0.4mm diameter, expanding to a thin wide-based lateral scapular blade with a stretched-triangular shape; the blade is 1.5mm long x 0.5mm high anteriorly. A rounded medial knob at the base of the scapular shaft is possibly a glenoid process. ANUV2969.8 (Fig. 4B) is a left scapulocoracoid, 3.6mm high. ANUV2939.6 is a left scapulocoracoid, 5mm high, with only the upper part of the lateral scapular blade preserved. Paratype ANUV2969.2 (Figs 3D-E,4C-D) is a right scapulocoracoid, 2.7mm high, with the scapular shaft, ?glenoid process, medial coracoid and lateral scapular blade all preserved. Some delicate perichondral granular mineralisation is preserved anteriorly, with no indication of a coracoid process or procoracoid.

*Denticulated fin spines* (Fig. 4H,L-Q). ANUV 2939.10 (Fig. 4N) is an almost complete, but fragmented, pectoral fin spine, 11mm long, curving slightly, and is from the left side; the main shaft has a circular cross-section and smooth sides, with a longitudinal ridge along the leading edge. The distal half to two-thirds of this ridge bears fine backward-pointing denticulations. The proximal end of the spine has a thin film of ossified cartilage across the triangular cleft between the two sides of the spine. This spine possibly articulated with the left scapulocoracoid described above. ANU-V2939.11 is a right pectoral fin spine, 11mm long but missing the proximal part; it is otherwise comparable to the left pectoral fin spine, having a circular cross-section and distal denticulations. These pectoral fin spines are not exactly symmetrical dorso-ventrally, having a smooth transition from the leading edge ridge to groove to main body of spine on one side, but with an abrupt, 'stepped-down' transition from the ridge to the main body of the spine on the other side. Paratype ANU V2969.6 (Fig. 4P-Q) is a complete, laterally flattened fin spine 14mm long, also showing slight longitudinal curvature. The pulp cavity is open along the proximal half of the trailing edge, and the distal half of the leading edge is denticulated. Other fin spine material in the samples includes short fragments of denticulated spines, including one in ANUV2941 and three in ANUV2939 (Fig. 4H). Paratype ANUV2969.1 (Fig. 4L-M) is the proximal 3mm of a ?pectoral fin spine which has a delicate sheet of perichondral ossification preserved across the longitudinal cleft. This sheet has three holes, each 0.2-0.3mm long: a proximal pair and a more distal single central hole, which probably represent the articulation points of the fin radials, showing that these fin elements were arranged in a triangle rather than linearly.

*Non-denticulated fin spines* (Figs 3G,4E-G,K). Paratype ANUV2969.5 (Fig. 4K) is a complete, symmetrical? spine 12mm long, with a smooth leading edge ridge and several (up to five) fine longitudinal ridges on each side. A delicate sheet of perichondral ossification is partly preserved boxing over the open pulp cavity of the proximal half of the spine, and is presumed to have covered the basal cartilage of the fin. As the spine is symmetrical, and dorsal fins are the only median fins for which basal cartilages have been recorded in any acanthodians, the spine is probably from the dorsal fin. Two fragments from sample ANUV2939 are proximal ends of spines,

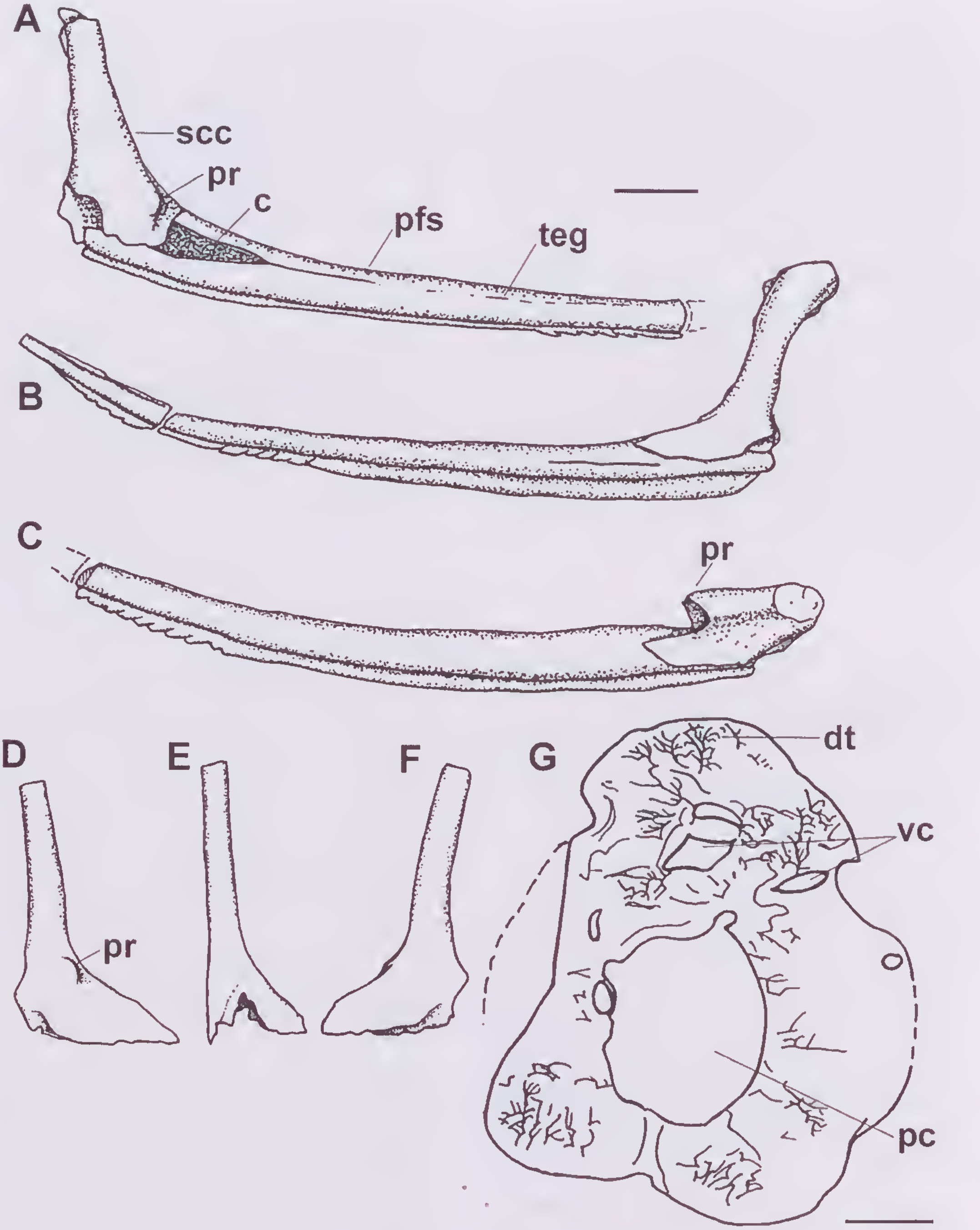

FIG. 3. Drawings of pectoral girdles and fin spine of *Teneracanthus toombaensis* gen. et sp. nov. from site GY11. A-C. Articulated right scapulocoracoid and pectoral fin spine ANU V2940. A, medial view, B, lateral view, and C, dorsal view. D-F. Right scapulocoracoid ANU V2969.2, in D, medial view, E, anterior view, and F, lateral view. G. ground thin cross-section of fin spine ANU V2939.9. Scale bar = 1.0mm in A-C, 0.5mm in D-F, 0.1mm in G. c, spine cleft; dt, dentine tubules; pc, pulp cavity; pfs, pectoral fin spine; pr. ?glenoid process; teg, trailing edge groove; vc, vascular canals.

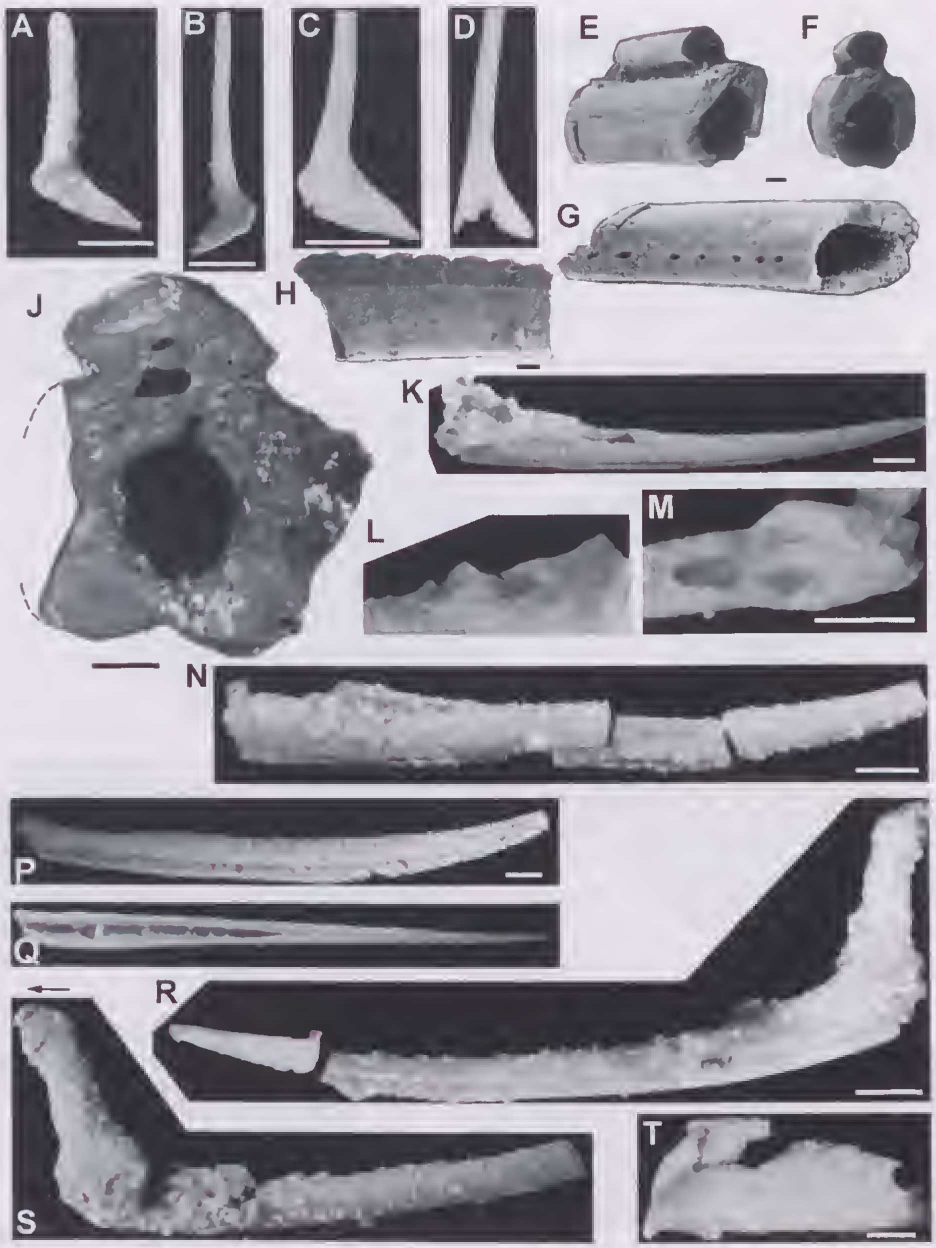

FIG. 4. Pectoral girdles, fin spines and palatoquadrate of *Teneracanthus toombaensis* gen. et sp. nov. from GY11. A, right scapulocoracoid, medial view ANUV2939.5; B, left scapulocoracoid, lateral view ANUV2969.8; C-D, right scapulocoracoid, medial and anterior views ANUV2969.2; E-G, non-denticulated spine fragment ANUV2939.8 E, lateral view, F, end-on view, and G, latero-basal view; H, lateral view denticulated fin spine fragment ANUV2939.7; J, transverse section ANUV2939.9, under cross nicols; K, median fin spine ANUV2969.5, showing perichondral ossification of basal cartilage; L-M, proximal cleft of pectoral fin spine ANUV2969.1, showing three holes in the perichondral ossification; N, ?left pectoral fin spine ANUV2939.10, dorsal view; P-Q, denticulated fin spine ANUV2969.6 P, lateral view, and Q, trailing edge view, R-S, articulated right scapulocoracoid and pectoral fin spine ANUV2940, R, lateral view, and S, medial view; T, fractured perichondral ossification of left palatoquadrate ANUV2969.4. Scale bar=1mm in A-D, K, N-S, 0.5mm in L-M, T, and 0.1mm in E-J; arrow to anterior.

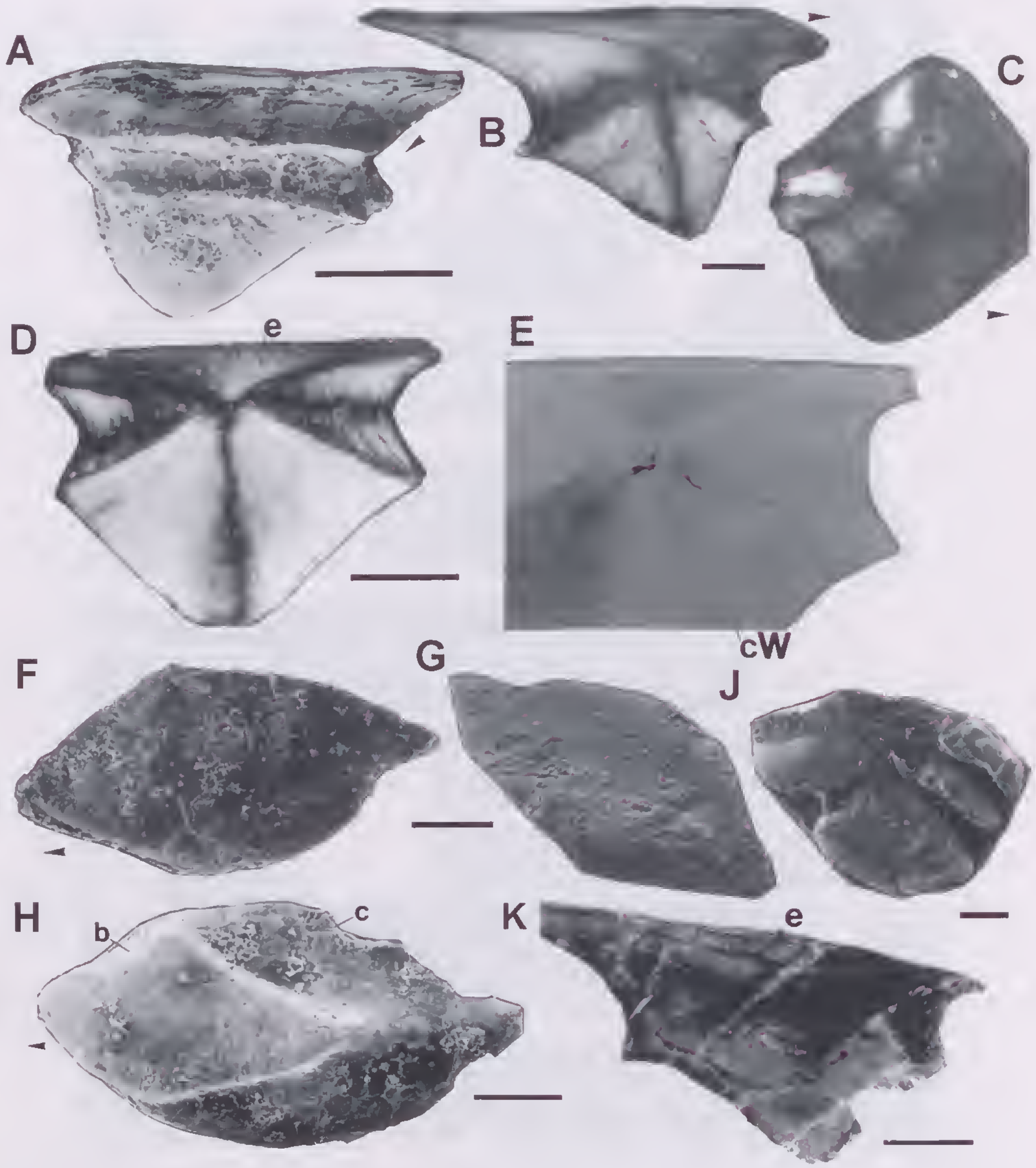

FIG. 5. Scales of *Teneracanthus toombaensis* gen. et sp. nov. from GY11 (A-J) and BRJ104B (K). A, antero-lateral view flank scale ANUV2939.12; B, vertical longitudinal section flank scale, ANU V2939.13, under cross nicols; C, horizontal section crown flank scale ANUV2939.14, under cross nicols; D, E, vertical transverse section flank scale ANUV2939.15, D under cross nicols; F, G, caudal scale (*sciotoensis* var.) ANUV2937.8, F, crown view, G, latero-crown view; H, caudal scale ANU V2939.16, basal view; J, ?cheek tessera ANUV2939.17, crown view; K, Vertical longitudinal section flank scale UQY9335. Scale bar=0.1 mm; arrow is anteriad; b = base, c =crown, cW =canals of Williamson, e = enameloid.

with part of the short striated insertion area preserved, and a wide open main central cavity. Most other fragments are short (Fig. 4E-G); two of the longer pieces are a mid-spine section, 4.2mm long, and a very slender distal fragment which is 2.5mm long. These are straight, laterally flattened, without denticulations and with two or more very fine longitudinal ribs per side on the main shaft of the spine. Irregularly-spaced rounded pores pierce the trailing edge groove (Fig. 4G).

*Scapulocoracoid plus pectoral fin spine* (Figs 3A-C,4R-S). Holotype ANUV2940, a fin spine, 12mm long, articulated with a scapulocoracoid, 3mm high (although the top of the shaft is broken off). Specimen heavily encrusted with small ?sand grains, obscuring finer details. Scapular shaft narrow with circular cross section. Scapulocoracoid attached to dorsal and lateral faces of the pectoral fin spine, with the straight ventral margin of the scapular blade paralleling the main longitudinal groove between the leading edge ridge and the main shaft of the spine. Medial coracoid blade of scapulocoracoid incomplete.

*Spine histology* (Figs 3G,4J). A wide central cavity extends through the length of the main shaft of the spine, with one or more longitudinal canals in the leading edge ridge. Other vascular canals are also visible, and denteons are developed near the central cavity and the vascular canals. Bone cell lacunae and lacunal widenings in dentine are lacking, with the hard tissue being relatively densely-branching, fine dentine tubules. A thin inner lamellar layer lining the central cavity is possibly present.

*Palatoquadrate* (Fig. 4T). ANUV2969.4, 2.8mm long, greatest height ca. 1.2mm, represents delicate, hollow perichondral granular mineralisation of most of a left upper jaw. A semicircular notch on the anterior edge resembles the embayment at junction of the metapterygoid and autopalatine cartilages on *Acanthodes bronni* (e.g. Miles, 1965: fig. 1A) and at the junction of the anterior and posterior parts of the palatoquadrate on *Mesacanthus mitchelli* (Watson, 1937), but there are no signs of separate ossification areas. Most of the palatoquadrate is preserved, including posterior part of the extrapalatoquadrate ridge and the hyomandibular groove, and the jaw joint articulation surface comprising prearticular and articular processes. Posterior edge of palatoquadrate almost vertical; anterodorsal part of the element missing, and thus presence or absence of a fenestra comparable to that in *Lodeacanthus* (Upeniece, 1996: fig. 1B,C) is unknown.

*Scale morphology* (Figs 5A,F-H). Translucent, amber to cream coloured, small with smooth flat crown. Square-crowned (Fig. 5A) 0.2 to 0.3mm wide and long, with concave neck and base with a central pointed, inverted pyramid-shaped swelling surrounded by a relatively flat perimeter. Elongated scales are 0.2mm wide and 0.3 to 0.4mm long, with a short neck, and a flat or slightly convex diamond-shaped base.

*Scale histology* (Figs 5B-E,K,6D-F). Thick enameloid is developed through the centre of the crown, with long ascending dentine tubules in the anterior and posterior crown; these tubules show minimal branching. There are no bone cell lacunae in the base or crown. A network of Williamson's canals penetrates the base.

REMARKS. The tall slender scapular shaft with its circular cross section and the smooth-crowned scales with *Acanthodes*-type histology indicate the elements derive from an acanthodiform acanthodian. Fin spines and scapulocoracoids of *Teneracanthus toombaensis* gen. et sp. nov. are similar to *Cheiracanthus* spp. in the shape of scapulocoracoids, type of articulation between scapulocoracoid and fin spine, and the structure of the fin spines. The shoulder girdle/pectoral fin spine arrangement is unclear in other cheiracanthids (i.e. acanthodiforms with ornamented scales); eg., *Carycinacanthus* (Novitskaya & Obruchev, 1967), *Protogonacanthus* and *Homalacanthus* (Miles, 1966). Whereas the reconstructions of *Cheiracanthus murchisoni* Agassiz, 1835 (1833-43) and *C. latus* Egerton, 1861 in Watson (1937: figs 12,13) have the pectoral fin spine detached from the scapulocoracoid, Miles (1973; also Egerton, 1861) indicated that these elements were articulated. In *Cheiracanthus*, the scapulocoracoid shaft leans slightly forward and has a circular cross section. The ventral blade widens out below the shaft, forming a triangular region with a long straight ventral margin (Miles, 1973: 157, text-fig. 22). The scapulocoracoids of *Teneracanthus toombaensis* gen. et sp. nov. share these features, but also have a medial blade of similar shape to the lateral blade, so that the element straddles the proximal end of the pectoral fin spine. Also, *Cheiracanthus* differs by having a procoracoid anterior to the scapulocoracoid and pectoral fin spine (although lacking a procoracoid process on the scapulocoracoid). No procoracoid is preserved on the

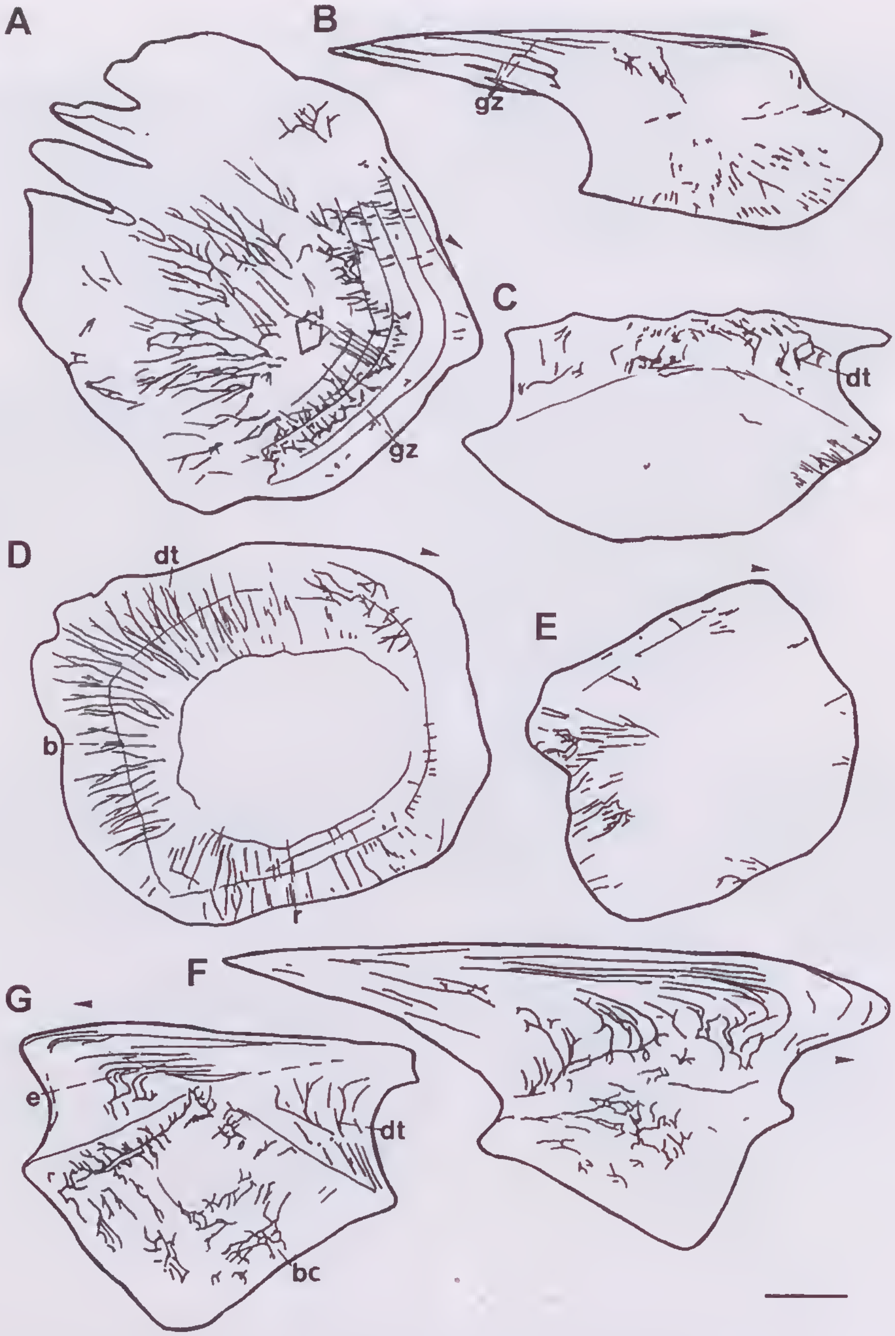

FIG. 6. Drawings of thin sections of scales from GY11. A-C, *Machaeracanthus pectinatus* sp. nov., ground thin sections. A, horizontal section crown ANUV2939.1; B, vertical longitudinal section ANU V2939.2; vertical transverse section C,ANUV2939.3. D-G, *Teneracanthus toombaensis* gen. et sp. nov. D, scale CPC20087.2 in anise oil; E-G, ground thin sections: E, horizontal section crown ANUV2939.4; F, vertical longitudinal section ANUV2939.13 ; G, vertical transverse section ANUV2939.15. Scale bar =0.1mm in A-F, 0.05mm in G; arrow to anterior; bc = cellular processes, dt =dentine tubule, gz growth zones.

Cravens Peak specimens, and the relatively complete scapulocoracoids have a smooth anterior face. Unlike cheiracanthids, which all have scales with ornamented crowns, the new taxon has the smooth-crowned scales which characterise the acanthodids and mesacanthids.

In acanthodids, the shoulder girdle structure and its articulation with the pectoral fin spine is well known in *Acanthodes bronni* (Lower Permian, Lebach, Germany). Unlike the new taxon, *Acanthodes* has a relatively short stout scapular shaft and an extensive coracoid flanking the fin spine medially, as does *Howittacanthus* (Long, 1986). Of mesacanthids (Table 1), *Mesacanthus mitchelli* (Egerton, 1861) from the Early Devonian of Scotland, has a simple scapulocoracoid attached to the inner face of the pectoral fin spine (Miles, 1973: text-fig. 23), and *Triazeugacanthus* Miles, 1966 from the Frasnian of Miguasha, Canada has a tall and anteriorly curved scapulocoracoid. Miles (1966) indicated that in *Triazeugacanthus* the scapulocoracoid was dorsal to the pectoral fin spine, but Gagnier (pers. comm.) suggested that it covers some of the 'inner' part of the pectoral fin spine.

The scapulocoracoid plus pectoral fin spine ANUV2940 complex is similar to that of the Emsian mesacanthid *Melanoacanthus minutus* Cumbaa & Schultze, 2002, but compares most closely with that of mesacanthid *Lodeacanthus gaujicus* Upeniece, 1996 from the lower Frasnian Lode Formation of Latvia. Upeniece (1996) described articulated specimens of both juveniles and adults of *Lodeacanthus*, ranging from 13.6-38.9mm in length. The flank scales are smooth-crowned, with conical bases in adults but with concave bases in juveniles. The palatoquadrate on *Lodeacanthus* is ossified as a single unit and has a large fenestra anterodorsal to the jaw articulation; prearticular and articular processes extend from the ventral shelf. ANU V2969.4 shows a comparable structure, although with the fractured and incomplete preservation of the dorsal region the presence or absence of a fenestra is unclear.

The scapulocoracoid in *Lodeacanthus* has a scapular shaft with a circular cross-section in adults and flattened oval cross-section in juveniles; the shaft is 4/5 total height of the scapulocoracoid. As on *Teneracanthus*, the ventral part of the scapulocoracoid divides into two blades straddling the cleft of the pectoral fin spine. In *Lodeacanthus*, the fin spines have an elliptical cross section and lack insertion areas. The distal leading edge of all fin spines, except intermediate ones, lack ornamentation in adults, but in juveniles all fin spines have a row of denticles on the leading edge. In the adults, the ratio of pectoral fin spine: total length of fish averages 0.15. By comparison, the *Teneracanthus toombaensis* gen. et sp. nov. fish which had the articulated scapulocoracoid/ pectoral fin spine is estimated to have been about 73mm long.

All *Teneracanthus toombaensis* gen. et sp. nov. scales have convex bases, indicating (cf. *Lodeacanthus*) they are from an adult rather than a juvenile. It differs from *Lodeacanthus* in having denticulated pectoral fin spines on adult fish and long-based scapulocoracoid blades. It is uncertain whether *Teneracanthus* had pre-pelvic fin spines; none of the fin spine fragments appear to be from small spines comparable to the pre-pelvic spines of *Lodeacanthus*.

Scale histology for *Teneracanthus toombaensis* gen. et sp. nov. shows numerous centrifugal, non-branching dentine tubules in the upper crown, indicating *Acanthodes*-type histology similar to that in scales of *Cheiracanthus latus*. They differ to *Acanthodes bronni* (Gross, 1947: fig. 18B) in lacking the fine network between the long dentine tubules. Scales of *Mesacanthus* spp. from England and Scotland are much smaller than those of other mesacanthids, and often have relatively wide vascular canals piercing the base in caudal scales (CJB, pers. obs.). However, they do have long dentine tubules typical of acanthodiforms (Denison, 1979). No description was given of *Lodeacanthus* scale histology.

Smooth-crowned scales of late Early to Middle Devonian age have traditionally been referred to *Acanthoides* Wells, 1944 or *Acanthodes*? spp. Scales of *Teneracanthus toombaensis* gen. et sp. nov. resemble those from the Eifelian bone beds of Ohio, Indiana and Kentucky in the U.S.A. assigned to *Acanthoides dublinensis* and *A. sciotoensis* by Wells (1944) and Storrs (1987: fig. 3.5,6). Although the crown shape is comparable, scales of *Acanthoides* have rounded rather than pointed bases. From the same U.S. bone beds are the fin spine fragments which Wells (1944: pl. 2.46,47) assigned to *Gyracanthus*? *eastmani*, and Storrs (1987: fig. 3.7) to 'acanthodian fin spine fragment', which resemble the denticulated spines of *Teneracanthus toombaensis* gen. et sp. nov. In Queensland, De Pomeroy (1996: fig. 3O,P) referred scales from the Papilio Formation (Givetian, mid *varcus* CZ) of the Broken River Province to *Acanthoides* sp. These were described as having a 'highly convex' base, which presumably means a rounded base. However, several scales which have the distinctively pointed base like those of *Teneracanthus toombaensis* gen. et sp. nov. are present in late Emsian/?early Eifelian limestones of the Broken River region, and are assigned here to the same taxon (Fig. 8G).

*Pectoral fin structure.* The knob shaped process posteromedial to the base of the scapular shaft is comparable to the structure which Miles (1973: text-fig. 40B) designated a glenoid process in *Diplacanthus striatus* Agassiz, 1844.

Three-D preservation of delicate perichondral granular mineralisation at the base of the pectoral fin spine is a unique record of the structure of the fin base. Three basal radials have previously been noted in *Acanthodes bronni* (Miles, 1973: 153, text-fig. 20), but in that species the three stout elements articulate against the margoradialis of the scapulocoracoid, aligned linearly perpendicular to the fin spine. This arrangement is drastically different to that in *Teneracanthus*, where three presumably uncalcified radials apparently issued from the proximal cleft of the pectoral fin spine. The near-complete scapulocoracoid ANUV2969.2 has clearcut ventral edges to the lateral and medial blades, indicating that the coracoid did not extend further ventrally, and thus negating the possibility of a fin radial articulation comparable to that of *A. bronni*. All reconstructions of pectoral fin radials in the latter species place them in a straight line, perhaps influenced by comparison with extant actinopterygians and chondrichthyans, with their long-based fins. It is unlikely, however, that *A. bronni* had a short-based, triangular arrangement like that in *Teneracanthus*, as *A. bronni* had a long narrow margo radialis (Miles, 1973: pl. 14.2). Several climatiid taxa, e.g. *Sabrinacanthus arcuatus* (Miles, 1973: text-fig. 29) and *Ptomacanthus* sp. indet. (Miles, 1973: text-fig. 32), have cartilage spanning the proximal cleft of the pectoral fin spine, which Miles (1973) interpreted as the margo radialis. Although the acanthodian endoskeletal shoulder girdle has been described as a 'scapulocoracoid', most taxa lack a distinguishable coracoid region. Thus in most acanthodians, as exemplified by *Teneracanthus*, it seems likely that the pectoral fin endoskeleton (if present) articulated with the cartilage which filled or covered the proximal cleft of the pectoral fin spine.

Recognition of the triangular arrangement of the pectoral fin radials in *Teneracanthus* encouraged consideration of the pectoral fin base in some of the earliest 'true' chondrichthyans which lack paired fin spines. This region on the Carboniferous chondrichthyan *Hamiltonichthys mapesi* Maisey, 1989 was reconstructed with the three fin basals aligned linearly (Maisey, 1989: fig. 14). According to Maisey (1989: 19), "articulation with the scapulocoracoid is mainly protopterygial, although the mesopterygium and metapterygium may also have met the shoulder girdle". Goujet (2001) noted that in chondrichthyans with a tribasal fin, only one element articulates with the girdle, with the other basal elements just overlapping rather than articulating with the girdle. As it now seems clear that proto-chondrichthyans had pectoral fin spines (Wilson & Hanke, 1998; Miller et al., 2003), the linear tribasal arrangement in 'true' chondrichthyans is possibly related to the loss of the articulation cartilage in the cleft of the pectoral fin spine. What can we infer for the plesiomorphic condition in acanthodians? The Placodermi are generally regarded as the sister group of all other gnathostomes. Goujet (2001) proposed that a monobasal pectoral fin is a general condition within the gnathostomes, and is plesiomorphic for placoderms. This contradicts the previously held view that a monobasal fin is a synapomorphy of the sarcopterygians (Janvier, 1996), but is supported by embryological studies of zebrafish as well as by the structure of the chondrichthyan 'tribasal' fin (Goujet, 2001). Unfortunately, the internal skeleton of the fins in Acanthodii is usually not preserved, or poorly ossified, and is thus poorly known. Although the margo radialis has been identified in several climatiids, the only acanthodian other than *A. bronni* in which pectoral fin radials have been identified is *Ischnacanthus* Powrie, 1864. Watson (1937) described four pectoral fin elements, which Miles (1973) interpreted as radials, in a specimen of *I. gracilis* (NMS 1891.92.258), but the arrangement of these elements has not been detailed. We can only presume that, if the general condition in gnathostomes is a monobasal pectoral fin as proposed by Goujet (2001), then if we accept the current view of gnathostome phylogeny, the stem acanthodian would either have had a monobasal fin, or have descended from a derived stem-group gnathostome which had already developed a tribasal pectoral fin.

### Order incertae sedis

### Family MACHAERACANTHIDAE fam. nov.

TYPE GENUS. *Machaeracanthus* Newberry, 1857, thus far the only known member.

DIAGNOSIS. Acanthodian fishes lacking paired and median fin spines of typical acanthodian structure (i.e. with a pulp cavity opening out along the proximal part of the trailing edge of the spine); having only paired fin spines, derived from internal fin rays or radials; scales with both apposed and superposed crown growth zones; perichondrally ossified scapulocoracoid with a relatively slender scapular shaft broadening out to a sub-triangular scapulocoracoid blade.

### **Machaeracanthus** Newberry, 1857

TYPE SPECIES. *M. peracutus* Newberry, 1857

REMARKS. Affinities of *Machaeracanthus* have been extensively debated over recent decades (Janvier, 1996), with some (e.g. Goujet, 1995) assigning the genus to the Chondrichthyes, others (e.g. Zidek, 1981) maintaining inclusion in Acanthodii (as first proposed by Fritsch, 1893), and yet others remaining equivocal (e.g. Mader, 1986, assigned *Machaeracanthus* to 'Gnathostomata incertae sedis'). The original material of *M. bohemicus* (Barrande, 1873) from the Pragian Dvorce prokop Limestone and the early Emsian Zlichov Formation of Bohemia included an uncatalogued specimen (Barrande, 1873: pl. 34.29-34) from the Dvorce prokop Limestone comprising fin spines associated with an ossified endoskeletal scapulocoracoid (the latter captioned as 'Ossement de nature indéterminée'). The part of the specimen has not yet been refound, but the counterpart (Barrande, 1873: pl. 34.33,34) was identified (by CJB) as specimen Lc 98 in the National Museum collection, Prague. As noted by Fritsch (1895) and Zidek (1975, 1981), this scapulocoracoid is comparable in shape and structure with those of climatiids and ischnacanthiforms. Gross (1973) assigned scales associated with *M. bohemicus* spines from the Lochkovian Radotin Limestone, Kosor to the taxon. These scales resemble those of poracanthodid scales in shape and ornament, but lack a pore canal system within the scale crown. Many of the fin spines have a calcified core; prismatic calcified cartilage was not associated with any of the specimens. As far as known, *Machaeracanthus* lacks features which indicate chondrichthyan affinity: no prismatic calcified cartilage, no loss of endoskeletal bone, no pulp canals piercing scale bases, and no chondrichthyan-type teeth, although Goujet (1993) suggested that *Leonodus* Mader, 1986 teeth could be from *Machaeracanthus*. However, Soler-Gijón & Hampe (2003) indicated that *Leonodus* had *Antarctilamna*-type scales and fin spines, based on an associated (but not articulated) assemblage of remains on a single slab from the type locality for *Leonodus*. No teeth from the Cravens Peak Beds localities are comparable with *Leonodus* teeth.

### **Machaeracanthus pectinatus** sp. nov
(Figs 6A-C,7A-L,8A-E)

1987 'shark scales comparable with those of *Gualepis*' Turner & Young: 233
1987 '*Machaeracanthus* spines and scales' Young et al.: 239
1991 'shark scales cf. *Gualepis*' Turner: fig. 5G-H, pl. 51
1991 '*Machaeracanthus*' Turner: tab. 3
1993 'scales similar to those called *Gualepis*' Turner: 184, fig. 8.4G-H
1993 '*Machaeracanthus*' Turner: 193
1993 'machaeracanthid acanthodians' Young: 224
1995 '*Machaeracanthus* scales' Turner: 683
2000 '*Machaeracanthus* sp.' Young & Turner: 464
2003 'Acanthodian remains', in parts Young & Goujet: 9.

ETYMOLOGY. Latin *pectinis*, comb.

MATERIAL. HOLOTYPE: Scale ANUV2936.10 (Fig. 7A); Locality GY11 (= BMR locality GEO 65/28; Fig. 1B), a small limestone outcrop in the S part of the Toomba Range, W flank of the Toko Syncline, Georgina Basin, western Queensland. PARATYPES: Scales ANUV2938.4, ANUV2938.2, ANUV2935.12, ANU V2938.1, ANUV2938.8, ANUV2937.5 (Fig. 7B-G) and thin sections of scales ANUV2939.1-3 (Figs 6A-C,7H,J,K). ADDITIONAL MATERIAL. Eighty-one scales including three ground thin sections from samples ANU V2935-41, and ca. 20 scales from ANUV2969, locality GY11; probably four scales including CPC20087/3 from sample 74710577 (locality GEO 65/28); possibly one scale from shot-point sample SP801; possible fin ray-type elements from localities GY10,11 (Fig. 1B).

DIAGNOSIS. Scales with four to twelve sub-parallel or sub-convergent ridges on the anterior part of the crown, and sub-parallel denticulations forming the posterior crown and extending behind the base; individual flank scales have a similar or equivalent number of ridges as denticulations; scale neck and base are of equal height; orthodentine forms most of the crown, with some mesodentine in the anterior part of the crown growth zones; growth zones are apposed in the posterior, and superposed in the anterior region of the crown.

GEOGRAPHICAL AND STRATIGRAPHIC DISTRIBUTION. Cravens Peak Beds (?late

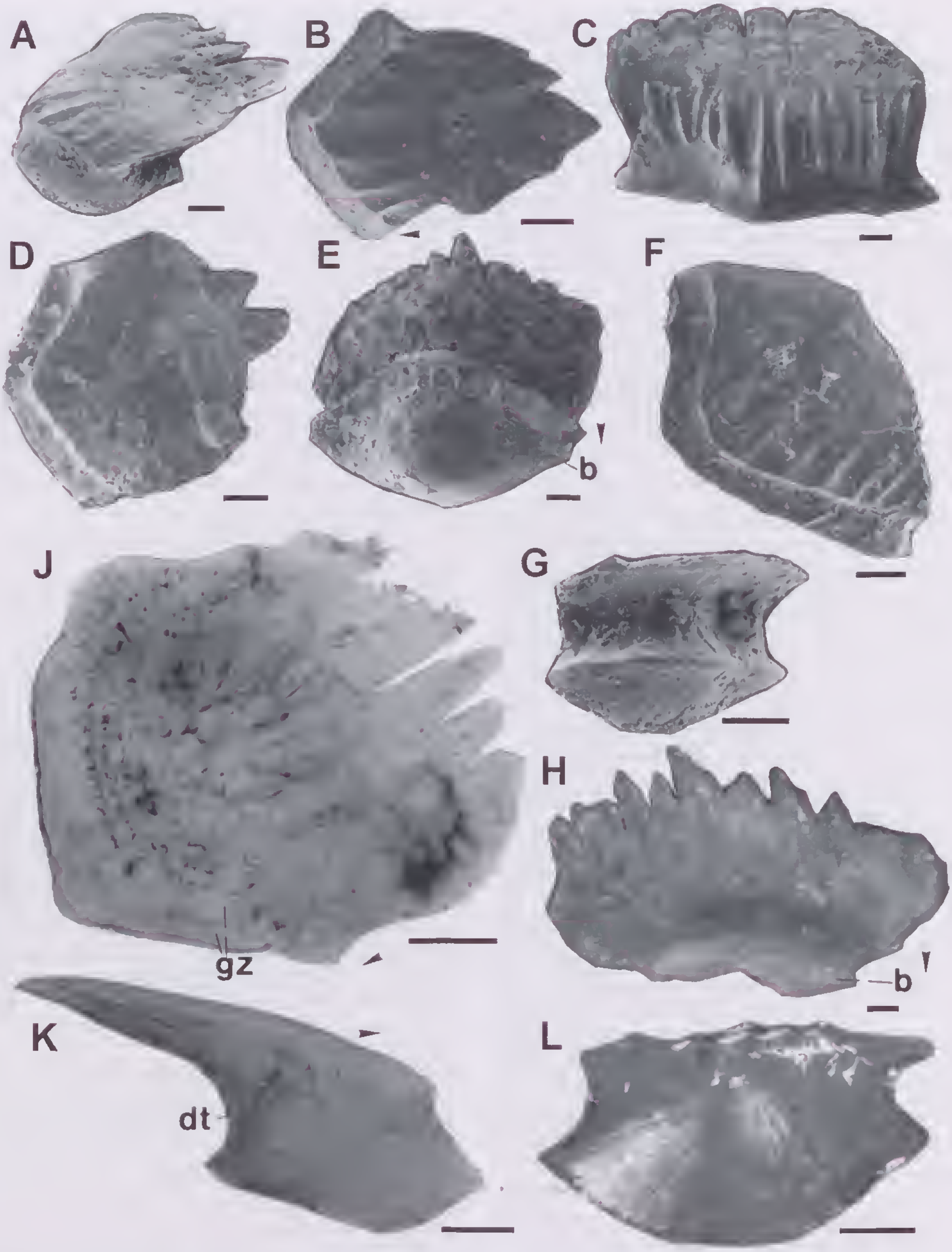

FIG. 7. Scales of *Machaeracanthus pectinatus* sp. nov. from site GY11. A, latero-crown view, ANUV2936.10; B, crown view, ANUV2938.4; C, antero-crown view, ANUV2938.2; D, crown view, ANUV2935.12; E, basal view, ANUV2938.1; F, crown view, ANU V2938.8, posterior crown section broken off; G, posterior view, ANUV2937.5; H, basal view, ANUV1649.1 anterior of scale broken off; J, horizontal section of crown ANUV2939.1; K, vertical longitudinal section ANUV2939.2; L, vertical transverse section ANUV2939.3, under cross nicols. Scale bar = 0.1 mm; arrow to anterior; b = base, dt = dentine tubules, gz = crown growth zones.

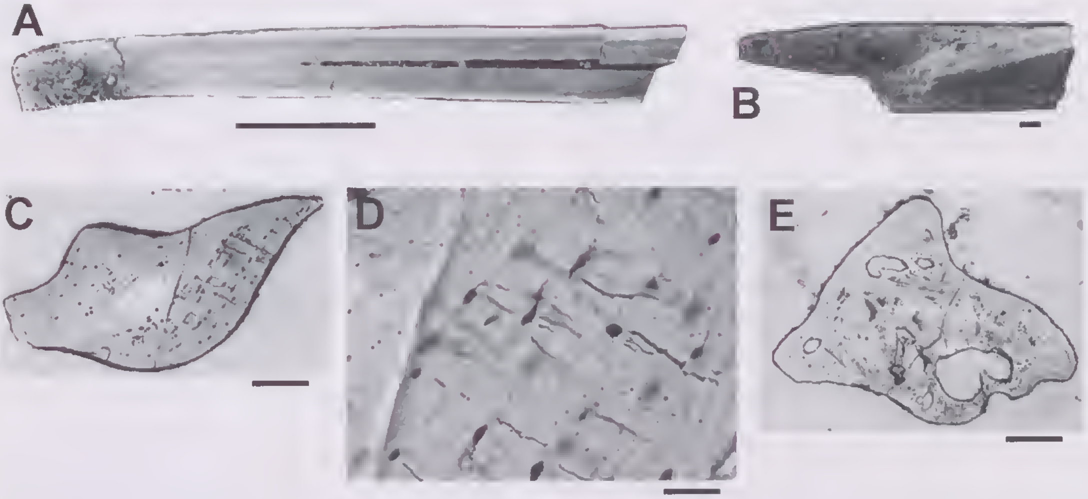

FIG. 8. Fin ray or spine elements possibly from *Machaeracanthus pectinatus* sp. nov. from GY10 (A,B) and GY11 (C-E). A, double element fused at base (left) ANUV2941.1; B, single element with narrow proximal end ANUV2941.2; C-D, transverse section from distal part of an element ANUV2939.18: C, showing whole section, D, close-up of bone cell lacunae and processes; E, transverse section from proximal part of an element ANUV2939.19. Scale bar = 1mm in A, 0.1mm in C,E, and 0.01mm in D; C-E, under cross nicols.

Emsian/early Eifelian), Toomba Range, Georgina Basin, western Queensland

DESCRIPTION. *Morphology* (Fig. 7A-H). Scales translucent, amber or cream coloured, with small red spots throughout the latter type; 0.7 to 1.2mm wide and long. Crown rises slightly or steeply antero-posteriorly, extending well beyond the posterior corner of base on well-preserved scales. Between four and twelve sharp ridges lead back from the anterior edge of the crown; on some scales these ridges tend to converge, while on others they run more or less parallel to each other. The posterior crown, when preserved, is divided into five to eleven long parallel denticulations. The neck is short and concave all round, with a sharp rim between the neck and base. Base shallow to moderately convex with swelling central, or sometimes forward of centre. Base protrudes only slightly in front of the anterior edge of the crown. Base and neck of the scales of equal height.

*Histology* (Figs 6A-C,7J-L). No bone cell lacunae or wide vascular canals are visible in the base or crown. Orthodentine tubules radiate through most of the crown, extending into the posterior crown 'fingers'; some mesodentine with a network of lacunae and short tubules is developed in the front of the crown. Apposed growth zones form the posterior crown, and superposed zones form the anterior crown.

?*Fin spines or rays* (Fig. 8A-F). 0.5 to 1mm wide, asymmetrical, slightly tapering along the main shaft. Surface smooth except for irregular longitudinal grooves of the vascular system visible towards proximal end. In cross-section of the distal ends, the 'dorsal' side has a rounded ridge, slightly off-centre, the 'ventral' side is bowl-shaped, and the edges flatten out to be relatively thick and blunt on one side, and thin and pointed on the other side. Elements have a dull, 'bony' lustre. ANUV2941.1 comprises two rays fused at the base (Fig. 8A). Histological structure of distal fragments (Fig. 8C,D) shows no dentine tubules or vascular canals, but abundant bone cell lacunae, some of which have ?Williamson's canals leading towards the exterior. Mid-shaft, the 'dorsal' ridge is very asymmetrical, curving over towards the side. Histological structure at this level (Fig. 8E) shows weak growth lines paralleling the external surface, with some short straight canals in these narrow outer growth zones. The inner part is formed of thick bone, similar to tissue described by Bystrow (1957) in non-dentinous placoderm bones, with abundant bone cell lacunae and wide, longitudinal vascular canals.

REMARKS. Scales are the only certain machaeracanthid elements in the Cravens Peak samples. *Machaeracanthus bohemicus* (Barrande, 1872) from Lochkovian to early Emsian limestones in the Czech Republic is the only *Machaeracanthus* with more than one type of element assigned to it: material from the Czech localities includes spines associated with scales, a scapulocoracoid and possibly the tip of a tooth (Zidek, 1985). Isolated scales from Early Devonian localities worldwide have been assigned to *Machaeracanthus* sp. (e.g. Goujet, 1976; Mader, 1986; Wang, 1993; Burrow, 1997). Scales from the Lochkovian of northern Spain assigned by Wang (1993) to *M. stonehousensis* have 'Stranggewebe'-like tissue (i.e. with close-set, parallel elongated lacunae) in the crown, and other *Machaeracanthus* sp. scales from the Early Devonian of Spain (Mader, 1986; Wang, 1993) and France (Goujet, 1976) have bone cell lacunae in the base, and vascular canals and probably mesodentine in the crown. Cravens Peak Beds machaeracanthid scales have similar histological structure to *M. bohemicus;* orthodentine forming most of the crown, on-layering or apposition of growth zones in the posterior crown denticulations (e.g. Gross, 1973: pl. 28.21a) and lacking bone cell lacunae. Scales of *M. pectinatus* sp. nov. differ to those of *M. bohemicus* by the comb-like structure formed by the sub-parallel denticulations of the posterior crown (in the latter species, the denticulations radiate from the centre of the scale) and having a shallower scale base.

Except for *Machaeracanthus pectinatus* sp. nov., all other *Machaeracanthus* scales are from Lochkovian strata. *Machaeracanthus* sp. scales from near Trundle, New South Wales are now thought to be from two taxa (Burrow, 2002). Older scales from the Connemarra Formation (= 'Trundle Beds B' in Burrow, 1997; late Lochkovian/ early Pragian) are now considered indeterminate, deriving from either *Machaeracanthus* sp. or the Poracanthodidae, while scales from the younger Troffs Formation (= 'Trundle Beds A' in Burrow, 1997) and Gleninga Formation (mid Pragian-early Emsian) are now assigned to *Cheiracanthoides wangi* (Basden et al., 2000; Burrow, 2002; Burrow et al., 2000). Turner (1991, 1993) compared some of Cravens Peak Beds *M. pectinatus* sp. nov. scales to those of the chondrichthyan *Gnalepis*. Several of the scales in the type material of *Gnalepis* Wang, 1984 from the Xitun Member, Cuifengshan Formation, China which were designated 'old' scales (e.g. those in Wang, 1984: figs 10D-E,11A-D) are possibly specialised ischnacanthid scales. Similar scales assigned to *Machaeracanthus pectinatus* sp. nov. probably lined sensory canals on the head of the fish. However, *Gnalepis* scales from the type locality in China which were described as juvenile scales appear to be chondrichthyan, not acanthodian.

Zidek (1981) characterised different species of *Machaeracanthus* by the cross-sectional shape of fin spines. Unfortunately, histological study of the spines is limited: no thin sections of *M. bohemicus* spines were located in the Czech National Museum collection. Large *Machaeracanthus* sp. spines have been described from the Lower or Middle Devonian of North and South America, Antarctica, Africa, Europe and the Falklands Islands (Maisey, 2002). While it is by no means certain that the fin ray-like elements from the Cravens Peak Beds belong to the same fish as the *M. pectinatus* scales, the elongated elements have a similar cross-sectional shape to spines of *M. major* (Zidek, 1981: fig. 2e). However, lack of an outer dentine layer and occurrence of fused elements in the Cravens Peak Beds elements indicate they are not homologous with normal acanthodian fin spines. Rather, they probably derived from internal fin rays. If so, they suggest an explanation for the difference between fin spines of *Machaeracanthus* and other acanthodians (if *Machaeracanthus* is indeed an acanthodian). Fin spines of acanthodians are typically found in front of all fins except the caudal, and in all other acanthodian genera they have a U-shaped cross section. *Machaeracanthus* has only asymmetrical, presumably paired, spines, in which the pulp cavity is always totally enclosed by the spine body. Perhaps *Machaeracanthus* fin spines are not homologous with those of other acanthodians, but developed from enlarged radials of the pectoral fins. All fins in the mesacanthid acanthodian *Triazengacanthus* (Gagnier, 1996: figs 8,14) have 'ceratotrichia' with a circular cross-section, and some of these elements are forked (P.-Y. Gagnier, pers. comm.), but they are only about 0.02mm wide (compared to their pectoral fin spines which are about 6mm long). Amongst the ischnacanthiforms, *Ischnacanthus gracilis* had 'ceratotrichia' (diameter ca. 0.01mm) in the proximal part of the fin web (Miles, 1970: fig. 8), articulating with basal radials. If machaeracanthids derived from an ischnacanthiform ancestor, perhaps *Machaeracanthus* spines developed by enlargement of the fin basals after loss of the pectoral fin spines. Although younger than *M. bohemicus*, *M. pectinatus* sp. nov. could represent an intermediate stage in phylogenetic development of *Machaeracanthus*. No dentinous *Machaeracanthus* fin spines have been recorded from Australia or any other region of East Gondwanaland, suggesting the *Machaeracanthus* lineage split before typical, large ?dentinous spines developed elsewhere. Development of spines from internal fin rays in the paired fins has occurred numerous times in different groups including extant fishes such as catfishes, lionfishes and bullheads, and perhaps also the enigmatic chondrichthyan *Menaspis armata* Ewald, 1848 from the Permian of Germany. Work on extant *Channallabes apus* (Adriaens et al., 2002) showed maximum variability in development of pectoral fins and spines, with individuals in one generation having these structures and some individuals in the next generation lacking them. In the light of such studies, the reinvention of a pectoral fin spine in *Machaeracanthus* is not unlikely.

Despite similarity between the Cravens Peak Beds asymmetrical fin rays and fin spines from *Machaeracanthus*, the possibility that they could be from one of the other types of fish in the samples must be considered. Unfortunately, the shape and histology of fin rays from other Mid-Palaeozoic fish have only rarely been described (e.g. Goodrich, 1904). Reconstructions in Stensiö (1959) show pectoral fins in arthrodire placoderms with distally-branching radials. A totally bony structure is the norm for osteichthyan dermal fin rays (as opposed to lepidotrichia, which are specialised scales). The Carboniferous sarcopterygian *Rhizodus* had bifurcating fin rays, but these have a circular cross-section (Andrews, 1985: fig. 4d-f). Some actinopterygians (e.g. *Pachyrhizodus* from the Cretaceous of Queensland) had fin rays with a cross-sectional shape and internal structure similar to the Cravens Peak Beds elements. Fin rays of the dipnoan *Scaumenacia curta* (Goodrich 1904: fig. 33A) and the osteolepiform *Eusthenopteron foordi* (Goodrich, 1904: fig. 45B) have a histological structure which also is comparable with that of the Cravens Peak Beds elements, but the cross-sectional shape of the rays in these sarcopterygian taxa is sub-circular. In conclusion, an assignation of the fin rays to *Machaeracanthus pectinatus* is only tentative.

## CONCLUSIONS

Differences in the vertebrate taxa from the SP799 shot-point locality and the other localities indicate different ages. SP799 vertebrate fauna includes scales of thelodont *Turinia* sp., rare scales of *Nostolepis* sp. cf. *N. striata*, and *Radioporacanthodes?* sp. (Burrow, 2002). All three are also found in the ?late Lochkovian/ early Pragian Martins Well Limestone. The acanthodians *Teneracanthus toombaensis* gen. et sp. nov. and *Machaeracanthus pectinatus* sp. nov. are added to the extensive late Early to early Middle Devonian vertebrate faunal list from the Cravens Peak Beds (Young & Goujet, 2003). As all other scale-based species of *Machaeracanthus* are from the Lochkovian or Pragian, *M. pectinatus* sp. nov. is the youngest *Machaeracanthus* species for which scales have been identified. The oldest mesacanthid taxon *Mesacanthus mitchelli* is Early Devonian (Lochkovian), and the youngest mesacanthid taxa are the Late Devonian (Frasnian) *Lodeacanthus gaujicus* and *Triazeugacanthus milesi*. *Teneracanthus toombaensis* gen. et sp. nov. appears intermediate between these taxa, being most closely related to *Lodeacanthus*.

## ACKNOWLEDGEMENTS

CJB acknowledges the support of an ARC Postdoctoral Fellowship 2002-4, an APSF grant for equipment, the Zoology & Entomology Department and Centre for Microscopy and Microanalysis, University of Queensland, for provision of facilities, and in particular, Boris Ekrt and Stan Stamberg (Czech Republic) for locating and assisting with the study of specimens in the National Museum collection, Prague. GCY thanks the Department of Earth and Marine Sciences, Australian National University, for provision of facilities. We thank John Long (Museum of Victoria) for reviewing the manuscript.

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## ADDITIONAL SPECIMENS OF *BOHRA* (MARSUPIALIA: MACROPODIDAE) FROM THE PLIOCENE OF QUEENSLAND.

*Memoirs of the Queensland Museum 51(1): 26.*

*Bohra paulae* Flannery & Szalay, 1982 was erected for a macropodine taxon considered to be a giant tree kangaroo. Holotype AMF62099, a large calcaneum, has relative dimensions found only in dendrolagin taxa (Flannery & Szalay, 1 982) including the ratio of relative height (h) to width (w) of the calcaneal-cuboid articulation (cca) (Flannery & Szalay, 1982; 84, Table 1) and relative calcaneal length (cl) to calcaneal tuberosity length (ctl) (Flannery & Szalay, 1982; 87, Table 3). Dentition in the type species is unknown.

Dawson (2004) described *Bohra wilkinsonorum* from the Pliocene, Chinchilla Sands, south east Queensland, based on a juvenile right maxillary fragment (QMF43277). Dentition shows features plesiomorphic within Dendrolagini and given its much larger size than *Dendrolagus*, it was considered to be *Bohra*. Recent discovery of *Bohra* from Chinchilla is intriguing because of a long history of collecting and abundance of macropodid material recovered (Rich, 1991; Hocknull, pers. obs.). Hocknull (2005) identified *Bohra* from the Early Pliocene of Mt Etna, central eastern Queensland, basing identification on a calcaneum which has relative dimensions similar to *B. paulae* but smaller in size. Audit of Chinchilla collections at the Queensland Museum was made to determine the additional material referable to members of the Dendrolagini. A calcaneum confirms the presence of *Bohra* in the Chinchilla Local Fauna. Abbreviations used in the text: AMF (Australian Museum Fossil); QMF (Queensland Museum Fossil).

**Description.** (Fig. 1) QMF49453; right calcaneum bearing a stout calcaneal tuberosity, broad astragular-fibular articulation, shallow and narrow calcanela-cuboidal articulation, and broad rugose, plantar surface. Posterior medial and lateral margins of the tuberosity abraded, ventral portion of the calcaneal-cuboid articulation missing to the plantar surface. Dimensions cl: 43.64mm; ccaw: 18.72mm; ccah: 11.31mm (est.); calcaneal-astragular articulation length: 21.01mm.

**Remarks.** QMF49453 is similar in morphology to *Bohra paulae* except it is approximately 20% smaller. QMF49453 differs from *Bohra paulae* by a relatively narrower cca (e.g. ccah/ccaw; QMF49453, 0.604 versus *Bohra paulae*, 0.686 and species of *Dendrolagus* 0.601-0.702); and a relatively longer ct (e.g. ctl/cl; QMF49453, 0.481 versus *Bohra paulae*, 0.442 and species of *Dendrolagus* 0,46-0.512 (data from Flannery & Szalay, 1982)). QMF49453 is most similar to *Bohra* sp. (QMF51762) from Mt Etna but differs by a relatively narrower fibular-calcaneal articulation.

A low representation of *Bohra* within the Chinchilla Local Fauna (1 calcaneum, 1 maxilla) is apparent when compared to other macropodids (68 or more calcanea; 120 or more maxillae) from Chinchilla. This may explain why *Bohra* has not been previously recorded from Chinchilla. A greater representation of dendrolagin calcanea in the Early Pliocene Mt Etna Local Fauna is due to the abundance of *Dendrolagus* (Hocknull, 2005). Yet *Bohra* remains rare in both Queensland sites. Representation of *Bohra* from the type locality is unknown due to the uncertainty surrounding its stratigraphic context. Flannery & Szalay (1982) considered *Bohra paulae* not to be a rainforest taxon, however, it probably inhabited wooded areas due to its size and hypothesised arborealism. Dawson (2004) considered *Bohra* to be plesiomorphic to *Dendrolagus*, possessing a broad ecological tolerance and inhabiting a mosaic of vegetation including forest and open woodlands. Hocknull (2005) identified *Bohra* sp. as sympatric with *Dendrolagus* and other specialist taxa inhabiting rainforest. Considered together, *Bohra* represents a rare taxon with possible specialisations for arborealism, whilst possessing a broad habitat tolerance throughout the Plio-Pleistocene.

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*Scott A. Hocknull, Queensland Museum, 122 Gerler Rd. Hendra, Queensland 4011; 1 January 2005*

FIG 1. A, *Bohra paulae*, right calcaneum (cast of AMF62099). B, *Bohra* sp.; QMF51762, right calcaneum. C, *Bohra* sp.; QMF49453, right calcaneum. Scale bar = 10mm.

# AN UNUSUAL NEW ELASMOSAURID PLESIOSAUR (SAUROPTERYGIA) FROM THE UPPER HAUMURIAN (MAASTRICHTIAN) OF THE SOUTH ISLAND, NEW ZEALAND

NORTON HILLER AND AL A. MANNERING

Hiller, N. & Mannering, A.A. 2005 05 31: A new elasmosaurid plesiosaur (Sauropterygia) from the Upper Haumurian (Maastrichtian) of the South Island, New Zealand. *Memoirs of the Queensland Museum* **51**(1): 27-37. Brisbane. ISSN 0079-8835.

An unusual new elasmosaur is described from postcranial elements preserved in a large concretionary mass from the Conway Formation (Haumurian; Maastrichtian) of the Waipara River area, North Canterbury, South Island, New Zealand. The specimen, representing the youngest plesiosaur described so far from New Zealand, is distinguished by characters of the pectoral girdle, particularly the elongate, rod-like ventral process and the symphyseal fossa on the fused coracoids. ❒ *Elasmosaur, Late Cretaceous, New Zealand.*

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A large concretion containing reptile bones was discovered on the left bank of the Waipara River, North Canterbury (Fig. 1B) in late 1982. The discovery was reported to Canterbury Museum and a team recovered the remains the following year. Preparation of the specimen over a period of several years revealed the almost completely disarticulated partial skeleton of an elamosaurid plesiosaur.

The area in which the specimen was found has produced fossil marine reptiles for many years. Indeed, New Zealand's first vertebrate fossils were reported from that area in 1859 (Hood, 1870). This started a golden age of fossil reptile discoveries in New Zealand, and extensive collecting by Hood, Haast, Hector and McKay led, by the mid-1870s, to the recognition of nine species of plesiosaur and two species of mosasaur (Hector, 1874). The bulk of these fossil remains came from exposures along the Waipara River and at Haumuri Bluff (Fig. 1B).

There followed a period of almost 100 years during which very few new discoveries were recorded. Then came the seminal work of Welles and Gregg (1971) in which they reviewed all the reptile material known at the time, provided a history of the early discoveries and described several new finds. They rationalised the plesiosaur material into a single acceptable taxon, the elasmosaur *Mauisaurus haasti* Hector, 1874, and placed many specimens as indeterminate except to family level at best.

More recent finds of marine reptiles, including plesiosaurs, have been made at Hawke's Bay (Fig. 1A: HB) in the North Island (Wiffen, 1980; 1990; Wiffen & Moisley, 1986) and at Shag Point (Fig. 1A: SP) near Dunedin (Cruickshank & Fordyce, 1996; 2002; Fordyce, 1983). Wiffen & Moisley (1986) provided the first description of skull material from a New Zealand plesiosaur and placed it in a new elasmosaurid genus, *Tuarangisaurus*. They attributed some post-cranial elements from the same locality to *Mauisaurus*. The large, substantially complete skeleton described from Shag Point by Cruickshank & Fordyce (2002) belongs to a new genus, *Kaiwhekia*, which has been placed in the Cryptoclididae by the authors. However, following recent cladistic analyses of plesiosaurs by O'Keefe (2001) and Gasparini et al. (2003b), some authors may dispute such a placement.

As rock enclosing the new specimen was gradually removed, it became clear that the neck and skull were missing but many diagnostic elements were present. It was also clear this specimen was unlike any previously recorded. In this paper we describe this new addition to the southwest Pacific Late Cretaceous marine reptile fauna.

## MATERIAL

The specimen here described was preserved in a very large concretionary mass (estimated weight about 10 tonnes) that had broken into two very large blocks and a third much smaller one. The blocks were discovered where a portion of the cliffs overlooking the Middle Waipara River had slumped following a flood event.

After recovery, blocks were transported to Christchurch where they were further split, using drills and wedges, into smaller blocks that could be manhandled into the Canterbury Museum

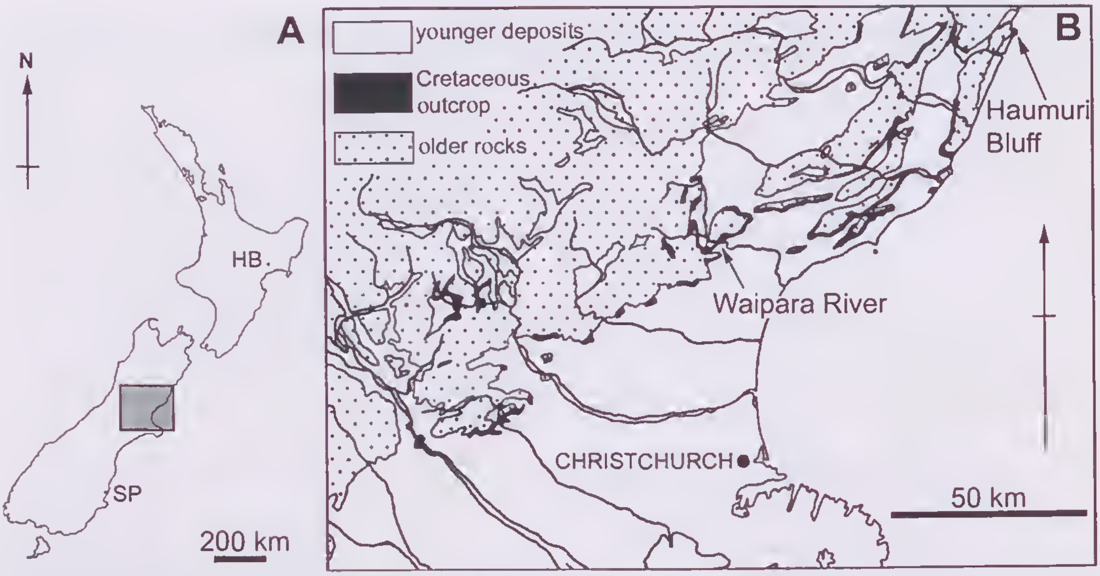

FIG. 1. Locality maps. A, map of New Zealand showing the locations of the North Canterbury region (shaded square), Shag Point (SP) and Hawke's Bay (HB). B, simplified geological sketch map of North Canterbury showing the Cretaceous outcrop and the locations of the Waipara River and Haumuri Bluff.

workshop. Although the matrix is calcareous, mechanical preparation was preferred over acid treatment as the separation between bone and matrix was good. Most bones were not removed completely from the matrix to preserve their context for a separate taphonomic study (Fig. 2).

CM Zfr 145 comprises an incomplete individual represented by the vertebral column from the anterior dorsal region to the tail, elements of the right fore limb and both hind limbs, major bones from the pectoral and pelvic girdles and an assortment of ribs and gastralia. Scattered among the bones are more than 340 gastroliths, mostly of resistant siliceous lithologies, in the size range 11-58 mm.

The preserved bones are scattered over an area of about 5 $m^2$; disarticulation is almost complete with only a few dorsal vertebrae retaining any original association. Disarticulation may have resulted from explosive degassing of a semi-buoyant carcass although some redistribution of bones probably occurred through the action of scavengers. Some vertical movement of small bones has taken place as a result of bioturbation.

Bones are generally well preserved with very little evidence of fragmentation or abrasion, suggesting a minimum of transport by current activity. However, several articulation surfaces, such as the capitulum of both the femur and humerus, and a number of vertebral centra show marked degradation. Whether this is the result of chemical attack or bioerosion is difficult to determine, but it suggests that the bones were partially exposed for some time on the sea floor prior to burial.

## AGE, STRATIGRAPHY AND GEOLOGICAL SETTING

The specimen was recovered from the Conway Formation, which crops out across a wide area of North Canterbury and southern Marlborough (Fig. 1B) and has been the main source of marine reptile fossils in the South Island. Throughout most of its outcrop area, the Conway Formation is a soft, easily eroded dark grey massive jarositic siltstone or silty sandstone in which pervasive bioturbation has all but obliterated primary sedimentary structures. Large subspherical calcareous concretions are a distinctive feature of the unit, particularly in the lower part. Warren & Speden (1978) estimated that about 25% of these concretions contain reptile bones at Haumuri Bluff, about 95 km northeast of the Waipara River (Fig. 1B).

The Conway Formation contains few macrofossils other than the reptile remains. In some places, where the siltstone has not been completely decalcified, a few species of molluscs

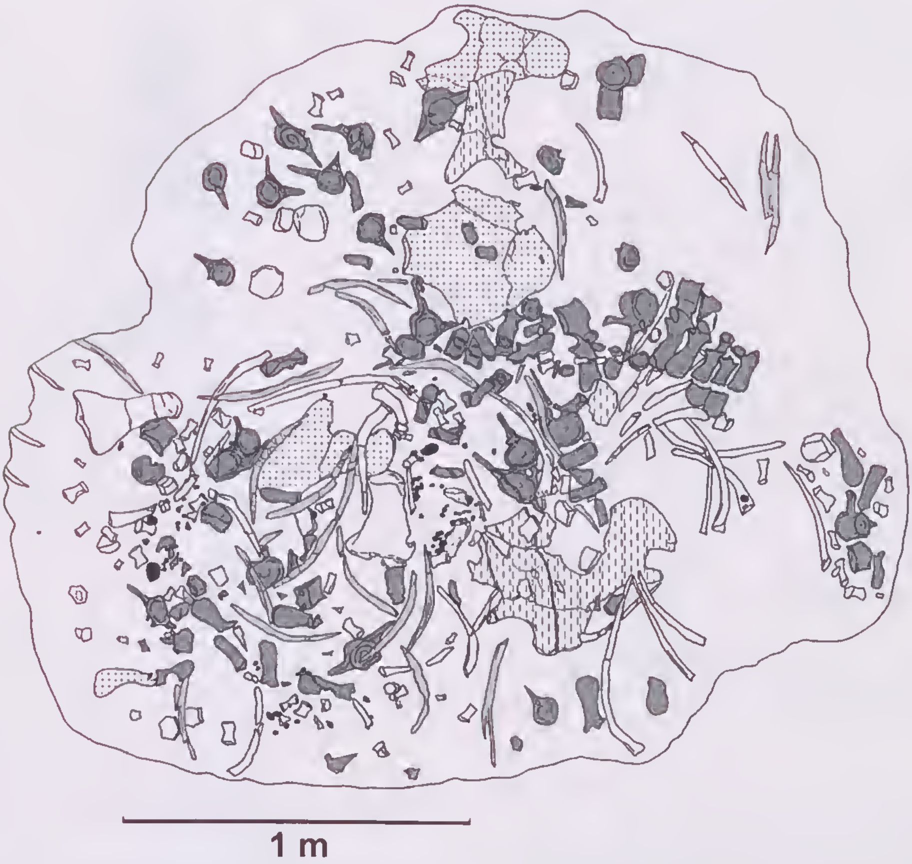

FIG. 2. Map of bone distribution of CM Zfr 145 in the concretion. Dark grey: vertebrae and neural spines; pale grey: gastralia; stipple: pelvic girdle elements; dashed: pectoral girdle elements; white: limb bones and ribs.

have been found, but generally calcareous shelled invertebrates, including foraminifera, are very rare and poorly preserved. Non-calcareous remains, such as phosphatic-shelled brachiopods, sharks' teeth, teleost bones and scales, and plant material, are present but uncommon. However, rich dinoflagellate assemblages are present.

Sedimentary and geochemical characteristics of the Conway Formation suggested to Warren & Speden (1978) that it was deposited in an area of sea floor free from strong current or wave activity in which oxygen-poor conditions prevailed. They favoured a barred submarine depression or series of depressions, as the depositional setting and drew analogy with the present day Santa Barbara Basin off California.

The Conway Formation is generally regarded as belonging within the Haumurian Stage of the local New Zealand time scale, although Browne & Field (1985) suggested that it might range up into the overlying Teurian Stage. The Haumurian Stage was once correlated with the Maastrichtian Stage on the European time scale (Wellman, 1959) but more recently has been shown to be the equivalent of the Upper Santonian to end-Maastrichtian portion of the international scale (Crampton et al., 2000). The revised correlation is based, in part, on the development of a refined biostratigraphy founded on dinoflagellates (Roncaglia & Schiøler, 1997; Roncagli et al., 1999; Schiøler & Wilson, 1998). Application of this biostratigraphical scheme to the Conway Formation shows it to range from lower Middle Campanian at Haumuri Bluff in the north to Upper Maastrichtian at Waipara River

(Roncaglia and Schiøler, 1997; Roncagli et al., 1999) (Fig. 3). Recently, Wilson et al. (in press) have used dinoflagellates to date individual reptile specimens within this scheme.

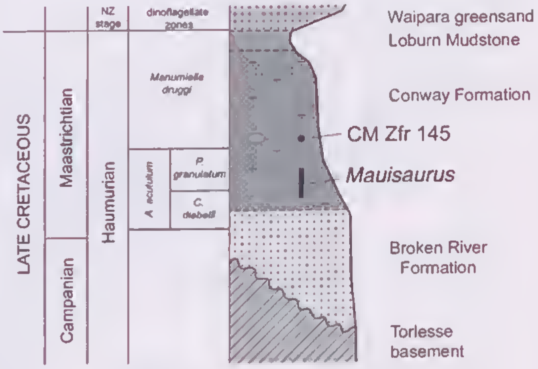

FIG. 3. Stratigraphic section of the Cretaceous sequence exposed in the Waipara River showing levels from which the elasmosaurs *Mauisaurus* and CM Zfr 145 have been recovered. (follows Roncaglia et al., 1999 and Wilson et al., in press).

## SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Linnaeus, 1758
Order SAUROPTERYGIA Owen, 1860
Suborder PLESIOSAURIA de Blainville, 1835
Superfamily PLESIOSAUROIDEA (Grey, 1825) *sensu* Welles, 1943
Family ELASMOSAURIDAE Cope, 1869

### **Elasmosaurid** indet.

MATERIAL. CM Zfr 145 from the Conway Formation on the left bank of Middle Waipara River about 1 km upstream from the old Laidmore Bridge (New Zealand Fossil Record File No. M34/f462).Upper Haumurian (Late Maastrichtian) *Manumiella druggi* zone (Wilson et al., in press) (Fig. 3).

DESCRIPTION. The skeleton is interpreted as belonging to a 'young adult'. The neural arches of some dorsal and caudal vertebrae appear firmly fused to their centra but among the bones there are dissociated neural arches that clearly are not fused to centra. This would place the specimen between the 'juvenile' and 'adult' categories defined by Brown (1981). The specimen lacks the skull, cervical vertebrae and the major limb bones from the left side (Fig. 4).

An estimate of body length indicates the animal to have been a minimum of about six metres long in life. This is based on an estimate of 2 m for the trunk, 1 m for the tail and an assumption that the neck makes up about one-half of the total body length.

*Axial skeleton*. Seventeen dorsal vertebrae, three sacral vertebrae, 30 caudal vertebrae and 16 dissociated neural spines are present. Dorsal vertebrae typical of an elasmosaur, with subcircular articular faces on reel-like centra (Fig. 5A-B). Where measurements are possible, dorsal vertebrae show vertebral length indices (Brown, 1981) in the 0.75 – 0.77 range. Both anterior and posterior zygapophyses are separated pairs.

Sacral vertebrae have transversely ovoid articular faces (Fig. 5C) and in each case the sacral ribs, which taper distally, are firmly fused to the centra. Two nutritive foramina are present on the ventral surface of each.

Anterior caudal vertebrae are similar in shape to the sacrals, although a little shorter, but further back in the series they become more hexagonal in cross-section (Fig. 5D), with the smallest examples being almost cylindrical. Anterior centra have two ventral foramina but this is reduced to one further back in the series. Chevron facets are not seen on the anterior caudal vertebrae but are well developed on the more hexagonal centra, at the posterior end of low rounded ventral ridges (Fig. 5E). Caudal ribs are

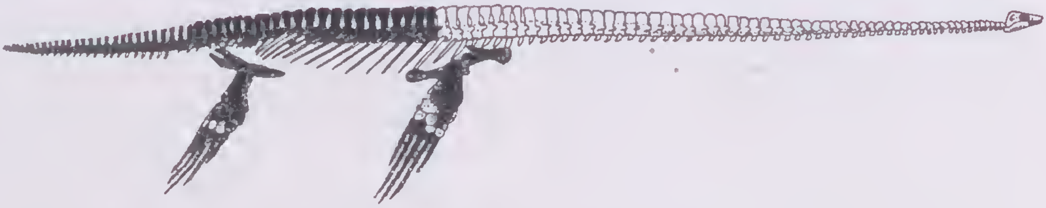

FIG. 4. Diagram showing (in black) the bones represented in CM Zfr 145.

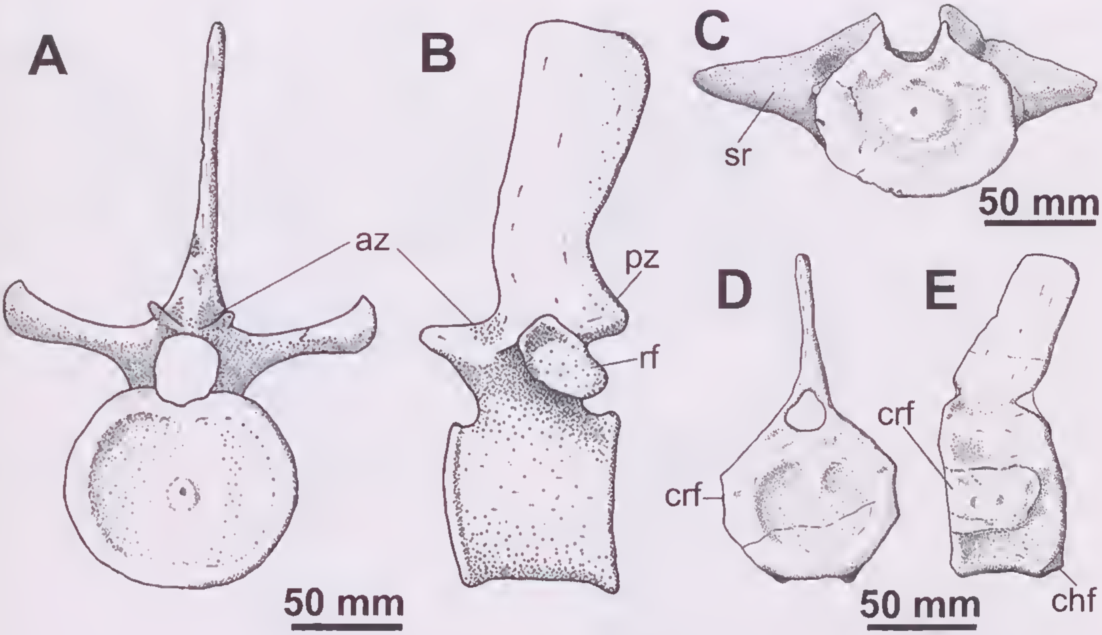

FIG. 5. Dorsal, sacral and caudal vertebrae of CM Zfr 145. A, restored mid-dorsal (based on three actual examples) in anterior view. B, restored mid-dorsal in left lateral view. C, sacral in anterior view showing firmly attached sacral ribs. D, caudal in anterior view. E, caudal in left lateral view. Abbreviations: az, anterior zygapophyses; chf, chevron facet; crf, caudal rib facet; pz, posterior zygapophyses; rf, rib facet; sr, sacral rib.

short (maximum length about 120 mm), about 25-30% as wide as long, flat with parallel sides and rounded distal terminations.

*Girdles*. In the pectoral girdle, the right scapula, complete right coracoid and partial left coracoid are preserved. As in other New Zealand plesiosaurs, no clavicles or interclavicles have been recognised. Possibly these were cartilaginous and not preserved.

Scapula characteristically a triradiate bone with the angle between the ventral and dorsal rami, measured at the ridge on the ventral surface where they meet, being about 140° (Fig. 6D). Dorsal ramus is a relatively short, tapering blade-like structure with a rounded distal margin (Fig. 6A-C). Ventral ramus has a subrectangular outline and is gently convex upwards (Fig. 6A-C). Although it may have suffered some damage, very little seems to be missing from the bone. The square anterior margin suggests that a clavicle may have been present in life.

In outline, coracoids show the typical "hour-glass" shape seen in elasmosaurs (Fig. 7). They meet and are firmly fused along the anterior portion of the symphysis, which extends forwards beyond the level of the glenoids as an elongate anterior process (Fig. 7A). This process projects steeply downwards anteroventrally (Fig. 8 C-C'). It does not seem likely that a full midline bar was developed in this specimen. Fusion of the coracoids is complete with no suture visible between the right and left portions. On the ventral surface, about midway along the anterior symphysis, a prominent cylindrical process, buttressed by ridges, extends ventrally (Fig. 7B-C). Posteriorly, the coracoids are separated by a large heart-shaped intracoracoid foramen. The dorsal (visceral) surface of each coracoid is flat, with no sign of any transverse thickening of the bone between the glenoids. An unusual feature of the pectoral girdle is that the dorsal surface of the conjoined coracoids is cleft by an elongate boat-shaped trough (Fig. 8). This trough, here named the symphyseal fossa, extends from just behind the anterior process to a point posterior of the ventral process. It is unclear just how far back this feature is present, but it is believed to be connected to an elongate oval foramen that opens on the ventral surface of the coracoids posterior of the ventral process (Fig. 7A).

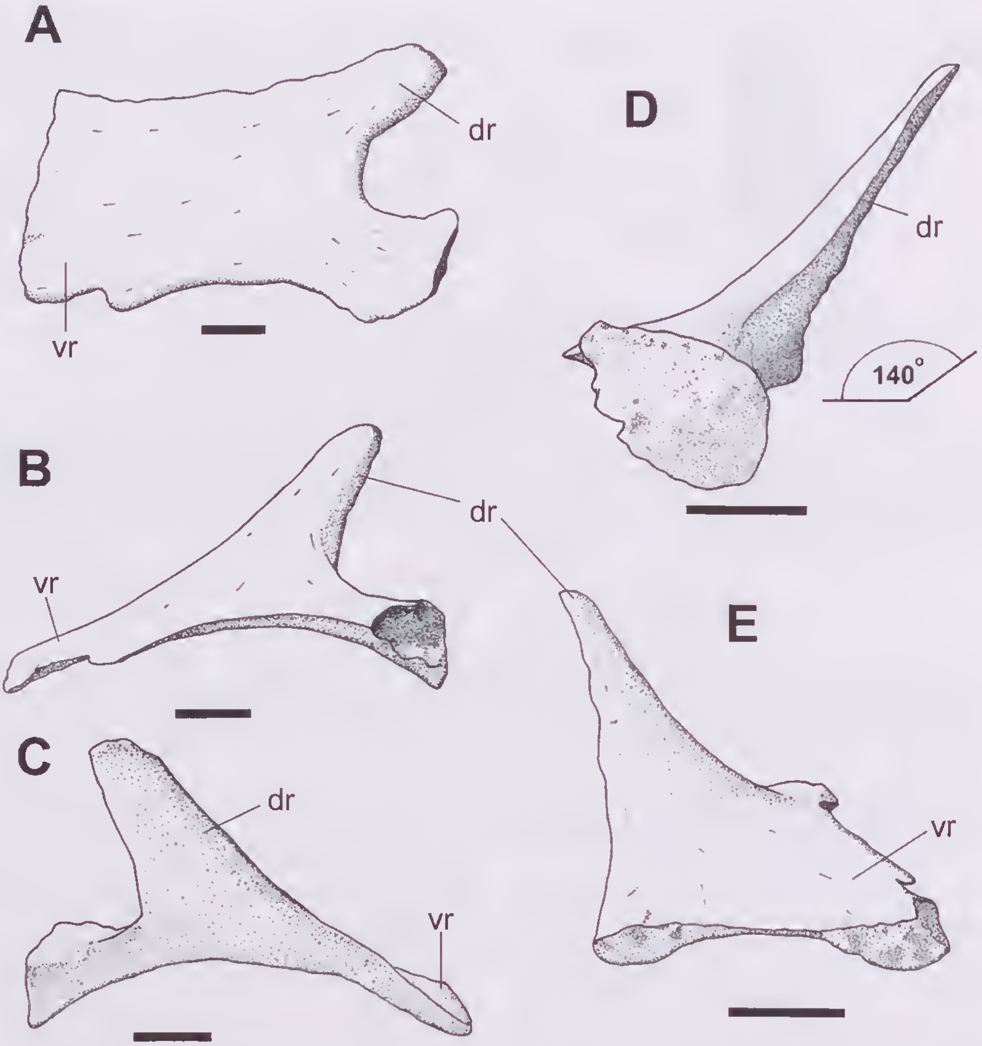

FIG. 6. Right scapula of CM Zfr 145. A, dorsal view. B, internal lateral view. C, external lateral view. D, posterior view. E, anterior view. Note slightly different scales; scale bars = 50 mm. Abbreviations: dr. dorsal ramus; vr, ventral ramus.

The pelvic girdle is represented by both ilia, both ischia and the left pubis (Fig. 9). Ilia (Fig. 9A) are robust curved rods with expanded proximal (ventral) ends bearing facets for junctions with the ischia and acetabula. Their distal (dorsal) ends are parallel sided with 'square' terminations.

The pubis (Fig. 9B) is a large subquadrate plate-like bone, thickest at the acetabulum and very thin in its central part. The lateral and posterior margins are concave; the anterior and medial margins are gently convex.

Ischia (Fig. 9C) are elongate "hatchet-shaped" plates in which the maximum width, measured at right angles to the median line, is about three-quarters of the maximum length. Their ventral surfaces are almost planar while the dorsal surfaces have a broad convex ridge extending from the symphysis towards the lateral ramus. Along the symphysis, each ischium bears a short anterior projection with a 'square'

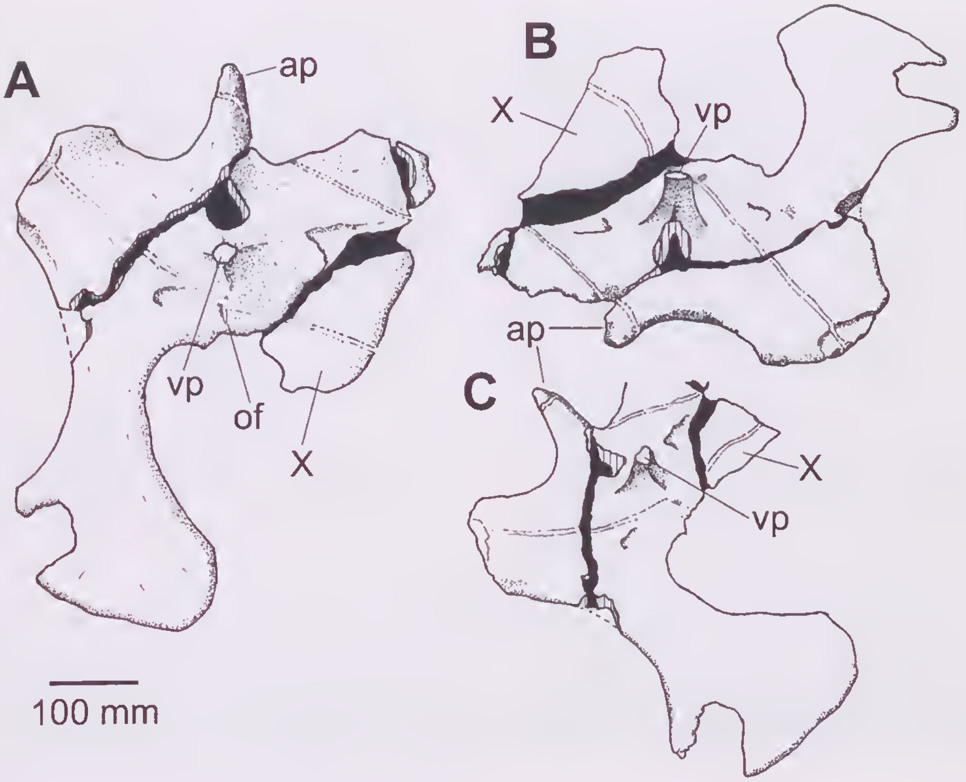

FIG. 7. Coracoids of CM Zfr 145. A, ventral view. B, anteroventral view. C, posteroventral view showing the preserved outlines and the rod-like ventral process. Fragment X does not lie in the same plane as the rest of the bone. Abbreviations: ap, anterior process; of, elongate oval foramen; vp, ventral process.

termination. These projections do not extend as far forward as the facet where the ischium meets the pubis. In life, the ischia and pubes sloped upward and outward from the symphysis to form an upwardly concave visceral cup (Fig. 10E). Restored outlines of both pectoral and pelvic girdles are presented in Fig. 10.

*Limbs.* Limb elements are not in association, making identification of those distal to the epipodials difficult. The right humerus, right femur, four epipodials from three limbs, 15 metapodials and 77 phalanges are scattered among the other bones. Humerus (Fig. 11) has a width/length ratio of about 82% and the femur (Fig. 12) about 73% but each has a damaged capitulum and so maximum length is difficult to measure accurately. The femur is slightly longer and more slender than the humerus, which has a more markedly asymmetrical outline.

Among the epipodials are one radius, two tibiae and a fibula. In the fore paddle, we can only identify one radiale of the proximal carpal bones, two distal carpals that we have designated dcIV, and a metacarpal identified as mc1. In the hind paddles, the proximal tarsals are represented by both tibiales, both centrales and a fibulare. Four distal tarsals have been identified, two of which are designated dtII+III, one as dtI and one as dtIV. Two metatarsals are identified as mt1. A partial reconstruction of the right rear paddle based on the elements recognised is given in Fig. 12.

REMARKS. It was deemed inadvisable to establish a new taxon without skull material but we believe that the features of the postcranial skeleton serve to separate CM Zfr 145 from all previously described elasmosaurs. In particular, characters of the pectoral girdle can be used to distinguish the new form. In addition, the ischia seem to be unusually long compared with those of other Late Cretaceous elasmosaurs.

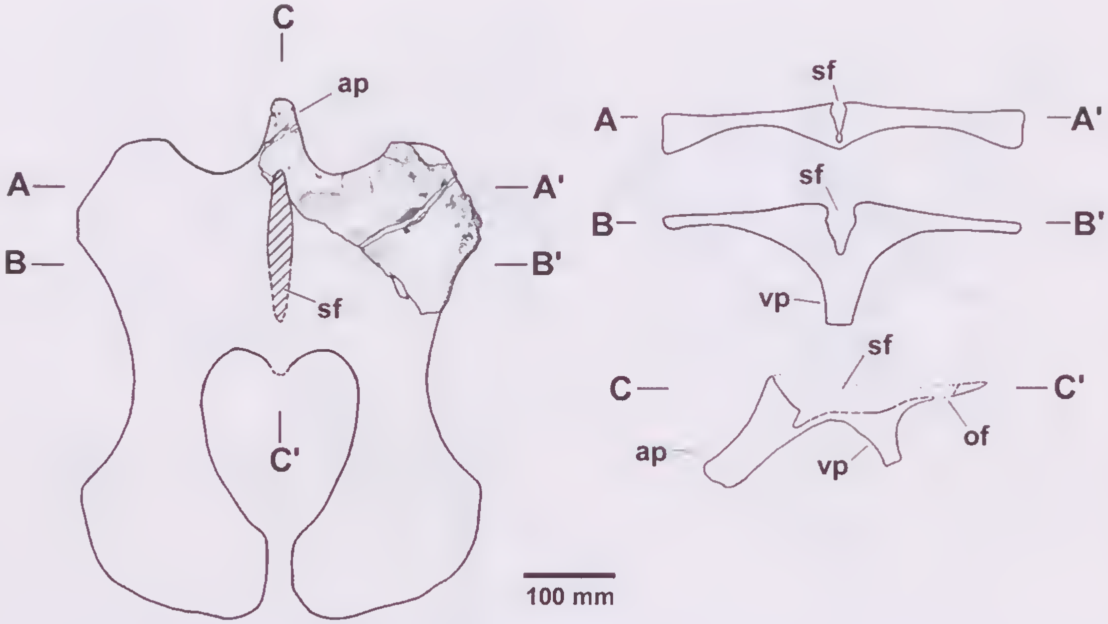

FIG. 8. Restoration of the dorsal surface of the coracoids showing the position and supposed extent of the symphyseal fossa, and transverse and longitudinal cross-sections illustrating the shape of the feature. Abbreviations: ap, anterior process; of, elongate oval foramen; sf, symphyseal fossa; vp, ventral process.

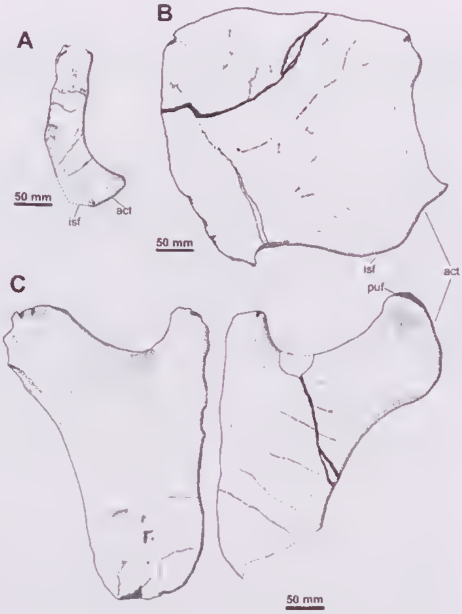

FIG. 9. Pelvic girdle elements of CM Zfr 145. A, right ilium in lateral view. B, right pubis in ventral view. C, ischia in ventral view. Abbreviations: act, acetabulum; isf, ischial facet of ilium and pubis; puf, pubic facet of ischium.

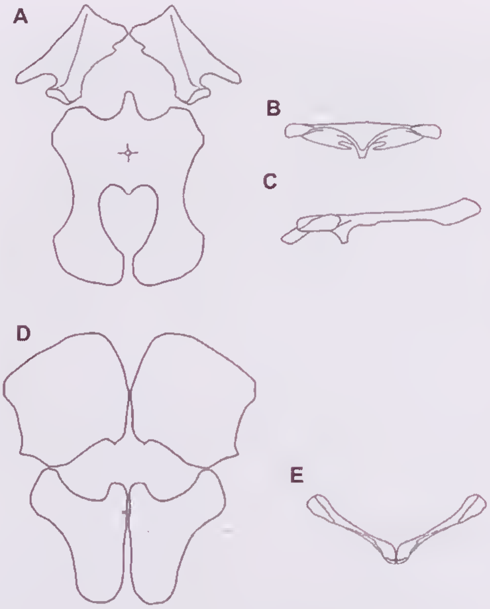

FIG. 10. Reconstructed outline of the pectoral and pelvic girdle elements. A, ventral view of scapulae and coracoids. B, anterior view of coracoids. C, left lateral view of coracoids. D, ventral view of pubes and ischia. E, anterior view of ischia.

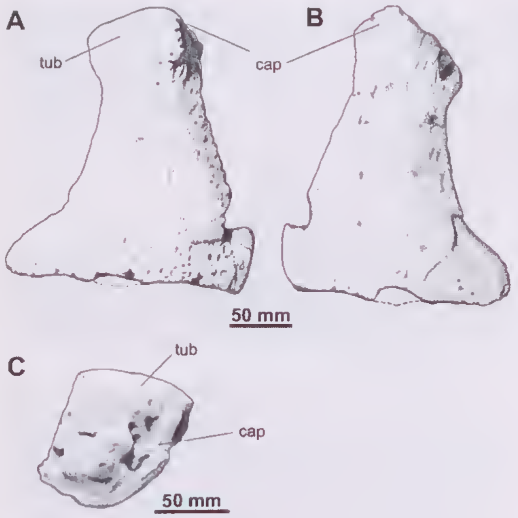

FIG. 11. Right humerus of CM Zfr 145. A, dorsal view. B, ventral view. C, proximal end view. Note damage to capitulum. Abbreviations: cap, capitulum; tub, tuberosity.

Of the two previously described New Zealand elasmosaurs, both of which are slightly older than CM Zfr 145, only *Mauisaurus haasti* Hector, 1874 can be directly compared with the new taxon. The other, *Tuarangisaurus keyesi* Wiffen & Moisley, 1986, is known only from its skull and several anterior cervical vertebrae. A new description of *M. haasti*, based on a more complete specimen than previously available, has recently been prepared by Hiller et al. (in press). This shows that the scapulae and coracoids are quite different from the same bones in CM Zfr 145. In *Mauisaurus*, the angle between the dorsal and ventral rami of the scapula is 130°, the dorsal ramus has parallel sides and has a square termination, and the ventral plate has a convex anterior margin. In CM Zfr 145 the angle between dorsal and ventral rami of the scapula is 140°, the dorsal ramus tapers distally and has a rounded termination. The ventral plate has a straight anterior margin.

The coracoids of CM Zfr 145 are particularly unusual. They are firmly fused anterior of the intracoracoid foramen, unlike the situation in *Mauisaurus* and many other elasmosaurs where the coracoids remain separate, even in very mature adults. They are flat and plate-like and show no signs of the transverse thickening observed on the dorsal surface of the coracoids in *Mauisaurus*. On the ventral surface, they bear an elongate rod-like projection quite unlike the rounded conical ventral process of *Mauisaurus* and some other elasmosaurs. Indeed, this feature is unknown in any elasmosaur described so far, although we have been made aware of an undescribed specimen in Canada that shows a similar feature (E. Nicholls, pers. com.). The Canadian specimen differs from CM Zfr 145 in that although its coracoids may be fused they have a distinct suture between the two halves (P. Druckenmiller, pers. com.). Also, the posterior ends of the coracoids of the Canadian specimen differ markedly in shape from those of CM Zfr 145. Another unusual feature of the coracoids in CM Zfr 145, not reported from any other elasmosaur, is the symphyseal fossa on the dorsal surface. Conceivably, this might be interpreted as an area of incomplete fusion, still occupied by cartilage, along the inter-coracoid contact. However, given the intimate fusion of the coracoids, which must have occurred at a very early ontogenetic stage, it seems more likely that the symphyseal fossa is a real character. This interpretation is supported by the 'clean' edges of the feature (Fig. 13), although there has been some post mortem modification of the walls of

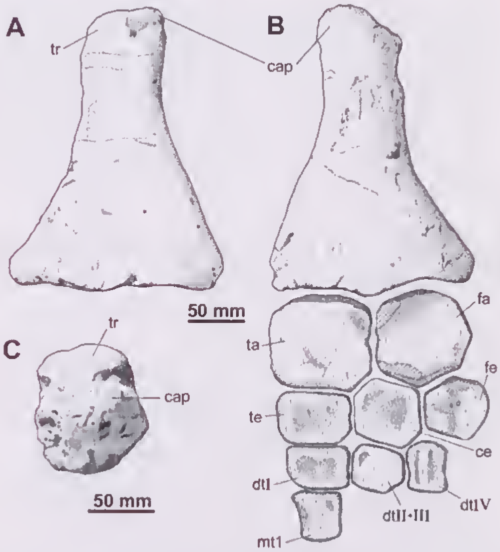

FIG. 12. Right hind limb of CM Zfr 145. A, dorsal view of femur. B, ventral view of femur and paddle elements. C, proximal end view. Note damage to capitulum. Abbreviations: cap, capitulum; ce, centrale; dt, distal tarsal; fa, fibula; fe, fibulare; mt, metatarsal; ta, tibia; te, tibiale; tr, trochanter.

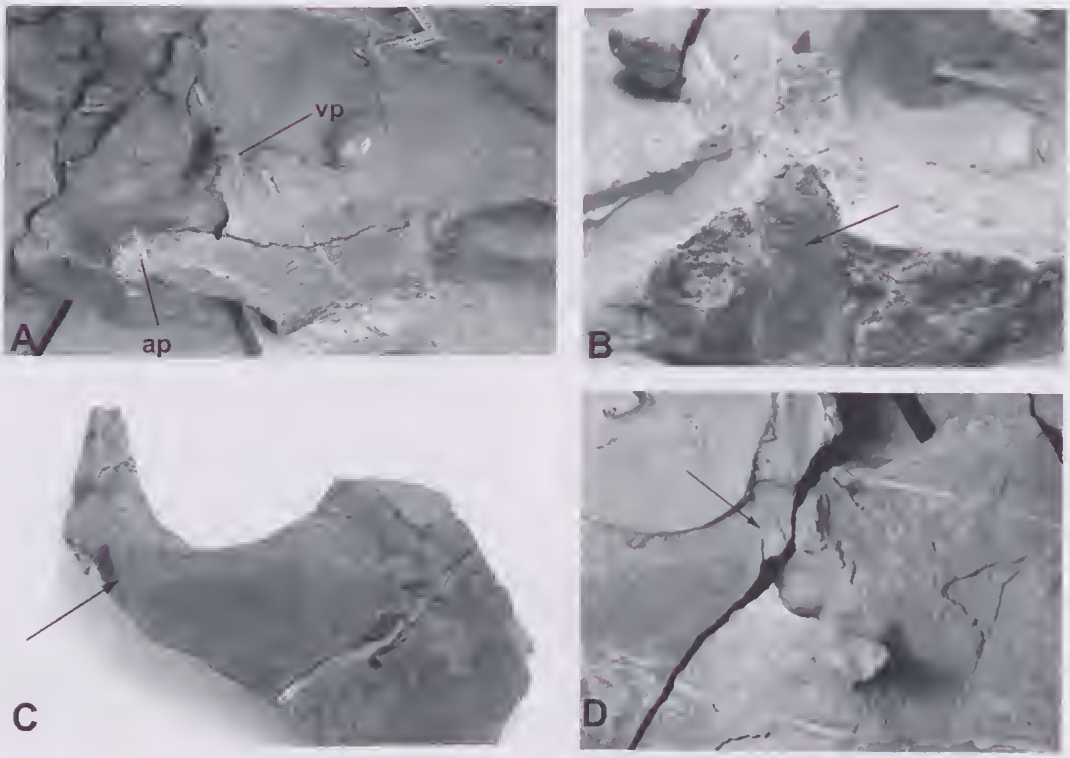

FIG. 13. Photographs of fused coracoids, CM Zfr 145. A, oblique view ; ventral surface of coracoids showing the elongate anterior process (ap) and the pillar-like ventral process (vp). Hole immediately anterior of ventral process is a drill hole used in splitting the blocks. Right anterior portion of the coracoid detachable and seen inverted in C. B, close-up of ventral process with view of internal structure afforded by drill hole. Note sediment fill of symphyseal fossa (arrowed) and lack of suture along midline. C, dorsal view of detached portion of coracoid showing anterior margin of symphyseal fossa (arrowed). Note lack of suture along midline. D. close-up of area from which right anterior portion of coracoid has been removed and showing imprint of anterior end of symphyseal fossa (arrowed).

the fossa as has occurred in other bones while they lay exposed on the sea floor.

Comparisons with other Late Cretaceous austral elasmosaurids are made difficult by the incompleteness of the specimens. Chatterjee & Small (1989) described a number of indeterminate elasmosaurids, represented by postcranial remains, from Seymour Island, Antarctic Peninsula. Three of their specimens preserve parts of the pectoral girdle. They show that the coracoids were not fused and on the ventral surface a transverse ridge extends from the glenoid to the median symphysis, a feature not seen in CM Zfr 145.

Gasparini et al. (2003a) described several specimens from northern Patagonia, drawing similarities between them and other New Zealand taxa. One of their specimens, *Tuarangisaurus? cabazai*, is evidently a juvenile but the characters of its coracoid immediately distinguish it from CM Zfr 145. Their other specimens, assigned to cf. *Mauisaurus* sp., preserve very few girdle elements but the ilia appear very different to those of CM Zfr 145. They are gently curved and lack the distinct knee seen in those of CMZfr 145.

We conclude that, in spite of its incompleteness, CM Zfr 145 represents a distinctive new elasmosaur and adds to the Late Cretaceous radiation of marine reptiles in the southwest Pacific.

## ACKNOWLEDGEMENTS

Financial assistance from the Robin S Allan Memorial Trust at Canterbury Museum is gratefully acknowledged. We are grateful to Dr Arthur Cruickshank for commenting on an early draft of the manuscript and to Dr Margaret Bradshaw, Dr Karen Watson and Craig Jones for their work during the earliest stages of this project. Our thanks also go to Dr Ben Kear whose comments helped improve the quality of the manuscript.

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LATE PLEISTOCENE-HOLOCENE OCCURRENCE OF *CHAEROPUS* (PERAMELIDAE) AND *MACROTIS* (THYLACOMYIDAE) FROM QUEENSLAND. *Memoirs of the Queensland Museum 51(1): 38.* Recent collections of vertebrate remains from cave systems in central-eastern and north-eastern Queensland have yielded diverse small-sized mammalian taxa. Within these faunas, four perameloid genera are present and include species of *Isoodon, Perameles, Chaeropus* and *Macrotis*. The presence of *Perameles* and *Isoodon* in these deposits is not surprising because they occur at the localities in the present day. However, Hocknull (2005) and Price (2004) report on the most easterly extent of *Perameles bougainville*, a typically arid distributed taxon. In addition, the presence of *Macrotis* and *Chaeropus* significantly increases the easterly distributions of these distinctly arid-adapted taxa. Muirhead & Godthelp (1995) reported on fossil *Chaeropus ecaudatus* from Chillagoe, northeastern Queensland, considering the age of the material to be late Pleistocene. Hocknull (2005) reported late Pleistocene *Chaeropus ecaudatus* and *Macrotis lagotis* from Mount Etna, central eastern Queensland. A new locality has yielded a specimen of *Macrotis* Thomas, 1887 and is presented herein. The locality (QML1287) is considered to be Late Pleistocene - Holocene in age based on the subfossil preservation of the excavated specimens, distinctly modern associated fauna, and the lack of associated megafauna.

### Family THYLACOMYIDAE (Bensley, 1903)

### **Macrotis** sp. (Fig 1)

Locality. QML1287, 'Dodgey's Cave', Dosey Limestone Kart, Broken River Province, 120km NW Charters Towers.

**Description.** QMF41971 is a left $M^2$ with little ware, broken root base. Max. length, 4.66mm; ant. width, 3.42mm; post. width, 2.67mm. Bulbous, sub-rectangular tooth in occlusal aspect, bearing three distinct anterior cusps (protocone, paracone and conical stylar cusp '?B'); two distinct posterior cusps (metacone and conical stylar cusp '?D'). Metaconule absent. Open, dumbbell-shaped roots. Anterior cingulum present.

**Remarks.** Identification of the tooth as *Macrotis* was based on the massively inflated, rectangular-ovoid occlusal crown, dumbell-shaped molar roots, absence of the metaconule and conical stylar cusps. Muirhead (1994) listed characteristics of the dentition for both species of *Macrotis, M. lagotis* and *M. leucura*. Unfortunately, comparative specimens of *M. leucura* were not available for study, therefore, verification of *M. leucura* requires additional specimens and a morphometric appraisal of both species' dentition.

Figure 2 illustrates the distributions (recent and fossil) of *M. lagotis, M. leucura* and *Chaeropus ecaudatus*. This is the second record of *Macrotis* in the fossil record of Queensland.

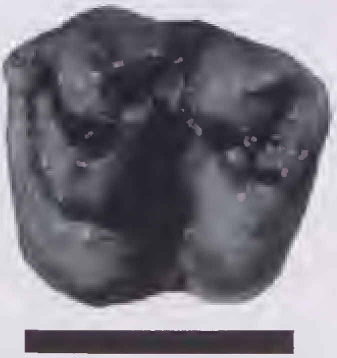

FIG 1. QMF41971, $LM^2$ in occlusal view. Scale bar = 4mm.

FIG 2. Distribution map of fossil and recent populations of A. *C. ecaudatus* (solid square), B. *M. leucura*, C. *M. lagotis* (solid circle) and *Macrotis* sp. (solid star). Recent bandicoot distributions from Strahan (1998).

The massive difference in the ranges of these three taxa when comparing late Pleistocene-Holocene to pre-European distributions indicates considerable contraction into the arid interior during the Holocene. A more detailed chronology of retraction is required to elucidate the factors influencing such a massive decline prior to European arrival, whether they be climatic, biotic and/or anthropogenic.

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# ECOLOGICAL SUCCESSION DURING THE LATE CAINOZOIC OF CENTRAL EASTERN QUEENSLAND: EXTINCTION OF A DIVERSE RAINFOREST COMMUNITY

SCOTT A. HOCKNULL

Hocknull, S.A. 2005 05 31: Ecological succession during the late Cainozoic of central eastern Queensland: extinction of a diverse rainforest community. *Memoirs of the Queensland Museum* **51**(1): 39-122. Brisbane. ISSN 0079-8835.

New late Cainozoic faunal assemblages are preliminarily identified and described from central eastern Queensland. Biocorrelation of the sites has determined that the oldest faunal assemblages are Early Pliocene in age, with younger faunas from the Plio-Pleistocene, late Pleistocene and Holocene. Pliocene faunal assemblages are characterised by rainforest-specialist frog, squamate and mammalian taxa. These include new Pliocene records for frogs; *Kyarranus, Lechriodus, Nyctimystes* and microhylids, squamates; *Cyclodomorphus gerrardii,* a new species of *Tiliqua* and typholopids, and mammals; *Bohra* sp., *Pseudochirulus* spp., new petaurids and dasyurids, *Dactylopsila*, petauroid *incertae sedis, Acrobates, Cercartetus, Uromys/Melomys, Mesembriomys* and *Pogonomys.* Ecological signals derived from the faunal assemblages correlate well with dated palynological records from central eastern and northern Queensland (ODP815, Aquarius Well and Lynch's Crater). Combined Early Pliocene palynological and faunal records strongly indicates a nonseasonal, mesothermal, angiosperm-dominant rainforest with emergent gymnosperms at Mount Etna. A Plio-Pleistocene seasonal, open ecology indicated by the palynological record is corroborated by fauna from similar-aged sites, although several rainforest taxa persist. Increasing aridity during the late Pleistocene is suggested by a distinctly arid-adapted faunal assemblage in late Pleistocene sites, including eastern-most records of *Tympanocryptis, Macrotis lagotis, Chaeropus ecaudatus, Perameles bougainville, Sminthopsis macroura* and *Notomys.* Faunal succession from the Early Pliocene to Holocene is characterised by the extinction of most rainforest groups by the late Pleistocene, being replaced by more xeric-adapted forms. Several of the Early Pliocene taxa show resilience to extinction by remaining, albeit rare, in the late Pleistocene fauna, probably in local refugia. These include *Dendrolagus* sp., a new petauroid, *Thylogale, Macroderma gigas, Sarcophilus laniarius* and *Thylacinus.* Presence of rainforest murids in the Early Pliocene of Australia significantly predates previous estimates for their dispersal onto mainland Australia.❒ *Pliocene, Pleistocene, ecological succession, rainforest fauna, Queensland, Australia, fossil vertebrates.*

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The succession of faunal assemblages during the late Cainozoic of Australia is unknown for large parts of the continent. Where present, the records are extremely patchy when compared to similar-aged faunal records for other continents (e.g. North America (Stirton, 1936); Africa (Bishop et al., 1971); China (Flynn et al., 1991); and Eurasia (Azzaroli et al., 1988)). A majority of the Australian late Cainozoic Local Faunas have either been the focus of long term, low yield, sporadic collecting with little systematic documentation or once-off, large-scale excavations of a single fossil specimen, site or horizon (Rich, 1991). Typical examples of these sites include the Plio-Pleistocene sites of the Darling Downs southeast Queensland, which, for over 150 years have yielded large collections of specimens with little or no field data due to the ad hoc nature of the collecting (Molnar & Kurz, 1997). These specimens are usually collected as single miscellaneous finds from along creek banks and riverbeds and have, until recently, possessed little documentation associated with the specimen. Such specimens are mostly out of stratigraphic context making them basically useless for detailed palaeoecological reconstruction and biostratigraphy.

In contrast, once-off large-scale excavations have either occurred in response to a major find, such as a complete skeleton(s), or the impending destruction of a fossil site by human impact (Archer, 1978; Long & Mackness, 1994). Material recovered from these sites usually possesses good field data, however, very rarely spans the temporal scale needed to document the succession of faunas for a single region over large periods of time.

There have been several attempts to tie together Pliocene and Pleistocene sites in an effort to develop a biochronological and evolutionary framework for the late Cainozoic fossil communities of Australia (Archer & Wade 1976; Lundelius, 1983, 1989; Woodburne et al., 1985; Rich, 1991; Tedford et al., 1992; Tedford, 1994; Archer et al., 1995a; Archer et al., 1999; Dawson et al., 1999).

A review of literature for Australian Plio-Pleistocene faunas show some distinctive trends: 1) The majority of sites determined as Pliocene in age are considered to be from the Early Pliocene (5.2-3.4 Mya); Bluff Downs (Mackness et al., 2000); Chinchilla (Tedford et al., 1992); Rackham's Roost (Archer et al., 1995b): QLD; Curramulka (Pledge, 1992; Tedford, 1994), Tirari Formation (Tedford et al., 1992), Sunlands (Pledge, 1987): SA; Forsyth's Bank (Tedford, 1994); Hamilton (Rich, 1991); Parwan (Tedford, 1994); Boxlea (Tedford, 1994); Coimadai (Turnbull et al., 1992) VIC; Big Sink (Dawson et al., 1999); and Bow (Flannery & Archer, 1984) NSW. These sites include the only radiometrically or magnetostratigraphically dated sites of the Pliocene: Bluff Downs 3.6 Mya; Hamilton 4.5Mya and the Tirari Formation 3.4-3.9Mya. 2) When Early Pliocene faunas are compared with the few identified Late Pliocene sites (3.4-2.0Mya): Dog Rocks in Victoria (Tedford, 1994); Bone Gultch and Fisherman's Cliff in New South Wales (Tedford, 1994); and Quanbun in Western Australia (Flannery, 1984; Rich, 1991), there is a distinct 'modernisation' of the fauna as suggested by Tedford (1994). These faunas possess several extant and extinct genera and species that become dominant during the Pleistocene and are the typical suite of taxa found in the late Pleistocene (Bartholomai, 1977; Archer, 1978; Hope, 1978; McNamara, 1990; Dawson & Augee, 1997; Molnar & Kurz, 1997; Reed & Bourne, 2000). The apparent faunal mixing of plesiomorphic and stratigraphically older taxa with younger, derived taxa, makes biochronology of the Late Pliocene and early Pleistocene difficult via stage-of-evolution criteria. Direct dates are needed to calibrate the timing of faunal changeover from the Pliocene to Pleistocene.

One notable near absence from the Pliocene to Pleistocene record is that of the diverse rainforest communities that distinguished many of the older Oligo-Miocene faunas of Australia (Archer et al., 1995a; Archer et al., 1999). A palaeoecological succession for the Pliocene through medial Pleistocene of southeastern Australia has been proposed by Tedford (1994). This includes the Early Pliocene Hamilton Fauna (Turnbull & Lundelius, 1970; Flannery, 1992; Rich, 1991; Macphail, 1996), the only representation of a post Early Miocene rainforest community in southern Australia. Additional Pliocene and Pleistocene faunas from southeastern Australia support several rainforest components, however, these accounts are usually interpreted as part of a patchy assemblage and do not dominate the ecological reconstruction (Tedford, 1994; Archer et al., 1999).

Tedford (1994) concluded that the rainforest communities of southeastern Australia are missing by the Late Pliocene. Archer et al. (1995a) reviewed the Tertiary biotic change in Australia and concluded that by the Late Pliocene central Australia was becoming arid, coastal regions were forested and open, and rainforest persisted in northeastern Queensland as refugia. Macphail (1997) showed distinctly drier-adapted flora throughout the Late Pliocene of Australia.

A unique opportunity to access a late Cainozoic terrestrial fossil record from central eastern Queensland has been made possible via a series of open-cut limestone quarries and cavernous systems running along the coast to the north and south of Rockhampton (Fig. 1). Exposures of extensive fossiliferous deposits in stratigraphic context allow for this first account of a faunal succession spanning the Pliocene to Holocene in Queensland, including a distinctive Pliocene-aged rainforest community.

## HISTORY OF COLLECTION

Collection of vertebrate remains from cave and fissure deposits in central eastern Queensland (CEQ) occurred sporadically for over 90 years, but few papers have appeared on fossils collected from these sites (Longman 1921, 1924, 1925a, 1925b; Hocknull, 2003).

Central eastern Queensland contains several limestone blocks with known karstification. Of these, Marmor and The Caves are the only two areas where vertebrate fossils have been found prior to 2002.

In 1910 G.E. Blundell collected a tooth from Marmor Quarry, S of Rockhampton, which made its way to the British Museum of Natural History

(BMNH10257) identified as *Macropus brehus*, now identified as *Palorchestes*.

First vertebrate remains acquired by the Queensland Museum QM were from guano mining in caves on Reserve Holding 272, Limestone Ridge, east of Mount Etna (R444),between 1920-1921. A mandible assigned to *Sarcophilus laniarius* was presented to Heber A. Longman in 1921 by P.H. Ebbott of Mount Etna Fertilisers Ltd (Longman, 1921). Shortly thereafter, Samuel Evans, mine manager of Marmor Quarry, presented several small collections of fossils unearthed during quarrying. In 1924, Longman collected the QM's first representative samples from CEQ; from Olsen's Cave, SE of Mt Etna and Marmor Quarry, publishing the combined material collected from Marmor Quarry (Longman, 1924, 1925a & b). Longman's faunal records from Marmor Quarry included; *Diprotodon australis* (herein ?Zygmaturinae), *Phascolomys* sp. (herein, *Vombatus urinus mitchellii*), *Thylacoleo carnifex* (herein *Thylacoleo* sp.), *Thylacinus spelaeus* (herein *Thylacinus cynocephalus*), *Sarcophilus laniarius*, *Macropus anak* (herein *Macropus titan*), *Phascogale flavipes* (herein *Antechinus* sp. 2), *Petrogale* sp. cf. *P. inornata* (herein *Petrogale* sp.) and *Megalania prisca*. Smaller fauna included snake and rodent remains. Fossils collected from Olsen's Cave remained unpublished.

In 1925 Evans presented a second Marmor Quarry collection to Longman. F.W. Whitehouse collected bones from Johannsens Cave on Limestone Ridge in 1926, during the peak of guano mining. A hiatus of nearly 30 years followed. In 1954 and 1957 two collections of bones were presented to the QM from Marmor Quarry, by O. Anderson and J.E. Joyce, respectively. Final collections of large pieces of bone-bearing cave breccia were taken from Marmor Quarry in 1964-5 by Bartholomai and Joyce. This breccia is currently being prepared and contains remains of some very large vertebrates, including *Macropus titan*, as well as many smaller-sized species. No collecting has been possible from Marmor Quarry since 1964.

In 1972, Mike Murray donated small surficial collections from Old Timbers, Lion's Den and Johansen's Cave, Mount Etna area.

A second hiatus from the 1970's to mid 1980's occured when concerns regarding the conservation of several caves on Mount Etna were at their greatest (Bourke, 1970; Vavryn, 1987). Two cave systems, Speaking Tube Cave and Elephant Hole Cave, were under threat from quarrying operations on the W flank of Mt Etna. In 1986, Kerry Williamson & Dianne Vavryn removed two sacks of loose bone and sediment from the floor of Elephant Hole Cave before mining operations broke into the cave. The small collection was sent to the QM later that year.

Mining operations continued on the western ridge of Mount Etna until early 2004. During the initial stages of operation, the two known caves were broken into and cave breccias exposed. A deposit was unearthed in 1992 when breaking into Speaking Tube Cave. Then mine manager M. Barton, with assistance from David Kershaw and Don Kime, kindly donated bone-breccia samples to the QM and kept a stockpile of bone breccia material on the eastern side of Mount Etna on a flat bench below Main Cave (QML1313).

The author, Paul Tierney and members of the Central Queensland Speleological Society, mounted expeditions to Mt. Etna in 1998, 2000 and 2001. Several sites were successfully located and collected within the Mt. Etna Caves National Park and Mt. Etna Limestone Mine.

Extensive fossiliferous deposits on Limestone Ridge were found in 1998 which included considerably diverse faunas from several distinct ecologies, including rainforest. Twice in 2000, the QM and University of New South Wales systematically collected material from sites on Limestone Ridge and Mt. Etna.

In 2001 collections were made from the Mt Etna Limestone Mine, with the discovery of, inter alia, faunal assemblages of similar diversity and age to those from Limestone Ridge. Deposits represent a series of cave-fills exposed in cross-section by mining operations. Examination of these units has enabled development of a preliminary chronology of the faunas. Continued fieldwork in 2002 and 2003 increased the number of distinct sites on the mining lease and located a remnant chamber of Speaking Tube Cave. In mid-2002 a limestone at Mount Princhester, 50kms north of Mount Etna, was investigated and small deposits of exposed fossiliferous cave floor sediment collected. Further fieldwork (2003) resulted in discovery of new sites in Olsen's Cave and Karst Glen, SE of the main Mount Etna and Limestone Ridge blocks.

## METHODS

FOSSIL SITES (Figs. 1-3). Preliminary site geology, including simplified sedimentological descriptions are provided herein. Cave names

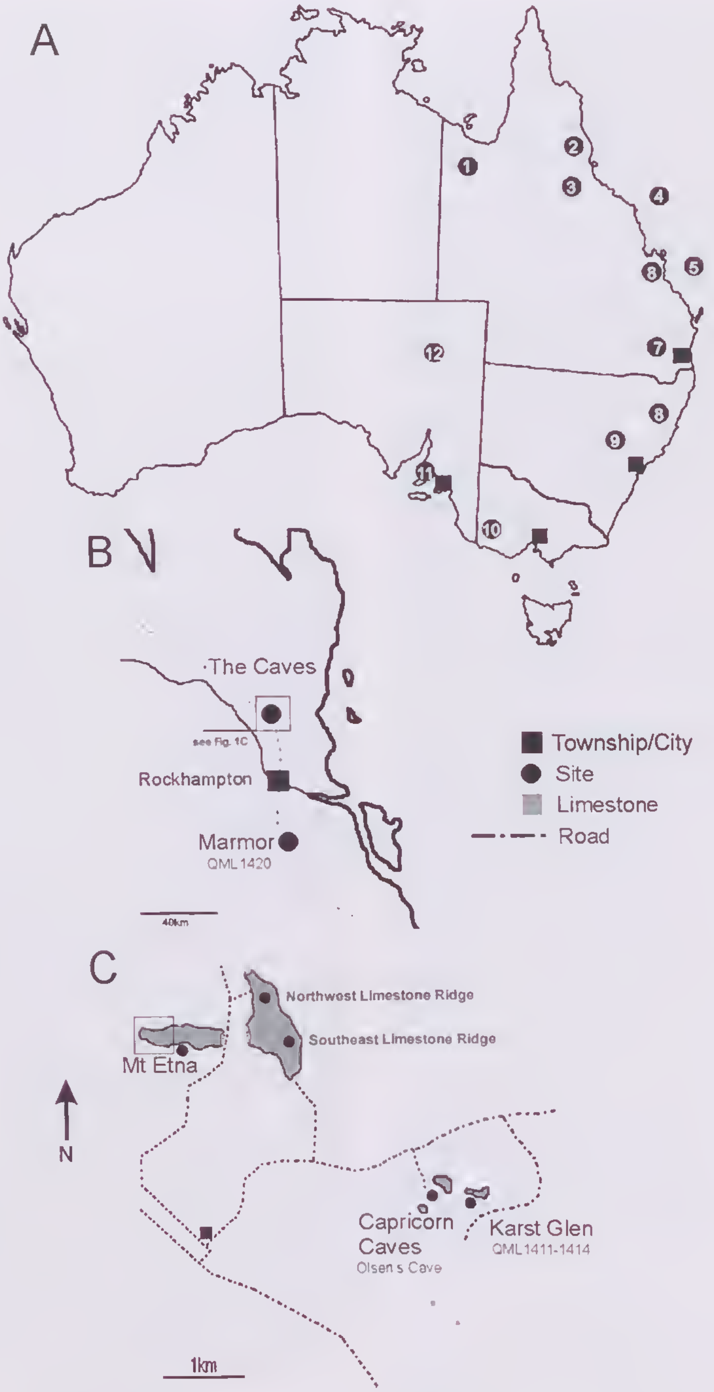

FIG 1. Map of fossil localites. A, Major localities mentioned in text, 1. Riversleigh; 2. Lynch's Crater; 3. Bluff Downs; 4. ODP815, Marion Plateau; 5. Aquarius Well, Capricorn Trough; 6. Mt Etna/Marmor; 7. Chinchilla; 8. Bow; 9. Big Sink, Wellington; 10. Hamilton; 11. Curramulka; 12. Tirari Formation, Lake Eyre. B, 6. expanded. C, The Caves area.

follow (Shannon, 1970b). Fossil sites are given a QML number (Queensland Museum Locality). Superpositional and stratigraphic data was collected from all localities with the exception of Marmor Quarry. Data collected included, stratigraphic context, breccia components, bone preservation, tooth preservation, shell preservation and a facies interpretation. Where possible, sampling bias was reduced by collecting and processing equal amounts of material from each site.

TAXONOMY. A brief systematic account of the taxa found from each site is tabulated (Table 1-3, Appendix 1)with abbreviated systematic descriptions of relavant taxa given below. A selection of the best-preserved specimens was used to provide the identifications that follow. All specimens are held at the Queensland Museum, (prefix QMF). Frog osteological nomenclature and taxonomy follows Tyler (1976) and Cogger (2000) respectively. Squamate nomenclature follows; Hutchinson (1992) for scincids, Hutchinson (1997) for pygopodids and gekkonids, Hecht (1975) for varanids, Hocknull (2002) for agamids, Smith (1976) for elapids and Holman (2000) for typholopids. Squamate taxonomy follows Cogger (2000); crocodylian nomenelature and taxonomy follows Willis (1995); mammalian nomenclature follows Archer (1984) for tooth morphology and Luckett (1993) for tooth positions. Mammalian taxonomy follows Strahan (1995) and Flannery (1994). Fossil mammal taxonomy follows Long et al. (2002). Avian nomenclature follows Gilbert et al. (1981) and taxonomy Lindsey (1992).

FAUNAL ASSEMBLAGES (LOCAL FAUNA). Similarities between site faunas were computed using PAUP (Swofford, 2000) and MacClade software (Maddison & Maddison, 2000), where sites defined as 'taxa' and the taxa as 'characters'. 'Characters' were given the states of either being absent (0) or present (1) (Appendix 1).

Small-sized mammals (smaller than and including *Petrogale*) were chosen for the analysis because they were represented in all of the sites and are least affected by taphonomic bias. The dominant accumulating agent for each site was either via a pit-trap and/or owl/bat roosts. This biases the preservation of large-sized vertebrate taxa, thus they are excluded from the analysis.

A mammal list was constructed to define the present day small mammal fauna for Mount Etna. This list was derived from mammal species surveyed directly at Mount Etna (Horsup et al., 1993; Dwyer, 1970) and those species found in habitat similar to that of present day Mount Etna (semi-evergreen vine thicket), which are also found within the central eastern Queensland region today (Horsup et al., 1993). The present day fauna was fixed in position for the analysis as the 'outgroup'. Present day mammal species not found in the fossil record were excluded from the 'ingroup' analysis because they were simply counted as autapomorphies and uninformative. A dendrogram of relationship was constructed using both PAUP and MacClade parsimony analyses (heuristic search; 1000 replicates).

FAUNAL ASSEMBLAGE AGE. Biocorrelated taxa were used to provide an estimated date for each of the sites. Palaeoecological signals generated from well-constrained palynological records off the coast of central eastern Queensland (Hekel, 1972; Martin & McMinn, 1993) were correlated with palaeoecological signals generated from site faunas. Direct dating of one site, QML1312, was possible via Thermal Ionisation Mass Spectrometry (TIMS) Uranium-series dating. Dating was carried out on a *Petrogale* jaw. The date is considered to be a minimum age based on late-stage uptake of Uranium into bone and dentine (Ayliffe & Veeh., 1988; Shen et al., 2001; Zhoa et al., 2002).

## GEOLOGICAL SETTINGS

The geological history of the limestone blocks containing cave and fissure deposits of the present study have been subject to debate (Kirkgaard et al., 1970; Shannon, 1970a; Willmott et al., 1986; Barker et al., 1997; Simpson et al., 2001). Sites occur in cavern and fissure systems within Early Devonian limestone blocks (Philip & Pedder, 1967) of the Mount Alma Formation (*sensu* Barker et al., 1997). Limestone blocks are irregular in shape and are scattered randomly throughout the formation. The southern extremity of the limestone blocks occurs in the Marmor-Raglan area 50 kms S of Rockhampton. The northern extension of the limestone outcrops as a series of small limestone bluffs at The Caves township (25km N of Rockhampton) and at Princhester (50km N). Sediments from these sites have yielded an enormous and varied vertebrate fossil record.

Palaeontological and structural evidence suggests the limestones are allochthonous blocks within Late Devonian Mount Alma Formation (Barker et al., 1997).

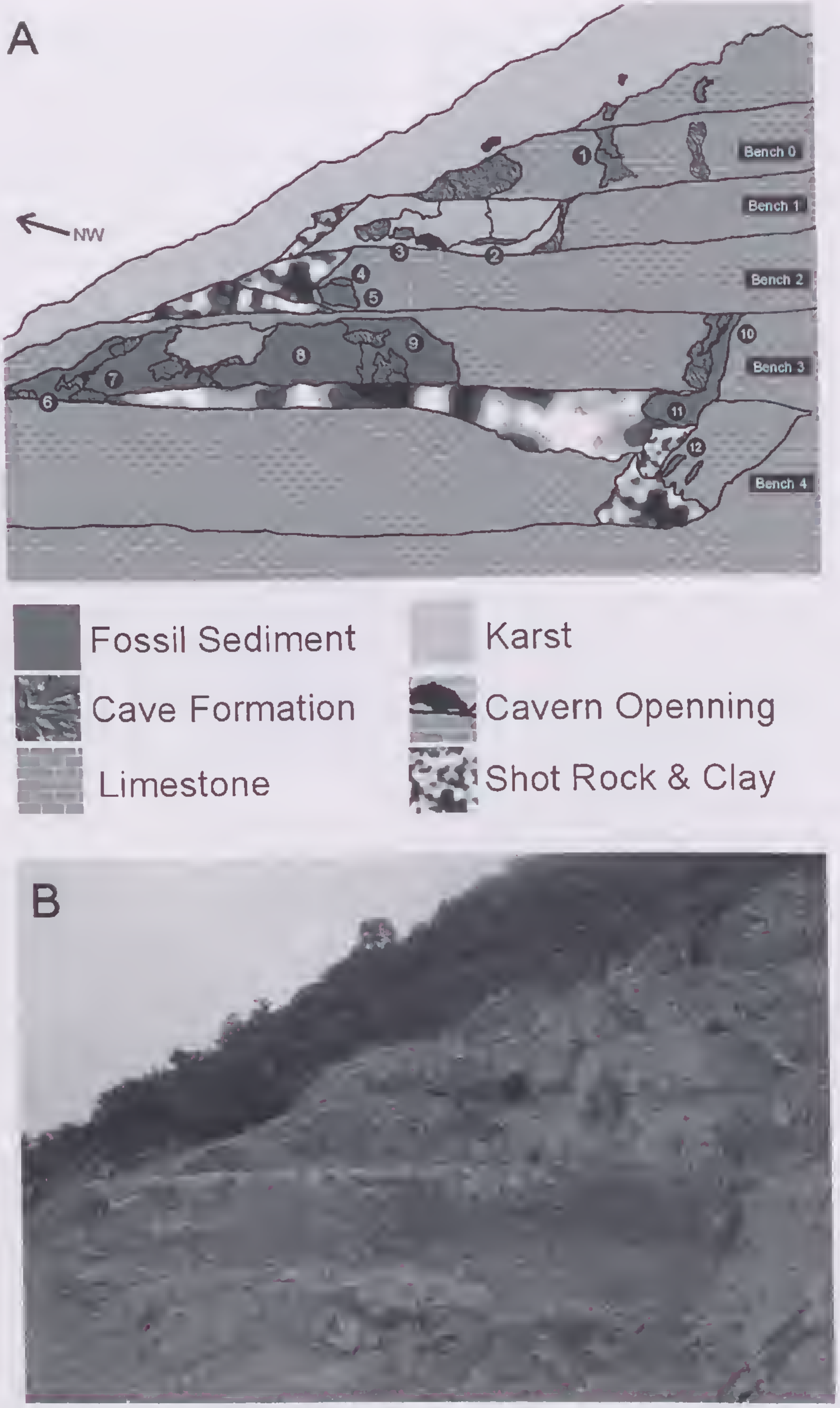

FIG. 2. Fossil localities on the western benches of Mount Etna Limestone Mine. 1. QML1419; 2. QML1313, 3. QML1383, 4. QML1310 Unit 1, 5. QML1310 Unit 2, 6. QML1311 A/B, 7. QML1311 C/D, 8. QML1311 F, 9. QML1311 H, 10. QML1398U, 11. QML1384L, 12. QML1385.

The structural history of these limestone blocks which includes their distance and position from one another, irregular bedding planes, faulting, and complex joint systems, has had a direct influence on the sedimentology of the varying vertebrate fossil deposits found within them (Willmott et al., 1986). Structural history has also influenced the terrestrial communities occupying the limestone (caverns and surrounds) through the past and in the present. Modern ecologies on these limestones strongly reflect this influence because most of the bluffs act as present day refugia for flora and fauna (Horsup et al., 1993).

## SITE LIST

**Mount Etna Limestone Mine and National Park**

*Speaking Tube Cave System*

Bench 0, QML1419*
Bench 1, QML1313 (=QML1313 & QML1288)**
Bench 1, QML1383*
Bench 2, QML1310 Unit 1
Bench 2, QML1310 Unit 2*
Bench 3, QML1311 Unit A*
Bench 3, QML1311 Unit B*
Bench 3, QML1311 Unit C**
Bench 3, QML1311 Unit D**
Bench 3, QML1311 Unit F*
Bench 3, QML1311 Unit H**

*Elephant Hole Cave System*

Williamson & Vavyrn Collection, QML1312**
Bench 3, QML1384 Upper Unit**
Bench 3, QML1384 Lower Unit**
Bench 4, QML1385**

**Northwest Limestone Ridge**

*Johansen's Cave System*

QML1314, Guano deposit**
QML368, Flowstone (False Floor) Unit**
Southeast Limestone Ridge

*Mini Cave System*

Mini Cave Chamber Deposit, QML1284**
Mini Cave Surface Deposit, QML1284a**
Leo's Lunch Site, QML1382*

**Olsen's Cave System****

Karst Glen System
KG3 Surface Deposits, QML1411-1414*

**Marmor Quarry**

Marmor Bone Breccia collection, QML1420**

* Sites with fauna

** Sites with fauna presented herein

## MOUNT ETNA LIMESTONE MINE AND NATIONAL PARK

Approximately 40% of Mount Etna is massive recrystalised limestone with the remainder a combination of faulted sedimentary and volcanogenic units of the Mount Alma Formation (Shannon, 1970a; Barker et al., 1997). Limestone on Mount Etna dips steeply to the SW, with major joints oriented along a NW axis. Joints are predominantly vertical and control cave development (Shannon, 1970b). Phreatic enlargement has occurred along these vertical planes producing deep chambers with sculptured phreatic pendants. Vadose cave development is marked by extensive speleothem formation and cave entrance development. Bone breccias and cemented cave floors are common throughout, occurring within functional cave systems or exposed on weathered and collapsed dolines. Two major cave systems on Mount Etna are the focus of the present study; Speaking Tube and Elephant Hole Cave systems.

Speaking Tube Cave system occupies two major joint controlled rifts running down the mountain in a NW-SE direction. Phreatic chambers developed at depth are linked to the surface by long solution pipes. Elephant Hole Cave system is a third joint-controlled rift to the SE of the Speaking Tube Cave system. It is also linked to the surface by large solution pipes. A geochronological summary of sites found on the western benches of Mount Etna Limestone Mine is provided in Fig. 3.

### Speaking Tube Cave System

SPEAKING TUBE CAVE: E7. *"This cave has nine entrances at middle to highest levels on the West flank of Mt. Etna. It is a very complicated active inflow cave with three active sumps."* (Shannon, 1970b: 25)

It is obvious from the many and varied bone breccias recovered that Speaking Tube Cave system has had a long and complex history. No substantial collections were made from Speaking Tube Cave before it was broken into by mining operations. In 1992, bone breccias were exposed close to surface karst and stockpiled by Pacific Lime Pty Ltd operators. A small sample of these bone breccia blocks was sent to the Queensland Museum marked "Speaking Tube Cave". In 2000 the stockpile was located on the eastern side of

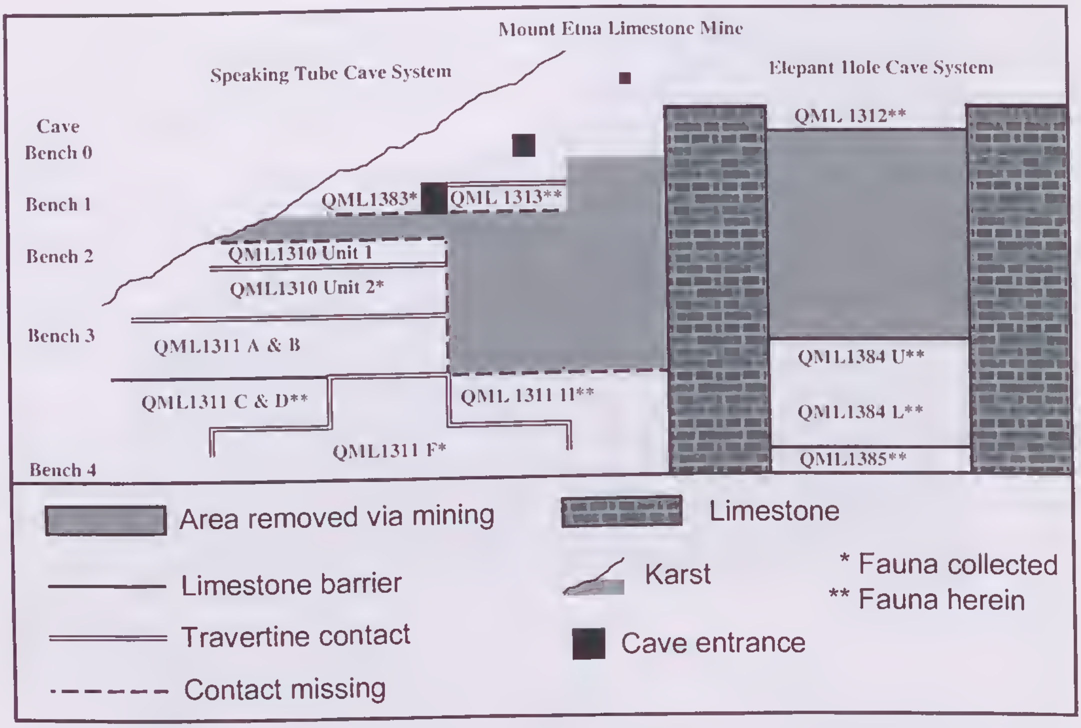

FIG 3. Schematic diagram illustrating the relationships between fossil deposits on the western benches of the Mount Etna Limestone Mine, Mount Etna. * Fauna collected. ** Fauna presented herein.

Mount Etna by the QM and collected, given the site name 'Mat's Menagerie' (QML1313). The original location of the bone breccia was unknown until 2002 when equivalent material was found in situ on Bench 1 of the western benches. Five main benches are considered to preserve portions of the Speaking Tube Cave system, including an entrance to the cave through an exposed chamber on Bench 1.

BENCH 0, QML1419. A thin veneer of limestone covered a solution tube until 2003 when it collapsed and revealed a breccia-filled tube. It was discovered in mid 2003. The solution pipe contains several levels of varyingly indurated fossiliferous sediment.

BENCH 1, QML1313 (=QML1313 & QML1288). A small amount of bone breccia received from Pacific Lime in 1992 and labeled as 'Speaking Tube Cave' (QML1288) was rediscovered by the Queensland Museum as a stockpile on the eastern face of Mount Etna, subsequently named "Mat's Menagerie Site" (QML1313). The bone breccia originated on the western benches where its exact locality was unknown. Inspection of the Bench 1 cliff line relocated lithologically identical bone breccia adhering to an exposed cave chamber wall. The material follows a cave wall demarcated by cave formations along the middle length of the bench. The breccia runs in a northwest/southeast axis toward an opened chamber. The chamber constitutes a known chamber within Speaking Tube Cave. Bone breccia received by the museum, stockpiled on the eastern face and adhering to the southeast side of the cave wall on Bench 1, western benches, constitutes the same unit.

*Stratigraphic context.* There is no preserved contact of this unit with any of the other deposits on the mountain. The area in which a contact may have occurred has been mined. There are no clasts of other bone breccias within the matrix. The only breccia that shows similarities in sedimentology to QML1313 is QML1311 (Unit A) of Bench 3, which indicates that this unit was very extensive and formed deep within the system. It is sedimentologically distinct from the only other breccia found on Bench 1(QML1383), which occurs to the northwest of the open chamber.

*Breccia components.* Distinctly bright yellow to orange coloured, heavily cemented containing large angular clasts of parent limestone, flowstone and smaller clasts of allochthonous rock; abundant bone, teeth and skulls of variable sizes; snails common; large calcite vugs. Small clasts of red to brown clay; pisolites of ironoxide and calcite; bedding chaotic.

*Bone preservation.* Articulated and semi-associated skeletal elements; well-preserved material with no apparent dominant bone orientation; calcite growth within bone vacuities; bones variable in size, from large limb bones (10-15cm) to grain-sized bone fragments.

*Tooth preservation.* Teeth usually in jaws.

*Shell preservation.* Shells complete and isolated.

*Facies Interpretation.* Abundant large angular clasts, articulated and semi-articulated large-sized bones, large complete shells and no dominant bedding or clasts indicates an entrance facies talus and scree.

BENCH 1, QML1383. Located to the northwest of the open chamber, QML1383 is a large fossiliferous unit.

*Stratigraphic context.* Sedimentologically this unit is similar to QML1311 (Unit B) of Bench 3 and QML1310 (Unit 2) of Bench 2. QML1310 (Unit 1) of Bench 2 divides the contact between QML1383 and QML1310 (Unit 2) so it is suggested here that QML1383 is stratigraphically younger than both QML1310 and QML1311. The site has an analogous depositional facies.

*Breccia components.* Dark red to pink clay, heavily cemented with minor clasts of decalcified limestone, allochthonous sediments and pisolites; abundant bones, teeth and shell.

*Bone preservation.* Bones fragmentary and small; no distinct large bone orientation; smaller bone fragments occur in fine lenses which are horizontally bedded.

*Tooth preservation.* Usually isolated and well preserved.

*Shell preservation.* Abundant in small lenses.

*Facies Interpretation.* Lack of large angular clasts, large bones and the lack of distinct large bone orientation indicates a depositional facies away from an entrance and having not been subject to significant water transport. Abundance of small fragments of bones and isolated teeth indicates a possible predator accumulation. Thin irregular lenses of material suggest that accumulation occurred from slumping of upper roost deposits, probably *Macroderma*. The deposit seems to occur within an old aven when viewed in sectional profile.

BENCH 2, QML1310. Bench 2 lacks large deposits of breccia, with the two units described here only found on a small pinnacle left from mining operations.

**Unit 1**; *Stratigraphic context.* Unit 1 is younger than Unit 2 with a distinct cave floor formation between the two horizons.

*Breccia components.* Mottled red/grey horizons; lacks bone and teeth; small clasts of allochthonous sediments; heavily cemented.

*Bone, tooth and shell preservation.* Rare to nil.

*Facies Interpretation.* Lack of fossil material and major clasts indicates a non-entrance facies. The mottling of the rock indicates the presence of dense rootlets and thus the base of a chamber.

**Unit 2**; *Stratigraphic context.* Occurs below and is older than Unit 1. Several thick bands of flowstone occur through the top of this unit, demarcating different levels of formation. Toward the base there is a considerable reduction in flowstone. The base of Unit 2 appears to be very similar in depositional style to QML1311 (Unit B) of Bench 3 and is interpreted as the top of this unit.

*Breccia components.* Flowstone-dominated light red coloured, heavily cemented bone breccia; flowstones irregular in shape and domed at the middle of the exposure; bones abundant and small; shell abundant in small lenses, associated with flowstones; small, grain-sized clasts of allochthonous sediment.

*Bone preservation.* Disarticulated, disassociation within the accumulation; large numbers of bones from small animals, usually broken into grain-sized particles.

*Tooth preservation.* Isolated teeth, well preserved, no rounding.

*Shell preservation.* Small snail shells, in bands usually associated with flowstone unit.

*Facies Interpretation.* The mass of banded flowstones at the top of QML1310 Unit 2 indicates a major increase in speleothem genesis over that found in QML1311, Unit B. It is unknown whether this was a rapid phase of precipitation or it was a gradual increase over time. The reason for this is because the contact between QML1311, Unit B and the base of QML1310 Unit 2 has been removed by mining. The presence of the flowstones and a domed lamination indicates a series of cave floors, probably in the shape of a sediment cone. Absence of large angular clasts and large bones indicates a chamber facies. The sediment cone was probably produced at the base of a bat roost because there are no additional chambers above the deposit that could have acted as a sump.

BENCH 3, QML1311

**Unit A;** *Stratigraphic context.* Unit A in contact with Unit B. Unit A formed before Unit B. Unit A is considered lithologically equivalent to QML1313 sediment although found deeper within the system. This is reflected in the breccia components, bone preservation, greater bedding and speleothem genesis of Unit A sediments.

*Breccia components.* Yellow, grey and pink coloured clay; heavily cemented; massive flowstones and travertine throughout (ranging from 5-20cm thick); cave formations preserved within breccias. Large clasts of allochthonous sediments and semi-rounded parent limestone. Drusy calcite vugs and well preserved bone.

*Bone preservation.* A semi-articulated, associated accumulation with some patches of sorted large bone; limb bones well preserved with most elements complete; small bones in apparent association; bone vacuities infilled with calcite.

*Tooth preservation.* Teeth usually found in complete or near complete jaws.

*Shell preservation.* Snails abundant, isolated, and well preserved.

*Facies Interpretation.* Unit A is considered a talus accumulation below the entrance facies of QML1313.

**Unit B;** *Stratigraphic context.* Unit B occurs in two areas along Bench 3. Unit B contacts Unit A on its north-western extremity and occurs above Unit C/D toward the center of Bench 3. Unit B is divided from Unit C/D by a massive limestone wall, varying from 5-10m thick. Unit B is considered so close in lithology to the sediment at the base of QML1310 Unit 2, Bench 2, that it is considered here to have had a conformable contact between these two units.

*Breccia components.* Light red heavily cemented clay; numerous clasts of decalcified parent limestone, cave wall travertine and allochthonous sediments, including gravel. Cave formation dominates the clasts, followed by allocthonous sediment and parent limestone. Bone and tooth fragments abundant; small drusy calcite vugs; isolated iron-oxide pisolites.

*Bone preservation.* Disarticulated accumulation with some sorting of small bone elements. Sorting is localised and not common; large bones are rare; small bone well preserved with teeth in jaws. Long bones badly preserved, mostly broken at both proximal and distal ends; numerous grain-sized bone particles occur in irregularly graded lenses. Calcite growth within bone vacuities.

*Tooth preservation.* Well preserved tooth rows.

*Shell preservation.* Shell abundant and usually associated with bone sorting.

*Facies Interpretation.* Unit B is considered the base of a talus from a well-developed sediment cone. The base being Unit B and the top being QML1310 Unit 2 Bench 2. The lack of large bone accumulations and the abundance of small bone fragments suggest a similar predator accumulation as to QML1310 Unit 2 Bench 2 within an aven chamber.

**Unit C** ; *Stratigraphic context.* Unit C grades into Unit D but with less mottling. Unit C and D are considered equivalent in age. Unit C is separated from Unit A & B by a large limestone wall, varying from 5-10m thick. Units C and D unconformably overlies Unit F on a decalcified and eroded travertine surface formed on Unit F and included as clasts in Units C & D. Units C and D are thus considered to be younger than Unit F.

*Breccia components.* Red/yellow/grey clay, moderately cemented; drusy calcite vugs formed within rootlet vacuities; isolated iron-oxide pisolites; small clasts of decalcified parent limestone and allochthonous sediments. Isolated clasts of broken and transported travertine; large bones, isolated teeth and numerous complete small bones; large bones fractured and exploded by clay matrix; no travertine formation other than calcite formation between Unit C and F. Small clasts of Unit F at the southeast extremity of unit C.

*Bone preservation.* Disarticulated accumulation with little bone sorting; large long bones missing proximal and distal ends; vertebrae missing processes. Large bones have been transported some distance. Small bones variably preserved; complete elements to grain-sized particles; bone vacuities filled with clay.

*Tooth preservation.* Large teeth usually preserved within the jaw. Small teeth usually isolated and associated with edentulous jaws.

*Shell preservation.* Rare to absent.

*Facies Interpretation.* Unit C is considered to be a deep chamber deposit based on the lack of large angular inclusions and large well-preserved, semi articulated or associated bone. There are no indications that this deposit is a predator accumulation. The lack of sorting of clasts and no distinct bedding planes indicate that stream and channel action was not the main mode of transport and deposition here. The presence of large bones and very few well-preserved snails indicates a deposit where the larger elements have been transported from an entrance facies into a lower chamber probably via extensive slumping, requiring little water transport.

**Unit D;** *Stratigraphic context.* Unit D is a mottled breccia very close in lithology to Unit C and is considered equivalent in age. Unit D conformably grades into Unit C without any distinctive demarcation.

*Breccia components.* Mottled red/yellow/grey clay, loosely cemented; drusy calcite vugs formed within rootlet vacuities. Unit D possesses distinctive mottling due to penetration of the clay load by rootlets. Isolated iron-oxide pisolites; small clasts of decalcified parent limestone and allochthonous sediments; rare large bones and isolated teeth; no travertine formation other than calcite formation between Unit C/D and F.

*Bone preservation.* Disarticulation accumulation with little bone sorting; large long bones missing proximal and distal ends. Bone vacuities filled with clay.

*Tooth preservation.* Small teeth usually isolated and associated with edentulous jaws.

*Shell preservation.* Rare to absent.

*Facies Interpretation.* As for Unit C but with a greater influence from rootlets altering the general colouration and texture of the sediments.

**Unit F;** *Stratigraphic context.* Unit F is located between Units C & D and Unit H. There are contacts between Unit F and Unit C on the northwest flank, and with Unit H on the southeast flank. These contacts are demarcated by cave wall formation in the form of travertine and decalcified, detached flowstones with Units C, D and H. All three Units have been secondarily capped by a more recent travertine. Based on the contact zone, Unit F formed before Units C, D and H.

*Breccia components.* Bright yellow sandy, clay-rich; cemented; travertine distinct and demarcates contacts with younger sediment; little internal flowstone formation. Interspersed small, rootlet-shaped drusy calcite vugs; minor clasts (0.5-2cm) of decalcified parent limestone with chalky texture. Small patches of highly fragmented bones and teeth.

*Bone preservation.* Disarticulated accumulation with no bedding or sorting; bones small and hollow in cross section; no large elements, mostly postcranial.

*Tooth preservation.* Mostly fragmented rodent incisors.

*Shell preservation.* Shell absent.

*Facies Interpretation.* The sediment is unlike any other found in the study area. The paucity of bone, internal speleothem genesis and clasts indicates a possibly dry accumulation. Further investigation of this deposit is needed. The lack of fossil specimens may also indicate a relatively old age for the deposit, before there was major connection of the solution pipes with the surface and well before karstification.

**Unit H;** *Stratigraphic context.* Unit H contacts the travertine wall enclosing Unit F and is younger. Unit H has formed at a similar depth to Units C, D and QML1384 Lower Unit, however, their superpositional relationships are unknown, possibly contemporaneous.

*Breccia components.* Red to dark brown clay, heavily compacted but not heavily cemented; numerous small clasts of altered serpentinite, clasts of decalcified parent limestone and iron-oxide pisolites; large and small bone fragments; isolated teeth and jaws. Minor travertine inclusions from Unit F.

*Bone preservation.* Dissarticulated accumulation with no distinct bedding or sorting of elements. Tightly packed bone accumulations; large bones are commonly long bones. Long bones usually with broken proximal and distal ends; shafts fractured and exploded by clay matrix; vertebrae usually missing transverse processes and neural spines; metatarsals commonly missing one disal end: small bones include variously fragmented skeletal elements; usually preserving epiphyses. Ranging from complete bone elements to grain-sized bone particles.

*Tooth preservation.* Mostly edentulous jaws and numerous isolated teeth. Large (e.g. large macropodid) teeth usually remain within the jaw. Teeth variably preserved with tooth roots.

*Shell preservation.* Nil.

*Facies Interpretation.* Absence of angular limestone blocks and dipping beds indicates a non-entrance facies. The lack of cementation indicates a period of saturation of the sediment or the inclusion of humic acids into the cavern, both similarly retarding the precipitation of calcite within the sediment, however, geochemical analyses will be needed to clarify this.

### Elephant Hole Cave System

ELEPHANT HOLE CAVE: E8. *"On the West flank of Mt Etna. The cave [Elephant Hole Cave] has three middle level entrances, all containing vertical pitches. An active inflow cave. From the main entrance a talus slope leads to the drop into two large caverns. ...The cave has little decoration, but has some breccia deposits which include bone material."* Shannon (1970b: 25)

**Williamson & Vavyrn Collection, QML1312;** a sample of unconsolidated floor sediment from an earth floor within Elephant Hole Cave in 1986.

*Stratigraphic context.* Of unknown stratigraphic context. TIMS U-series date based on *Petrogale* dentition (minimum age) 149,000 ± 611 ybp. Considered to be young based on the preservation state of the material. Younger than QML1384 and QML1385 deposits.

*Breccia components.* Sediment and bone that was collected is derived from a loosely compacted cave floor (Vavryn & Williamson pers coms.) which is almost entirely made-up of fine, dark to light brown or red clay. Sediment breaks down easily in water and contains small, angular fragments of cave wall and roof, which show some signs of weathering and decalcification. Bone appears to be subfossil, with minimal bone discolouration, except for black manganese-oxide surface stains.

*Bone preservation.* Disarticulated, semi associated; bone small to medium-sized (<100mm in length) with portions of larger limb elements; very well preserved with most of the long bones retaining epiphyses and skull bones intact. Bone cavities free of calcite and sediment.

*Tooth preservation.* Most mandibles and maxillae retain teeth and most molar rows.

*Shell preservation.* Fragmentary and rare.

*Facies Interpretation.* Abundance of small bones of mammals, lizards, frogs and passerine birds suggests that a fraction of the deposit be derived from a predator accumulation. Some gnaw marks have been found and identified as rodent gnawings. Present in the deposit are owl *(Tyto* sp.) and ghost bat (*Macroderma gigas*) remains indicating that typical cave dwelling predators were present in Elephant Hole Cave during deposition. Well-preserved and semi-associated large vertebrate remains attaining a maximum size of the macropodine *Petrogale*, indicate an accumulation close to an entrance.

No orientations of the bones were taken with the collection so it is unclear whether water was involved in the accumulation. No speleothem or cementing has occurred, suggesting the sediment was not water transported. Some sediment clods remained within the deposit and were not broken down during collection, transport or preparation. These compacted sediment clods are thick with bones and teeth with their orientations relatively random. The lack of water transport, compaction and calcite precipitation indicates a very dry accumulation close to an entrance, with input from a predator's roost.

BENCH 3, QML1384 UPPER UNIT. In 2000 whilst collecting on the western benches of Mount Etna Mine, a site (QML 1384U) was discovered with a similar sedimentology to that seen in the material recovered from Elephant Hole Cave by Williamson & Vavyrn in 1986 (QML1312). Based on the position of the deposit on the mine site, it would have occupied a deep chamber within the Elephant Hole Cave system.

*Stratigraphic context.* QML 1384 is considered to be older than QML1312 because it is found much deeper and is more compacted and lightly cemented. There is no distinct reworking of bone material and the bone has a greater degree of alteration than the bone from QML1312.

*Breccia components.* Cave earth compacted, only lightly cemented, breaking down easly in weak acidic solution. Sediment possesses a strikingly similar colour and texture to QML1312, including an abundance of brown to red clay, angular cave wall and roof inclusions.

*Bone preservation.* Bones disarticulated; subfossil preservation; similar in preservation to QML1312, especially by the presence of the black manganese oxide staining. The completeness of cranial and postcranial bones also indicates close similarities because no other site at Mt Etna, other than the Elephant Hole Cave collection, has such a high density of perfectly preserved elements. Bones infilled with clay.

*Tooth preservation.* Complete jaws with tooth rows preserved.

*Shell preservation.* Rare and fragmentary.

*Facies Interpretation.* The chambers of Elephant Hole Cave were large and vertical. It is therefore considered that QML1384U is simply a lower and older extension of the entrance and predator accumulation identified as the QML1312 deposit.

BENCH 3, QML1384 LOWER UNIT.

*Stratigraphic Context.* QML1384L is lithologically similar to QML1384U. There is no distinct contrast between the upper and lower unit except for a darker colour of the clay in the Lower Unit. The Lower Unit is considered to be continuous with and therefore older than the sediments collected from the upper unit.

*Breccia components.* Sediment unconsolidated, extremely clay-rich, dark brown in colour. The clay is very greasy in texture; isolated allochthonous cobbles and gravel are dispersed throughout the clay load. Bone rare; little flowstone and few autochthonous clasts are present in the sediment.

*Bone preservation.* Bone rare and fragmented, where present relatively unaltered, possessing simple maganese staining. Larger bone vaculities free of clay. Similar in preservation to the upper unit, except for greater manganese staining.

*Tooth preservation. Rare and isolated.*

*Facies interpretation.* Lower Unit is simply an extension of a large vertically oriented solution pipe which fed into a large chamber housing phreatic pendants. The lack of distinctive vadosely developed flowstones within the sediment suggest that, like QML1311 Units C, D and H, the lower unit was accumulating within a water-saturated chamber, or one with sufficient acidity to prevent carbonate precipitation. This would also explain the lack of carbonate to indurate the clay sediment. The sediment looked to continue deeper within the system and certainly down to the level of Bench 4 (QML1385) deposit. This lower unit may contact QML1385 and be a source for the bone accumulations in it.

BENCH 4, QML 1385. In 2002 a small deposit of bones was discovered further down the mine site benches, in a direct line below QML1384L. The deposit is the lowest found so far on Mount Etna. This deposit is unlike any found on Mount Etna, however, it occurs closest to the base of the QML1384L. It is here considered to be part of the Elephant Hole Cave system, however, it may be independent of all accumulations on the mountain. A large wedge of limestone covers any potential connection between QML1384L and QML 1385 below it.

*Stratigraphic context.* Although the relationship of the deposit to the Elephant Hole Cave system is unclear, it is considered older than both QML1312 and QML1384 based primarily on the preservation of the bones, cementing of the breccia and great depth on the mountain.

*Breccia components.* The bone breccia contains deep red coloured clays, well sorted, well rounded pebbles and gravel and abundant fossilised bones and teeth. The breccia is heavily cemented but lacks distinctive speleothem genesis. Clasts of gravels are distinctly allochthonous with few parent limestone fragments.

*Bone preservation.* Disarticulated, slight reworking and rounding of dark-coloured bones. The majority of the bones are discoloured to some degree with crystalisation occurring within the bone. Long bones are usually found in parallel orientations but are not associated.

*Tooth preservation.* Variably preserved either within jaws, isolated and complete, or isolated and tumbled with smoothed edges.

*Shell preservation.* Rare.

*Facies Interpretation.* QML1385 is a complex mixture of accumulation processes. Bones and teeth are variably preserved and show differing degrees of preservation and alteration. A small portion of the bones and teeth are tumbled and rounded indicating stream or channel deposition. Many bones, especially frog ilia and mammal and bird limb bones show signs of predation, including bite marks (bat) and semi digestion (owl). The site is interpreted as a mixed deposit of material accumulated by reworking and water transportation of a predator accumulation. The material was then washed deep within the mountain to form well-sorted stream gravel deposits. Lack of travertine clasts or travertine development may indicate the deposition into a water-filled pool or a recently opened chamber.

## LIMESTONE RIDGE

Limestone Ridge occurs directly to the east and southeast of Mount Etna (Fig 1, C) and may have been connected to Mt. Etna in the past. The ridge is bisected by a large siltstone/mudstone unit of the Mount Alma Formation, therefore, the cave systems presented herein are best described in two sections, northwest Limestone Ridge and southeast Limestone Ridge. The limestone blocks do not dip to the southeast as seen at Mount Etna and overall cave system development is along a horizontal joint axis.

Within a horizontally controlled joint system phreatic enlargement has developed long, 'ballroom' shaped and sized chambers. The presence of massive speleothems illustrates a long vadose history. Some horizontal development of the caves has been due to the influence of intrusive sills of volcanogenic material, such as Ball Room Cave J8 and Lost Paradise Cave J7 (Shannon, 1970a).

## NORTHWEST LIMESTONE RIDGE

### Johansen's cave system

JOHANSEN'S CAVE J1 AND J2. *"This is at present the largest cave in the Mt Etna district"* Shannon (1970b: 29).

Johannsens Cave is characterised by its abundance of bat guano. In 1919 guano mining began in Johansen's Cave. A discovery by P.H. Ebbott of a mandible of *Sarcophilus laniarius* (Longman, 1921) from within a guano matrix may be attributed to guano mining in Johansen's or Bee Cave. In 1926 Whitehouse recovered a small surface collection of bones from the guano in Johansen's Cave, all being from modern local species. In 1972 Mike Murray collected kangaroo mandibles, an edentulous *Sarcophilus harrisii* mandible and a crocodilian premaxilla from Lower Johansen's Cave. The mandibles were obviously from guano accumulations as guano still adheres to the bone. A note on the specimen label for the crocodile premaxilla (QMF17071) reads "In flowstone bed, above Tas. Devil level, Lower Johansen's Cave.".

In 2002 the author visited Johansen's Cave, in particular Lower Johansen's Cave (J2), to relocate the flowstone bed with a guano unit below it. A distinctive thick (10-30cm) flowstone bed occurs along a small section of the back chamber with a large unit of mined guano below it. Preliminary inspection of the chamber located large vertebrate bones, including macropod metarsals within the flowstone and similar-sized but differently preserved bone in the guano. The flowstone bed forms a false floor across a small portion of the chamber with a secondary filling of guano.

QML1314, Guano bed below flowstone *Stratigraphic context.* Guano occurs throughout the cave and has an amorphous sedimentological structure. It is considered younger than the flowstone unit because of the false floor nature of the flowstone.

*Breccia component.* Fine-grained dark brown to black guano, heavily organic; large and small bones of variable size and parent limestone fragments.

*Bone preservation.* Disarticulated, well preserved bone with long bones preserving ephiphyses.

*Tooth preservation.* Variably preserved jaws with teeth preserved or isolated.

*Snail preservation.* Abundant, complete snail shells. Colour patterning present.

*Facies Interpretation.* A guano deposit with minor stream and channel movement within a large chamber.

QML368, FLOWSTONE (FALSE FLOOR) UNIT *Stratigraphic context.* A distinct false floor developed over an older sediment, which has been subsequently eroded leaving the false floor. Guano fills within a vacuity under the false floor. Thus, the flowstone unit is considered to be older than the guano beneath it.

*Breccia components.* Fine-grained yellow to brown clays with very well preserved, heavily cemented travertine. Numerous large bones and land snails occur within these flowstone bands.

*Bone preservation.* Disarticulated. Well preserved bones with most epiphises preserved.

*Facies Interpretation.* Flowstone false floor.

*Surface collection*: no stratigraphic context.

SHUFFLE CAVE NO E NO: bone collection QML371

OLDER TIMBERS CAVE J31: surface collection QML372 & 1315

## SOUTHEAST LIMESTONE RIDGE

### Mini cave system

MINI CAVE J12. *"Small horizontal ... active inflow cave. The single entrance leads to a tunnel cavern 60 feet long then a short crawl to an end [second] chamber"* (Shannon, 1970b: 32).

At the end of the first chamber is a small shelf of heavily cemented bone breccia. The existing breccia is the remainder of a more substantial deposit that would have filled at least 40% of the first chamber.

QML1284, MINI CAVE CHAMBER BRECCIA, *Stratigraphic context.* The chamber breccia occurs lower on Limestone Ridge than both surface breccias (QML1284a and QML1382), however, they are considered to be contemporaneous deposits. QML1284a illustrates an entrance facies, which would be expected to occur above the QML1284 section, feeding material into the chamber.

*Breccia components.* Consists of fine-grained yellow to red coloured clay, bedded travertine, small angular clasts of parent limestone, allochthonous siltstone and serpentinite, small black goethitic and lighter coloured carbonate pisolites. The oxide pisolites are considered to be allochthonous, the carbonate pisolites autochthonous (cave pearls). The sediments are layered with speleothem, producing distinct sections throughout the deposit. These layers are continuous throughout the deposit and are interpreted as a series of sump deposits flowing into permanent rim pools.

*Bone preservation.* An articulated assemblage of small cave dwelling species such as snakes, frogs and bats. Bones well preserved in a halo of carbonate. Bones vary in size from tiny osteoderms to pockets of larger bone up to 100mm in size. All skeletal elements are well preserved, even the minute osteoderms from skinks. Little evidence of bone gnawing or digestion from predators.

*Tooth preservation.* Teeth usually in jaws and well preserved tooth rows, mostly molar rows and isolated incisors. Majority of teeth are from small taxa, however, isolated teeth from large-sized taxa occur randomly in the lenses.

*Shell preservation.* Snail shells well preserved, usually complete shells of varying sizes.

*Facies Interpretation.* Presence of distinct rim pool formations (basin-shaped travertine, abundant carbonate pisolites, and sorting of sediment matrix) indicates the deposit was at the base of a chamber being fed from above. The entrance is thought to have been higher than the current Mini Cave entrance and QML1284a is in a suitable position to be this entrance facies. The abundance of articulated or associated specimens indicates that many vertebrates including frogs, bats, rodents and snakes inhabited the chamber.

QML1284A, ABOVE MINI CAVE. Located above and to the northwest of the Mini Cave entrance is a heavily weathered bone breccia, which is interpreted as the upper level of the Mini Cave System, and an old cave chamber collapse.

*Stratigraphic context.* QML1284a deposit sits above QML1284 sediments but is considered to be relatively contemporaneous as it is believed that QML1284a is the entrance facies for the same series of accumulations making up the deeper rip pool deposits of QML1284. QML1382 is a lateral extension of the QML1284a entrance facies, therefore, is of similar age also.

*Breccia components.* Pink-grey coloured clay, heavily cemented with thinly bedded travertine throughout. Irregular bedding within breccia blocks. Large clasts of parent limestone, with smaller clasts of oxide and carbonate pisolites, allochthonous gravels and large calcite vugs.

*Bone preservation.* Well preserved, complete bones and associated specimens. Bones showing predation and partial digestion. Snail shells complete and associated with travertine.

*Tooth preservation.* Teeth usually in jaws and well preserved.

*Shell preservation.* Well preserved, complete.

*Facies Interpretation.* Large angular limestone clasts and irregular bedding suggests a facies close to an entrance. The presence of a distinct predator accumulation and a small contribution of larger vertebrate remains suggests a chamber was close to an entrance, which was big enough to support a bat or owl's roost.

QML1382, LEO'S LUNCH SITE. Located to the north of QML1284a, QML1382 is interpreted as a lateral extension of the QML1284a collapse line.

*Breccia components.* A grey-pink, heavily cemented bone breccia with large clasts of parent limestone, smaller clasts of flowstone, pisolites and allochthonous sediment.

*Bone preservation.* Small grain-sized fragments , isolated limbs and vertebrae within flowstones.

*Tooth preservation.* Isolated teeth.

*Shell preservation.* Snail shells associated with flowstone.

*Facies Interpretation.* A lateral extension of the entrance facies of QML1284a, with greater flowstone development and irregular bone accumulations.

*Surface collections*: no stratigraphic context.

LOST PARADISE CAVE J7: bone collection, stream channel first chamber.

BALL ROOM CAVE J8: bone collection, stream channel southern end of main chamber.

## OLSEN'S CAVE SYSTEM

**Olsen's cave.**

*"Essentially only one cave system of sixteen interconnected caverns, usually joint-controlled*

*and of varying dimensions...*" Shannon (1970b: 36).

*Stratigraphic context.* Unknown, however, bone preservation suggests relatively young deposit.

*Breccia components.* Dark brown coloured clay sediment. Loosely consolidated and cemented cave floor sediment. No major clasts present.

*Bone preservation.* A mass of disarticulated, unsorted, tightly compacted fragmentary bone.

*Tooth preservation.* Jaws with teeth and most molar rows. Exclusively small vertebrates.

*Shell preservation.* Nil.

*Facies Interpretation.* Tightly compacted bone accumulation of predominantly small vertebrate remains suggests a typical predator accumulation such as an owl's roost accumulation. Some encorporation of isolated macropod teeth.

## KARST GLEN SYSTEM

To the southwest of Olsen's Cave is another isolated outcrop of limestone known as Karst Glen. Several small to medium sized caves occur in this limestone block and possess associated fossil deposits. Tall karst towers on the northern aspect of the limestone outcrop demarcate a collapsed cliff line following an intersecting vertically jointed system. These collapses have exposed a series of bone breccias and cemented cave floor sediments. Amongst the karst scree, several in situ fossil deposits can be found, generally near to, or beneath, a present cave entrance. Within the chambers, deep sequences of breccia are associated with extensive speleothems. Collections were not made within the caves of these breccias, however, outcrops of surface breccia were located and collected.

### **QM1411-1414, KG3 surface breccia**

QML1411, KG3 BRECCIA UPPER BRECCIA SITE. Located as an exposed fissure deposit near the top of the karst limestone at Karst Glen, QML1411 connects with the sediment found deeper within the limestone caverns. Lithologically it is unique amongst the cave deposits for central eastern Queensland being a markedly pisolitic conglomerate rather than a breccia..

*Stratigraphic context.* QML1411 occurs high on the open karst as a fissure deposit dipping at approximately 45° and running the length of a NW joint. It is stratigraphically higher than any of the other units currently at Karst Glen and is considered to be a very old fissure fill system. The age of the sites in relation to the other sites on Karst Glen is unknown.

*Breccia components.* The rock unit at QML1411 is best considered a pisolitic conglomerate. The majority of the unit contains large and small, well rounded conglomerate of black oxide pisolites. The rock is heavily cemented with the matrix a grey-coloured carbonate clay. Small clasts of parent limestone occur throughout the conglomerate.

*Bone preservation.* Very well rounded and reworked medium-sized bones that are heavily oxidised and shiny black in colour and lustre.

*Tooth preservation.* Nil.

*Shell preservation.* Nil.

*Facies Interpretation.* A heavily reworked channel fill occurring within the confines of a limestone fissure.

QML1412 & QML1413, KG3 B ENTRANCE BRECCIA.

QML1412 and QML1413 occurs beneath and to the southeast of "B" entrance within the KG3 Cave complex at Karst Glen. The unit follows a collapsed joint running NE-SW. The breccia is the remnant sediment fill within the vertical joint that has collapsed. Several of the blocks are *in situ*, forming the source for a large breccia scree found working its way downslope throughout the thick vegetation. Large patches of flowstone exposed on the surface can also be found closer to the present cliff line.

*Stratigraphic context.* QML1412 and QML1413 are of unknown stratigraphic context to other sites on KG3 and within the Cave systems. As the deposits are all joint controlled, each joint may contain contemporaneous sediment without stratigraphic contact.

*Breccia components.* A fine grained, red coloured matrix that is heavily cemented. Very small allochthonous gravel and pisolite clasts. Sediment is clay dominant. Weathered flowstone found in patches throughout the site.

*Bone preservation.* Bone mostly small and well sorted into fine lenses forming the main irregular bedding planes. Finest portion of bone material, small and sand grain-sized. Bone well preserved, however, most elements are fragmentary with epiphyses missing.

*Tooth preservation.* Teeth usually associated with jaws. Almost entirely comprised of small jaws of rodents, possums, bats and dasyurids. Very few larger vertebrates present.

*Shell preservation.* Very little shell present. Some well preserved isolated large snails.

*Facies Interpretation.* The lack of large angular limestone clasts, patchy travertine and abundant clay load indicates a non-entrance facies. The fine lenses of grain-sized bones and massive accumulation of small vertebrates indicates a possible predator accumulation.

### MARMOR QUARRY

QML1420.

Bone breccia collected by Bartholomai in 1964

*Stratigraphic context.* Unknown.QML1420 has been treated as a single fauna because none of the fossils are in stratigraphic context. Two factors suggest that the fossils have been derived from similarly aged sediment, probably the same breccia: 1. The lithology of the matrix adhering to all of the material collected is very similar. When known sites of different age are compared at Mount Etna, the matrix differs dramatically in sediment colour, cementation and bone preservation (e.g. QML1312 versus QML1311). Therefore, it seems likely that the material from Marmor Quarry is derived from the same unit. 2. Two collections have been used for this analysis: One by Longman in the 1920's and one by Bartholomai in the 1960's. Both collections used the mine manager of-the-day as a source of historical knowledge for site location, plus they both collected similar fauna, such as *Macropus titan, M. agilis siva,* and *Sarcophilus laniarius.*

Both collections contain similar species of rodents and bandicoots, with the small mammals derived from Bartholomai's collection via acid etching of bone breccia. This breccia also contained megafauna such as *Macropus titan.*

*Breccia components.* Grey to brown clay, lightly cemented; clasts of limestone only.

*Bone preservation.* Bone preserved as grain-sized fragments, isolated large long bone elements and occasional large vertebrate remains.

*Tooth preservation.* Small-sized vertebrates are generally preserved as isolated teeth without jaws. Large-sized vertebrates present as isolated mandibles and maxillae with preserved teeth.

*Shell preservation.* Isolated large snails.

*Facies Interpretation.* The sediment type and bone preservation is very similar to the guano found in Lower Johansen's Cave, the major difference being the degree of cementation. Marmor Quarry sediment is considerably more cemented than the guano found at Lower Johannsen's Cave. It is therefore considered that the breccia recovered by Bartholomai in 1964 comes from a cemented guano deposit.

## FAUNAS

Many of the sites individually represent diverse faunas and their constituent taxa are tabulated (Tables 1-3, Appendix 1). Higher level taxa which are represented by few or one elements but are noreworthy are listed below. In addition the murids are listed below but will be described in another work.

### UNDESCRIBED TAXA

Teleost indet. QMF51442, vertebra, QML368.

Microchiropterans; QMF48001-48108; QMF48160-QMF48165; All localities (except QML1420).

Bats are found in all faunal assemblages except QML1420 and range in size from very small species of *Miniopterus,* to the very large *Macroderma gigas* (Fig. 29A-E.). Identification of the numerous small species of bats was outside the scope of the present study.

Murids: Rodents are a conspicuous element of all sites and faunal assemblages. At least ten genera have been identified (Author and H. Godthelp). The taxa range in size from the large arboreal *Melomys/Uromys* and aquatic *Hydromys*, to the very small arboreal *Pogonomys* and terrestrial *Leggadina.* Specific identifications will be determined in a full review of the rodents. A preliminary list is provided below with identified specimens.

**Conilurus** sp. Fig. 30A: QMF52052; QML1312.

**Hydromys** sp. QMF52056; QML1420.

**Leggadina** sp. Fig. 30B: QMF52040-QMF52042, QML1312; Olsen's Cave; QML1314.

**Uromys/Melomys** sp. Fig. 30C-D; QMF52014-QMF52021; QML1284; QML1284a; QML1313; QML1420; QML1311; QML1384L.

**Mesembriomys** spp. QMF52028-QMF52032, QML1284; QML1384L; QML1385; QML1313; QML1311.

**Notomys** spp. Fig. 30I; QMF52036-52039; QML1312.

**Pogonomys** sp. nov. Fig. 30G QMF52022-QMF52027; QML1313; QML1284; QML1284a; QML1384U; QML1384L; QML1385; QML1311.

**Pseudomys** spp. Fig. 30E-F; QMF52043-QMF52051; All Localities.

**Rattus** spp. Fig. 30J; QMF52033- QMF52035; QML1312; QML1384U; Olsen's Cave; QML1420.

**Zyzomys** spp. Fig. 30H; QMF52053-QMF52055; QML1284; QML1284a; QML1312.

## SYSTEMATIC PALAEONTOLOGY

### Order ANURA Rafinesque, 1815
### Family HYLIDAE Rafinesque, 1815

### **Cyclorana** Steindachner, 1867

### **Cyclorana** sp.
(Fig. 4G)

MATERIAL. QMF51443 & QMF51444 ; Olsen's Cave.

Two ilia represent this genus. Both ilia possess very large acetabular fossae with thin acetabular rims; distinct but small dorsal acetabular expansion; small and rounded ventral acetabular expansion; narrow preacetabular zone; slight curvature of the ilium; distinct dorsal prominence; anteroventrally and laterally orientated dorsal protuberance. Dorsal prominence almost entirely anterior of the acetabular rim. Superior acetabular rim margin above the level of the ventral margin of the ilial shaft. Lateral rim and medial groove absent. Ilial crest absent.

Identified as *Cyclorana* on comparison with Tyler's description of the genus (Tyler, 1976; Tyler et al.,1994). Identified as being close to *Cyclorana cultripes* by the presence of the large acetabular fossa, distinct dorsal prominence and protuberance and laterally projecting protuberance. Comparative specimens of the many species of *Cyclorana* were not available for this study, therefore, no specific assignment is warranted.

### Litoria/Nyctimystes

Menzies et al. (2002) illustrated the problems associated with identifying fossil hylids from their pelvic elements, especially differentiating species of *Litoria* and *Nyctimystes*. Using the diagnostic features described by Tyler (1976) and Menzies et al. 2002) for *Litoria* and *Nyctimystes*, it was clear that both these taxa are present within the faunal assemblages. Identification to species level was not possible, except for those fossil specimens closely allying taxa with available comparative specimens such as *Litoria caerulea*.

Specimens assigned to *Litoria* were so based on the presence of the following distinctive features; 1. Ovoid dorsal protuberance, 2. Dorsal ilial crest absent, 3. Large acetabular fossa. Specimens assigned to *Nyctimystes* were so based on the presence of the following additional features to those seen in *Litoria*; 1. Ventral acetabular expansion rounded. 2. Very broad preacetabular zone.

### **Litoria** Tschudi, 1838

### **Litoria** sp. 1
(Fig. 4D)

MATERIAL. QMF51445; QML1385.

Small *Litoria* with: 1. acetabular fossa large and shallow with distinct peripheral rim. 2. dorsal prominence anterior to acetabular rim. 3. dorsal protuberance a distinct ovoid, laterally developed, knob. 4. small fossa posterior of the protuberance and at the base of prominence. 5. ridge runs anteriorly from base of protuberance to medial side of ilial shaft. 6. Ilial shaft slightly curved. 7. dorsal acetabular expansion and ventral acetabular expansion reduced. 8. narrow preacetabular zone. 9. broad ilial shaft.

Differs from all other *Litoria* within the assemblages by possessing an anterior ridge of the dorsal prominence running from the base of the dorsal protuberance to the medial side of the ilial shaft. Differs from *Litoria* sp 2 by possessing a narrow preacetabular zone and a shorter dorsal acetabular expansion. Differs from *Litoria* sp. 3 by being smaller and possessing a smaller dorsal protuberance and a narrower preacetabular zone. Differs from *Litoria* sp. 4 by being smaller and having a more ovoid, and better-developed dorsal protuberance.

### **Litoria** sp. 2
(Fig. 4E)

MATERIAL. QMF51446; QML1385.

Medium-sized *Litoria* with the following: 1. broad, oval, and shallow acetabular fossa. 2. distinct acetabular rim. 3. Narrow preacetabular zone. 4. Elongàte dorsal acetabular expansion. 5. Well developed and rounded ventral acetabular expansion. 6. Low dorsal prominence. 7. Dorsal protuberance ovoid and laterally developed. 8. Ilial shaft straight.

Differs from *Litoria* sp. 3 by being larger, having a smaller dorsal protuberance and an elongate dorsal acetabular expansion, which extends superiorly of the line of the dorsal protuberance. Differs from *Litoria* sp. 4 by being larger, possessing a well-developed dorsal protuberance and broad preacetabular zone.

### **Litoria** sp. 3
(Fig. 4B)

MATERIAL: QMF51447-51449; QML1385.

A medium-sized *Litoria* possessing the following features: 1. Large, half-moon shaped acetabular fossa. 2. Reduced dorsal acetabular expansion. 3. Ventral acetabular expansion well developed and rounded. 4. Narrow preacetabulae zone. 5. Dorsal prominence reduced. 6. Dorsal protuberance as a massive ovoid knob with a distinct ventral groove.

Differs from *Litoria* sp. 4 by being larger and possessing an enormous ovoid dorsal protuberance with a ventral groove.

TABLE 1. Faunal lists for fish and amphibians

| | QML368 | QML1284 | QML1284a | QML1312 | QML1314 | QML1384U | QML1385 | Olsen's Cave |
|---|---|---|---|---|---|---|---|---|
| Teleosti indet | x | | | | | | | |
| *Cyclorana* sp. | | | | | | | | x |
| *Litoria* sp. 1 | | | | | | | x | |
| *Litoria* sp. 2 | | | | | | | x | |
| *Litoria* sp. 3 | | | | | | | x | |
| *Litoria* sp. 4 | | x | | | | | x | |
| *Litoria caerulea* | | | | | x | | | |
| *Nyctimystes* sp. 1 | | | | | | | x | |
| *Nyctimystes* sp. 2 | | x | x | | | | | |
| *Etnabatrachus maximus* | | x | | | | | x | |
| *Crinia* sp. | | | | | | | x | |
| *Kyarranus* sp. | | x | x | | | x | x | |
| *Limnodynastes* sp. 1 | | | | | | | x | |
| *Limnodynastes* sp. 2 | | x | | x | | | x | |
| *Limnodynastes* sp. 3 | | | x | | | | | |
| *L. tasmaniensis* sp. grp. | | | | | | | x | |
| *L. spenceri* sp. grp. | | | | | | | x | |
| *L.* sp. cf. *L. peronii* | | x | | x | | | | |
| *Lechriodus* sp. | | x | | | | | | |
| *Neobatrachus* sp. | | | | | | | x | |
| microhylid sp. 1 | | x | x | | | | | |
| microhylid sp. 2 | | x | x | | | | | |
| microhylid sp. 3 | | x | | | | | | |

### **Litoria** sp. 4
(Fig. 4C)

MATERIAL. QMF51450-51456; QMF51463-51464, QML1385; QML1284.

A small-sized *Litoria* possessing the following features; 1. Reduced, triangular-ovoid acetabular fossa. 2. Dorsal acetabular expansion and ventral acetabular expansion reduced. 3. Dorsal prominence reduced. 4. Dorsal protuberance conical-shaped and laterally produced. 5. Ilial shaft straight.

Differs from *Litoria conicula* by possessing a larger conical protuberance, smaller acetabular fossa, less developed ventral acetabular expansion and a narrow preacetabular zone.

### **Litoria caerulea** (White, 1790)

MATERIAL. QMF51457-51462; QML1314.

A large-sized *Litoria,* possessing the following features: 1. Medial and lateral groove absent. 2. Dorsal acetabular expansion reduced. 3. Ventral acetabular expansion gently curved. 4. Dorsal prominence and protuberance low on the ilial shaft. 5. Dorsal protuberance elongate-ovoid and slightly produced laterally.

Closely resembles comparative material available for *L. caerulea* from Queensland, especially the distinctly low dorsal prominence and ovoid protuberance.

Two smaller morphs of *Litoria* are present in subfossil accumulations from QML1314. It is uncertain whether these represent different taxa or a highly variable *Litoria caerulea.*

## **Nyctimystes** Stejneger, 1916

### **Nyctimystes** sp. 1
(Fig. 4F)

MATERIAL. QMF51465; QML1385.

A large *Nyctimystes* possessing the following features of the ilium; 1. Moderately large triangular acetabular fossa. 2. Reduced dorsal acetabular expansion. 3. Ventral acetabular expansion gently rounded and expanded, spatulate-shaped. 4. Preacetabular zone broad. 5. Dorsal prominence low with small indistinct ovoid protuberance. 6. Posterior ridge of dorsal prominence tapers to anterior base of dorsal acetabular expansion. 7. Ilial shaft straight, medio-laterally compressed and broad.

Differs from *Nyctimystes* sp. 2 by lacking a well-developed dorsal prominence and laterally developed dorsal protuberance. Further differs by lacking a distinctive groove ventral of the dorsal protuberance.

### **Nyctimystes** sp. 2

MATERIAL. QMF51466-51468; QMF51469-51471, QML1284; QML1284a.

A large *Nyctimystes* possessing the following features of the ilium; 1. Large ovoid acetabular fossa. 2. Reduced and pointed dorsal acetabular expansion. 3. Ventral acetabular expansion rounded and very broad. 4. Preacteabular zone broad and gently curved to the base of the ilial shaft. 5. Dorsal prominence and protuberance low on the ilial shaft. 6. Dorsal protuberance distinct and laterally developed into an elongate-ovoid knob. 7. Beneath the dorsal protuberance runs a distinct lateral groove. 8. Dorsal protuberance above anterior-most margin of acetabular rim.

*Nyctimystes* sp. 2 most closely resembles *N. disrupta* and *N. zweifeli* from illustrations and descriptions available from Tyler (1976) and Menzies et al. (2002).

### **Etnabatrachus** Hocknull, 2003

### **Etnabatrachus maximus** Hocknull, 2003
(Fig. 6B)

MATERIAL. QMF44207, QMF44208; QML1385, QML1284.

A giant frog probably from the Hylidae, based on the large rounded dorsal protuberances. Previously described by Hocknull (2003) and currently endemic to the Plio-Pleistocene of Mount Etna and Limestone Ridge.

## Family LEPTODACTYLIDAE Werner, 1896

### **Crinia** Tschudi, 1838

### **Crinia** sp.
(Fig. 4A)

MATERIAL. QMF51472, QML1385.

A small leptodactylid. Only the rim of acetabular fossa preserved, indicating a large rounded and shallow fossa. Other features include: 1. Dorsal acetabular expansion short and pointed. 2. Ventral acetabular expansion broken and insignificant. 3. Preacetabular zone narrow. 4. Dorsal prominence low and long, running halfway anterior of the acetabular rim. 5. Dorsal protuberance inconspicuous. 6. Long thin median groove running the length of the ilial shaft. 7. Ilial shaft curved and slender.

*Crinia* sp. is identified as *Crinia* based on its small-size, reduced dorsal prominence and protuberance, slender curved ilial shaft, large acetabular fossa and longitudinal medial groove.

### **Kyarranus** Moore, 1958

### **Kyarranus** sp.
(Fig. 5F)

MATERIAL. QMF51488, QMF51489, QMF51490, QMF51491; QML1284a; QML1284, QML1385, QML1384U.

Large sub-triangular acetabular fossa. Acetabular rim distinct and high. Dorsal acetabular expansion expressed as a triangular point at an equivalent height to the dorsal prominence and protuberance. Ventral acetabular expansion narrow and anteriorly projecting. Preacetabular zone narrow. Dorsal prominence high and anterior of acetabular rim. Dorsal protuberance is an elongate antero-dorsally projecting process from dorsal prominence. Small fossa at the posterior base of the dorsal prominence. Ilial shaft long, slender and curved.

*Kyarannus* is a distinctive leptodactylid, possessing an elaborate dorsal prominence and anteriorly projecting protuberance. The combination of this feature with a long, curved ilial shaft and a high acetabular rim identify *Kyarranus* here. Specific placement will be considered in later works.

### **Limnodynastes** Fitzinger, 1843

Tyler et al. (1998) describes all species of *Limnodynastes* as possessing an extremely large dorsal prominence and protuberance, and a high and steep dorsal acetabular expansion of the ilium. Within the genus there is considerable variation of these features, with the development of an ilial crest in some taxa (Tyler 1976). Specimens possessing these features are here assigned to *Limnodynastes*.

### **Limnodynastes** sp. 1

MATERIAL. QMF51473-51474; QML1385.

Acetabular fossa large and high, with a distinct acetabular rim. Dorsal acetabular expansion rises steeply from the shaft to an acute point. Ventral acetabular expansion is gracile and rounded. Preacetabular zone narrow and runs beneath the rim of the acetabulum. Dorsal prominence rises high above ilial shaft and positioned anterior of the acetabular margin. Dorsal prominence antero-dorsally oriented and distinct. A short

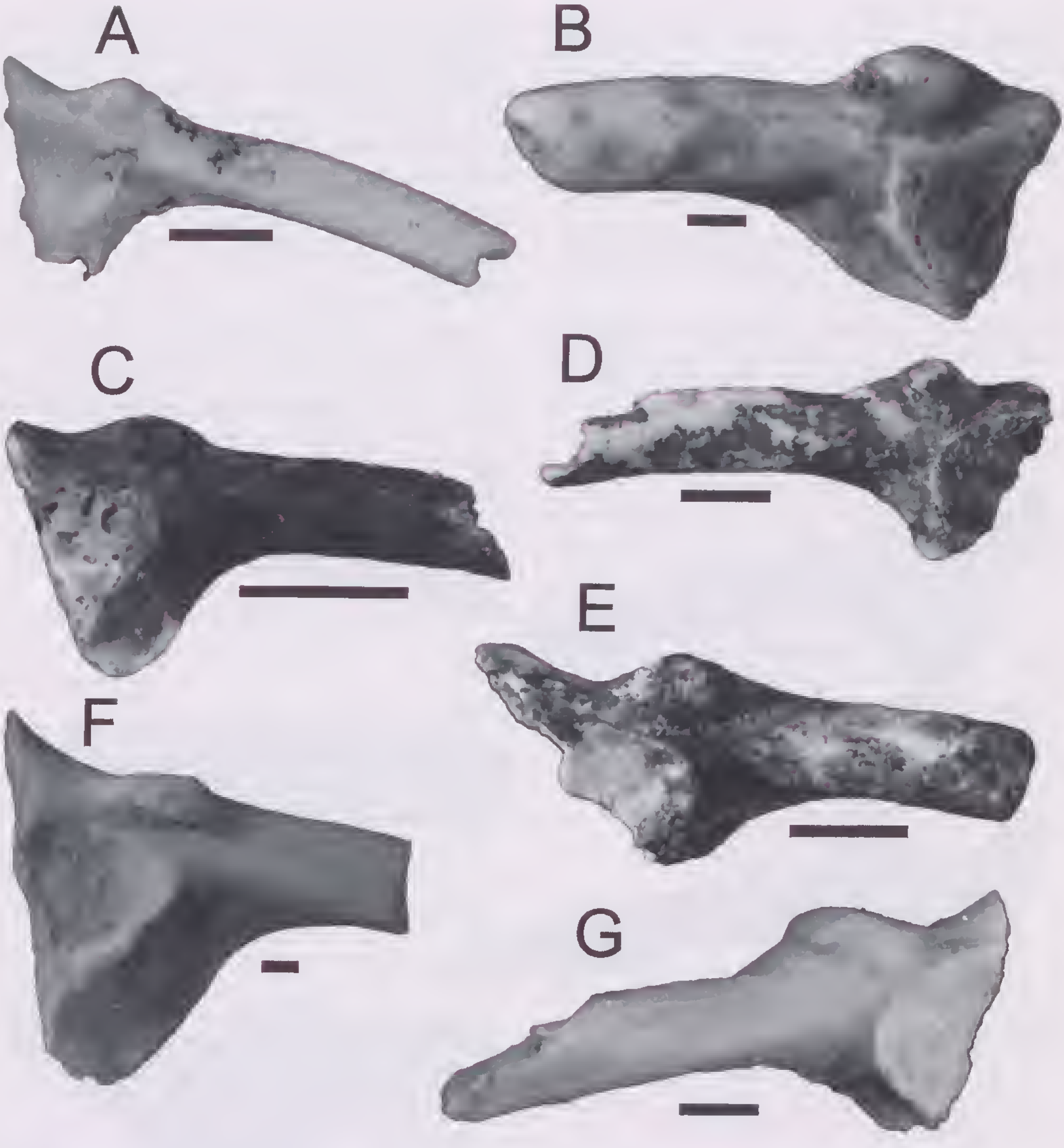

FIG. 4. A, *Crinia* sp.; QMF51472, right ilium. B, *Litoria* sp. 3; QMF51447, left ilium. C, *Litoria* sp. 4; QMF51450, right ilium. D, *Litoria* sp. 1; QMF51445, left ilium. E, *Litoria* sp. 2; QMF51446, left ilium. F. *Nyctimystes* sp. 1; QMF51465, left ilium. G. *Cyclorana* sp.; QMF51443, left ilium. Scale bar = 1mm.

lateral groove runs 1/3 the length of the ilial shaft, originating just anterior to the base of the dorsal prominence. A long median groove runs the length of the ilial shaft. Ilial shaft slightly curved.

Differs from *Limnodynastes* sp. 2 by possessing a median groove, a larger dorsal prominence and protuberance and missing a pocket on the ventral acetabular expansion, situated beneath the acetabular rim. Differs from *Limnodynastes* sp. 3 by lacking a lateral groove ventral to the dorsal prominence and possessing a better-developed dorsal protuberance. Differs from *Limnodynastes tasmaniensis* sp. group by possessing a median groove on the ilium. Differs from *Limnodynastes spenceri* sp. group by lacking a dorsal ilial crest. Differs from *Limnodynastes peronii* by being much smaller and lacking the massive development of the dorsal prominence and protuberance.

### **Limnodynastes** sp. 2
(Fig. 5E)

MATERIAL. QMF51476-51477, QMF51478-51481, QMF41864, QMF41856, QMF33383; QML1284, QML1385, QML1312.

Acetabular fossa broad and shallow, subtriangular in lateral view. Acetabular rim high. Dorsal acetabular expansion elongate and pointed reaching much higher than the tip of the dorsal protuberance. Ventral acetabular expansion rounded. Preacetabular zone narrow, running beneath the acetabular rim. A dorsal pocket occurs beneath the rim and at the origin of the ventral acetabular expansion. Dorsal prominence low and inconspicuous. A small fossa is located at the posterior base of the prominence. Dorsal protuberance equally inconspicuous being low and only slightly conical. Ilial shaft laterally compressed, narrow and curved.

Differs from *Limnodynastes* sp. 3 by possessing a pocket on the ventral acetabular expansion and a lower dorsal prominence. Differs from *Limnodynastes tasmaniesis* group

FIG. 5. A, *Limnodynastes* sp. 3; QMF51486, right ilium. B, *Limnodynastes* sp. cf. *L. peronii*; QMF41793, left ilium. C, *Limnodynastes* sp. 1; QMF51473, right ilium. D, *Limnodynastes spenceri*; QMF51484, left ilium. E, *Limnodynastes* sp. 2; QMF51476, right ilium. F. *Kyarranus* sp.; QMF51489, right ilium. Scale bar = 1mm.

by possessing a lower prominence, indistinct protuberance and lacking a lateral groove. Differs from *Limnodynastes spenceri* group by lacking a dorsal ilial crest. Differs from *Limnodynastes peronii* by lacking a massively developed dorsal prominence and protuberance.

### **Limnodynastes** sp. 3
(Fig. 5A)

MATERIAL. QMF51486; QML1284a.

Acetabular fossa ovoid and deep, rim elevated. Dorsal acetabular expansion elongate and pointed dorsally. Ventral acetabular expansion rounded and gracile. Preacetabular zone narrow. Lateral groove absent. Dorsal prominence low. Dorsal protuberance distinct, as a point projecting antero-dorsally from the prominence. Ilial shaft slightly curved. Median groove running the length of the ilial shaft.

Differs from *Limnodynastes tasmaniensis* group by possessing a median groove along the shaft and lacking a lateral groove. Differs from *Limnodynastes spenceri* group by lacking an ilial crest. Differs from *Limnodynastes peronii* by lacking a massive dorsal prominence and protuberance.

### **Limnodynastes tasmaniensis** Günther, 1858 sp. group.

MATERIAL. QMF51482-51483; QML1385.

Acetabular fossa distinctly rounded and elevated from the shaft. Dorsal acetabular expansion elongate, tapering to a point at an equivalent level to the dorsal protuberance. Ventral acetabular expansion narrow and tapered. Preacetabular zone narrow and concave. Lateral groove present on the shaft just ventral to the dorsal prominence. Dorsal prominence distinct, triangular shaped. Dorsal protuberance elongate, ovoid and projecting antero-dorsally. Ilial shaft curved.

Differs from *Limnodynastes spenceri* group by lacking a dorsal ilial crest. Differs from *Limnodynastes peronii* by lacking the massive dorsal prominence distinctive of *L. peronii.*

### **Limnodynastes spenceri** Parker, 1940 sp. group.
(Fig. 5D)

MATERIAL. QMF51484-51485; QML1385.

Small ilium possessing a distinct dorsal ilial crest and prominent antero-dorsally oriented dorsal protuberance. Acetabular fossa small and rounded. Acetabular rim distinct. Dorsal acetabular expansion unknown in the specimens. Ventral acetabular expansion unknown in specimens. Preacetabular zone narrow and close to the acetabular rim. Ilial shaft relatively straight.

Differs from all other *Limnodynastes* species by possessing an ilial crest. Differs from the only other taxa with ilial crests, *Rana, Mixophyes* and *Lechriodus,* by lacking the extreme dorsal development of the crests.

### **Limnodynastes** sp. cf. **L. peronii** Duméril & Bibron, 1841
(Fig. 5B)

MATERIAL: QMF41793, QMF41801, QMF41812, QMF41821, QMF41827, QMF33380, QMF41863, QMF41865-41866; QML1284; QML1312.

Acetabular fossa large and rounded. Rim elevated and thick. Dorsal acetabular expansion elongate and tapered, steeply pointed. Ventral acetabular expansion rounded and broad. Preacetabular zone narrow and concave. Fossa present at the posterior base of the dorsal prominence. Dorsal prominence distinct and anterior of acetabular rim. Dorsal protuberance large and well developed. Protuberance anterior projecting. Ilial shaft broad and slightly curved.

Specimens assigned to *L. peronii* from QML1284 differ from conspecific specimens from QML1312 in possessing a distinct fossa and a more anteriorly projecting dorsal prominence. This variation is considered to be within the possible range of variation for this taxon.

### **Lechriodus** Boulenger, 1882

### **Lechriodus** sp.
(Fig. 6A)

MATERIAL. QMF51492; QML1284.

Ilial crest present. Dorsal protuberance ovoid and level with the acetabular rim. Dorsal acetabular and ventral acetabular expansions narrow and short. Preacetabular zone narrow. Broad semicircular acetabular fossa. Shallow lateral groove runs the length of the ilial crest.

### **Neobatrachus** Peters, 1863

### **Neobatrachus** sp.
(Fig. 6C)

MATERIAL. QMF51487; QML1385.

Acetabular fossa very small and rounded. Acetabular rim low and distinct from preacetabular zone. Dorsal acetabular expansion very broad and high, coalescing with the posterior margin of the dorsal prominence. Ventral acetabular expansion narrow and pointed. Preacetabular zone narrow and close to acetabular rim. Dorsal prominence is large with a tiny point making up the dorsal protuberance. Ilial shaft nearly straight and laterally compressed.

*Neobatrachus* possesses distinct ilial characteristics not found in other leptodactylids, including the elaboration of the dorsal acetabular expansion and its coalescence with the dorsal prominence, small acetabular fossa and reduced ventral acetabular expansion. Specific assignment is not justified at this stage due to the lack of comparative specimens.

### Family MICROHYLIDAE Günther, 1858

Microhylids have been identified from some of the faunal assemblages based on their small size, very large acetabular fossa, curved shaft and diminutive posteriorly placed dorsal prominence and protuberance.

#### microhylid sp. 1
(Fig. 6C)

MATERIAL. QMF51493-51494, QMF51495; QML1284, QML1284a.

Large rounded acetabular fossa which is distinct from the shaft and possesses a distinct acetabular rim. Dorsal acetabular expansion short and pointed. Ventral acetabular expansion short and rounded. Preacetabular zone narrow and constricted toward the acetabular rim. Dorsal prominence low with a conical protuberance posterior of acetabular rim. Ilial shaft recurved without dorsal crest.

Differs from microhylid 2 by possessing a curved shaft and less ridged dorsal protuberance. Differs from microhylid 3 by lacking a dorsal crest.

#### microhylid sp. 2
(Fig. 6F)

MATERIAL. QMF51496, QMF51497; QML1284, QML1284a.

Acetabular fossa large and rounded. Distinct acetabular rim. Dorsal acetabular expansion and ventral acetabular expansion unknown, however, inferred to be reduced. Preacetabular zone narrow. Dorsal prominence low, dorsal protuberance small and ridged. Ilial shaft slightly curved and slender. Differs from microhylid 3 by lacking a dorsal crest.

#### microhylid sp. 3 cf. **Hylophorbus** Macleay, 1878
(Fig. 6D-E)

MATERIAL. QMF51498; QML1284.

Large rounded acetabular fossa. Distinct acetabular rim, set high above ilial shaft. Dorsal acetabular expansion elongated to a sharp dorsal point. Ventral acetabular expansion anteriorly deflected and rounded. Preacetabular zone narrow. Dorsal prominence inconspicuous, forming the posterior margin of a dorsal crest. Dorsal protuberance elongate and antero-dorsally projecting. Ilial shaft curved. Dorsal crest laterally compressed, angled medially, running almost the entire length of the ilial shaft.

The form of the ilium, distinct ilial crest, and curvature of the shaft ally this taxon very closely to *Hylophorbus* from Papua New Guinea as described and figured in Menzies et al. (2002). More specimens and access to comparative *Hylophorbus* will be needed to clarify its taxonomic placement within the Microhylidae.

## Order TESTUDINES Linnaeus, 1758

### Family CHELIDAE Gray, 1825a

#### chelid indet.
(Fig. 7G-H)

MATERIAL. QMF52061, QMF52062, QMF52063; QML1311(H); QML1384L; QML1311(C/D).

Several pieces of carapace and plastron represent remains of freshwater turtles. The portions of carapace are thick, with distinct suture lines. A single posterior portion of a plastron is very thin and preserves pelvic sutures from the left side.

## Order NEOSUCHIA Benton & Clark, 1988
### Family CROCODILIDAE Cuvier, 1807

#### Mekosuchinae indet.
(Fig. 7A-F)

MATERIAL. QMF51499-51505, QMF52064-52065, QMF17071; QML1311 (H), QML1384L, QML368, QML1313.

Fragmentary remains, including a serrated ziphodont tooth, a portion of an edentulous premaxilla, two partial vertebrae, three scutes, the proximal end of a femur and an ungual represent crocodilians. The tooth has a distinctly serrate carinae and is ziphodont in form. A wear facet can be seen on the ?mesial margin of the tooth. The premaxilla is rounded with three alveoli, linked to one another by thick ridges on the lateral premaxillary margin. The vertebrae are antero-posteriorly compressed and squat, preserving both the condyle and cotyle. Scutes, small and thin, with a flat ventral surface and a keeled dorsal surface. Rows of pits occur on the dorsal surface of the scutes.

FIG 6. A, *Lechriodus* sp.; QMF51492, right ilium. B, *Etnabatrachus maximus*; QMF44208, left ilium. C, *Neobatrachus* sp.; QMF51487, right ilium. D-E, microhylid sp. 3; QMF51498, left ilium in mesial and lateral view. F, microhylid sp. 2; QMF51496, left ilium. G, microhylid sp. 1; QMF51493, right ilium. Scale bar = 1mm.

The overall shape and size of the premaxillary bone, tooth and femur are similar to that of *Baru huberi* (QMF31061) but differs by having a deep reception pit for the first dentary tooth, that breaks the dorsal surface of the premaxilla.

## Order SQUAMATA Oppel, 1811
## Family AGAMIDAE Hardwicke & Gray, 1827

### **Amphibolurus** Wagler, 1830

#### **Amphibolurus** sp.

(Fig. 8D)

MATERIAL. QMF43893; QML1312.

Right maxilla bearing two pleurodont tooth loci, both broken at the base. Nine acrodont tooth loci. The dorsal maxillary process is broken dorsal to the narial basin.

QMF43893 is placed within *Amphibolurus* on the basis of the following combined features: 1. Possessing a significantly reduced, near absent, naris ridge. 2. Dorsal maxillary process constricted superiorly and broad inferiorly. 3. Two pleurodont teeth with $P^1$ approximately three quarters the size of $P^2$. 4. Less than fifteen acrodont teeth. 5. Angular dorsal maxillary process. 6. Hooked anterior profile.

### **Diporiphora** Gray, 1842

#### **Diporiphora** group 2 (*sensu* Hocknull, 2002)

(Fig. 8)

MATERIAL. QMF51507; Olsen's Cave.

A left maxilla bearing one large pleurodont and six acrodont teeth. Maxilla broken posterior to $A^6$. Pleurodont tooth large, recurved and orientated labially. Angulate dorsal maxillary process.

Identified as a species within *Diporiphora* group 2 *sensu* Hocknull (2002) on the basis of the following combined features: 1. Naris ridge absent. 2. Broad dorsal maxillary process, narrowed superiorly. 3. One large caniniform maxillary pleurodont tooth.

### **Hypsilurus** Peters, 1867

#### **Hypsilurus** sp.

MATERIAL. QMF51506; QML1313.

Half of a badly preserved right dentary (Length: 12.13+mm) bearing 11 acrodont and one tiny pleurodont tooth represents a medium-sized agamid. The dentary is broken posteriorly of $A_{11}$ and is gracile, tapering anteriorly with little curvature. Four visible foramina are present on the labial side of the dentary, with the last occurring below $A_{11}$. The dental sulcus is narrow along its length and tapers markedly anteriorly. The dentary symphysis is small and ovoid. Acrodont dentition is badly weathered, however, there are distinct mesoconids and small antero and posteroconids. Tooth size changes markedly between tooth position $A_5$ and $A_6$.

Agamid dentaries are difficult to identify, however, only five Australian agamid genera possess such distinctively diminutive pleurodont dentition of the dentary: *Chelosania*, *Hypsilurus*, *Physignathus*, *Moloch* and *Pogona* (Hocknull, 2002). The fossil is most similar to *Hypsilurus* by sharing one very tiny pleurodont tooth (*Hypsilurus* possesses one or two) and a very gracile, tapered dentary outline. The fossil dentary differs from all of the other four genera by possessing a much more gracile dentary and narrowly tapered dental sulcus. The fossil specimen differs further from *Chelosania* by being larger and possessing less tricuspid acrodont dentition. The fossil differs further from *Physignathus* by being smaller and possessing one versus three pleurodont dentary teeth. The fossil differs further from *Pogona* by possessing less rounded acrodont dentition and relatively shallower posterior and anterior margins.

### **Pogona** Storr, 1982

#### **Pogona** sp. (small morphotype)

(Fig. 8C)

MATERIAL. QMF41969; QML1312.

Left maxilla with the anterior and posterior margins broken. Twelve acrodont teeth present.

*Pogona* has been identified from QML1312 by the presence of the following feature of the maxilla: 1. Posterior region deep. 2. Rounded acrodont teeth with large mesocones. Based on its size, the specimen allies the smaller *Pogona* species, such as *P. mitchelli* and *P. minor*.

### **Tympanocryptis** Peters, 1863

#### **Tympanocryptis** sp. cf. **T. cephalus** Günther, 1867

(Fig. 8A)

MATERIAL. QMF41963; QML1312.

A nearly complete right maxilla, which is broken posteriorly to $A^{12}$. Twelve acrodont and two pleurodont teeth preserved. Dorsal maxillary process broken at the dorsal margin.

Specimens referred here to a species of *Tympanocryptis* have been identified based on the following combined features; 1. Naris ridge present. 2. Naris ridge borders narial basin. 3.

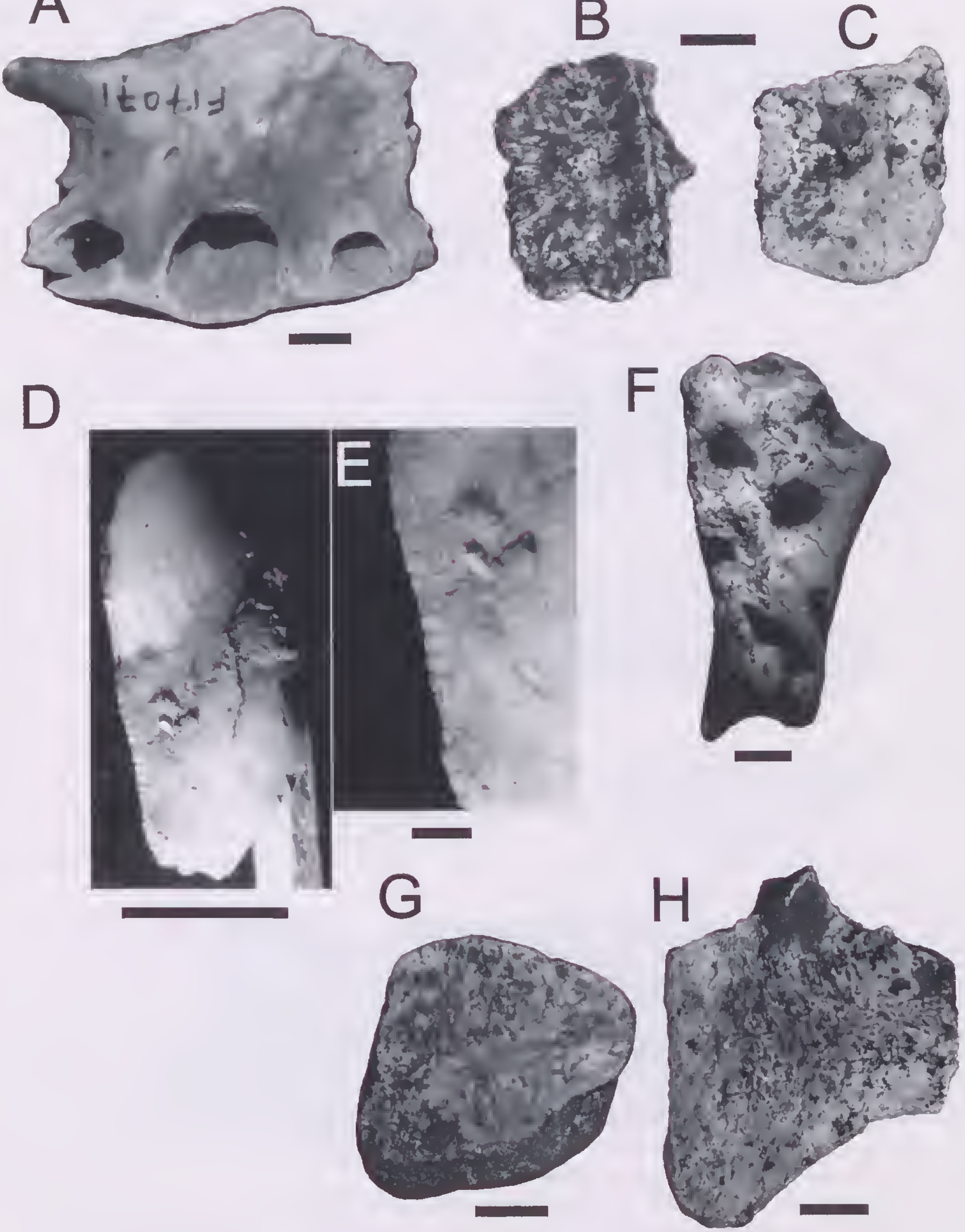

FIG. 7. A-F, Mekosuchinae; A, QMF17071, premaxillary. B, QMF52064, scute. C, QMF52065, scute. D, QMF51503, ziphodont tooth. Scale bar = 5mm. E, QMF51593 closeup of carinae (Scale bar = 1mm). F. QMF51505, scute. G-H, Chelidae; G. QMF52061, carapace. H, QMF52062, plastron.

TABLE 2. Faunal lists for reptiles and birds.

| | QML368 | QML1284 | QML1284a | QML1311H | QML1311CD | QML1312 | QML1313 | QML1314 | QML1384U | QML1384L | QML1385 | QML1420 | Olsens Cave |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| chelid indet. | | | | x | x | | | | | x | | | |
| mekosuchine indet. | x | | | x | | | x | | | x | | | |
| *Amphibolurus* sp. | | | | | | x | | | | | | | |
| *Diporiphora* sp. | | | | | | | | | | | | | x |
| *Hypsilurus* sp. | | | | | | | x | | | | | | |
| *Pogona* sp. | | | | | | x | | | | | | | |
| *Tympanocryptis* sp. cf. *T. cephalus* | | | | | | x | | | | | | | |
| agamid indet | x | x | x | x | x | x | x | | x | x | x | x | |
| *Tiliqua* sp. | | x | | | | | | | | | | | |
| *Tiliqua scincoides* | | | | | | | x | x | | | | | |
| *Cyclodomorphus gerrardii* | | x | x | x | x | | x | | x | x | x | x | x |
| *Egernia* spp. | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Eugongylus* Group | | x | x | | | | | | | | | | |
| *Sphenomorphus* Group (gracile) | | x | x | | | x | x | | | | x | | |
| *Sphenomorphus Group* (robust) | | | | | | x | | | | | | | x |
| gekkonid (large) | | x | x | | | | x | | | | | | |
| gekkonid (small) | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Varanus* sp. 1 | | | | x | | x | | | | | | | |
| *Varanus* sp. 2 | | | | x | x | x | x | | | | | | |
| *Megalania prisca* | | | | | | | | | | | | x | |
| elapid indet. | x | x | x | x | x | x | x | x | x | x | x | x | x |
| pythonine indet. | x | x | x | x | x | x | x | x | x | x | x | x | x |
| typholopid | | x | x | | | | | | | | | | |
| Galliformes | | | | | | x | | | | | | | |
| Gruiformes | | | | | | x | | | | | | | |
| Passeriformes | | x | | | | x | | | | | | | |
| Strigiformes | x | x | x | x | x | x | x | x | x | x | x | | x |

Two unequally-sized pleurodont teeth with $P^2$ caniniform. 4. Distinct notch anterodorsally of $P^1$. QMF41963 shares very close similarities to *T. cephalus*. $P^1$ and $P^2$ are parallel to one another, which is not found in *T. tetraporophora* and *T. intima*. Also, *T. intima* is considerably larger than the specimen and comparative *T. cephalus*. The posterior "molar" acrodont teeth do not show the marked size change typical of *T. lineata* and *T. intima* (Hocknull, 2002). The lateral margin of the premaxillary/maxillary suture is higher and the naris ridge contributes more to this than it does in *T. lineata*. The $P^1$ is very small, which is more usual in *T. cephalus* specimens, than *T. lineata*. The total number of acrodont teeth is unknown in this specimen, however, judging from the amount of missing maxilla, the number of teeth would be thirteen or more. Thirteen or more acrodont teeth in the maxilla is more commonly found in *T. cephalus* with tooth counts of 13-14 than *T. lineata* with 11-13.

### agamid indet.

MATERIAL: QML1284, QML1284a, QML1311, QML1313, QML1384, QML1385; QML1420

Several maxillary and dentary fragments bearing acrodont dentition are recorded in most sites, however, most of these are unidentifiable because they do not preserve the anterior diagnostic elements needed (Hocknull, 2002). The majority of the specimens show characteristics typical of juvenile agamids, including large acrodont teeth relative to jaw depth, lack of distinct wear facets on the acrodont teeth and dental bone, and overall bone fragility.

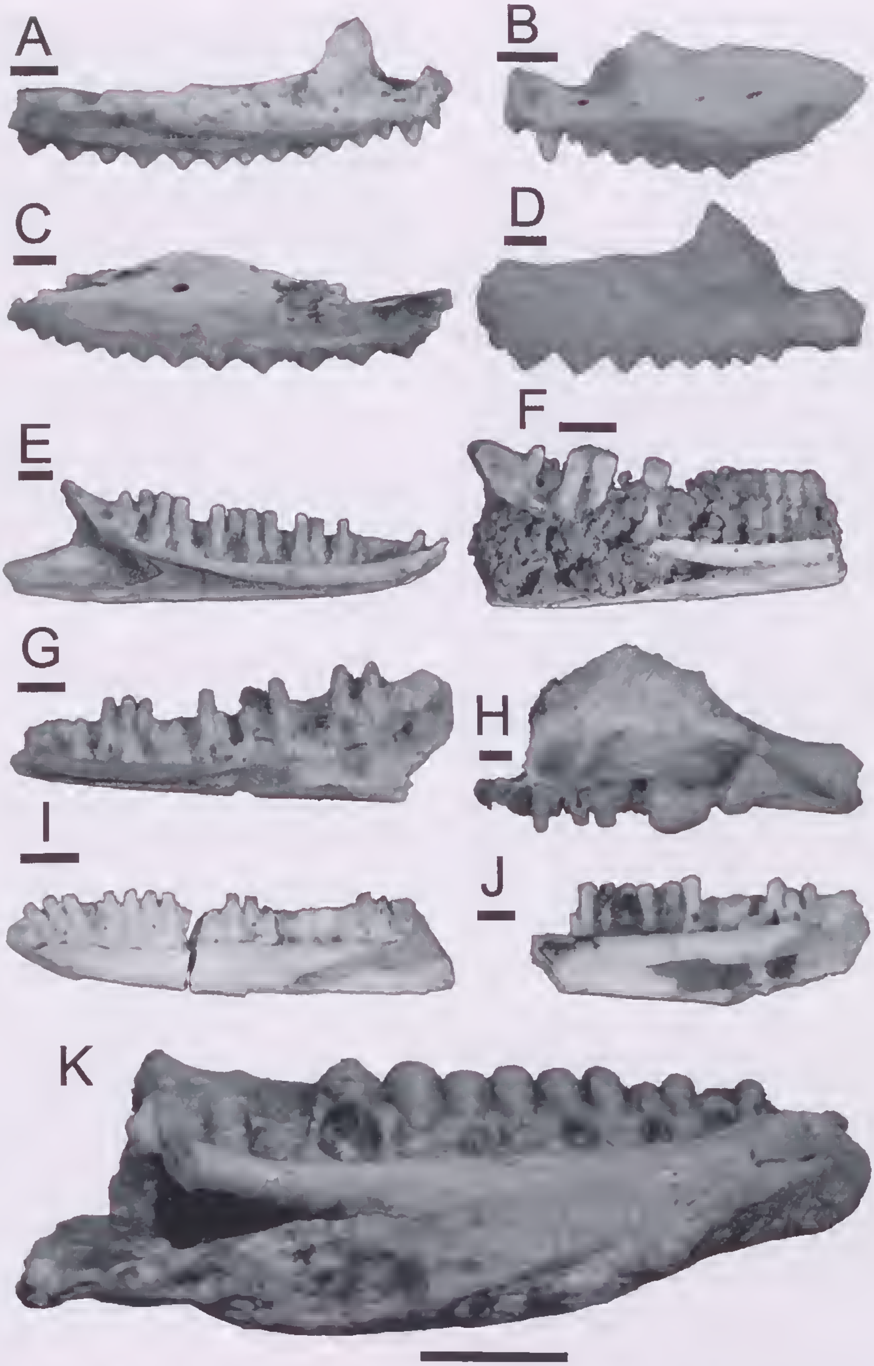

FIG. 8. A-D, Agamidae; A, *Tympanocryptis* sp. cf. *T. cephalus*; QMF41963, right maxilla. B, *Diporiphora* group 2; QMF51507, left maxilla. C, *Pogona* sp.; QMF41969, left maxilla. D, *Amphibolurus* sp.; QMF43893, right maxilla. E-K, Scincidae; E, *Sphenomorphus* group (robust morph); QMF51543, left dentary. F, *Egernia* sp.; QMF51529, left dentary. G, *Sphenomorphus* group (gracile morph); QMF51537, right dentary. H, *Cyclodomorphus gerrardii*; QMF51519, right maxilla. I-J, *Eugongylus* group; QMF51535 & QMF51536, right dentaries. K, *Tiliqua* sp.; QMF51516, left dentary. Scale bar = 5mm.

### Family SCINCIDAE Oppel, 1811

### **Egernia** Group *sensu* Greer, 1979

### **Tiliqua** Gray, 1825

### **Tiliqua** sp nov.
(Fig. 8K)

MATERIAL. QMF51516; QML1284.

A robust left dentary, broken posterior to the splenial notch. Eleven conical, haplodont teeth are preserved with four addition tooth loci. Symphysial crest extends to below the eighth haplodont tooth locus. Symphysis elongate, tapering sharply to the posterior and rounded anteriorly. The labial side of the dentary bone is distinctly inflated to the posterior, giving the dentary a very robust appearance in lateral view. Teeth gradually increase in width toward the posterior, all retaining their conical grooved tooth crowns. Dental shelf deep along its length.

The closed Meckelian groove places this specimen with the *Egernia* and *Eugongylus* groups within the Lygosominae (Greer, 1979). The enlarged posterior conical teeth place this specimen within the *Tiliqua* lineage (Shea, 1990). The presence of a long symphysial crest, bunched haplodont dentition and the absence of a single massive posterior durophagous tooth excludes this specimen from being *Cyclodomorphus*. *Tiliqua* sp. differs markedly from all living and fossil *Tiliqua* so far described and is most probably a new species.

### **Tiliqua scincoides** (White, 1790)

MATERIAL. QMF51517; QMF51518; QML1313, QML1314.

*Tiliqua scincoides* is best represented by a single right dentary possessing nine teeth and twelve tooth loci. The largest tooth is toward the posterior and is characterised by having a rounded durophagous tooth crown . The elongate symphysial crest places this specimen within *Tiliqua*, its size and tooth morphology place it firmly within *Tiliqua scincoides* by being much smaller and more gracile than both *T. gigas* and the large *Tiliqua* species from Mini Cave.

### **Cyclodomorphus** (Fitzinger, 1843)

### **Cyclodomorphus gerrardii** (Gray, 1845)
(Fig. 8H)

MATERIAL. QMF51519-QMF51527; Olsen's Cave, QML1284, QML1284a, QML1311(H), QML1311(C/D), QML1384 U, QML1313, QML1385, QML1420.

Several isolated maxillae and dentaries possess a massively rounded posterior tooth in both jaw elements, a short symphysial crest and a concave anterior portion of the dental sulcus. Maxillae preserve up to ten haplodont teeth in varying degrees of replacement. Dentaries usually exhibit some form of abrasion on the smaller anterior haplodont teeth.

The identification of *Cyclodomorphus gerrardii* was based on the presence a single massive durophagous maxillary and dentary tooth, concave anterior dental sulcus and short symphysial crest.

### **Egernia** Gray, 1838

### **Egernia** spp.
(Fig. 8F)

MATERIAL. QMF51529-51534; all localities.

Dentaries and maxillae large, possessing at least 12 haplodont teeth with chisel-shaped crowns. Meckelian groove closed. Posterior portion of the jaw robust and deep. Large inferior mental foramen.

### **Eugongylus** group (*sensu* Hutchinson, 1992)
(Fig. 8I-J)

MATERIAL. QMF51535-QMF51536; QML1284, QML1284a.

Large-sized scincid possessing a slender dentary, wedge-shaped, tightly spaced haplodont teeth and a closed Meckelian groove.

The large size, slender dentary, closed Meckelian groove ally these specimens to the *Eugongylus* Group *sensu* Hutchinson (1992).

### **Sphenomorphus** Group (*sensu* Greer, 1979)

### gracile morphotype
(Fig. 8G)

MATERIAL. QMF51537-QMF51541; QML1284a; QML1284, QML1312, QML1313, QML1385.

Small-sized dentary with closely-spaced haplodont teeth. Teeth with pointed crowns. Meckelian groove open along its length to symphysis. Dentary shallow and symphysis small.

The small gracile form of the dentary and the open Meckelian groove place these specimens within the gracile morphotype of *Sphenomorphus* Group sensu Hutchinson (1992).

### robust morphotype
(Fig. 8E)

MATERIAL. QMF51543, QMF51544; QML1312, Olsen's Cave.

Large-sized dentary with elongate blunt-crowned haplodont teeth. Meckelian groove open along its length to symphasis. Dentary deep at posterior, tapering markedly to ovoid symphysis.

The open Meckelian groove, large size, robust tooth morphology and deep jaw place these specimens within the robust morphotype of *Sphenomorphus* Group sensu Hutchinson (1992).

### Family GEKKONIDAE Oppel, 1811

Fossil gekkonids have been found in several deposits and are abundant throughout. Unfortunately most of the maxillae and dentaries are preserved as fragments, which make identification very difficult. In addition to this, there is no premise for identification of fossil Australian gekkonid taxa based on maxillary and dentary characteristics, therefore, gekkonid specimens described here were only compared to the limited comparative collection available to the author.

### gekkonid (large)
(Fig. 9A-C)

MATERIAL. QMF51508, QMF51509, QMF51510; QML1284, QML1284a, QML1313.

Several large maxillary and dentary fragments preserving rows of closely-set, needle-like homodont teeth. Maxillae possess a dorsal process of the maxilla, which lies anterior to the orbit and contacts the nasal bones. The process borders the posterior margin of the narial opening. The morphology of this margin varies between gekkonid taxa and is distinctly broad in the fossil specimens. The most complete fossil dentaries indicate the presence of a very large gekkonid. The dentaries are characterised by being long and curved mesially, possessing many closely-spaced homodont teeth, a splenial notch and a small dental symphysis.

Based on its overall very large size, the fossil taxon must have reached a snout-to-vent length of 16 cm or more, making it similar in size to the largest extant Australian gekkonids (*Phyllurus, Cryrtodactylus*). The maxillae and dentaries of all three genera show similarities with the fossil taxon.

### gekkonid (small)
(Fig. 9B)

MATERIAL. QMF51511-51515; All localities.

Several small fragmentary dentaries and maxillae are preserved throughout the deposits, probably representing several taxa. A small maxilla (QMF51511; QML1284) is distinctive in possessing a relatively narrow dorsal process originating posterior of the narial opening and tapering markedly to the posterior of the maxilla. The dentition is simple, however several of the teeth are bicuspid. Dentaries are small, curved and slender.

On comparison with small-sized gekkonids, most of the gekkonid specimens cannot be adequately identified.

### Family VARANIDAE Hardwicke & Gray, 1827

Varanids are a conspicuous member of the lizard fauna. Varanids have been identified from isolated, recurved small and large-sized serrated teeth, an isolated parietal, quadrate, femur, dentary fragments and several isolated cervical, dorsal and caudal vertebrae.

### **Varanus** Merrem, 1820

### **Varanus** sp. 1

MATERIAL. QMF51546, QMF51547; QML1312, QML1311(H).

A medium-sized species of *Varanus* is represented by a parietal, two dentary fragments, an isolated dorsal and several caudal vertebrae. The fossils compare favourably with a similarily sized *Varanus varius*, particularly in the broad flat parietal with narrow, slender temporal ridges; small-sized teeth and a dorsal vertebrae that falls within measurements provided by Smith (1976) for *Varanus*. The dorsal vertebrae compare in size to either *V. varius* or *V. gouldi*.

### **Varanus** sp. 2
(Fig. 9D-E, G-H)

MATERIAL. QMF51548-QMF51550, QMF52066; QML1312, QML1311(H), QML1311(C/D), QML1313.

A very large varanid is represented by an isolated right quadrate, a cervical and several dorsal and caudal vertebrae. On prezygopophysis to postzygopophysis length alone, these specimens fall within the range of dorsal vertebral measurements provided by Smith (1976) for *V.giganteus* and below the range provided for a small species of *Megalania* from Chinchilla provided by Hutchinson & Mackness (2002). The dorsal vertebrae are most similar in length to *V. giganteus*, however, differ remarkably in the ratio defined by Smith (1976) as prezygopophysis- prezygopophysis (Pr-Pr) width over prezygopophysis- postzygopophysis (Pr-Po) length. In particular, when comparing this ratio to modern and fossil varanids the dorsal

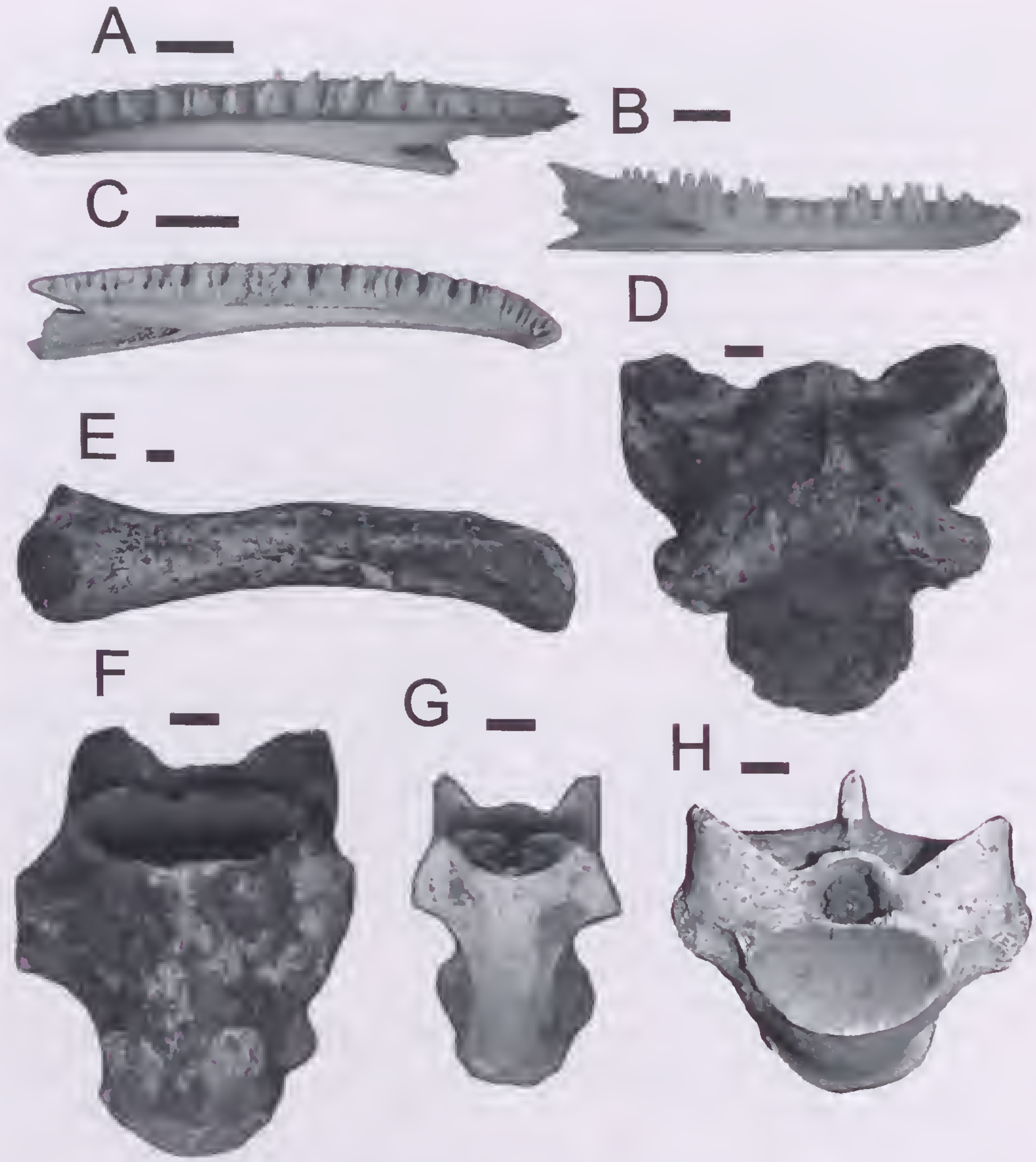

FIG 9. A-C, Gekkonidae; A&C, gekkonid (large morph); QMF51508, right dentary, QMF51510, left dentary. B, gekkonid (small morph); QMF51511, left dentary. Scale bar = 1mm. D-H, Varanidae; D-E, *Varanus* sp. 2; D, QMF51548, dorsal vertebra. E, QMF51549, femur. F, *Megalania prisca*: QMF1418, caudal vertebra. G-H, *Varanus* sp. 2; G, QMF51550, cervical vertebra. H, QMF52066, dorsal vertebra. Scale bar = 5mm.

vertebrae measured here attain a ratio of between 1.07 and 1.22. This indicates that the Pr-Pr width of the vertebrae are generally wider than the Pr-Po length. Interestingly, the measurements provided by Smith (1976) show that dorsal vertebrae of extant *Varanus* are mostly longer than broad with some being nearly equally as long as broad. Very few measured slightly broader than long.

Specimens referable to *Megalania* from both Chinchilla, Bluff Downs (Mackness &

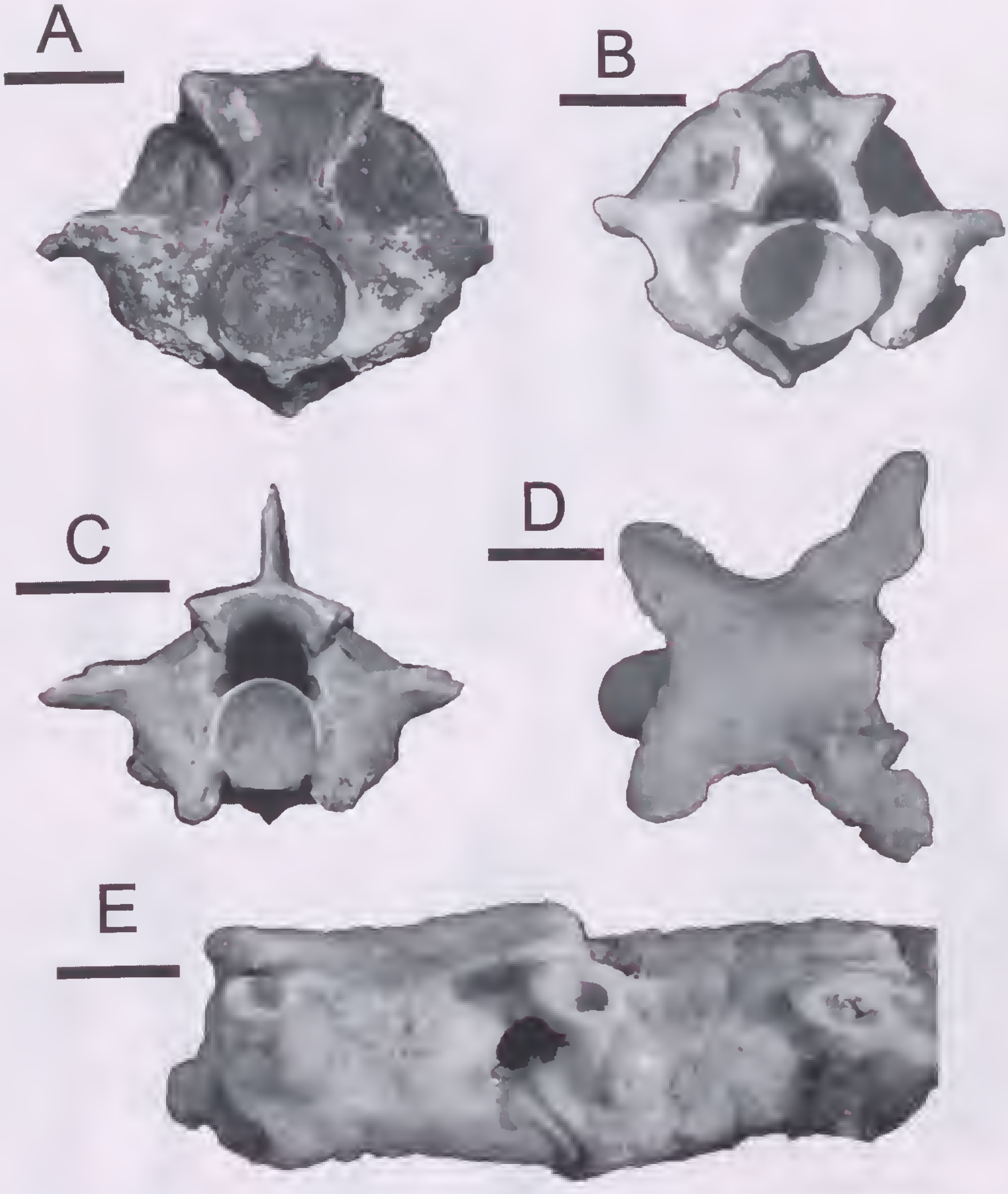

FIG 10. A-B, Pythoninae; A, QMF51560, dorsal vertebra. B, QMF51561, dorsal vertebra. C, Elapidae; QMF51551, dorsal vertebra. Scale bar = 5mm. D-E, Typholopidae; D, QMF51578, dorsal vertebra. E, QMF51579, three articulated dorsal vertebrae. Scale bar = 1mm.

Hutchinson, 2000; Hutchinson & Mackness, 2002) and the Darling Downs (Hecht 1975; pers. obs.) possess dramatically broader than long dorsal vertebrae. This feature is easily seen in the largest *Megalania prisca* dorsal vertebrae. Further comparisons of *Varanus* spp larger than *V. giganteus*, such as *V. komodoensis,* will be needed to verify the validity of these differences.

### **Megalania** (Owen, 1860)

### **Megalania prisca** (Owen, 1860)
(Fig. 9F)

MATERIAL. QMF1418; QML1420.

*Megalania prisca* is represented by a single varanid distal caudal vertebra, cotyle-condyle length: 28.80mm. The massive size of the

FIG 11. A-C, Galliformes; QMF51607-51609 (left to right), humeri. D-H, Gruiformes; D-F, QMF51610-51612 (left to right), humeri. G-H, QMF33458 & QMF33460 (left to right), carpometacarpi. I-L, Passeriformes; QMF51601-51604 (left to right), humeri. Scale bar = 5mm.

vertebra and the fact that it is a distal caudal vertebra indicates that the varanid was enormous, attaining the dimensions only seen in *Megalania*. Until the debate surrounding the generic validity of *Megalania* is resolved (Hecht, 1975; Molnar, 1990; Lee, 1996), this giant varanid will be placed within *Megalania*.

### Family ELAPIDAE Boie, 1827

### elapid indet.

Fig. 10C

MATERIAL. QMF51551-51559; All Localities.

Elapids have been identified based on the following features of the trunk vertebrae: 1. Elongate and high vertebrae, longer than broad. 2. Distinct hypopophyses. 3. High neural spine. 4. Aecute prezygopophyses. 5. Spherical condyle-cotyle articulation. Elapid specimens are variable in size with the largest specimen from QML1312, being at least twice the size of the the largest elapids from QML1284, 1284a and 1311.

### Subfamily PYTHONINAE Fitzinger, 1826

### pythonine indet.

(Fig. 10A-B)

MATERIAL. QMF51560-51569; All Localities.

In addition to maxillary and dentary remains, pythonines have been identified from the deposits based on the following features of the trunk vertebrae: 1. Short, stout vertebrae, as wide as long. 2. Robust zygantrum. 3. Thick zygosphene. 4. Ovoid condylar-cotylar articulation. 5. Hypopophysis tiny or absent. 6. Large ovoid prezygopophyses. 7. High neural spines with overhanging anterior and posterior margins.

### Family TYPHOLOPIDAE Gray, 1825

### typholopid indet.

(Fig. 10D-E)

MATERIAL. QMF51578-51582, QMF51583-51587; QML1284, QML1284a.

Typholopids have been identified on the basis of the following features of the trunk vertebrae: 1. Neural spine absent. 2. Neural arch low and thin. 3. Zygantrum narrow and deep. 4. Accute prezygopophyses. 5. Hypopophysis absent. 6. Hemal keel abent or only slight. 7. Neural canal very large relative to vertebral size.

## AVES

Bird postcranial elements are numerous throughout all of the sites, especially from those sites interpreted as predator accumulations with owls as the major accumulator. The largest bird elements are currently attributed to the owls (Strigiformes), the smallest from the song birds (Passeriformes).

### Galliformes

(Fig. 11A-C)

MATERIAL. QMF51607-51609; QML1312.

Quails are represented by several postcrania, including very distinctive humeri and carpometacarpi. The size of the humeri and presence of two proximal pneumatic fossae in the head of the humerus suggests the presence of a species of *Coturnix*.

### Gruiformes

(Fig. 11D-H)

MATERIAL. QMF33458, QMF33460, QMF51610-QMF51612; QML1312.

Buttonquails are represented by several postcrania, including humeri, carpometacarpi, femora, tarsometatarsi and sternal fragments. The distinctive larger pneumatic fossa in at the proximal head of the humerus and the large triangular intermetacarpal tuberosity ally these specimens closest to a species of *Turnix*.

### Passeriformes

(Fig. 11I-L)

MATERIAL. QMF51601, QMF51602-51606; QML1284 QML1312.

Passeriformes were identified from humeri possessing a distinct entepicondylar prominence, ectepicondyle distinct and distal to internal condyle, and a shallow pneumatic fossae.

### Strigiformes

(Fig. 12 A-K)

MATERIAL. QMF51578-51587; All localities except QML1420.

Owls were identified from numerous postcranial specimens including humeri, ulnae, carpometacarpi, phalanges, claws, femora and tarsometatarsi. Owls possess a distinct first phalange of the pes digits, with four tuberosities in each corner of the phalange. The phalange tends to be short and squat with a deep facet on the dorsal and distal margin.

FIG. 12. A-K, Strigiformes; A-B, QMF51578 & 51579, femora. C-D, QMF51580 & 51581, carpometacarpi. E-F, QMF51582 & 51583, ulnae. G-H, QMF51584 & 51585, carpometacarpi. I-K, QMF51586, 51581, 33361, phalanges. L-M, QMF33863 & 33864, claws. Scale bar = 5mm.

## MAMMALIA

### Family PERAMELIDAE Gray, 1825b

### **Perameles** Geoffroy, 1803

### **Perameles** sp. 1

(Fig. 13A)

MATERIAL. QMF51613-QMF51620; QML1284, QML1284a, QML1311(H), QML1313, QML1384U, QML1385, QML1420, QML1311(C/D).

A species of *Perameles* on the basis of the following combination of features; 1. Presence of fully developed anterior and posterior cingulae on $M^{1-3}$. 2. Triangular tooth crown with the para and metastylar corners outside the margin of the tooth crown. 3. Equidistant protoconid-metaconid, protoconid-paraconid distances on $M_{1-4.}$ 4. Absence of the anterior cingulid on $M_1$.

When compared to the modern species of *Perameles* the fossils differ as follows:

*Perameles* sp. 1 is larger than *P. bougainville* and has a more buccally developed posterior cingulum on $M^{1-3}$. The posthypocristid runs to the hypoconulid on $M_{1-3}$ whereas the posthypocristid only runs to the hypoconulid in $M_{1-2}$ of *P. bougainville*

*Perameles* sp. 1 is smaller than *P. nasuta*. The meta- and parastylar corners in unworn molars of the fossil taxon are bicuspid whereas *P. nasuta* possess single conical meta- and parastyle.

*Perameles* sp. 1. is smaller than *P. gunnii* and possesses a more buccally developed posterior cingulum on $M^{1-4}$. The posthypocristid runs to the hypoconulid on all lower molars in the fossil *Perameles*, whereas it only runs to the hypoconulid in $M_{2-3}$ of *P.gunnii.*

*Perameles* sp. 1. differs from *P. bowensis* by being larger, possessing larger hypoconulids, and a posthypocristid that runs to the hypoconulid on $M_3$. *Perameles* sp. 1. differs from *P. allinghamensis*, which is only known by an isolated upper molar, by being much smaller and possessing a posterior cingulum that terminates below and buccal to the metacone. *Perameles* sp. 1. differs from *P. sobbei*, which is only known from lower dentition, by possessing larger hypoconulids on $M_{1-3}$, a posthypocristid that runs to the hypoconulid on $M_{1-3}$, and by being smaller.

### **Perameles** sp. 2

(Fig. 13B)

MATERIAL: QMF51621-QMF51626; QML1284, QML1284a, QML1311(H), QML1313, QML1384U, QML1385.

A second medium-sized species of *Perameles* possesses the following features: 1. Anterior cingulid of $M_1$ absent. 2. Hypoconulid reduced on $M_{1-3}$. 3. Posthypocristid contacts the base of the entoconid $M_{1-3}$. 4. Trigonid cusps approximated. 5. Entoconid conical with a small preentocristid crest. *Perameles* sp. 2 differs from *Perameles* sp. 1 by being larger, possessing a posthypocristid that contacts the entoconid and a preentocristid crest. *Perameles* sp. 2 differs from *P. nasuta, P. bougainville, P. eremiana, P. bowensis* by possessing an $M_1$ with a posthypocristid that contacts the entoconid instead of the hypoconulid. *Perameles* sp. 2 differs from *P. gunnii* by being markedly smaller, possessing a more mesially terminating cristid obliqua and not possessing a simple conical entoconid. *Perameles* sp. 2 differs from *P. sobbei* by its smaller size, larger hypoconulid on $M_1$, narrower protoconid-metaconid distance and smaller paraconid.

### **Perameles bougainville** Quoy & Gaimard, 1824

(Fig. 12C-E)

MATERIAL. QMF51627-51630, QMF51631; QML1312; Olsen's Cave.

A small species of *Perameles* is present in the fauna recovered from QML1312 and a single specimen in Olsen's Cave. The fossils are identified as *Perameles* on the basis of the following combined features: 1. Para- and metastylar corners angular, occuring outside the peripherial margin of the tooth crown base, 2. The presence of a variably complete posterior cingulum. 3. Anterior cingulum on $M_{2-4}$ that originates well below the apex of the paraconid. 4. Gently curved ascending ramus. 5. Reduced metaconule.

When compared to the three available species of modern *Perameles* (*P. nasuta*, *P. gunnii* and *P. bougainville*) this fossil species was closest to *P. bougainville* in size. The fossils referred to here as *P. bougainville* differ from both *P. nasuta* and *P. gunnii* by; being considerably smaller; possessing small, isolated parastyles on $M^1$ instead of large, curved parastyles that are connected to the main tooth crown by a distinct preparacrista; possessing distinct protocones and metaconules on $M^{1-3}$; acute angle made by the postprotocrista and premetaconule crista; possessing a lower angle of the postmetacrista to the longitudinal axis of the tooth crown; more lingually oriented stylar cusp B & D. They differ from *P. allinghamensis* by being much smaller

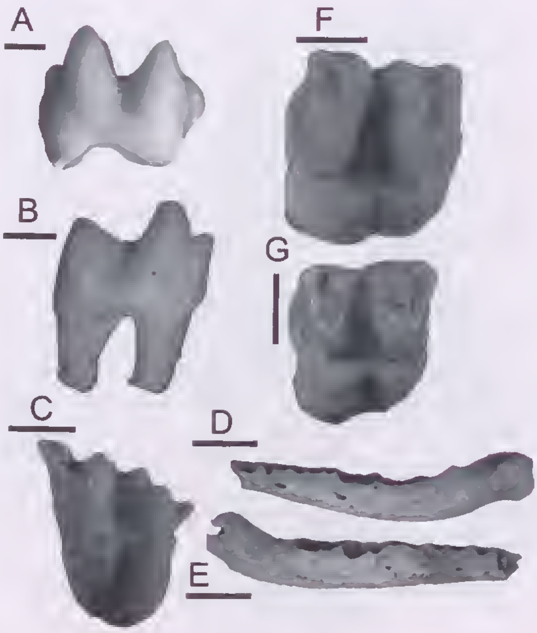

FIG. 13. A-G, Peramelidae; A. *Perameles* sp. 1; QMF51613, LM$_1$. B, *Perameles* sp. 2; QMF51621, RM$_1$. C-E, *Perameles bougainville*; QMF51627, RM$^1$. Scale bar = 1mm. D, QMF51628, left mandible. E, QMF51529, right mandible. Scale bar = 5mm. F, *Isoodon obesulus*; QMF51632, RM$^2$. G, *Isoodon* sp.; QMF51635, RM$^2$. Scale bar = 1mm.

and possessing a more triangular outline in occlusal view. They differ from *P. bowensis* by being larger and better developed posterior cingulum on M$^3$.

The fossils compare favourably with *P. bougainville* on the basis of: 1. Small size, though they are slightly larger than the samples measured by Freedman & Joffe (1966). 2. Form of the parastyle on M$^1$, being small, isolated and not connected to the preprotocrista. 3. Higher angle of the postmetacrista to the longitudinal axis of the tooth crown. 4. Lingually oriented stylar cusps B & D. 5. Incomplete posterior cingulum on M$^{1-2}$ with a short posterior cingulum on M$^3$.

The identification presented here is made with some caution due to the absence of *P. eremiana* from comparative collections available. However, Muirhead (1994) provides characteristics to split these two species. These features included the development of the posterior cingulum (complete on M$^1$ in *P. eremiana* and incomplete on M$^1$ of *P. bougainville*) and the hypoconulid. Features characteristic of *P. bougainville* are shared with the fossil over *P.eremiana.* It is unlikely that the fossil taxon represents an extinct species based on the closeness in morphology to *P. bougainville*. Instead, it may represent a larger-sized eastern population of the arid-adapted *P. bougainville*. This record represents the most easterly and northerly record of the small-sized, arid-adapted members of *Perameles*.

### **Isoodon** Desmarest, 1817

### **Isoodon obesulus** (Shaw, 1797)
(Fig. 13F)

MATERIAL. QMF51632-QMF51634; QML1312, QML1384U, QML1420.

*Isoodon* fossils are abundant in the QML1384U and QML1312 deposits. These specimens are referred to *Isoodon* based on the following combined features: 1. Well developed anterior and posterior cingulae on M$^{1-3}$; 2. Stylar corners well within the tooth crown margins on M$^{2-3}$; 3. Stylar cusps B & D oriented lingually; 4. Deep, dumb-bell shaped lingual root on upper molars; 5. Cuspid at the anterobuccal base of the hypoconid, 6. Anterior cingulae on M$^{2-4}$ terminates just ventral to the paraconid.

Morphologically, the fossils differ from *I. macrourus* and *I. auratus* in possessing distinct metaconules and protocones on M$^{1-3}$, where the postprotocrista and premetaconule crista form an acute angle between the two cusps. They also agree in size with modern *I. obesulus*.

### **Isoodon** sp.
(Fig. 13G)

MATERIAL. QMF51635-QMF51636; QML1384U, QML1312.

Specimens of a species of *Isoodon* represent a second species. The specimens are smaller than all three extant *Isoodon* species, being closer to *I. obesulus* than *I. macrourus* and *I. auratus*. In morphology the specimens differ from all species of *Isoodon* by possessing an incomplete anterior cingulum on M$^2$ and narrower metastyle-stylar cusp D and parastyle-stylar cusp B distances. The fossil specimens are all smaller than those teeth assigned to *I. obesulus* from the same deposit.

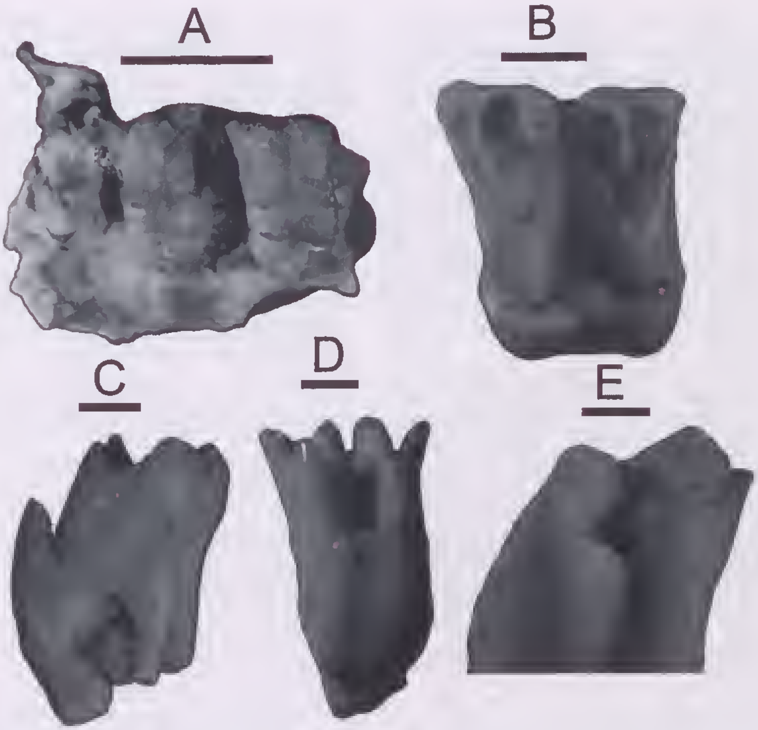

FIG 14. A-D, Peramelidae; A-D, *Chaeropus ecaudatus*; A, QMF51637, RM$^{3-4}$. Scale bar = 5mm. B-C, QMF515638, RM$^{2}$, occlusal & anterior views. D, QMF51639, RM$^{3}$. E, Thylacomyidae; *Macrotis lagotis*; QMF51642, RM$^{1}$. Scale bar = 1mm.

### **Chaeropus** Ogilby, 1838

### **Chaeropus ecaudatus** (Ogilby, 1838)
(Fig. 14A-D)

MATERIAL. QMF51637-51641; QML1312.

*Chaeropus ecaudatus* is only known from QML1312 and is the third most abundant bandicoot in that deposit. *C. ecaudatus* has been identified from upper molars using the following combination of characteristics defined by Muirhead and Godthelp (1995): 1. Near parallel preparacristae and postmetacristae to each other and almost perpendicular to the long axis of the tooth crown. 2. Absence of both an anterior and posterior cingulae. 3. Very tall and slender molar crowns. 4. Preprotocristae and postprotocristae terminate at the base of the paracone and metacone respectively. 5. Preparacristae straight with no anterior curvature.

## Family THYLACOMYIDAE (Bensley, 1903)

### **Macrotis** Reid, 1837

### **Macrotis lagotis** (Reid, 1837)
(Fig. 14E)

MATERIAL. QMF51642-51643; QML1312.

The Greater Bilby is an enigmatic species of bandicoot with a highly specialised and distinctive tooth morphology. Two molars have been recovered from QML1312. Identification of the teeth as *M. lagotis* was based on the following combination of features. 1. Absence of the paraconid, 2. Absence of the metaconule, 3. Rectangular-ovoid molar crowns, 4. Dumbell-shaped molar roots and 5. Large cuspid on the anterobuccal side of the lower molars (considerably larger than that found in *Isoodon*).

## Family INCERTAE SEDIS

Two new bandicoots are present in the fauna with uncertain family-level taxonomic position. Several indications of new bandicoot groups within the Late Tertiary have been made in the literature (Muirhead, 1994, 1999; Dawson et al., 1999; Long et al., 2002) without formal description. One family, the Yaralidae, are described from the Oligo-Miocene (Muirhead, 2000) and are thought to occur into the Pliocene (Long et al., 2003). Based on dentition alone, family-level taxonomy becomes complicated with several previously diffinitive features now thought to be plesiomorphies (Muirhead, 1994; 2000; Muirhead & Filan, 1995). It is for this reason that these two distinct bandicoots will remain *incertae sedis* with the possibility of their placement within the plesiomorphic family Yaralidae.

Recently, Turnbull et al., (2003) erected a new bandicoot taxon, cf. *Peroryctes tedfordi* from the Early Pliocene Hamilton Fauna. Although they place the taxon in the Peroryctidae, they did note its plesiomorphic features and similarity to *Yarala*. The taxa identified below are morphologically very similar to cf. *Peroryctes tedfordi*, however, I reserve the placement of these taxa into any perameloid family until a full revision of both the Hamilton and Mt. Etna material is available.

### Gen. et sp. nov. 1

(Fig. 15A)

MATERIAL. QMF51644; QML1311 (H).

A large species of perameloid, similar in size to *Echymipera rufescens*, possessing the following features: 1. A distinct anterior cingulum on $M_1$. 2. Trigonid extremely compressed with protoconid and metaconid cusps high and approximated. 3. Paraconid small. 4. Bladed entoconid. 5. Hypoconulid heavily reduced on $M_{1-2}$, less so on $M_3$. 6. $M_{2-3}$ trigonid with protoconid-metaconid relatively more broader than corresponding cusps on $M_1$. 7. Posthypocristid contacts the base of the entoconid on $M_{1-3}$. 8. Cristid obliqua terminates on the posterior trigonid flank, buccally of the tooth midine.

This taxon shares a complete and distinctive anterior cingulum with only one other published bandicoot, *Yarala burchfieldi* from the Oligo-Miocene of Riversleigh, Far North Queensland (Muirhead & Filan 1995). It differs from *Yarala burchfieldi* by possessing a bladed entoconid, smaller hypoconulids, posthypocristid that contacts the entoconid and a less posteriorly placed metaconid.

### Gen et sp. nov. 2

(Fig. 15B)

MATERIAL. QMF51645-QMF51650; QML1284, QML1284a, QML1311(H). QML1384U, QML1313, QML1385, QML1311 (C/D).

A medium-sized bandicoot possessing the following dental characteristic: 1. $M_1$ with anterior cingulid present as distinct antero-dorsally projecting cuspule. 2. A small buccal cuspule between metaconid and hypoconid. 3. Compressed trigonid with all three main cusps closely approximated. 4. Bladed entoconid on $M_1$. 5. Posthypocristid runs to the base of the entoconid on $M_{1-3}$. 6. Hypoconulid reduction on $M_1$, further reduction on $M_2$ and near absent on $M_3$. 7. Cristid obliqua runs to the middle of the posteroventral flank of the trigonid. 8. Talonid broadens consecutively along molar row.

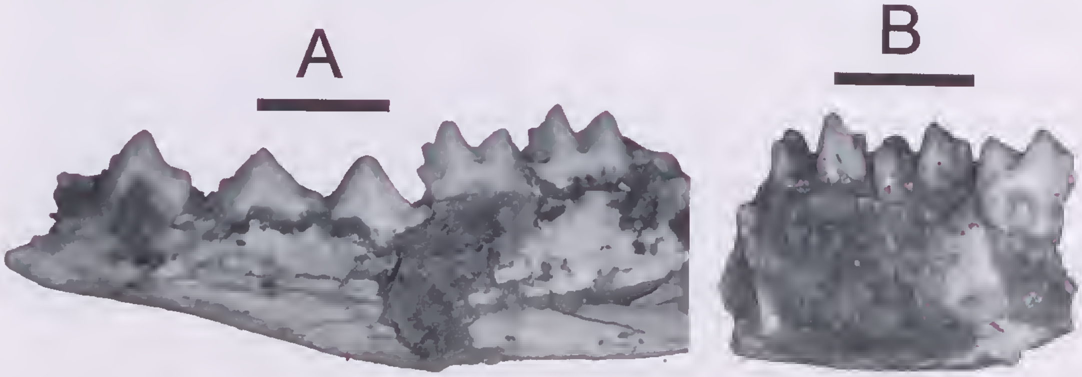

FIG 15. A-B, Family incertae sedis; A, Gen. et sp. nov. 1; QMF51644, $LP_1$-$M_3$. B, Gen. et sp. nov. 2; QMF51645, $RM_{1-3}$. Scale bar = 5mm

### Family DASYURIDAE Goldfuss, 1820 *sensu* Waterhouse, 1838

Dasyurids are a conspicuous part of all of the faunas, being represented by isolated teeth, nearly complete mandibles and maxillae, or even partial skulls. Identification of dasyurids follows the character states defined by Wroe and Mackness (1998) for *Dasyurus*, Van Dyck (2002) for *Antechinus*, Archer (1981) for *Sminthopsis*, Dawson (1982a) for modern and fossil *Sarcophilus*, Archer (1976) for *Planigale* and Wroe et al. (2000) for other dasyurid genera.

### **Antechinus** Macleay, 1841

*Antechinus* is a morphologically diverse group as defined by Van Dyck (2002). Specimens were identified as *Antechinus* on the basis of the combined features: 1. Complete posterior cingulum on upper molars. 2. $P_3$ / $P^3$ reduced. 3. Meta- and hypocristids not transverse to the longitudinal axis of the jaw. 4. Entoconid variably present.

### **Antechinus** sp. 1
(Fig. 16A)

MATERIAL. QMF51651-51653, QMF51654-51657; QML1313, QML1284a.

*Antechinus* sp. 1 is allied very closely to *Antechinus adustus* based on maxillary morphology. The fossil maxillae possessed the greatest number of maxillary character-states provided by Van Dyck (2002) for *A. adustus*, which included characters; 18-19, 22, 25-28, 30, 33, 36-37. Mandibles and isolated lower molars conform in size to the maxillary specimens, however, they do not conform in the character-states that are present in *A. adustus*. Instead, the mandibles show a greater similarity to *A. godmani* or *A.minimus* (characters 40-46; 48-54). Due to the very small sample size, these morphological variations may either constitute a single morphologically distinct new taxon or two similarly-sized known species of modern *Antechinus*. The most convincing characteristics seem to be from the maxilla, thus *A. adustus* would be considered the most likely taxon present in the deposits.

### **Antechinus** sp. 2

MATERIAL. QMF51663-51680; QML1284a, QML1385, QML1311(C/D), QML1420, QML1311(H), QML1313, QML1284.

A second species of *Antechinus* is present and differs from *Antechinus* sp. 1 by being larger in overall dimensions and possessing a relatively larger $P_3$. This species of *Antechinus* does not possess any greater similarity to any of the modern species of *Antechinus*.

### **Antechinus flavipes** (Waterhouse, 1838)
(Fig. 16B)

MATERIAL. QMF51681-51685; QML1312, QML1384U.

*Antechinus flavipes* has been identified by numerous fragmentary and complete maxillae and mandibles. The most complete specimens, which are also the easiest to identify, are the mandibles. Using the characteristics provided by Van Dyck (1982, 2002) and Smith (1972), which included: 1. Tiny and crowded $P_3$. 2. Transversely orientated $P_3$. 3. Small entoconids. 4. Small paraconid. 5. Size (7.54-7.66mm $M_{1-4}$ Length), I am able to differentiate this species from a second species present in the same deposit, *Antechinus swainsoni*.

### **Antechinus swainsoni** (Waterhouse, 1840)
(Fig. 16C)

MATERIAL. QMF51686-51688; QML1312.

*Antechinus swainsoni* is also represented by numerous maxillae and mandibles. Using features in Van Dyck (1982) that differentiate *A. flavipes* from *A. swainsoni*, this smaller species was able to be distinguished. The premolar row is not crowded as in *A. flavipes*, the mandible is gracile and $M_{1-4}$ length reaches 7.30-7.34mm.

### **Dasyurus** Geoffroy, 1796

*Dasyurus* was identified by the absence of $P^3$ or $P_3$ (except *Dasyurus dunmalli*) and its moderately large-sized molars and total mandibular dimensions (larger than *Phascogale*, smaller than *Sarcophilus* and *Glaucodon*).

### **Dasyurus hallucatus** Gould, 1842

MATERIAL. QMF51689, QML1312.

A small-sized *Dasyurus*, differing from other modern and extinct *Dasyurus* by possessing a relatively shorter metacrista length on $M^3$ than $M^2$, and a metacone on $M^1$ perpendicular to stylar cusp D.

### **Dasyurus viverrinus** (Shaw, 1800)
(Fig. 16K)

MATERIAL. QMF51690-51695; QML1312; QML1384U.

A medium-sized *Dasyurus*, differing from other modern and extinct *Dasyurus* by possessing a longer metacrista on $M^3$ than on $M^2$; metacone anterior to stylar cusp D; reduced paracones; not

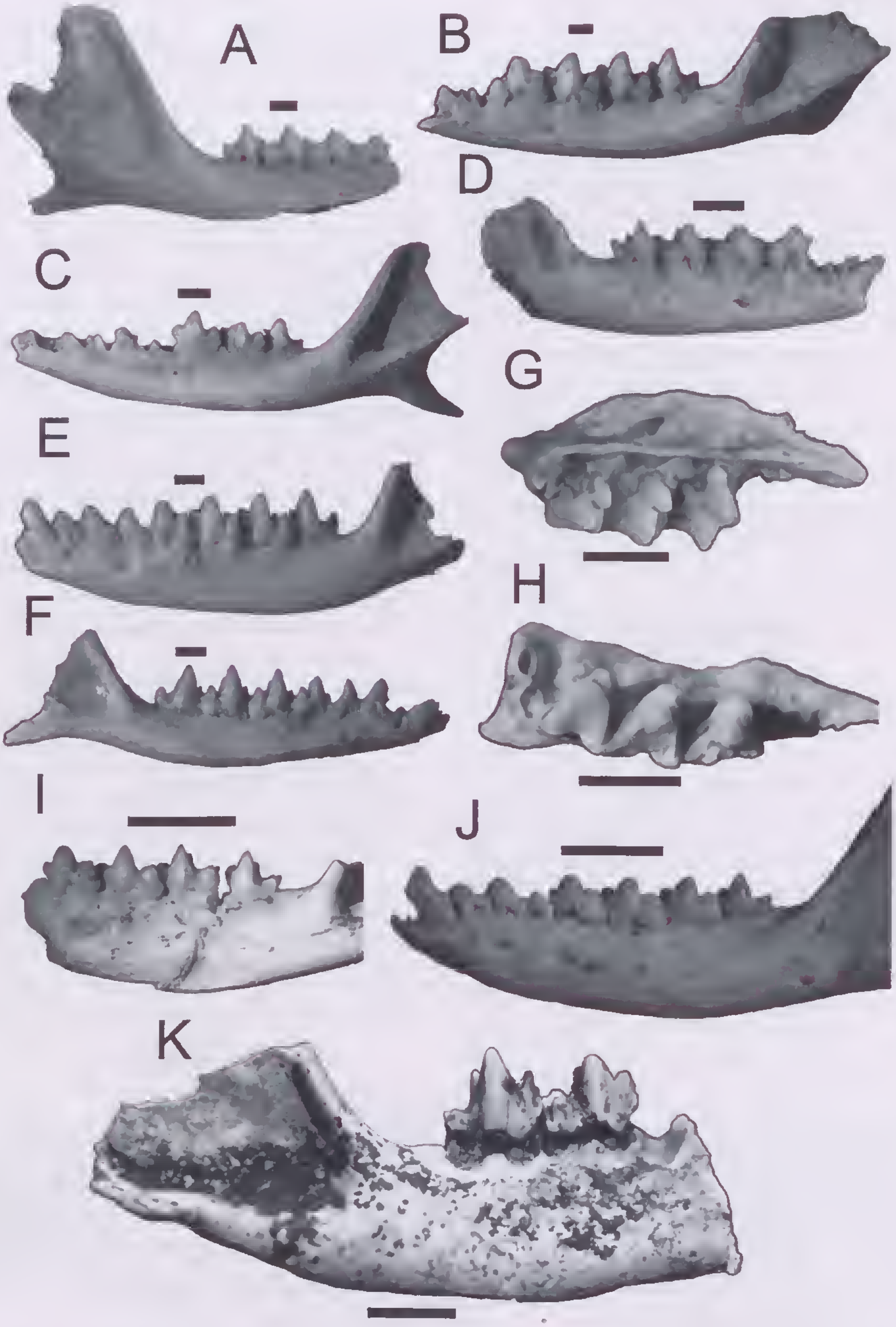

FIG 16. A-K, Dasyuridae; A-C, *Antechinus*; A, *Antechinus* sp. 1; QMF51651, RM$_{1-4}$. B, *Antechinus flavipes*; QMF51681, LP$_3$-M$_4$. C, *Antechinus swainsoni*; QMF51686, LM$_{2-4}$. D, *Planigale maculate*; QMF51707, RM$_{1-4}$. E-F, *Sminthopsis*; E, *Sminthopsis macroura*; QMF51715, LC$_1$-M$_4$. F, *Sminthopsis murina*, QMF51724, RP$_2$-M$_4$. G-H, Gen et sp. nov.; QMF51743, lingual and occlusal views. Scale bar = 1mm. I-J, *Phascogale*; I, *Phascogale* sp.; QMF51704, LM$_{1-4}$. J, *Phascogale topoatafa*; QMF51699, LC$_1$-M$_4$. K. *Dasyurus viverrinus*; QMF51690, RM$_{3-4}$. Scale bar = 5mm.

bulbous (as in *D. maculatus*); reduced metaconid. Differs specifically from *D. geoffroyi*, a species most similar to *D. viverrinus*, by having relatively longer metacristae. Fossil specimens show similarities to *D. maculatus*, including a small entoconid and a reduced posterior cingulid on M$_{1-3}$. These features are intriguing and with more specimens may constitute further review, however, at the present time there are significantly more morphological features shared with *D. viverrinus*.

### **Dasyurus** sp.

MATERIAL. QMF51696-51698; QML1313.

A medium-sized species of *Dasyurus* is represented by an isolated M$_2$, M$^{2+3}$. There are not enough features available on the specimen to warrant specific placement at the present time.

### **Phascogale** Temminck, 1824

Species of *Phascogale* are distinguished from other similar dasyurids by the P3 being higher than P2 and by being considerably larger than the only other dasyurid exhibiting the former trait, *Sminthopsis*.

### **Phascogale topoatafa** (Meyer, 1793)
(Fig. 16J)

MATERIAL. QMF51699-51703; QML1312.

*Phascogale topoatafa* is distinguished from *Phascogale calura* by being larger, possessing a small posterior cusp on P$^3$ and possessing a smaller protocone on M$^{1-3}$.

### **Phascogale** sp.
(Fig. 16I)

MATERIAL. QMF51704-51706; QML1420, QML1313.

A small, possibly undescribed, species of *Phascogale* is tentatively identified here based on the great number of similarities (as defined by Van Dyck (2002)) shared with both *P. topoatafa* and *P. calura*. Its smaller size seems to differentiate it from the two extant species of *Phascogale*, however, further analysis of *P. calura* is needed to determine whether the fossil specimens are within the variation for this species.

### **Planigale** Troughton, 1928

### **Planigale maculata** (Gould, 1851)
(Fig. 16D)

MATERIAL. QMF51707-QMF51711, QML1312; Olsens Cave.

A species of *Planigale* was identified based on its diminutive size, reduced single-rooted P$_3$, absent entoconid, present posterior cingulum and reduced stylar cusps, especially stylar cusp D on M$^{2-3}$. *P. maculata* was distinguished by its size, being smaller than *P. novaeguineae*, larger than *P. ingrami* and *P. tenuostris*, and by possessing P$_3$ (versus *P. gilesi*, which does not).

### **Sarcophilus** Cuvier, 1837

Species of *Sarcophilus* were determined by using criteria described by Dawson (1982a) for *Sarcophilus laniarius* and *Sarcophilus harrisii*. No site has yet been found where both taxa can be said to occur sympatrically, however, a fragment of a mandible which is referred to here as

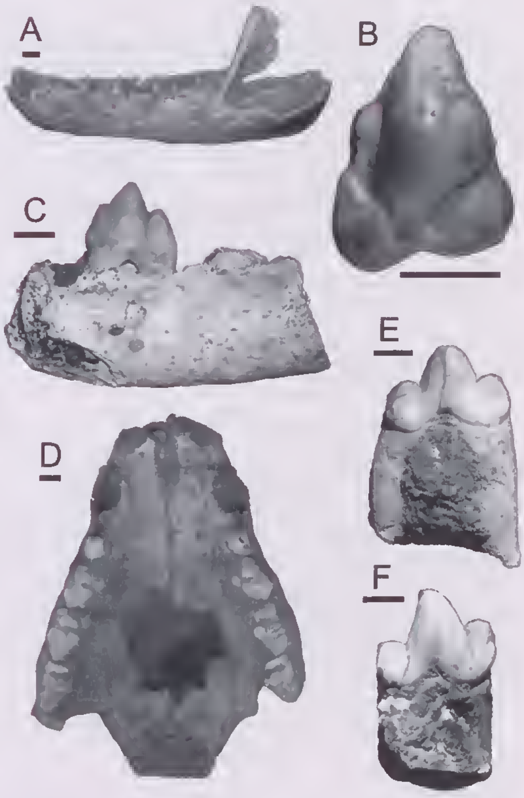

FIG 17. A-D, Dasyuridae; *Sarcophilus*; A, *Sarcophilus harrisii*; QMF51712, left mandible. B-D, *Sarcophilus laniarius*; B, QMF41997, LM$^1$. C, QMF51713, LM$_1$. D, QMF1872, partial skull. E-F, Thylacinidae; *Thylacinus cynocephalus*; E, QMF1737, RM$_2$. F, QMF51755, RM$_1$. Scale bar = 5mm.

*Sarcophilus laniarius* may have been derived from sediments from within Lower Johansen's Cave, a site containing the only representative of *Sarcophilus harrisii*.

### **Sarcophilus harrisii** (Boitard, 1841)
(Fig. 17A)

MATERIAL. QMF51712; QML1314.

*Sarcophilus harrisii* is represented by an edentulous left mandible ($M_{1-4}$ alveoli length: 39.50mm). The specimen differs markedly from *Sarcophilus laniarius* known from the Darling Downs and specimens from Marmor Quarry by being much smaller in size and having a more gracile lateral profile.

### **Sarcophilus laniarius** (Owen, 1838)
(Fig. 17B-D)

MATERIAL. QMF693, QMF1872, QMF51713-QMF51714, QMF41997; QML1420, QML1311(H), QML1312, QML1384U, QML1384L.

*Sarcophilus laniarius* is represented by isolated molars, a partial mandible and an almost complete palate. The distinctive large triangular dasyurid molars unquestionably place these specimens within *Sarcophilus*. The large size and robust nature of the palate and molars allies these specimens with those of typical *Sarcophilus laniarius* from the eastern Darling Downs and those measured by Dawson (1982a).

### **Sminthopsis** Thomas, 1887

Archer (1981) reviewed the taxonomy of *Sminthopsis*, providing keys to the species using either external or skeletal features. Species of *Sminthopsis* were identified on the basis of their compressed upper and lower molars; absent posterior cingulum on upper molars; transverse meta- and hypocristids; and subequal premolar heights.

### **Sminthopsis macroura** (Gould, 1845)
(Fig. 16E)

MATERIAL. QMF51715-QMF51723; QML1312, QML1384, QML1314.

*Sminthopsis macroura* was identified by possessing the following features: large and distinct entoconid; hypocristid that does not contact the entoconid; $C_1$ not enlarged; premolars longer than broad; medium-sized species ($M_{1-4}L$ = 5.8mm).

### **Sminthopsis murina** (Waterhouse, 1838)
(Fig. 16F)

MATERIAL. QMF51724-51739; QML1312, QML1313, QML1420, QML1284, QML1284a, QML1385, Olsen's Cave.

Difficulty was experienced in identifying a second species of *Sminthopsis*, distinguished by the absence of the entoconid. Very few features were available from Archer (1981) to distinguish species of this group based simply on mandibular or maxillary features. Three species were possible candidates; *S. butleri, S. leucopus* and *S. murina*. *S. butleri* was excluded because it apparently shows signs of tiny entoconids on $M_{1-3}$, the fossil specimens do not. *S. leucopus* was excluded because the fossil specimens show premolars that do slightly contact each other, a feature generally not seen in *S. leucopus*, however, this is a relatively variable trait. *S. murina* is preferred until further analysis is possible.

### Gen. et sp. nov.
(Fig. 16G-H)

MATERIAL. QMF51743-51754; QML1311(H), QML1385, QML1284, QML1284a, QML1313, QML1384U.

A tiny dasyurid, similar in size to *Planigale* and *Ningaui*, possesses heavily reduced upper dentition, including a significantly reduced protocone on $M^{1-3}$; an extremely reduced paracone on $M^1$; absent stylar cusps D and B on all molars; and a distinct ectoloph indentation. There are only four roots found between the canine root and $M^1$ suggesting the loss of $P^3$ as in *Planigale gilesi*. The possession of these distinctly derived traits (*sensu* Wroe et al., 2000) suggests the possible need to erect a new genus of dasyurid to accommodate this highly distinctive taxon. More complete material will soon be available and a more formal description and analysis is underway.

## Family THYLACINIDAE Bonaparte, 1838

### **Thylacinus** Temminck, 1824

### **Thylacinus cynocephalus** (Harris, 1808)
(Fig. 17E-F )

MATERIAL. QMF1737, QMF51755-QMF51757; QML1420, QML1313, QML1311(H), QML1311 (C/D), QML1312.

Several isolated molars and an almost complete skull and mandibles represent the marsupial carnivore, *Thylacinus cynocephalus*. They compare favourably with modern and fossil

TABLE 3. Faunal lists for large-sized mammal species

| | QML1284 | QML1284a | QML1311H | QML1311CD | QML1312 | QML1313 | QML1384U | QML1384L | QML1420 |
|---|---|---|---|---|---|---|---|---|---|
| *Thylacinus cynocephalus* | | | x | x | x | x | | | x |
| *Vombatus ursinus mitchellii* | | | | x | | | | | x |
| ?zygomaturine | | | | | | | | | x |
| *Palorchestes* sp. cf. *P. parvus* | | | x | x | | | | | x |
| ?diprotodontid indet | | | x | | | | | | |
| *Bohra* sp. | | | | x | | | | | |
| *Kurrabi* sp. | | | x | x | | | | | |
| *Protemnodon* sp. cf. *P. devisi* | x | | x | x | | | | | |
| macropodine indet. | x | x | x | | | | x | x | x |
| *Macropus* sp. 1 | | | | | x | | | | x |
| *Macropus* sp. cf. *M. agilis siva* | | | x | | | | | | x |
| *Macropus titan* | | | | | | | | | x |
| *Thylacoleo* sp. | | | | | | | | x | x |
| *Thylacoleo hilli* | | | x | | | | | | |

specimens assigned to *T. cynocephalus*, falling within the variation provided by Dawson (1982b).

### Family VOMBATIDAE Burnett, 1830

### **Vombatus** Geoffroy, 1803

### **Vombatus ursinus mitchellii** (*sensu* Dawson, 1983)
(Fig. 18A)

MATERIAL. QMF51758, QMF1420; QML1311 C/D, QML1420.

The only large marsupial with hypsodont molars, wombats are easily identified from any deposit. *Vombatus* is represented from QML1420, Marmor Quarry, by an incomplete left mandibular ramus with molars and insisor root preserved, and a partial right maxilla. A single tooth, within a partial maxilla has also been recovered from QML1311 Unit C/D. Based on size comparisons, the three specimens are much smaller than *Phascolonus* and slightly smaller than *Phascolomys medius*, falling within the size range of the Late Pleistocene *Vombatus ursinus mitchelli* (*sensu* Dawson 1983; Murray 1998) from the eastern Darling Downs.

### Family DIPROTODONTIDAE Gill, 1872

### ?zygomaturine
(Fig. 18B )

MATERIAL. QMF1419, QML1420.

Tooth fragments of a diprotodontid from Marmor Quarry which were initially identified by Longman (1925a) as *Diprotodon australis* are revised to ?zygomaturine. Two of the three tooth fragments come from the same molar. The fragments consist of a protolophid which possesses a narrow anterior cingulum. The third tooth fragment may come from the same molar and represents the posterior lingual side of the molar, preserving the lingual edge of the hypolophid. The tooth is low crowned and the lophs are relatively straight and narrow. Based on this, and comparing the molars to specimens of *Zygomaturus, Euryzygoma* and *Diprotodon*, it seems most likely that the tooth came from a species *Zygomaturus*. Phalanges and fragments of vertebrae have also come from Marmor Quarry, however, these do not aid in the identification of this relatively large form of diprotodontid.

### Family PALORCHESTIDAE (Tate, 1948)

### **Palorchestes** Owen, 1873

### **Palorchestes** sp. cf. **P. parvus** De Vis, 1895
(Fig. 18C-D)

MATERIAL. QMF51759-51760, QMF42635 (cast) / BMNH10257; QML1311(H); QML1311 (C/D), QML1420.

*Palorchestes* is represented by an isolated $M_2$, a left maxillary fragment preserving the posterior portion of $M^1$ and a complete $M^2$, and a left $I^{1-2}$. Left $I^1$ large, curved and broad distally. $LI^2$ broad with tapering root. $LM^1$ preserves a double midlink and a posterior-lingual fossette. $LM^2$ ovo-rectangular in occlusal view, lophs relatively narrow with the metaloph slightly narrower than paraloph. Single mid- and forelink. Anterior cingulum deep and completely running the length of the molar, bisected by forelink. Buccal cingulum present between paracone and metacone. Postero-lingual pocket. No posterior cingulum. $M_2$ rectangular in occlusal view, lophids high and narrow, distinct fore- and midlink, posterior cingulid absent.

These specimens cannot be assigned to a species of *Palorchestes* because they lack diagnostic features of the $M^1$ (Black, 1997). Based simply on size, the specimens are from a small species of *Palorchestes*, much smaller than

FIG 18. A, Vombatidae; *Vombatus ursinus mitchelli*; QMF1420, LM$_{1-4}$. B, ?Zygomaturine; QMF1419, fragmentary molar. C-D, Palorchetidae; *Palorchestes* sp. cf. *P. parvus*; C, QMF51759, RM$^2$ (partial M$^1$). D, QMF51760, LI$^{1-2}$. Scale bar = 10mm.

*P. azael* and very similar in size to *P. parvus*. The M$_2$ is larger than the species recovered from the Hamilton LF, which was considered by Turnbull & Lundelius (1970) to be *Palorchestes painei*. This identification has been challenged by Rich (1991) who considers it to represent a new taxon, illustrating the taxonomic uncertainty surrounding the smaller members of the Palorchestidae.

?diprotodontid indet.

MATERIAL. QMF51761; QML1311H.

Approximately a quarter of a lower molar possibly represents a small diprotodontid. The tooth is low crowned, lophodont and bears thick slightly crenulated enamel distinctive in several diprotodontian groups. The molar is distinctly not macropod based on the thickness of the enamel and the crenulations are not as distinct as those found in the Sthenurinae. The lophids are lower than those found in palorchestids.

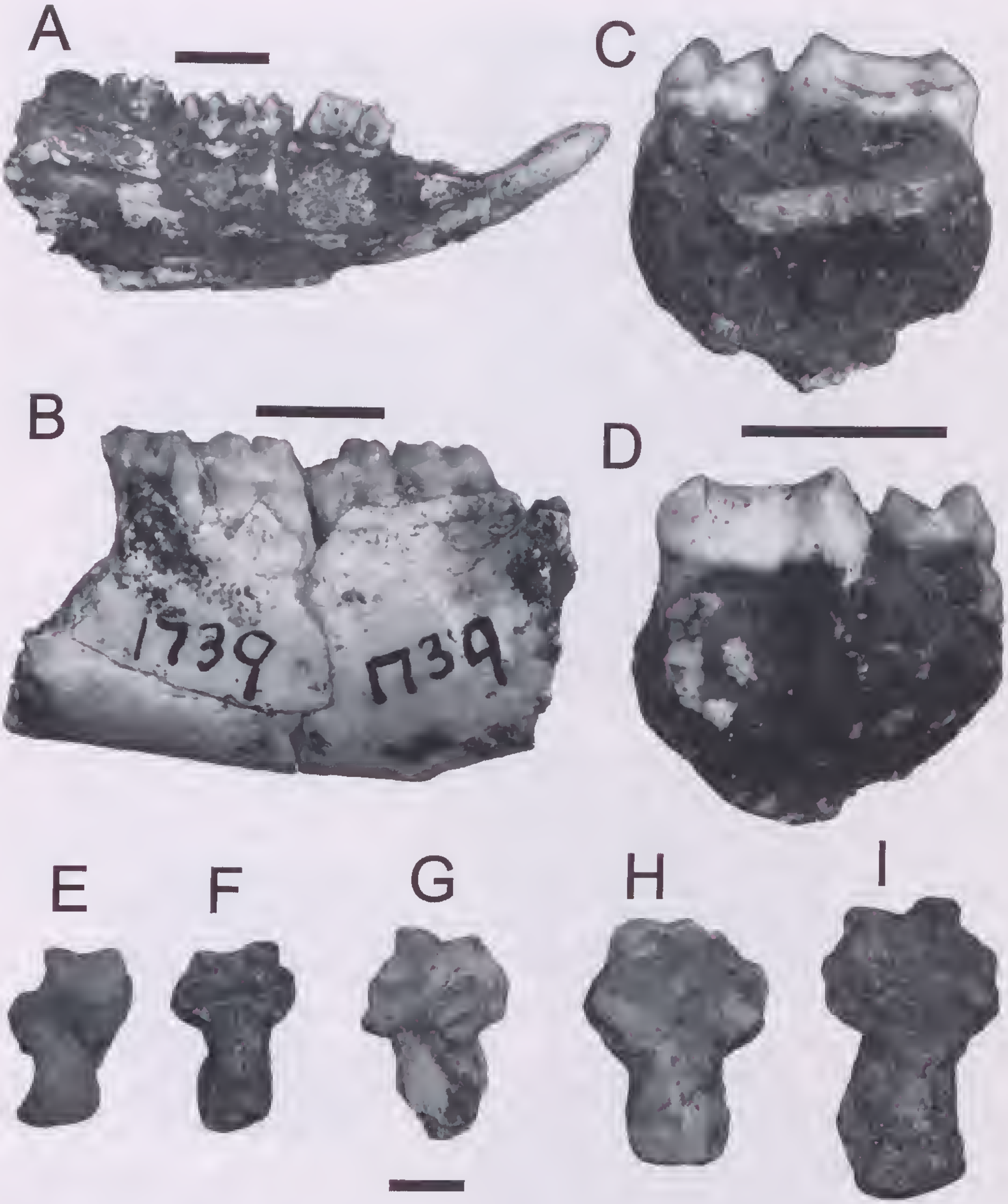

FIG19. A-I, Macropodidae. A-H, *Dendrolagus* sp.; A, QMF51770, RI$_1$-M$_4$. B, QMF1739, LM$_{1-4}$. C-D, QMF51771, RP$^3$-M$^1$ in lingual and buccal view (showing postero-buccal cuspule on P$^3$). E-H, Calcanea; QMF51772-51775 (left to right). I. *Bohra* sp.; QMF51783, calcaneum. Scale bar = 5mm.

## Family MACROPODIDAE Gray, 1821

### **Bohra** Flannery & Szakay, 1982

### **Bohra** sp.
(Fig.19I)

MATERIAL. QMF51762; QML1311C/D.

*Bohra* sp. is represented by a complete right calcaneum (Calcaneal Length: 46.79mm; Calcaneal-Cuboid articulation height 12.43mm and width 18.96; Astragalar-calcaneal articulation length 23.01mm). The calcaneum is placed within *Bohra* on the basis of the following features it shares with *Bohra paulae*: 1. Massive calcaneal size relative to all other dendrolagine macropods. 2. Height to width of calcaneal-cuboid articulation (Flannery & Szakay, 1982) (0.65). 3. Calcaneal length to astragalar-calcaneal articular length (Flannery & Szakay, 1982) (0.49).

### **Dendrolagus** Muller & Schkegel, 1839

### **Dendrolagus** sp.
( Fig. 19A-H)

MATERIAL. QMF51770-QMF51783; QML1284, QML1311(H), QML1311(C/D), QML1312, QML1385, QML1420.

*Dendrolagus* is represented by two nearly complete mandibles, three maxillary fragments, isolated premolars, molars and three calcanea. The mandibles are characterised by possessing low crowned, square molars and an elongate, blade-like $P_3$. $P_3$ blade bounded by a large anterior cusp and posterior cusp. A single intermediate cuspule is situated a third the way along the crest. The upper dentition is characterised by an ovo-rectangular $P^3$ in occlusal view, possessing low-crowned square molars with weak midlinks and absent forelinks. $P^3$ with both postero-buccal and postero-lingual cuspules. Paracone linked to metacone via a crested blade. A single vertical ridge runs to a small cuspule near the centre of the blade. A tiny accessory cuspule is present posterior to the main cuspule. Lingual cingulum runs the length of the tooth, terminating below the paracone. When compared to extant species of *Dendrolagus* the fossil taxon shares closest lower dentition morphology with *D. matschiei*, whereas the upper dentition most closely resembles *D. ursinus*. At present there are no morphological or morphometric features that suggest that the mandibles represent one taxon and the maxillae another. Further material will be needed to clarify the specific placement of these specimens, however, it seems most probable that the fossils represent an extinct taxon with phylogenetic links to both *D. matschiei* and *D. ursinus*.

Calcanea have been identified by possession of a distinctive squat shape, short calcaneal tuberosity, and broad anterior articular facets. Four specimens have been recovered so far and all four are distinctly different in size. The largest is from QML1420 Marmor Quarry (QMF51781), the second largest from QML1311 (QMF51780) and the smallest from QML1312. With so few calcanea available to compare, morphometric comparison with extant populations was not possible, however, the great difference in size between the largest and smallest calcanea may illustrate the presence of several species.

### **Kurrabi** Flannery & Archer, 1984

### **Kurrabi** sp.
(Fig. 20A-D)

MATERIAL. QMF51767-51769; QML1311(H), QML1311 (C/D).

Three isolated $P^3$'s represent a species of *Kurrabi*. Each premolar is elongate with two small vertical ridges on the longitudinal crest between the paracone and metacone. A moderate-sized fossette occurs on the posterior lingual side of the tooth. A lingual cingulum runs the length of the tooth, terminating just posterior of the base of the paracone. In size, the specimens are closest to *K. merriwaensis* (L: 9.2-11.5mm). Without more material specific diagnosis is not warranted.

### **Protemnodon** Owen, 1874

### **Protemnodon** sp. cf. **P. devisi** Bartholomai, 1973
(Fig. 20E-H)

MATERIAL: QMF41737, QMF41953, QMF51763-QMF51766, QMF52068; QML1284, QML1311(H), QML1311 (C/D).

*Protemnodon* sp. cf. *P. devisi* has been identified from an isolated premolar; a badly preserved palate with portions of $RP^2$, $RdP^3$, $RM^{1-3}$ and $LdP^3$, $RM^{1-2}$ preserved; a left mandible with $M_{2+3}$; left mandible preserving $P_3$; isolated $RM^1$, $LM^3$, $LM^4$, $LdP_3$, $LM_2$, $LM_3$ and an isolated $I_1$. Dimensions of the premolar and molars are within the range given for *P. devisi* by Bartholomai (1973). However, the specimens here differ from *P. devisi* from Chinchilla, but are similar to those of *P.* sp. cf. *P. devisi* described by Dawson et al. (1999) from Big Sink, in the

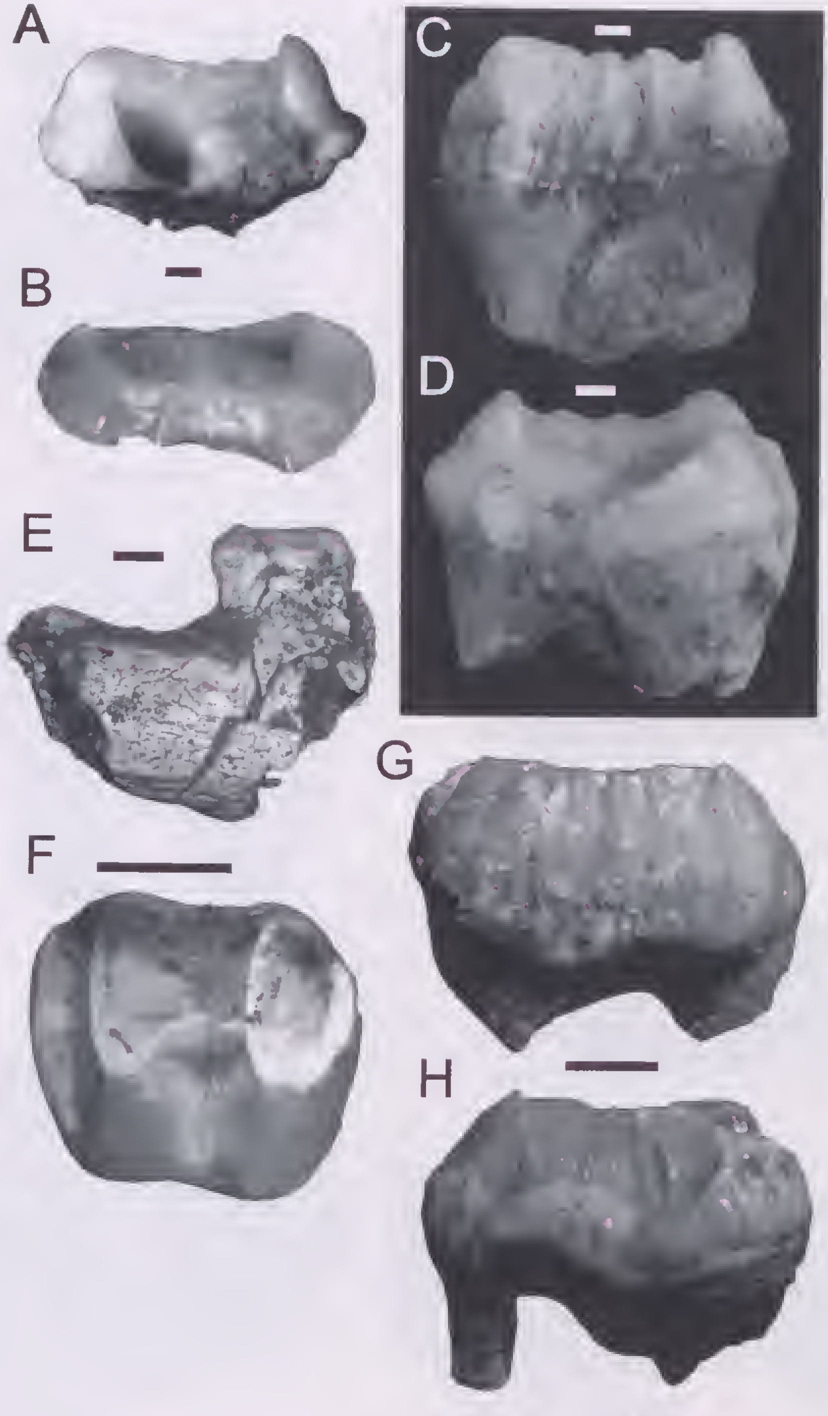

FIG 20. A-H, Macropodidae. A-D, *Kurrabi* sp.; A-B, QMF51767; RP$^3$ in lingual & occlusal views. C, QMF51768, LP$^3$. D, QMF51769, LP$^3$. Scale bar = 1mm. E-H, *Protemnodon* sp. cf. *P. devisi*; E, QMF41737, LP$_3$. F, QMF41953, LM$^3$. G-H, QMF51763; LP$^3$ in buccal & lingual views. Scale bar = 5mm.

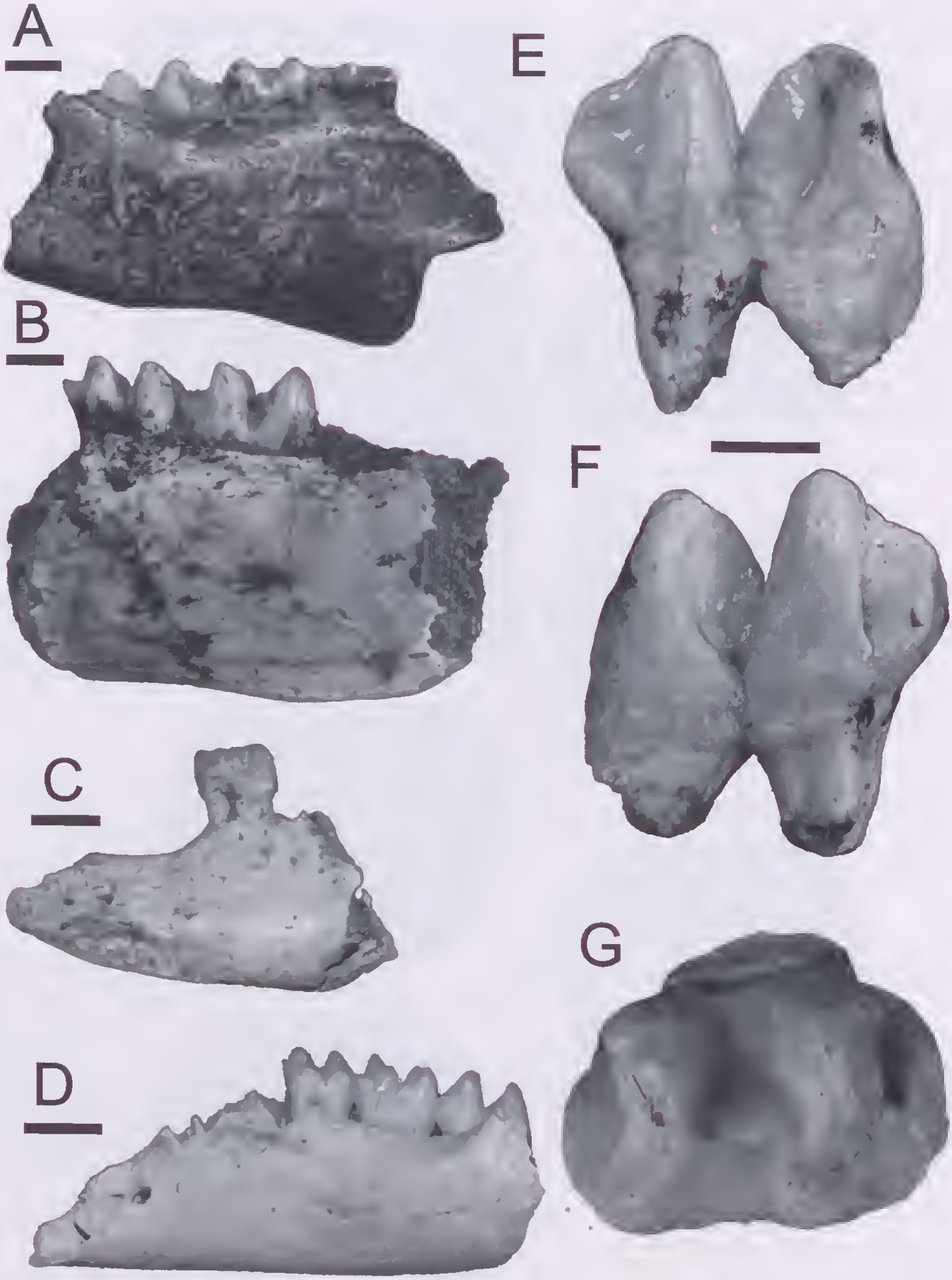

FIG 21. A-G, Macropodidae; A-B, *Macropus* sp. cf. *M. agilis siva*; A, QMF51829, RM$_{1-3}$. B, QMF51830, LM$_{1-2}$. C-D, *Petrogale* sp.; C, QMF51812, RP$_3$. D, QMF51813, LM$_{2-4}$. E-G, *Macropus titan*; QMF1697 in lingual (E), buccal (F) & occlusal (G) views. Scale bar = 5mm.

following ways: 1. Lower molars lack a posterior cingulum. 2. Upper molars lack a secondary link across the median valley. 3. $P^3$ has weak vertical ridges. The specimens do possess premetacristae, which the Big Sink specimens do not. The overall variation seen in the specimens of *P. devisi* from Chinchilla, Big Sink and Mount Etna is within that seen for similar cosmopolitan species such as *P. anak*.

### macropodine sp. indet

MATERIAL. QMF51802-51811; QML1284, QML1284a, QML1420, QML1384, QML1311(H).

Several isolated molars appear to represent a large species similar to species of *Thylogale*, however, being much greater in size. Other distinctive features of the molars include sharply crested postpara- and premetacrista running into the median valley; a sharply crested preparacrista linking onto the anterior cingulum, and a well-developed forelink.

The molar is high crowned, and similar in shape to some species of *Macropus*, however, the midlink is weakly developed and the cristae are sharp and elaborated unlike *Macropus*.

### **Petrogale** Gray, 1837

### **Petrogale** sp.
(Fig. 21C-D)

MATERIAL. QMF51812-51824; All localities.

*Petrogale* is represented by dozens of isolated mandibles, maxillae, molars, premolars, insisors and postcrania. The only taxa close to *Petrogale* are *Thylogale* and small members of *Macropus*. *Petrogale* differs from *Thylogale* in having lower-crowned molars, in the $I^3$ morphology (not having a longitudinal groove along the length of the $I^3$ crown) and the anterior morphology of the $P^3$ (not having a well-developed lingual cingulum with an anterior-lingual pocket). *Petrogale* differs from small-sized *Macropus* by being generally smaller, having a relatively longer $P^3$ and smaller $I^3$. The taxonomic diversity of modern species of *Petrogale* is not reflected in dental morphology, thus species placement is not warranted on the basis of available material.

### **Macropus** Shaw, 1790

Isolated molars and partial jaws represent species of *Macropus*. BarBtholomai (1975), Archer (1978) and Dawson & Flannery (1985) illustrate the difficulty in identifying species of *Macropus* on the basis of isolated molars or jaws without premolars and insisors. Distinction of different species of *Macropus* requires almost complete mandibles or maxillae. When dealing with isolated teeth, absolute size comparisons are the only features available for comparison to available data such as Bartholomai (1975). More complete specimens are required before specific allocations can be made.

### **Macropus** sp. 1

MATERIAL. QMF51825-51828; QML1312, QML1420.

A medium-sized *Macropus*, close to *Macropus dorsalis*, is represented by isolated molars that are larger in absolute size than those species of *Petrogale* but smaller than modern species of the size of *Macropus agilis*.

### **Macropus** sp. cf. **M. agilis siva** (De Vis, 1895)
(Fig. 21A-B )

MATERIAL. QMF51829-51834; QML1420, QML1311(H).

Isolated molars and a partial right mandible represent a medium-sized species of *Macropus*.

FIG 22. A-C, Macropodidae; *Thylogale* sp.; A, QMF51784, $LI_1$-$M_2$. Scale bar = 5mm. B, QMF51785, $LM_2$. C, QMF51786, $LM^2$. Scale bar = 1mm.

*Macropus agilis agilis* is closest in overall size to the fossil specimens from Marmor Quarry, however, there is overlap with *Macropus agilis siva* when comparing the mandible from Lost Paradise Cave (J7) and the maxilla and mandible from QML1311. All dental measurements fall within the range for *Macropus agilis siva* defined by Bartholomai (1975).

### **Macropus titan** (Owen, 1838)
(Fig. 21 E-G)

MATERIAL. QMF1697, QMF51835-51837; QML1420.

*Macropus titan* is a large macropod easily distinguished by its large high crowned molars, distinct mid- and fore-links and posterior hypolophid groove. Specimens referred to here are placed within *M. titan* based on these features and their similar size to samples taken from the Darling Downs (Bartholomai, 1975).

### **Thylogale** Gray, 1837

Two species of *Thylogale* have been identified based on the presence of high-crowned (relative to *Dendrolagus*), rectangular molars, poorly developed midlinks, an anterior cingulum that does not extend across the entire width of the upper molars, and an $I^3$ that has a complete longitudinal groove on the occlusal face. They have been differentiated from *Petrogale* by having weaker midlinks, an incomplete anterior cingulum on upper molars, smaller-sized molars, and better-developed cristae on dP3s and upper molars.

### **Thylogale** sp. 1
(Fig. 22A-C)

MATERIAL. QMF51784-51797; QML1284, QML1284a, QML1385, QML1384U.

A very small-sized new species of *Thylogale*, smaller than any extant or extinct species, including the smallest known species, *Thylogale christenseni* from Irian Jaya. The upper molars possess weakly developed midlinks, a reduced forelink and an anterior cingulum that only extends slightly more than half way across the front of the molar. These features are shared to a greater extent with *T. christenseni* and *T. billardierii*. With further specimens, this taxon will probably be a new species closely related to *Thylogale christenseni*.

### **Thylogale** sp. 2

MATERIAL. QMF51798-51801; QML1312, QML1420.

On the basis of molar size and morphology, differentiation of *Thylogale thetis* and *Thylogale stigmatica* is extremely difficult. The fossil specimens are within the range of both taxa and are very similar in overall morphology.

## Family PSEUDOCHEIRIDAE (Winge, 1893)

Pseudocheirids are represented by hundreds of isolated premolars and molars, molar rows and jaw fragments. The apparent morphological diversity in the collection is corroborated by the diversity in sizes, ranging from very small ringtails of similar size to *Pseudochirulus mayeri;* medium-sized similar to *Pseudochirulus forbesi*; large-sized *Pseudocheirops* and giant *Pseudokoala.* On reviewing the morphology of modern and Tertiary pseudocheirid taxa it became obvious that the most useful features for identification are found in the P3 and M1 of the upper and lower dentition. Based on characters from these key teeth, several groups emerged. More specific formal taxonomy will be provided in a future analysis as more complete material becomes available.

### **Pseudochirulus** Matschie, 1915

*Pseudochirulus* has been identified based on the following combined features: $P^3$ morphology; elongate-ovoid, preparacrista variably linked to paraconule by blade or valley, only two cusps, posterolingual cingulum variably expressed. $M^1$ morphology; molar profile elongate-rectangular, preprotoconule crista variably expressed, lingual cingulum absent. $P_3$ morphology; metaconid blade-like or absent, paraconid distinct and not linked to protoconid by blade, cristid obliqua distinct running from the hypoconid to protoconid. $M_1$ morphology; distinct paraconid; preprotocristid kinded buccally to paraconid, metaconid variably expressed, entostylid absent. Three species of *Pseudochirulus* have been identified, two small species similar in size to *Pseudochirulus mayeri* and one medium-sized species similar in size to *Pseudochirulus forbesi*.

### **Pseudochirulus** sp. 1
(Fig. 23 G-I, Fig. 24 E)

MATERIAL. QMF51838-51870; QML1385, QML1311(H), QML1311(C/D), QML1284, QML1284a, QML1313, QML1385L.

*Pseudochirulus* sp. 1 is the smallest of the pseudocheirid taxa represented and possesses the following distinctive features that distinguish it and differentiate this species from *Pseudochirulus* sp. 2 and 3: 1. Simple preprotoconule that does not connect to any other

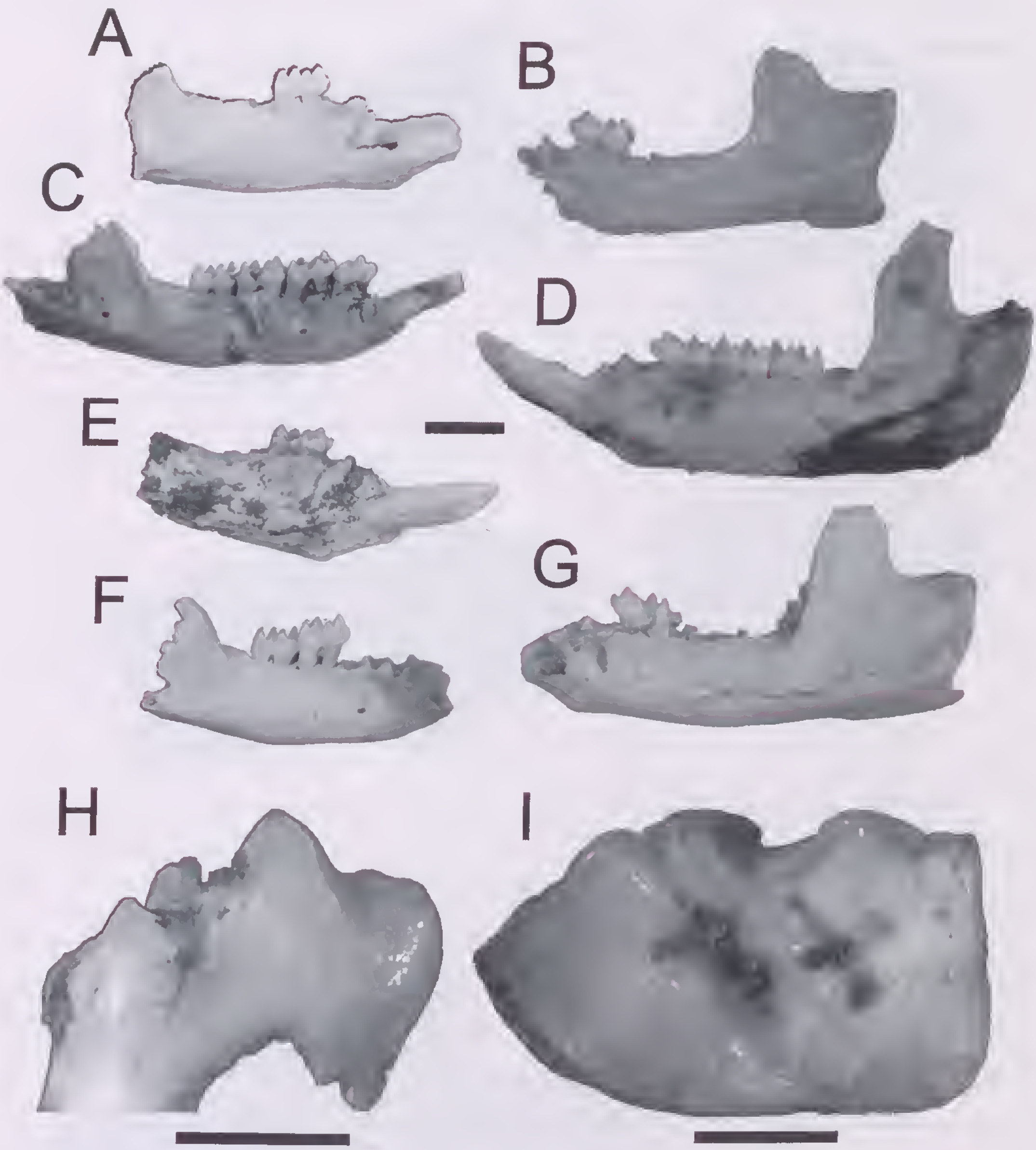

FIG 23. A-I, Pseudocheiridae. A, B, D, E & H, *Pseudocheirus* spp.; A, QMF51898, RM$_1$. B, QMF51899, RI$_1$-M$_3$. D, QMF51900, RM$_{2-3}$. E, QMF51901, RP$_3$. Scale bar = 5mm. H, QMF51840, LM$_1$. (Scale bar = 1mm). C, *Pseudochirulus* sp. 2; QMF51871, RI$_1$ & M$_1$. F, G & I, *Pseudochirulus* sp. 1; F, QMF51838, LM$_1$. G, QMF51839, LI$_1$ & M$_{1-3}$. Scale bar = 5mm. I, QMF51841. Scale bar = 1mm.

cristae. 2. Protostyle absent. 3. Lingual cingulum absent. 4. Anteriorlingual para- and metacristae absent. 5. Posterolingual para- and metacristae absent. 6. P$^3$ elongate-ovoid in occlusal view. 7. P$^3$ preparacrista does not connect to paraconule. 8. Distinct posterolingual cingulum on P$^3$.

*Pseudochirulus* sp. 1 is closest in morphology to the living *Pseudochirulus canescens* and

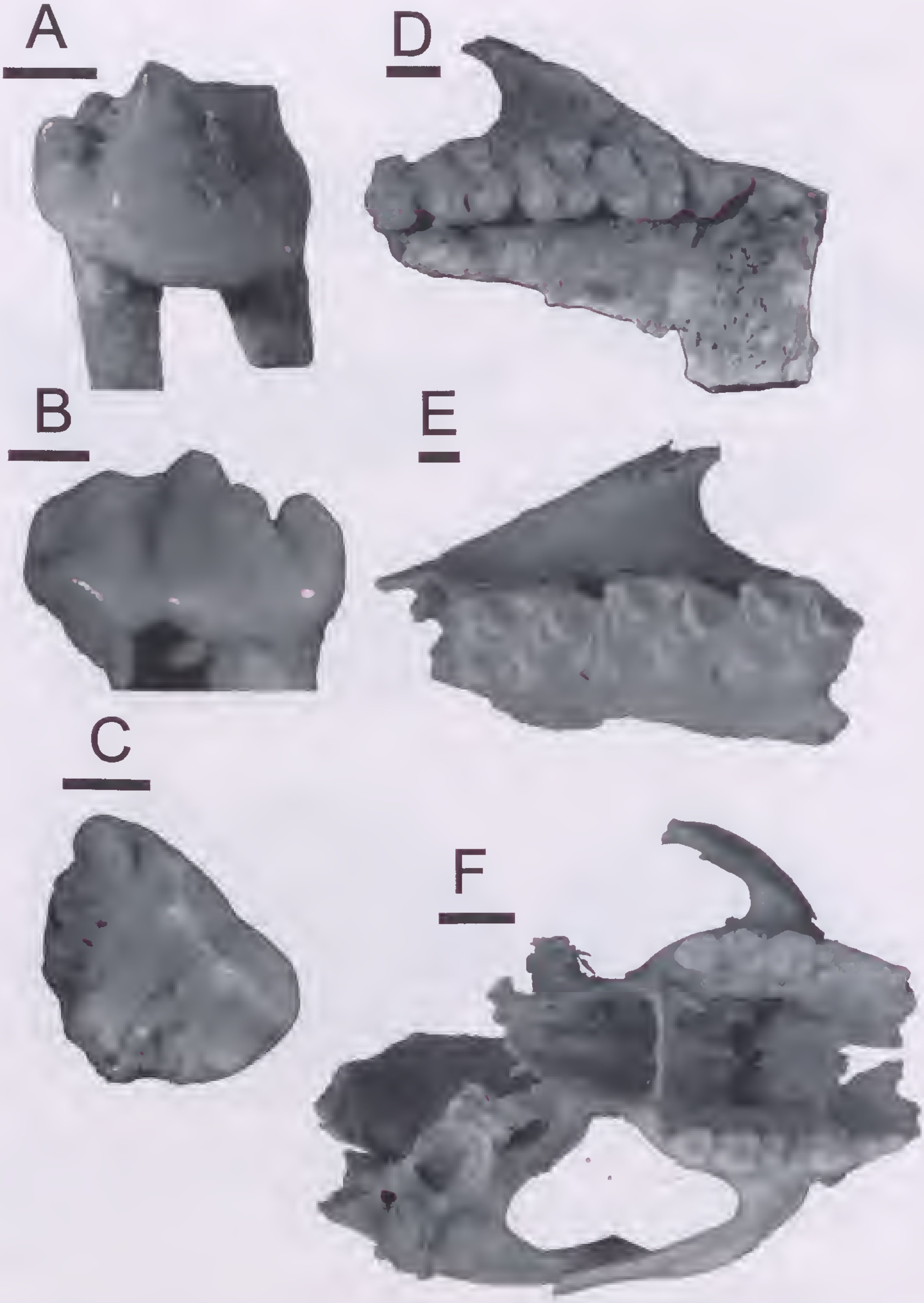

FIG 24. A-F, Pseudocheiridae; A-D, *Pseudocheirus* sp.; A, QMF51920, LP$^3$. B-C, QMF51921, LP$^3$ in buccal & occlusal views. E, *Pseudochirulus* sp. 1; QMF51870, RP$^3$-M$^3$ (broken). Scale bar = 1mm. F, *Pseudochirulus* sp. 2; QMF51887, partial skull. Scale bar = 5mm.

*Pseudochirulus mayeri* and the Early Pliocene *Pseudocheirus marshalli.*

### **Pseudochirulus** sp. 2
(Fig. 23C, Fig. 24F)

MATERIAL. QMF51871-51887; QML1284, QML1284a, QML1313, QML1311(H), QML1384U, QML1384L, QML1385.

*Pseudochirulus* sp. 2 possesses the following distinctive features, that when combined differentiate it from *Pseudochirulus* sp. 1 and 3: $P^3$ morphology; 1. $P^3$ elongate-ovoid. 2. Distinct paraconule. 3. Preparacrista contacts paraconule. 4. Broad posterolingual margin with indistinct cingulum. 5. Postparaconule crista distinct and terminates at the base of the paracone. $M^1$ morphology; 1. Preprotoconule crista contacts paracone butress. 2. Protostyle present and well-developed. Overall size larger than *Pseudochirulus* sp. 1.

When compared to modern species the fossil taxon is most similar to *Pseudochirulus cinereus* and *Pseudochirulus forbesi* in overall size. The $P^3$ of *Pseudochirulus* sp. 2 is distinctly more ovoid than the morphology seen in the modern species. The $P^1$ has large double roots, a feature seemingly unique to this taxon, having not being observed in any of the modern or fossil taxa.

### **Pseudochirulus** sp. 3

MATERIAL. QMF51888-51897; QML1284, QML1284a, QML1313, QML1311(H), QML1385, QML1384U, QML1384L.

*Pseudochirulus* sp. 3 possesses the following features that in combination differentiate it from *Pseudochirulus* sp. 1 and 2: $P^3$ morphology; 1. $P^3$ elongate-ovoid. 2. Preparacrista contacts paraconule. 3. Distinct posterolingual cingulum, variably cuspidate. 3. Kink in the posterobuccal end of the postparacrista.

When compared to modern species, the fossils are closest in morphology to both *Pseudochirulus mayeri* and *Pseudochirulus herbertensis*. The fossil specimens differ from these species in being larger than *Pseudochirulus mayeri* and smaller than *Pseudochirulus herbertensis.*

## **Pseudocheirus** Ogilby, 1837

### **Pseudocheirus** spp.
(Fig. 23A-B, D-E, H, Fig. 24A-D)

MATERIAL. QMF51898-51922; QML1284, QML1284a, QML1313, QML1311(H), QML1385, QML1384U, QML1384L.

*Pseudocheirus* has been identified on the basis of the following combined features: $P^3$ morphology; 1. Tricuspid, possessing a paracone, paraconule and an accessory cusp between and buccal to them. 2. Ovoid shape to the premolar in occlusal view. 3. Shallow, indistinct posterolingual basin. $M^1$ morphology; 1. Preprotoconule terminating at the base of the parastyle. 2. Protostyle distinct. 3. Lingual cingulum present between protocone and metaconule. 4. Lack postero- and anterolingual para- and metacristae. $P_3$ morphology; 1. Metaconid present as a distinct and high cusp. $M_1$ morphology; 1. Preprotocristid blade-like running to tip of paraconid. 2. Paraconid in line with protoconid. 3. Protostylid tall and crested, cloesly set against protoconid. 4. Entostylid absent. There are three species of *Pseudocheirus* represented from the sites, all three being markedly different in size but all significantly smaller than extant *Pseudocheirus*. Three species are considered to be new extinct species.

## **Petauroides** Thomas, 1888

### **Petauroides** spp.
(Fig. 25A-C)

MATERIAL. QMF51923-51935; QML1284, QML1284a, QML1313, QML1311(H).

*Petauroides* has been identified on the basis of the following combined features: $P^3$ morphology; 1. Ovoid shape in occlusal view. 2. Distinctly straight blade made by the crests running between the paraconule, paracone and posterobuccal margin of the premolar. 3. Posterolingual postparacrista running into posterolingual basin. 4. Posterolingual cingulum present. $M^1$ morphology; 1. Preprotoconule connects to preprotocrista. 2. Posterolingual para- and metacristae well developed as crests. 3. Protostyle absent. 4. Lingual cingulum absent. $P_3$ morphology; 1. Paraconid, protoconid and metaconid in a line along the longitudinal axis of the tooth crown. 2. Cristids variably expressed and probably constitute several species. 3. Small posterior pocket below the metaconid developed in some specimens.

The morphological diversity seen in specimens referred to here as *Petauroides* indicates a very complex fossil history leading to the modern *Petauroides* and *Hemibelideus*. The only $P^3$ specimen available is closest in morphology to *Hemibelideus*. $P_3$ morphology shows great degrees of morphological diversity albeit retaining typical *Petauroides* characteristics.

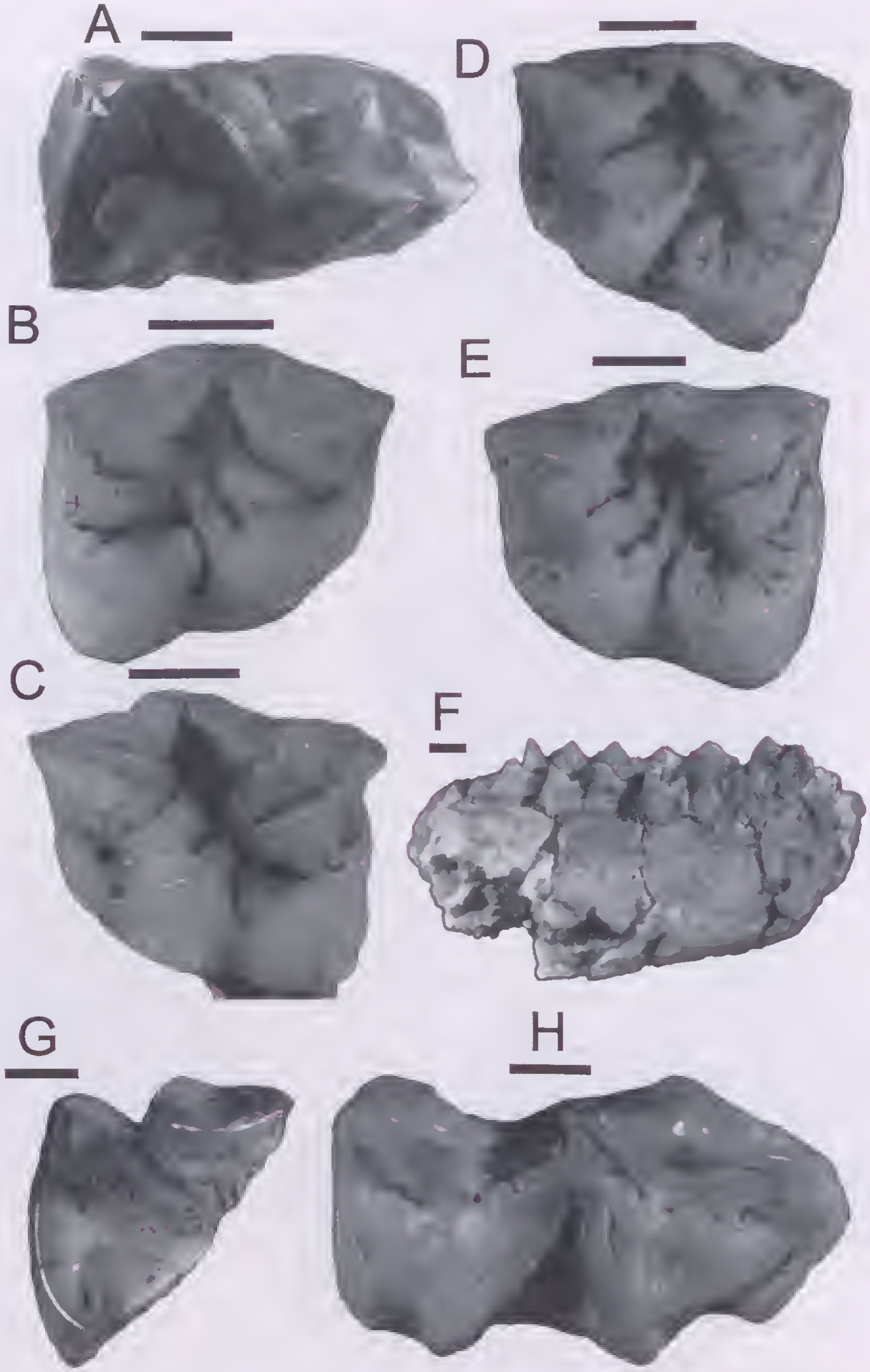

FIG 25. A-H, Pseudocheiridae; A-C, *Petauroides* sp.; A, QMF51923, RM$_1$. B, QMF51924, LM$^2$. C, QMF51925, RM$^2$. D-F, *Pseudocheirops* sp.; D-E, *Pseudocheirops* sp. 1; D, QMF51934, RM$^3$. E, QMF51935, RM$^2$. Scale bar = 1mm. F, *Pseudocheirops* sp. 2; QMF51937, RM$_2$. Scale bar = 5mm. G-H, Pseudokoala sp.; G, QMF51934, RM$^?$. H, QMF51939, RM$_2$. Scale bar = 1mm.

Five distinct morphologies are present, however, these will be treated as polymorphic until a larger collection is available. Even so, no $P_3$ clearly represents known species of *Petauroides* or *Hemibelideus*. $M_1$ morphology shares greater similarities with extinct species of *Petauroides* (*Petauroides stirtoni* and *Petauroides ayamaruensis*, see Long et al., (2002)) than with the modern *Petauroides volans* and *Hemibelideus lemuroides*.

### **Pseudocheirops** Matschie, 1915

*Pseudocheirops* has been identified on the basis of the following features: 1. Protostylid basin on $M_{1\text{-}3}$. 2. Elaborate crenulations on upper and lower molars. 3. Entosytlid present. 4. Posterior bifurcation of protoconule. 5. Protostyle present. 6. Crest present labial to protostyle. Two species of *Pseudocheirops* have been identified so far.

### **Pseudocheirops** sp. 1
(Fig. 25D-E)

MATERIAL. QMF51936, QMF51934-51935; QML1311(H), QML1384L.

*Pseudocheirops* sp. 1 is a right mandible preserving a partial $M_1$, complete $M_{2\text{-}3}$ and a partial $M_4$. Two upper right molars are also considered to be conspecific. The fossils compare favourably with *Pseudocheirops archeri* both in size, crenulations and development of the protostylid basin.

### **Pseudocheirops** sp. 2
(Fig. 25F)

MATERIAL. QMF51937; QML1284.

The second, much smaller species *Pseudocheirops* sp. 2, is only known from a right $M_2$. The crenulations are indistinct with a narrow entostylid and very small protostylid basin. The fossil is much smaller than any of the modern *Pseudocheirops* available to study, yet it is similar in size to the Pliocene *Pseudocheirops winteri* from Bluff Downs. The fossil differs from *Pseudocheirops winteri* by possessing a complete preentocristid-metacristid connection.

### **Pseudokoala** Turnbull & Lundelius, 1970

### **Pseudokoala** sp.
(Fig. 25G-H)

MATERIAL. QMF51938-51939; QML1385; QML1311 (C/D).

*Pseudokoala* has been identified from an isolated $M_2$ and a fragment of upper molar. It has been placed within *Pseudokoala* based on the following combined features: 1. Very large size. 2. Crenulations present but forming large buttresses, less crenulated than *Pseudocheirops* spp. 3. Lack of an entostylid. 4. Truncated posthypocristid. 5. Buccally buttressed protoconid.

When compared to the three species of *Pseudokoala*, *Pseudokoala* sp. is closest to *Pseudokoala erlita* in size ($M_2$L: 6.78mm *Pseudokoala* sp., $M_2$L: 6.2-7.3mm *Pseudokoala erlita* Turnbull & Lundelius (1970), $M_1$L: 10.7mm *Pseudokoala curramulkensis*, $M_1$L: 10.9mm *Pseudokoala cathysantamaria* Archer et al. (1997). The molar crown is simplified as in *Pseudokoala erlita*, however, due to the worn nature of the tooth no more specific comparisons can be made.

### pseudocheirid indet.

MATERIAL. QMF51940; Olsen's Cave.

A posterior fragment of an upper molar with distinctly selenodont morphology represents the only material of a pseudocheirid from the Olsen's Cave collection. The lack of crenulations and an anterolingual metacrista allies the specimen to a large member of *Pseudochirulus* or *Pseudocheirus peregrinus*.

## Family PETAURIDAE (Gill, 1872)

Petaurids are represented by several nearly complete maxillae, fragmentary mandibles, isolated insisors, premolars, molars and postcrania. Two genera are recorded, *Dactylopsila* and a new undescribed genus.

### **Dactylopsila** Gray, 1858

*Dactylopsila* has been identified based on the following combined features: 1. Possession of a distinct and large $M^1$ parastyle. 2. Reduction of the stylar margin with a distinct indentation between the paracone and metacone. 3. Reduced metaconule. 4. Procumbent $I_1$. 5. Bulbous, rectangular-ovoid lower molars.

### **Dactylopsila** sp. 1
(Fig 26E)

MATERIAL. QMF51943-QMF51946; QML1284; QML1284a; QML1384U; QML1385.

*Dactylopsila* sp. 1 is 10-12% smaller than the species of *Dactylopsila* available for study, *Dactylopsila trivirigata* and *Dactylopsila palpator*. The fossil species also differs from *D. trivirigata* and *D. palpator* by possessing less rounded and more gracile lower molars, a more buccal placement of the protoconid on $M_1$ and a

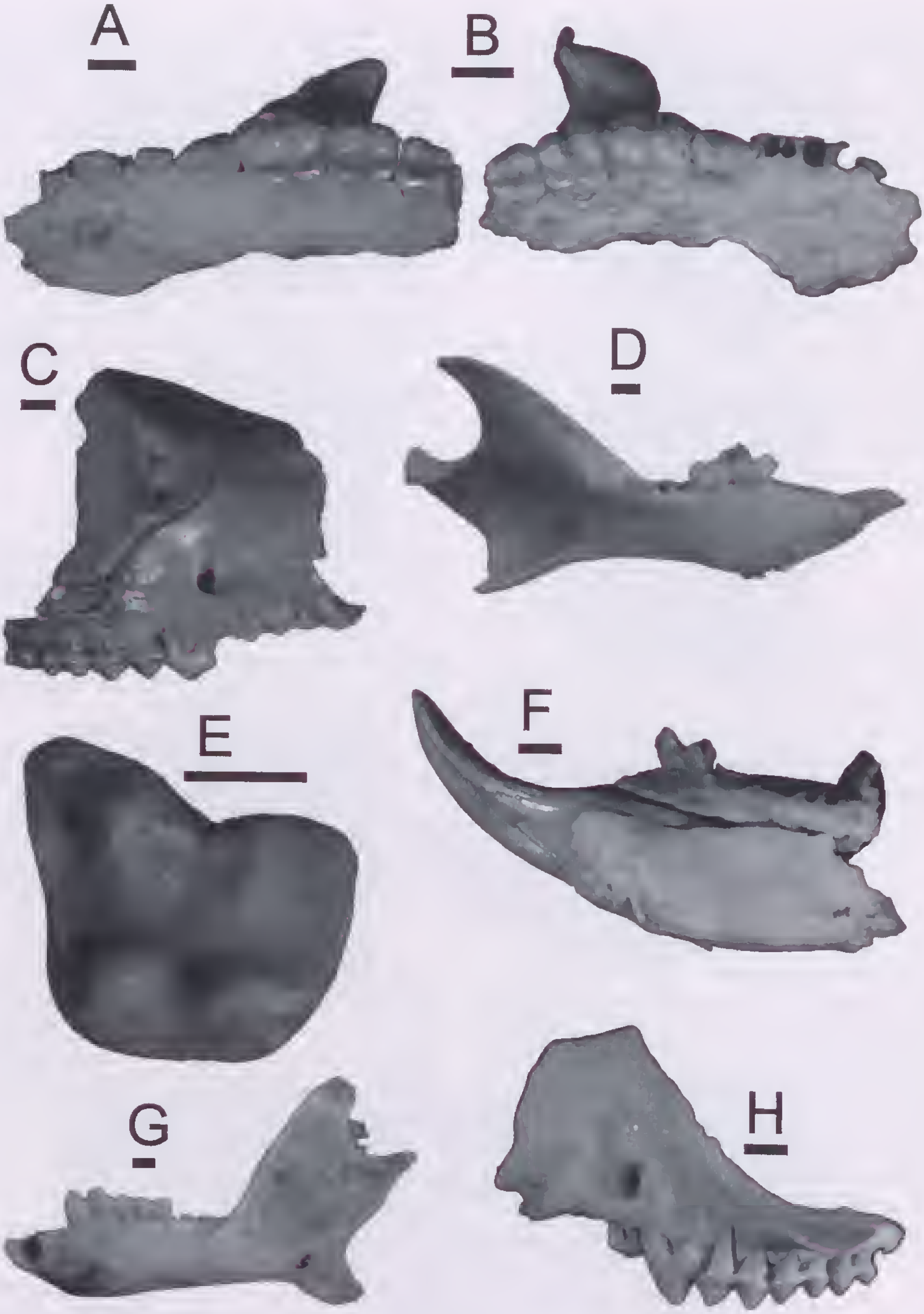

FIG 26. A-F, Petauridae, A-D, Gen. et sp. nov.; A, QMF51949, LP$^1$-M$^3$. B, QMF51950, RP$^3$-M$^3$. C, QMF54951, partial skull. D, QMF54952, left mandible (M$_{1-2}$). E, *Dactylopsila* sp. 1; QMF51947, LM$^1$. F, *Dactylopsila* sp. 2; QMF51948, RI$_1$ & M$_1$. G-H, Burramyidae; *Cercartetus* sp.; G, QMF51984, LP$_3$-M$_2$. H, QMF51985, LP$^2$-M$^3$. Scale bar = 1mm.

less distinct postprotocristid. When compared to the extinct *D. kambuayai* the fossil is approximately 20% larger, however, it does possess a similar gracile profile of the $M_2$.

### **Dactylopsila** sp. 2
(Fig. 26F)

MATERIAL. QMF51947-51948; QML1284.

A second, smaller species of *Dactylopsila* is represented by a fragmentary left mandible with $I_1$ and $M_1$. The $I_1$ is large and recurved, procumbent. $M_1$ gracile in occlusal profile, rectangular ovoid with conids without bulbous exterior margins. Protoconid mesially produced. Massateric fossa inserts below $M_{2-3}$. Very small alveoli for $P_{2-3}$.

When compared to *D. trivirigata* and *D. palpator*, *Dactylopsila* sp. 2 differs by being much smaller, a less recurved $I_1$, possessing a more gracile and unbuttressed hypoconid, and a more mesially oriented protoconid on $M_1$. *Dactylopsila* sp. 2 is similar in size and $I_1$ morphology to *D. kambuayai,* however, there are no specimens of $M_2$ available for direct comparison.

### Gen. et sp. nov. 1 & 2
(Fig. 26A-F)

MATERIAL. Sp 1: QMF51949-51969; QML1284, QML1284a, QML1313, QML1312, QML1385. QML1384U; QML1384L; QML1420, QML1311.

MATERIAL. Sp 2: QMF51970-51973; QML1284, QML1284a.

Two species of a new medium-sized petauroid are characterised by a dentition that possesses a combination of both plesiomorphic features found in Oligo-Miocene petauroid *Djaluganji yadjana* (Brammal, 1998), and the derived characteristics seen in modern *Petaurus.* The upper molar row is distinctly straight, not possessing the upward inflexion toward the posterior as seen in all modern petaurids. The presence of a distinct stylar basin in $M^1$ and $M^2$ distinguish this taxon from both the modern and described Oligo-Miocene petaurids. The reduction of the premolars and molar gradient is shared with *Petaurus* and *Gymnobelidius*, but not to the extent seen in these taxa. Two distinct species are present from the sites and can be distinguished from each other (and the Hamilton Fauna petaurids) on the state of the metaconule, postprotocristae, premetaconule cristae and stylar basin. The greater number of features shared with *Petaurus* and *Gymnobelidius* warrant its placement in the Petauridae at the present time.

## Family BURRAMYIDAE (Broom, 1898)

Burramyids were identified on the basis of their small-sized, square molars with reduced stylar shelf and distinctly high paracone and metacone. They were differentiated from acrobatids by possessing reduced P1 and P2 and the presence of M4. Burramyid specimens comprise the majority of the very small possums collected from the possum-rich localities of the present study. A conspicuous absence from the burramyid fauna is *Burramys*, with all of the specimens being placed within *Cercartetus.*

### **Cercartetus** Gloger, 1841

### **Cercartetus** sp.
(Fig. 26G-H)

MATERIAL. QMF51984-52002; QML1284, QML1284a, QML1385, QML1311(H), QML1313.

Several nearly complete mandibles, well preserved maxillae, dozens of isolated molars and premolars represent *Cercartetus.* These specimens have been placed within *Cercartetus* based on their size and the absence of the distinctly plagiaulacoid $P^3/P_3$, which is distinct in the only other burramyid, *Burramys*. On comparison with the four known species of *Cercartetus,* the fossil specimens differ least from *Cercartetus caudatus* by being very close in size, retaining M4 and possessing a $P^3$ with a single conical cusp. The specimens differ from all other species of *Cercartetus* by possessing an M4. *Cercartetus* sp. differs from *Cercartetus caudatus* by possessing a larger and double rooted $P^1$ and $P^2$, a larger $C^1$ root and a shorter diastema between $C^1$ and $P^1$. Additionally, it differs from all extant species of *Cercartetus* by only possessing two individual roots between $I_1$ and $P_3$, instead of three. The homology of the missing root is unknown. With further analysis, *Cercartetus* sp. probably represents a new extinct species closely related to *Cercartetus caudatus*.

## SUPERFAMILY INCERTAE SEDIS

### Gen et sp. nov.
(Fig. 27B-C)

MATERIAL. QMF51974-51981; QML1284, QML1284a, QML1311(H), QML1385.

A medium-sized possum, similar in size to *Petaurus*, represents a new taxon of uncertain affinities. The closest morphologies to this taxon can be found within both the Acrobatidae and the

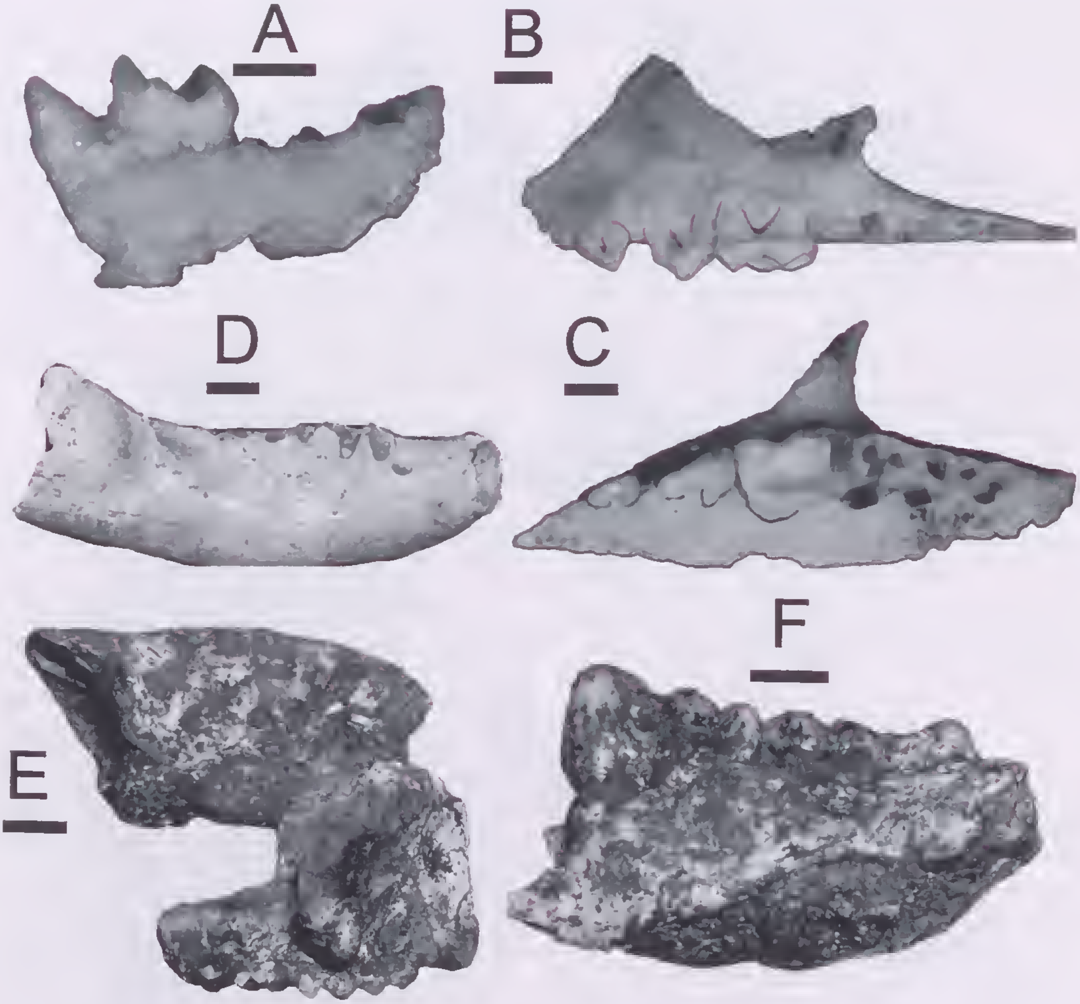

FIG 27. A, Acrobatidae; *Acrobates* sp.; QMF51982, RP$_3$-M$_1$. Scale bar = 1mm. B-C, Superfamily incertae sedis; QMF51974 in buccal & occlusal view. Scale bar = 1mm. D-F, Phalangeridae; D, *Trichosurus* sp. 1; QMF52009, right mandible. E, *Trichosurus* sp. 2; QMF52012, partial skull. F, *Strigocuscus* sp.; QMF52003, LP$_3$-M$_3$. Scale bar = 5mm.

Burramyidae, where features they share include: 1. Enlarged paracones and metacones on M$^{1-4}$. 2. Very reduced stylar margin. 3. Distinct molar size gradient from M$^{1-4}$. 4. Double-rooted P$^{2-3}$. The taxon differs from the majority of these taxa by features that are considered plesiomorphic within the two families (Archer, 1984), including: 1. Presence of M$^4$ (*Burramys parvus* and *Cercartetus caudatus*). 2. Subequal metaconule with protocone. 3. Double-rooted P$^2$.

The taxonomic placement within either of these families would require further material and a review of pygmy-possum higher taxonomy, which is under considerable confusion at present (Archer, 1984; Strahan, 1998).

### Family ACROBATIDAE Aplin, 1987

Acrobatids are easily distinguished and are here represented by the very small-sized *Acrobates*. The fossil specimens have been identified as acrobatid based on the large sized premolars and the premolariform shape to the $M_1$ trigonid (Archer, 1984).

### **Acrobates** Desmarest, 1818

### **Acrobates** sp.
(Fig. 27A)

MATERIAL. QMF51982- QMF51983; QML1385, QML1284.

*Acrobates* sp. has been identified based on its diminutive size and the presence of a large $P_3$, which distinguishes it from the only other member of the Acrobatidae, the New Guinea genus *Distoechurns*. On comparison with *Acrobates*, the specimens are very similar in size and overall morphology. There is only a slight difference in the posterobuccal morphology of the $P_3$. The variation of this feature is unknown, therefore, the identification will remain conservative.

## Family PHALANGERIDAE Thomas, 1888

Phalangerids have been found in most localities and either represent rainforest phalangerids or the more sclerophyl woodland species of *Trichosurus*. There is considerable difficulty when identifying phalangerids from partial jaws and isolated teeth because the best diagnostic features seem to be from the periotic (Crosby, pers.com.) and basicranial region (Flannery et al., 1987). Morphological conservatism obvious in fossil phalangerid taxa, including the Miocene *Strigocuscus reidi* and Early Pliocene *Strigocuscus notialis*, makes identification of this material particularly difficult. However, using features defined by Flannery et al. (1987) it is possible to refine the identification of phalangerids to generic level.

### **Strigocuscus** Gray, 1862

### **Strigocusus** sp.
(Fig. 27F )

MATERIAL. QMF52003-QMF52008, QMF52071; QML1284, QML1284a, QML1384U, QML1385, QML1384L.

*Strigocuscus* sp. is represented by two partial right mandibles, a partial left mandible and several isolated premolars and molars. The specimens are placed within *Strigocnsus* based on the presence of the following features: 1. P3 at an oblique angle to the molar row. 2. P3 has more than four cuspules. 3. P3 hypertrophic. 4. P3 highest anteriorly. 5. Molars without complex crenulations. 6. Preprotocrista contacts parastyle on $M^1$. The fossils share their greatest similarity with *S. gymnotis* and *S. notialis*, which includes a distinctly large, antero-buccally oriented P3 and a single-rooted $P_2$. The specimens differ from *S. gymnotis* by being only slightly larger, possessing more cuspules on P3 and having a distinct contact of the preprotocrista to parastyle. [Note: AMR22155, *S. gymnotis* from Parkop Village PNG does possess an $M^2$ with a preprotocrista contacting the parastyle albeit not as distinct as the fossil]. *S. reidi* Flannery & Archer, 1987 from the Miocene and *S. notialis* Flannery et al.,1987 from the Early Pliocene are phenetically very similar to *S. gymnotis*, however both possess distinct preparacristae contacting the parastylar corner of $M^1$. Additionally *S. reidi* is larger than *S. gymnotis* and *S. notialis* is smaller. On balance, *Strigocucus* sp. shares most features with *S. notialis*, except for being larger.

### **Trichosurus** Lesson, 1828

### **Trichosurus** sp. 1
(Fig. 27D)

MATERIAL. QMF52009-QMF52011; QML1312, QML1314, QML1420.

*Trichosurus* sp. 1 is represented by an edentulous right and a partial left mandible, two left partial maxillae, isolated molars and premolars. *Trichosnrus* sp. 1 has been identified based on the following combined features: 1. $P_2$ absent. 2. P3, rectangular-shaped in lateral profile (as high anteriorly as posteriorly). 3. Gracile mandible in lateral profile.

Archer (1978) could not adequately differentiate modern species of *Trichosurus* based on molar morphology and size, this mainly being due to the extreme variation seen in the cosmopolitan *T. vulpecula*. One feature of note, present in both fossil mandibles, is a large cavity situated above the posterodorsal margin of the mandibular symphasis, which penetrates the lower incisor alveolus. This feature has not been seen in any phalangerid examined for this study yet the feature is present in both mandibles referred to *Trichosurus* sp. 1. Also, both jaws are from different faunas, being split by almost 100km. The association of the cavity with the incisor root suggests that this may be a pathology, which affected a large population of *Trichosurus* in central eastern Queensland.

### **Trichosurus** sp. 2
(Fig. 27E)

MATERIAL. QMF52012, QMF52070; QML1311(H), QML1384L.

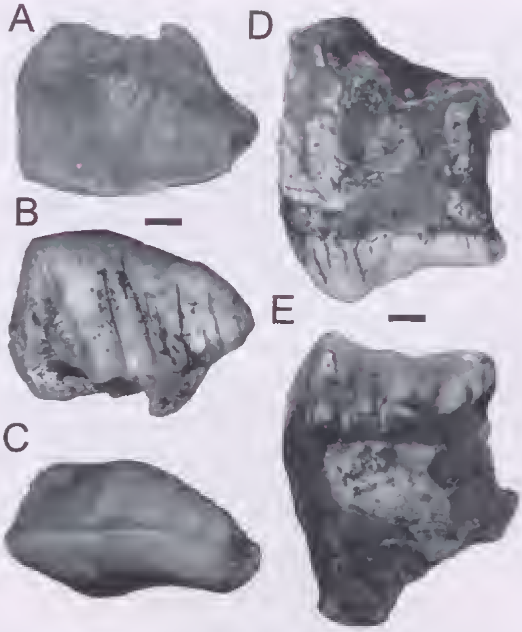

FIG 28. A-E, Thylacoleonidae; A-C, *Thylacoleo* sp.; QMF52069, $RP^3$ in lingual, buccal & occlusal views. D-E, *Thylacoleo hilli*; QMF52013, $RP^3$ in buccal & lingual views. Scale bar = 5mm.

A second, small species of *Trichosurus* is known from a single left mandible fragment preserving $P_3$ and $M_1$ and a portion of skull with right maxilla ($P^3$-$M^4$). The specimen is placed within *Trichosurus* based on: 1. A rectangular $P_3$ in lateral profile. 2. $M_1$ with distinct metaconid, positioned posterolingually to protoconid. 3. Reduced $P_3$ cuspules. 4. $P_3$ smaller than $M_1$. 5. Preprotocristid crest to paraconid. When compared to *T. vulpecula* and *T. caninus*, the fossil species is markedly smaller with a relatively larger $M_1$ to $P_3$. *Trichosurus* sp. 2 differs from the Early Pliocene *T. hamiltonensis* by possessing a smaller $P_3$ relative to $M_1$ and by being smaller in overall size. *Trichosurus* sp. is closest in morphology and size to *T. dicksoni* from the Miocene of Riversleigh. Because direct comparison to all trichosurin phalangerids, such as *T. arnhemensis,* was not possible a specific assignment will be left for a later analysis.

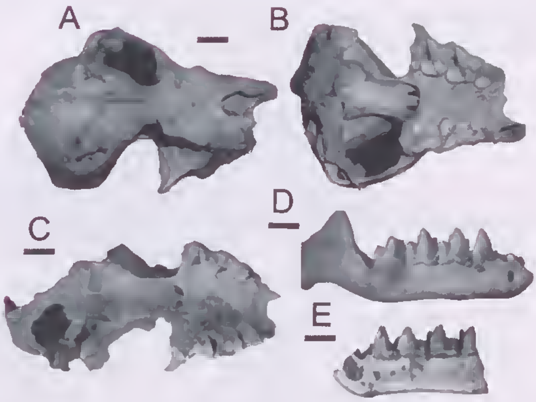

FIG 29. A-E, Megadermatidae; *Macroderma gigas*; A-B, QMF48021, partial skull in dorsal & ventral views. C, QMF48022, partial skull. D, QMF48006, $RP_3$-$M_3$. E, QMF48591, $LP_4$-$M_3$. Scale bar = 5mm.

## Family THYLACOLEONIDAE Gill, 1872

### **Thylacoleo** Gervais, 1852

### **Thylacoleo** sp.
(Fig. 28A-C )

MATERIAL. QMF1338, QMF52069; QML1420, QML1384L.

An isolated $P_3$ (QMF1338) and $P^3$ (QMF52069) represent the distinctive marsupial carnivore, *Thylacoleo.* Comparison of the premolars with *Thylacoleo carnifex* and *T. crassidentatus* does not resolve its taxonomic position, because the posterior portions of both premolars are broken, thus a full morphometric analysis was not possible. Interestingly, both specimens show very little wear.

### **Thylacoleo hilli** Pledge, 1977
(Fig. 28D-E)

MATERIAL. QMF52013; QML1311(H).

A single left $P^3$ represents the smallest known species of *Thylacoleo, Thylacoleo hilli.* Identification of small thylacoleonid P3's has been subject to speculation that they may be deciduous premolars of larger species (Pledge, 1977; Archer, 1984; Archer & Dawson, 1982b). Archer & Dawson (1982) suggest that *Thylacoleo* probably did not have a significant deciduous premolar since no thylacoleonid material so far found preserves a $dP^3$. The lack of a molariform premolar, resorbtion pits for the

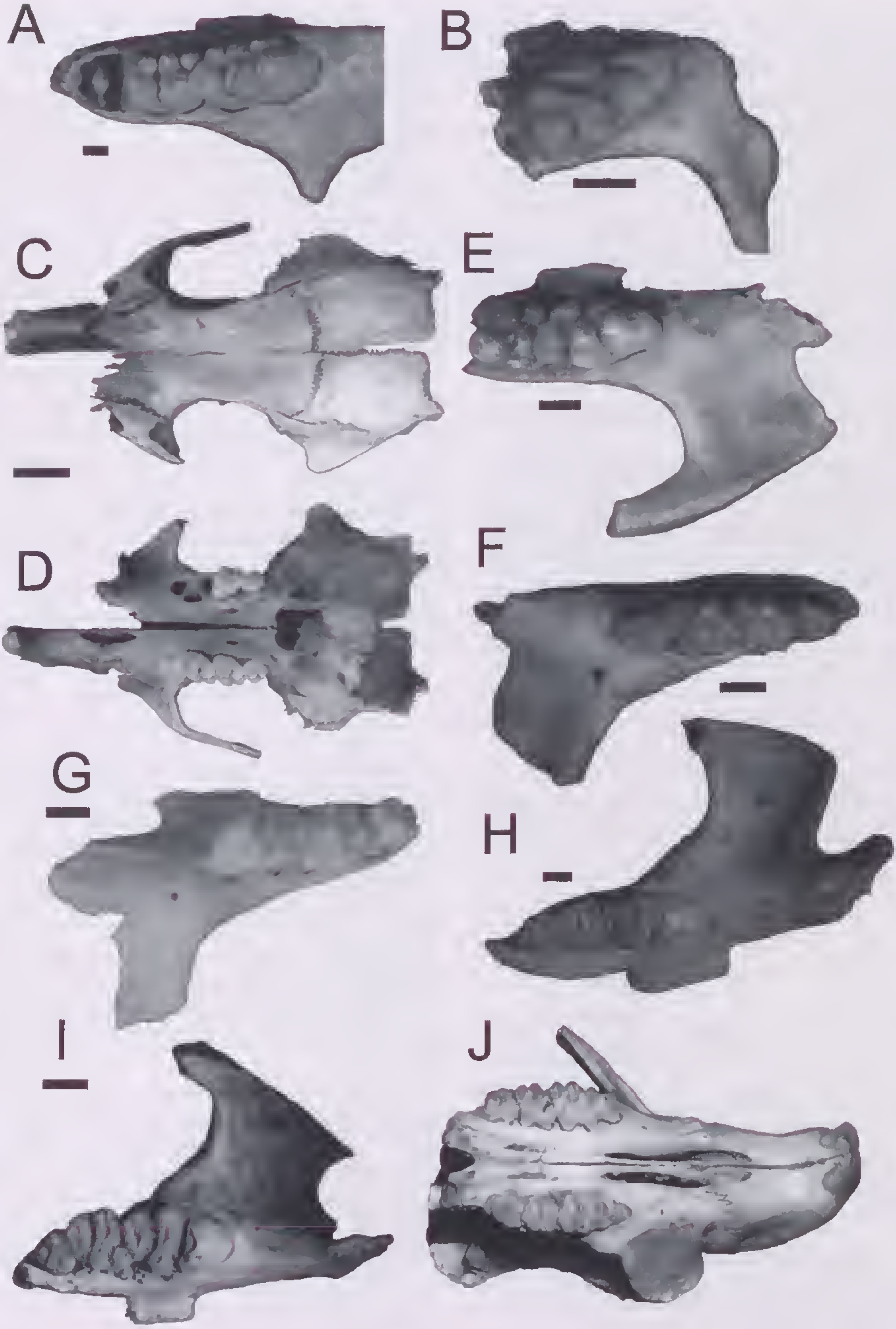

FIG 30. A-I, Muridae; A, *Conilurus* sp.; QMF52052, LM$^{1-2}$. B, *Leggadina* sp.; QMF52040, LM$^{1}$. Scale bar = 1mm. C-D, *Uromys/Melomys* sp.; QMF52014, skull in dorsal & ventral views. Scale bar = 5mm. E-F, *Pseudomys* spp.; E, QMF52043, LM$^{1-2}$. F, QMF52044, RM$^{1-3}$. G, *Pogonomys* sp.; QMF52022, RM$^{1-3}$. H, *Zyzomys* sp.; QMF52053, RM$^{1-3}$. Scale bar = 1mm. I, Notomys sp.; QMF52036, RM$^{1-3}$. J, *Rattus* sp.; QMF52033, partial skull. Scale bar = 5mm.

premolar roots and the presence of a relatively well used wear facet along the longitudinal shearing blade of the fossil premolar indicate that this specimen was from an adult. Comparison to obvious juvenile *T. carnifex* from Naracoorte Caves, shows that *Thylacoleo* did not have any deciduous dentition (pers. obs.). The specimen is therefore assigned to the Late Miocene to Pliocene *T. hilli* based on its diminutive size (24.4mm in *T. hilli* (Pledge, 1977) and 22.23mm for QMF52013), simplified posterior margin of the premolar and overall similarity to the holotype described by Pledge (1977).

## BIOCHRONOLOGY

In order to develop a faunal chronology of the sites, each site needed to be grouped based on their faunal similarity and these groups placed in geochronological order. Presence/absence data was used to produce a dendrogram of similarity for sites using small-sized mammalian taxa (excluding bats) represented at each site (Appendix 1; Fig. 31). The analysis grouped sites with progressively dissimilar faunas from those of the present day. Fig. 31 shows the relationship of sites based on small-sized mammal fauna.

Olsen's Cave fauna shares the greatest similarity with the present day fauna. Five faunas fall successively further away from the Olsen's Cave fauna, first QML1312, then QML1420, QML1384U, QML1384L and QML1311C/D. A final group of five faunas (QML1284, 1284a, 1385, 1313 and 1311H) remain unresolved (polytomy) by the analysis and are considered to possess, equally, the least number of taxa shared with the present day.

FIG 31. Dendrogram illustrating faunal similarity derived from small-sized mammal species from sites presented herein. Present day small-sized mammal fauna placed as the outgroup.

When compared to the available site geochronologies, the faunal dendrogram correlates well with the sites from the Elephant Holes Cave System but not as well with the sites from the Speaking Tube Cave System. Geochronologically, the Elephant Hole Cave System sites range from the oldest (QML1385) through QML1384L and QML1384U to the youngest (QML1312). The faunal dendrogram correlates with the geochronology, by QML1312 sharing the most taxa with the present day and QML1385 the least. Within the Speaking Tube Cave System, QML1311(H) and QML1311 (C/D) are considered to be geochronologically contemporaneous, with QML1313 possibly being younger. The faunal dendrogram does not provide any further resolution to these sites, all of which share similarily few taxa with the present day.

## ASSEMBLAGE AGE

A complete absence from the sites of mammalian taxa known from the Oligocene-Miocene ( possible exceptions being *Thylacoleo hilli* and *Trichosurus* sp. 2) confines biocorrelation to sites of post Late Miocene age. Radiometrically-dated and biocorrelated vertebrate faunas from the Pliocene were used to hypothesise the age of the oldest of the sites at Mount Etna and Limestone Ridge. Table 4 presents a summary of the taxa shared between the Mount Etna and Limestone Ridge sites and other Pliocene vertebrate communities throughout eastern Australia. Two sites possessed mixed faunas of Pliocene and Pleistocene taxa. These two sites were simply classified as Plio-Pleistocene, being younger than the biocorrelated Early Pliocene sites and older than the dated late Pleistocene, QML1312. Table 5 summarises the hypothesised ages for each site yielding fauna identified herein.

**Early Pliocene.** The most dissimilar assemblages to those of the present day fauna possess several taxa confined to the Pliocene in other parts of Australia. These taxa include, *Thylacoleo hilli*, *Kurrabi* sp., *Protemnodon* sp. cf. *P. devisi* and the new perameloids. Of these taxa, *Thylacoleo hilli* and *Kurrabi* sp. are confined elsewhere in Australia to the Early

Pliocene (Pledge, 1977; Flannery & Archer, 1984; Flannery et al.,1992). Several undescribed taxa presented here share their closest morphological similarities with taxa only known from the Early Pliocene. These taxa include, *Strigocuscus* sp. close to *Strigocuscus notialis* (Hamilton LF); *Trichosurus* sp. 2 close to *Trichosurus hamiltonensis* (Hamilton LF); *Petauroides* spp. close to *Petauroides stirtoni* (Hamilton LF; Big Sink LF); *Pseudochirulus* sp. 1 close to *Pseudocheirus marshalli* (Hamilton LF); *Pseudokoala* sp. close to *P. erlita* (Hamilton LF); and *Kurrabi* sp. close to *K. merriwaensis* (Bow LF; Big Sink LF).

Noticeable occurrences of believed Pleistocene-aged taxa are also present in these assemblages, including *Macropus agilis siva* and *Sarcophilus laniarius*. There is uncertainty surrounding the identification of *Macropus agilis siva* in the fauna, therefore it may be incorrectly identified. *Sarcophilus laniarius* is positively identified here and is considered to be the earliest age for this taxon, rather than a younger age of the fauna. The previously oldest record of *Sarcophilus* is from the early Pleistocene of Nelson Bay (Gerdtz & Archbold, 2003) although Tedford (1994) has identified possible *Sarcophilus* from Parwan (Early Pliocene). Gerdtz & Archbold (2003) record the presence of *Sarcophilus harrisii* and *Sarcophilus moornaensis* during the early Pleistocene of Victoria, indicating a pre-Pleistocene origin of *Sarcophilus* and supporting the presence of *Sarcophilus* in the Pliocene of Australia.

Overall, the majority of biocorrelatable taxa indicate an Early Pliocene age for the following sites: QML1284, QML1284a, QML1384L, QML1311 C/D, QML1311 H, QML1313 and QML1385.

**Plio-Pleistocene.** Two sites, QML1384U and QML1420 are considered to be dated sometime between the Late Pliocene and middle Pleistocene. Both sites possess similar small mammal faunas, with QML1384U sharing a similar large portion of its small mammal fauna with the Early Pliocene sites. Unfortunately QML1384U is yet to yield megafauna, however, it is considered to be faunally intermediate between the Early Pliocene assemblage and QML1420. QML1420 fauna lacks the restricted Early Pliocene taxa and possesses Plio-Pleistocene and Pleistocene species, including; *Palorchestes* cf. *P. parvus, Macropus titan, Macropus agilis siva,* and *Megalania prisca.* Additionally, QML1420 is considered to be pre-late Pleistocene in age based on its intermediate small mammal fauna between the Pliocene-aged assemblages and the dated late Pleistocene QML1312 fauna.

**Late Pleistocene.** QML1312 has been TIMS U-series dated using *Petrogale* dentition, providing a minimum age of 149,000 +/- 611 ybp. Faunally, QML1312 is intermediate between QML1420 and Olsen's Cave. The only distinctly Pleistocene taxon within the deposit is *Sarcophilus laniarius*. There are some elements of the fauna that show a lingering relationship to the older faunas, namely *Dendrolagus*, new genus of petauroid and *Thylacinus cynocephalus*.

**Holocene.** Olsen's Cave and QML1314 are considered to be post-late Pleistocene and probably Holocene in age based on the complete lack of megafauna (even though QML1314 site does collect large-sized macropodines) and the exclusive presence of extant taxa. Olsen's Cave fauna possesses the most similar small mammal fauna to the present day and the accumulation is subfossil in preservation.

## FAUNAL SUCCESSION

To adequately reconstruct the faunal and palaeoecological succession from Early Pliocene through to the present day taphonomic processes must be considered and the maximum available source area of fauna must be estimated for each fossil site. This may be predicted by examining the gross taphonomic processes dominating the deposition of each faunal assemblage.

Two predominantly allocthonous accumulation modes are identified as accounting for all of the sites; these being pit-trap and/or predator accumulations. Thus, all large-sized fauna, which would have been too large for owls and Ghost Bats to dispatch, would have been derived from the immediate vicinity of the cave/fissure entrance. There is no indication for denning of large marsupicarnivores or major fluvial deposition as evidenced by the lack of gnaw marks on long bones and fluvially transported sediments. Smaller vertebrates would have been collected from the vicinity of the cave entrances as either allochthonous or autochthonous (cave dwelling) assemblages. Additionally, small vertebrates would have also been collected within the hunting ranges of both the Ghost Bat and owl, the only known cave-dwelling predators within the deposits.

| | **Mount Etna LF** | **Bluff Downs LF** | **Rackham's Roost LF** | **Chinchilla LF** | **Big Sink LF** | **Bow LF** | **Kanunka LF** | **Town Well Cave** | **Hamilton LF** |
|---|---|---|---|---|---|---|---|---|---|
| | QLD | QLD | QLD | QLD | NSW | NSW | SA | | VIC |
| | Early Pliocene | Early Pliocenc | Early Pliocene | late Early Pliocene | Early Pliocene | Early Pliocene | Late Pliocene | Mio-Pliocene | Early Pliocene |
| MYA | | 3.8 | 3-5 | 3.4 | 3-5 | 3-5 | 3.4 | | 4.46 |
| *Thylacinus* | *cynocephalus* | | | *cynocephalus* | sp. | | | | |
| *Antechinus* | spp. | | | | sp. | | | | sp. |
| *Sminthopsis* | *murina* | | sp. | | spp. | | | | |
| *Dasyurus* | sp. | *dunmalli* | | *dunmalli* | | *dunmalli* | | | |
| Perameloid | gen. nov. | | | | gen. nov. | gen. nov. | | | cf. *Peroryctes tedfordi* |
| *Perameles* | sp. 1 & sp. 2 | | | *bowensis* | | *bowensis* | | | |
| | | *allinghamensis* | | | | *allinghamesis* | | | |
| *Thylacoleo* | sp. | *crassidentatus* | | *crassidentatus* | *crassidentatus* | *crassidentatus* | | | |
| *Thylacoleo* | *hilli* | | | | | *hilli* | | *hilli* | |
| *Protemnodon* | cf. *devisi* | *snewini* | cf. *snewini* | *devisi* | *devisi* | *chinchillaensis* | cf. *devisi* | | sp. |
| *Kurrabi* | sp. | | | | cf. *merriwaensis* | *merriwaensis* | sp. | | *plechenorum* |
| *Bohra* | sp. | | | *wilkinsonorum* | | | | | |
| *Dendrolagus* | sp. | | | | | sp. | sp. | | sp. |
| *Macropus* | sp. | spp. | | spp. | | spp. | spp. | | sp. |
| *Thylogale* | spp. | | | | | | | | *ignis* |
| *Palorchestes* | cf. *parvus* | *selestiae* | | *parvus* | | cf. *parvus* | | | sp. nov. |
| Vombatidae | *Vombatus* | *Ramsayia* | | *?Vombatus* | | *Phascolonus* | *Vombatus* | | gen. indet. |
| *Strigocuscus* | sp. | | | | | | | | *notialis* |
| *Trichosurus* | sp. 2 | | | | | | | | *hamiltonensis* |
| Burramyidae | *Cercartetus* | | | | *Cercartetus* | | | | *Burramys* |
| *Pseudokoala* | sp. | | | | | | | | *erlita* |
| *Pseudocheirus* | spp. | | | | | | | | *marshalli* |
| *Petauroides* | spp. | | | | cf. *stirtoni* | | | | *stirtoni* |
| *Pseudocheirops* | spp. | *winteri* | | | | | | | |
| Petauridae | gen. nov. | | | | | | | | *Petaurus* |
| *Macroderma* | *gigas* | | *gigas* | | *koppa* | | | | |

TABLE 4. Biocorrelations of taxa in the hypothesised Early Pliocene Mount Etna Local Fauna.

Owls have hunting ranges of up to 10km$^2$ (Lindsey, 1992) and *Macroderma gigas* ranges over an area of 2km$^2$ (Toop, 1985; Nelson, 1989). Thus owls would have had the potential to collect vertebrates from both the limestone bluff and the surrounding lowlands. The present day range of an owl at Mount Etna would encompass both closed vegetation typical of limestone bluffs out into lowland open vegetation. Small creeks are present within the owl's range and thus provide a third possible hunting habitat along riverine areas. Ghost Bat foraging areas would be considerably smaller and source the majority of its prey from the immediate vicinity of the feeding roost.

Owls are not considered to be an active accumulator at Marmor Quarry and Ghost Bats are considered to have had little input into the small vertebrate accumulation, therefore, Marmor Quarry is considered to have collected most of its fauna from the immediate vicinity of the pit-trap entrance.

Where possible, fossil sites were equally sampled to remove any potential collecting bias at each of the sites. Only presence/absence data are used for faunal and palaeoecological successions, with no analysis of relative abundance, which would be most affected by sample size. Collections from QML1312 are restricted due to the site's destruction prior to the expeditions in 2000.

On balance, the majority of faunas described here are considered to have been representative of the ecologies in direct vicinity of the cave entrances for both Mt Etna and Marmor Quarry.

*Anurans*. Greatest diversity of frogs occurs in the Early Pliocene sites from Mount Etna and Limestone Ridge. Of the 22 frog taxa identified here, 20 are found in the Early Pliocene sites. *Cyclorana* is restricted to the Holocene Olsen's Cave fauna and is not present in any of the older sites. New fossil frog records for Australia include the Early Pliocene species of *Nyctimystes*, *Etnabatrachus maximus* and microhylids. New frog records for the Early Pliocene include species of *Crinia*, *Kyarannus*, *Lechriodus*, *Limnodynastes* and *Litoria*. The majority of the species present in the Early Pliocene are locally extinct by the late Pleistocene, leaving only a single species of *Limnodynastes*. Species of *Litoria* and *Cyclorana* occur in the Holocene assemblages. The present day frog fauna includes at least, *Cyclorana*, *Litoria*, *Limnodynastes* and *Pseudophryne*. The retention of *Litoria* and *Limnodynastes* into the present day fauna is not suprising as these genera are cosmopolitan in their distribution and habitat preferences.

TABLE 5. Summarised ages for The Caves & Marmor fossil sites.

| | |
|---|---|
| Holocene | Olsen's Cave<br>QML1314 |
| Late Pleistocene | QML1312 |
| Plio-Pleistocene | QML1420<br>QML1384U |
| Early Pliocene | QML1313<br>QML1384L<br>QML1311C/D<br>QML1311H<br>QML1284<br>QML1284a<br>QML1385 |

Occurrence of *Neobatrachus* in the Early Pliocene is peculiar, representing a burrowing frog with a present day distribution restricted to arid areas. *Neobatrachus* has been recorded from the Pliocene of South Australia (Tyler, 1988; Tyler, 1994) in a palaeoecology that was wetter than today. Its presence within a predominantly rainforest frog fauna may be explained in a similar way as to the presence of the marsupial mole family, Notoryctidae, which occurs in a predominantly rainforest mammal fauna in the Oligo-Miocene of Riversleigh, yet it is confined to the arid zone of Australia today (Long et al., 2002). Adaptation for burrowing in soft rainforest soils may have allowed notoryctids to be pre-adapted to a later arid environment with soft sands. Similarly, it may be conceived that a burrowing frog that originated in rainforest would then be pre-adapted to life in the arid zone.

*Chelids*. Turtle fossils are restricted to the Early Pliocene localities and are a rare component of the assemblages. Freshwater turtles occur throughout the region today and are almost never encountered on the limestone karst. Turtle fossils would become absent from the record as karstification developed inhospitable ground for turtles to traverse.

*Crocodilians*. Crocodile specimens are generally restricted to the Early Pliocene sites and are rare. A single specimen is known from QML368 which has yet to yield a contemporaneous large-sized fauna that can be biocorrelated, however, the small-mammal fauna suggests a Pleistocene age.

*Squamates.* Agamids (Dragons) are rare, but have been found in all deposits from the Early Pliocene through to the present. Early Pliocene agamid remains are mostly unidentifiable, however, a single specimen is referable to a species of *Hypsilurus*. Diversity of agamids is greatest in the late Pleistocene with species of *Amphibolurus*, *Pogona* (small-morph) and *Tympanocryptis* present. *Diporiphora* replaces these in the Holocene. The present agamid fauna includes, *Diporiphora*, *Chlamydosaurus* and *Pogona barbata* (large-morph).

Gekkonids (Geckoes) have been found throughout the Pliocene to present, except in QML1420. Absence of gekkonids from QML1420 is considered an artefact of small collection size and the absence of a distinct predator accumulation. The large gekkonid form is present in the Early Pliocene sites but missing in the late Pliocene to present day. Due to their general rareness within the Early Pliocene sites, it is uncertain whether the absence of the large gekkonid from younger sites is a taphonomic bias or a Plio-Pleistocene extinction. The small gekkonid forms are present throughout the Pliocene to the present, however, they probably constitute several distinct taxa.

Large scincids (Skinks) are conspicuous in the Early Pliocene deposits. *Tiliqua* is known from the Early Pliocene and Holocene, but does not occur in the Late Pliocene-Pleistocene or late Pleistocene faunas. Species of *Tiliqua* are rare within any assemblage, represented by single specimens. Its absence from sites cannot be determined as either ecological or taphonomic. *Cyclodomorphus gerrardii* is the most common large skink and is found from the Early Pliocene to the present day, with the exception of site QML1312. The absence of *Cyclodomorphus* from QML1312 is not considered to be due to taphonomic bias because abundant remains of other large-sized skinks are present in this fauna. Instead, *Cyclodomorphus* is considered to have become locally extinct due to late Pleistocene aridity. By the present day, *Cyclodomorphus* had dispersed back into the Mt. Etna region. *Egernia* sp. is present throughout the Early Pliocene to Holocene. Large skinks found at Mount Etna today include *Tiliqua scincoides* and *Cyclodomorphus gerrardii*.

Varanids (Goannas & Monitors) are found from the Early Pliocene to the present day, with the exception of the Holocene faunal assemblage. This absence at Olsen's Cave is considered to be a taphonomic bias against large squamates (as with large mammals) because the deposit is derived from an owl roost. Two varanids are present in the Early Pliocene, one the size of modern *Varanus varius*, the second much more massive but not attaining the size of Pliocene or Pleistocene species of *Megalania*. These two taxa persist into the late Pleistocene, however, are missing from QML1420. Varanids are represented at QML1420 by the giant varanid *Megalania prisca*.

Elapids (Venomous snakes) are found from the Early Pliocene to the present day. Conspicuous size difference can be seen when comparing the largest vertebrae of elapids in the Pliocene-Pleistocene with those from the late Pleistocene. The late Pleistocene elapids are up to twice the size of their Early Pliocene relatives.

Pythonines are found from the Early Pliocene to the present day. Madstoiids have not been found. Python vertebrae tend to remain large-sized throughout the Pliocene to present day.

Typholopids (Blind snakes) are only found in the Early Pliocene sites. This is the second record of fossil blind snakes in Australia and the first from the Pliocene. The first record was from the Oligo-Miocene Riversleigh deposits from far north Queensland (Archer et al., 1995b).

Typholopids are a peculiar fossorial group with a cosmopolitan range today. A nocturnal ant/termite feeder, typholopids represent a specialised niche within the Early Pliocene faunal assemblage at Mount Etna. The typholopids seem to represent yet another group of fossorial animals, like the notoryctids (marsupial moles) and leptodactylids (*Neobatrachus*), which have utilised their adaptation for burrowing in ancient rainforests as an adaptative advantage with subsequent increasing aridity.

*Aves.* Four bird groups have been identified, including the quails (Galliformes), button quails (Gruiformes), song birds (Passeriformes) and owls (Strigiformes). The owls are a conspicious component of all the fossil assemblages except QML1420. Their absence at QML1420 is considered to be due to taphonomic processes. All four groups exist in the area today. The Early Pliocene occurrence of owls is the oldest known in Australia.

*Thylacinidae. Thylacinus cynocephalus* is present from the Early Pliocene to late Pleistocene. *Thylacinus cynocephalus* is absent from the Plio-Pleistocene site QML1384U, which is probably due to the taphonomic bias in that deposit toward smaller-sized mammals. *Thylacinus* is absent by the Holocene.

*Dasyuridae. Antechinus* spp. are present from the Early Pliocene through to the present day. During the Early Pliocene, *Antechinus* is represented by two species. By the late Pleistocene, these two species are extinct, having been replaced by *Antechinus flavipes* and *Antechinus swainsoni. Dasyurus* spp. are also present from the Early Pliocene through to the present day. During the Pliocene *Dasyurus* is represented by a medium-sized species. This species is replaced by *Dasyurus hallucatus* and *Dasyurus viverrinus* during the late Pleistocene. *Dasyurus hallucatus* and *Dasyurus maculatus* are found in the Holocene and present day fauna repectively. *Phascogale* has a possible appearance in the Early Pliocene with a small undescribed species. This species continues into the Pleistocene, however, it is extinct by the late Pleistocene, having been replaced with *Phascogale topoatafa. Planigale maculata* appears in the late Pleistocene and remains in the Holocene and present day fauna. An extinct, undescribed, small planigale-like dasyurid is present in the Pliocene but is extinct by the Pleistocene. Species of *Sarcophilus* are present from the Early Pliocene to late Pleistocene and possibly Holocene. *Sarcophilus laniarius* is known to occur from the Early Pliocene to late Pleistocene. A single specimen of *Sarcophilus harrisii* is present in the late Pleistocene-Holocene from Lower Johansen's Cave (QML1314). Species of *Sminthopsis* occur in the Early Pliocene but are rare within the Pliocene assemblages. During the late Pleistocene *Sminthopsis* represents the most abundant small-sized dasyurid, represented by two species, *Sminthopsis murina* and *Sminthopsis macroura*.

*Vombatidae*. A species of *Vombatus* is represented by three specimens, one in the Early Pliocene and two in the Plio-Pleistocene site QML1420. *Vombatus* is not present in the area by the late Pleistocene.

*?Zygomaturine*. This large-sized diprotodont is only known in the region from the Plio-Pleistocene (QML1420).

*Palorchestidae. Palorchestes* sp. cf. *P. parvus* is present in the Early Pliocene and in the Plio-Pleistocene (QML1420).

*Macropodidae. Bohra* sp. is only present in the Early Pliocene. Species of *Dendrolagus* are present from the Early Pliocene to late Pleistocene. Species of *Thylogale, Petrogale* and *Macropus* are all present from the Early Pliocene to the present day. *Protemnodon* sp. cf. *P. devisi* and *Kurrabi* are only present in the Early Pliocene. *Macropus titan* is restricted to the Plio-Pleistocene of Marmor Quarry and is absent from the late Pleistocene. This is the first record in Australia of *Dendrolagus* in the Pleistocene and the second record of *Bohra* in the Pliocene (Dawson, 2004).

A conspicuous absence from the macropod fauna are the morphologically distinct potoroids, inparticular *Potorous* and *Hypsiprymnodon*. Although they may turn up in future collections, the sample sizes at present suggest that this may be unlinkly and that this group of macropods was absent from the Early Pliocene of Mt. Etna. Interestingly, the small macropod fauna at Mt. Etna includes several small-sized macropodids, namely *Thylogale* sp. 1, which is very similar to the Irian Jayan *Thylogale christenseni*. Furthermore, there are no potoroids known from the present day or fossil record of Papua New Guinea and Irian Jaya, yet the small macropodid faunas tend to be either species of *Thylogale* or *Dorcopsis*. The disjunct nature of this macropodid fauna, where the Early Pliocene Mt. Etna fauna more closely resembles those from Papua New Guinea and Irian Jaya, is also seen in the Pseudocheiridae.

*Pseudocheiridae*. Pseudocheirids are considerably diverse during the Pliocene but are locally extinct by the late Pleistocene, returning in the Holocene as a rarity and abundant in the present day as a single taxon, *Pseudocheirus peregrinus*.

*Pseudochirulus* spp. are present in the Early Pliocene, including *Pseudochirulus.* sp. 1 which is very similar to the Early Pliocene Hamilton Fauna *Pseudochirulus marshalli* and the modern Papua New Guinean *Pseudochirulus canescens* and *Pseudochirulus mayeri*. Similarily, taxa referred to here as *Petauroides* share closer taxonomic affinities with species from both the Early Pliocene Hamilton Fauna and the late Pleistocene Irian Jayan Fauna, than they do to the modern *Petauroides* and *Hemibelideus* from far north Queensland forests and rainforests.

*Petauridae*. The new genus of petaurid is present with two species in the Pliocene and one species in the Plio-Pleistocene and late Pleistocene. It is extinct by the Holocene. *Dactylopsila* is present in the Pliocene but is locally extinct by the Pleistocene. This is the first post Miocene, and pre Holocene, record of *Dactylopsila* in Australia. *Dactylopsila* sp. 2 is diminutive in size relative to any living species, however, it is very close to the extinct Irian Jayan taxon, *Dactylopsila kambuayai*, which along with the macropodids and pseudocheirids illustrates a possible faunal connection to Papua New Guinea and Irian Jaya during the Early Pliocene.

*Superfamily* incertae sedis. A new genus and species of possum with unknown phylogenetic and taxonomic affinities is present in the Early Pliocene but has yet to turn up in younger sediments.

*Acrobatidae. Acrobates* occurs in the Early Pliocene and has not been found in younger sediments. This is the first record of acrobatids in the Pliocene of Australia.

*Burramyidae. Cercartetus* occurs in the Pliocene but is not found in younger sediments. The only other Pliocene record of *Cercartetus* is from the Big Sink Fauna (Dawson et al., 1999).

*Phalangeridae. Strigocuscus* is present in the Pliocene but is absent by the Pleistocene. *Trichosurus* is represented by two species, the first confined to the Early Pliocene and the second found in the Pleistocene, Holocene and present day.

*Thylacoleonidae.* Two species of *Thylacoleo*, one small and one large species, occur in the Early Pliocene whilst one large species has been found in the Plio-Pleistocene (QML1420). No remains of *Thylacoleo* have yet been found in late Pleistocene deposits.

*Peramelidae.* Species of *Perameles* occur throughout the Pliocene and into the present day. During the Pliocene and Plio-Pleistocene times, *Perameles* was represented by two extinct species. By the late Pleistocene to Holocene, these species were replaced by *Perameles bougainville* and eventually *Perameles nasuta. Isoodon* occurs in the Plio-Pleistocene to present day. *Isoodon* is represented by two small-sized species in the Plio-Pleistocene and late Pleistocene sites, *Isoodon obesulus* and *Isoodon* sp. During the Holocene, small-sized *Isoodon* were replaced with the larger *Isoodon macrourus.* During the late Pleistocene both *Chaeropus* and *Macrotis* appeared, leaving no further record.

*Perameloid* incertae sedis. An enigmatic family of bandicoots possibly related to the Oligo-Miocene Yaralidae are restricted to the Pliocene-aged deposits.

*Muridae.* Rodents are a conspicuous element of every deposit. Early Pliocene rodents include the first records of many rainforest taxa with no previous fossil records in Australia. Several taxa are found to dominate the Pliocene sites with possible Plio-Pleistocene records. These include *Melomys/Uromys*, *Pogonomys* and *Mesembriomys. Zyzomys* is present from the Pliocene to late Pleistocene. *Leggadina* is found in the late Pleistocene to Holocene. *Conilurus* is found in the late Pleistocene. *Rattus* is found from the Plio-Pleistocene to present day. *Pseudomys* is found from the Pliocene to present day. *Notomys* is restricted to the late Pleistocene. *Hydromys* has been recovered from the Early Pliocene, Plio-Pleistocene (QML1420) and present day faunas.

*Microchiropterans.* Bats are found in all deposits, except QML1420. *Macroderma gigas* is found from Early Pliocene to the present day.

## PALAEOECOLOGICAL SUCCESSION

### EARLY PLIOCENE.

*Nonseasonal, Mesothermal, angiosperm-dominant rainforest with emergent gymnosperms; minor grassy understory.*

Rainforest has been indicated both locally by the fauna and regionally through palynological studies of the Early Pliocene. Two pollen cores, Aquarius Well (Fig. 1A,5) (Hekel, 1972) and ODP815 (Fig. 1A,4) (Martin & MacMinn, 1993), located off the central eastern Queensland coast are close to the fossil sites. The Aquarius Well core was taken from the edge of the Capricorn Trough, which is located to the NE of Mount Etna and Marmor Quarry (Fig 1). Hekel (1972) published the palynological record of Aquarius Well, showing a dramatic increase in rainforest flora in the region post Late Miocene and dominating the entire Early Pliocene.

ODP815 drill core (Martin & MacMinn, 1993) from the Marion Plateau to the NE of Mount Etna shows an Early Pliocene dominated by rainforest flora. Macphail (1997) reviewed both the Aquarius Well and ODP815 records and concluded that the dominant vegetation type during the Early Pliocene would have been an angiosperm-dominated mesotherm rainforest with Araucaraceae. Low pollen counts for rainforest angiosperm taxa were considered to be an artefact of taphonomic bias toward more dispersible taxa, however, no conclusions could be drawn as to how dominant or complex the rainforest angiosperms were. Macphail (1997) suggests that the climate required to support such a vegetation structure would include temperatures greater than $20^0$C, and an annual precipitation rate of between 1300 and 2000mm.

Fauna recovered from Early Pliocene-aged sites within the local area of Mount Etna and Limestone Ridge support the presence of rainforest at the time, as follows;

*Anurans*. Microhylids are recorded from the Early Pliocene deposits and, although rare, indicate a very moist rainforest environment. *Nyctimystes* is presently known from rainforests of far north Queensland and Papua New Guinean, whilst *Lechriodus* is known from rainforest in southeastern Queensland and Papua New Guinea. *Kyarranus*, although not exclusively rainforest dwelling, is restricted to areas of constant moisture in areas close to or within montane rainforest or wet sclerophyll. Interestingly, the suite of frog genera identified in the Early Pliocene is similar to that recorded from the interpreted rainforest ecologies present during the Oligo-Miocene of Riversleigh (*Litoria*, *Limnodynastes*, *Kyarranus*, *Lechriodus*, and *Crinia*) (Tyler, 1991; Tyler 1994) and to those identified from the montane rainforests of Papua New Guinea (Menzies et al., 2002).

The overall abundance and diversity of small-sized frogs and the presence of only a single, rare, monotypic giant frog (*Etnabatrachus maximus*) indicates that the area experienced a reliable (non-seasonal) precipitation regime (Tyler, 1994).

*Squamates*. Several squamates indicate a predominantly rainforest ecology during the Early Pliocene. The most abundant large-sized squamate present in any of the Early Pliocene deposits is *Cyclodomorphus gerrardii*. Although also found in dry sclerophyllous vegetation today, *Cyclodomorphus gerrardii* is most frequently encountered in wet sclerophyll and rainforest. *Hypsilurus* sp. has been identified from the Early Pliocene. This agamid genus is rainforest-restricted, present only in rainforests of southeastern Queensland, the Wet Tropics and Papua New Guinea.

*Mammals*. Several analyses of Australian mammal biogeography have focussed on determining correlative values that describe the patterns seen in rainforest mammal distributions (Braithwaite et al.,1985; Williams, 1997; Kanowski et al., 2001; Kanowski et al., 2003; Winter, 1988; Winter, 1997; Laurance, 1997; Nix & Switzer, 1991). These correlative values encompass several different categories into which the mammals found in rainforests have been placed. These categories include broad definitions such as "Rainforest Specialists Species", "Forest Generalists Species", "Rainforest Ecotone Species", "Generalist Species" and "Independent Species" (Winter, 1988); or more specific definitions, such as the eleven defined tropical mammal guilds of Braithwaite et al. (1985). Williams (1997) used Braithwaite et al.'s guilds to describe patterns seen in mammal species of the Wet Tropics rainforest. Other authors (Kanowski et al., 2001; Kanowski et al., 2003; Winter, 1997; Laurance, 1997; Nix & Switzer, 1991) have either focussed on a single or a combination of ecological parameters to describe patterns in rainforest mammal species-richness. These parameters include; modelled palaeoclimate, floristics, altitude, geology, precipitation, rainforest shape and size, latitude, temperature, habitat fragmentation and predators. These criteria developed for modern rainforest mammals have been utilised here in identifying the palaeoecological parameters of the Early Pliocene environment, since several extant mammal genera (and possibly species) with obvious rainforest affinities occur in the Early Pliocene sites.

### *Ecological Specialisation.*

Forteen extant mammal species were identified by Winter (1988) to be rainforest specialists and restricted to northern Queensland. Of these taxa, eight are considered to be rainforest specialist genera (*Phalanger, Uromys, Pogonomys, Pseudocheirops, Pseudochirulus, Hypsiprymnodon, Hemibelideus* and *Dendrolagus*). In the Early Pliocene assemblages, five of these eight genera are present, with the absence of *Phalanger, Hypsiprymnodon* and *Hemibelideus*.

Rainforest-restricted mammal species were determined for Australia and New Guinea by using Strahan (1995) and Flannery (1994) respectively. The genera *Strigocusus* and

| Fossil Taxon | Present Day Analogue | Guild |
|---|---|---|
| Thylacinidae | | |
| *Thylacinus* | *Thylacinus cynocephalus* | VLTC |
| Dasyuridae | | |
| *Antechinus sp. 1* | *Antechinus* | SSI |
| *Antechinus sp. 2* | *Antechinus* | SSI |
| *Dasyurus sp.* | *Dasyurus* | MSI/C |
| *Phascogale sp.* | *Phascogale* | SSI |
| *Sarcophilus laniarius* | *Sarcophilus harrisii* | LTC |
| *Sminthopsis murina* | *Sminthopsis murina* | SSI |
| dasyurid new | *Planigale* | STI |
| Vombatidae | | |
| *Vombatus ursinus mitchelli* | *Vombatus ursinus* | VLTH |
| *Palorchestes sp.* cf. P. parvus | None | VLTH |
| diprotodont indet | None | VLTH |
| Macropodidae | | |
| *Bohra sp.* | None | LSH |
| *Dendrolagus spp.* | *Dendrolagus* | LAH |
| *Thylogale sp. 1* | *Thylogale christenseni* | MTH |
| *Thylogale sp. 2* | *Thylogale stigmata* | LTH |
| *Petrogale* | *Petrogale* | LTH |
| *Macropus sp. 1* | *Macropus dorsalis* | LTH |
| *Protemnodon cf. P. devisi* | None | VLTH |
| *Kurrabi* | None | LTH |
| Pseudocheiridae | | |
| *Pseudochirulus sp. 1* | *Pseudocheirulus mayeri* | SAH |
| *Pseudochirulus sp. 2* | *Pseudocheirulus canescens* | MAH |
| *Pseudochirulus sp. 3* | *Pseudocheirulus herbertensis* | SAH |
| *Pseudocheirus spp* | *Pseudocheirulus spp.* | SAH |
| *Petauroides* | *Petauroides/Hemibelidius* | SAH |
| *Pseudocheirops sp. 1* | *Pseudocheirops* | MAH |
| *Pseudocheirops sp. 2* | *Pseudocheirops* | MAH |
| *Pseudokoala* | None | LAH |
| Petauridae | | |
| gen. et sp. nov. 1 | *Petaurus* | SAN-I |
| gen. et sp. nov. 2 | *Petaurus* | SAN-I |
| *Dactylopsila sp. 1* | *Dactylopsila* | SSI |
| *Dactylopsila sp. 2* | *Dactylopsila* | SSI |
| Incerti Sedis | | |
| gen. et sp. nov. | None | SAN-I |
| Acrobatidae | | |
| *Acrobates sp* | *Acrobates* | SAN-I |
| Burramyidae | | |
| *Cercatetus sp.* | *Cercatetus* | SAN-I |
| Phalangeridae | | |
| *Strigocuscus* | *Strigocuscus* | LAH |
| *Trichosurus sp. 2* | *Trichosurus* | LAH |
| Thylacoleonidae | | |
| *Thylacoleo hilli* | None | LSC |
| *Thylacoleo sp.* | None | VLSC |
| Peramelidae | | |
| Perameles sp. 1 | *Perameles* | MTO |
| Perameles sp. 2 | *Perameles* | MTO |
| Perameloid fam. Incertae sedis | | |
| gen. et sp. nov. 1 | *Perameles/Peroryctes* | MTO |
| gen. et sp. nov. 2 | *Perameles/Peroryctes* | MTO |
| Muridae | | |
| *Hydromys* | *Hydromys* | MQO |
| *Pseudomys spp* | *Pseudomys* | STO |
| *Zyzomys* | *Zyzomyz* | STO |
| *Uromys/Melomys* | *Uromys/Melomys* | SSH |
| *Pogonomys* | *Pogonomys* | SSH |
| *Mesembriomys* | *Mesembriomys* | MSO |

TABLE 6. Mammalian guilds defined for the Early Pliocene. Guild traits expanded from Braithwaite et al., (1985). Abbreviations: Size; S. Small, <200g; M. Medium 200g-3kg; L. Large 3kg-20kg, VL Very Large >20kg. Microhabitat: A. Arboreal, T. Terrestrial, S. Scansorial, Q. Semi-aquatic. Diet: N-Nectarivore, I - Insectivore, O – Omnivore, C - Carnivore, H - Herbivore.

*Dactylopsila* are presently rainforest-restricted and are found in the Early Pliocene at Mt Etna.

Additionally, *Cercartetus* sp. is considered to be very close to, if not conspecific with, *Cercartetus caudatus*, and although *Cercartetus* is not a rainforest-restricted genus, *Cercartetus caudatus* is a distinct rainforest specialist (Winter, 1988). *Antechinus* sp. 1 is considered to be very close to the rainforest-restricted *Antechinus adustus* (Van Dyck & Crowther, 2000).

### *Mammal guilds and species richness*

Palaeoecological reconstruction using extant rainforest-restricted and specialist taxa as analogues provides good evidence for the presence of rainforest during the Early Pliocene. Defining the different mammalian guilds and the species richness present at sites allows for an extension of the palaeoecological reconstruction to include possible correlations with floristic diversity and climate as seen in modern day rainforest studies (Braithwaite et al., 1985; Heads, 2002; Williams, 1997).

Braithwaite et al. (1985) defined Australian tropical mammal guilds on the basis of three traits; 1. Body size (small <200g, medium 200-3kg, and large 3kg-10kg); 2. Microhabitat (arboreal, scansorial and terrestrial); and 3. Diet (insectivore, nectavore, folivore/frugivore (here classed as herbivore), carnivore, omnivore and granivore). Allocation of these three traits to the taxa from the Early Pliocene was achieved by choosing the closest living analogue or determining each trait from morphology. Table 6 lists the Early Pliocene mammalian fauna, their modern analogues and defined guild type based on Braithwaite et al's traits.

Most of the fossil taxa were able to be assigned to their equivalent modern day analogue by means of genus-level identity. Most species within the analogue genus shared traits defined for that genus' guild, with the possible exception of size. For genera with unknown modern analogues, the closest living taxon to the extinct taxon was used, with inferences drawn for each trait based on family-level trait similarity. For example, *Pseudokoala* was defined as being a large-sized (>3kg), arboreal herbivore, based on its much larger size when compared to the largest living pseudocheirid (*Pseudocheirops* - <3kg); and because all living pseudocheirids are arboreal and herbivorous.

The remaining taxa are those with no family-level trait similarities to modern groups (Diprotodontidae, Palorchestidae and Thylacoleonidae). All three of these families are characteristised by being very large-sized (>20kg), with the exception of *Thylacoleo hilli*, which is considered here to be large-sized (between 10 and 20kg) (Wroe et al.,2004). Based on the very-large size of these mammals, a fourth body size trait is added here. Two mammal families are considered to be terrestrial in their microhabitat due to their very large size, with the acception of *Thylacoleo*, which is here considered to be scansorial. Diprotodontidae and Palorchestidae are considered to be herbivores and members of the Thylacoleonidae to be carnivores.

All of the guilds defined by Braithwaite et al. (1985) were present in the Early Pliocene at Mt Etna. Nine new guilds were identified that did not fit the 11 guilds defined by Braithwaite et al. (1985) and are here considered to be either present in the Wet Tropics, Papua New Guinea/Irian Jaya or extinct from rainforests today. These nine guilds were; 1. Small-sized, arboreal, herbivore (SAH) (e.g. *Pseudochirulus mayeri*, *Pseudochiruhus* sp 1., *Pseudocheirus* sp. 1-2). This guild is present today in Papua New Guinea and Irian Jaya; 2. Medium-sized arboreal herbivore (MAH) (e.g. *Pseudochirulus* spp., *Pseudocheirops* spp.). Today present in the The Wet Tropics, Papua New Guinea and Irian Jaya; 3. Large-sized, scansorial carnivore (LSC) (e.g. *Thylacoleo hilli*), which is extinct; 4. Medium-sized terrestrial herbivore (MTH) (e.g. *Thylogale* sp. 1, *Thylogale christenseni*), recently extinct in Irian Jaya (Hope, 1981); 5. Medium-sized, semi-aquatic omnivore (MQO) (e.g. *Hydromys*), present in the Wet Tropics, PNG and Irian Jaya; 6. Large-sized, scansorial herbivore (e.g. *Bohra* sp.), which is now extinct; 7. Very large-sized, terrestrial herbivore (VLTH) (e.g. *Palorchetes*, diprotodont), extinct; 8. Very large-sized terrestrial carnivore (VLTC) (e.g. *Thylacinus*), extinct; and 9. Very large-sized scansorial carnivore (VLSC) (e.g. *Thylacoleo*), extinct.

Braithwaite et al. (1985) illustrates that the greatest number of mammalian guilds found in the Australian tropics are located in the habitat classified as rainforest. Williams (1997) illustrates that three guilds; small, scansorial, insectivores; large, arboreal, herbivores; and small, scansorial, omnivores, are important in determining species richness in modern rainforest of the Wet Tropics and are also the most extinction prone. All three of these guilds are present in each of the interpreted Early Pliocene sites at Mt. Etna.

Williams (1997) also shows that overall species richness in rainforest is positively influenced by guild diversity, rainforest shape, area and habitat diversity (rainfall and vegetation diversity). According to Williams (1997), the number of small to large-sized mammalian guilds present in the most species rich locations of the present day Wet Tropics is nine. The number of small to large sized mammalian guilds from individual sites in the Early Pliocene of Mount Etna ranges from ten to thirteen.

Williams (1997) identifies two regions of the northern Queensland Wet Tropics that possess the greatest species richness (21-26 spp), greatest number of endemic mammal species (4-8 spp.) and thus the greatest number of guilds (9) of rainforest mammals in Australia. These two areas are defined by Williams as the Windsor and Carbine Uplands, and the Lamb, Atherton, Bellenden-Ker/Bartle-Frere & Kirrama Uplands. Both regions have their greatest area above 1000m altitude and possess the greatest vegetation diversity of the Wet Tropics. The present day climatological parameters needed to sustain such a large number of guilds and high species richness for these two upland regions is a high consistent (nonseasonal) precipitation rate (>2000mm) with a moderately cool to cool annual temperature regime (meso-megathermal; 21-23°C) (Nix, 1982; Winter, 1997).

Rainforest areas of the Papua New Guinean central highlands show similar species richness of mammals (24-29 spp) (Heads, 2002). These regions are defined by Nix (1982) as a nonseasonal mesothermal-microthermal (12-14°C) climate.

The similarities seen here for both the Wet Tropics and Papua New Guinea suggest that both regions possess their greatest mammalian species richness and guild diversity in areas that have a relatively cool climate with nonseasonal high annual rainfall. Each of the Early Pliocene sites from Mt. Etna possess from at least 21 to 30 small to large-sized mammal species. This species richness is similar to that found in Papua New Guinea and the Wet Tropics of today, however, this does not account for the very large-sized taxa also present in the Early Pliocene.

When considered together; guild diversity, species richness, specialist and endemic taxa, the Early Pliocene faunal assemblage strongly indicates the presence of a diverse rainforest habitat, which was subject to regular nonseasonal high rainfall in a mesothermal climate regime (20-23°C). The entire fauna strongly indicates a vegetation structure that included several levels of complexity to house diverse guilds containing, arboreal, scansorial, terrestrial, fossorial, semi-aquatic and aquatic niches. On the basis that the fossil sites are not found higher than 200m above sea level today, the Early Pliocene rainforest could be considered to be lowland rainforest. The diversity of mammalian nectavores, herbivores and insectivores indicates the presence of an equally diverse angiosperm flora, possibly more diverse than what is indicated in the ODP 815 and Aquarius Well pollen cores. The very rare occurrence of grazing macropods and a single wombat specimen indicates the presence of small areas of grasslands or grassy understorey within the Mt. Etna area.

## PLIO-PLEISTOCENE.

*Seasonal, mesothermal, mosaic rainforest-sclerophyl forest with chenopod, asteraceae and grassy understorey.*

The Plio-Pleistocene pollen record for central eastern Queensland shows an increased seasonality toward the end of the Late Pliocene and into the Pleistocene with an increase in the sclerophyllous vegetation and decrease in several rainforest groups (Martin & McMinn, 1993). Podocarps, aruarcarians and ferns decrease with an increase in Casuarinaceae in the Aquarius Well core (Hekel, 1972). Similarly gymnosperms, rainforest angiosperms and ferns decrease during the Plio-Pleistocene of ODP815. A sudden increase in Chenopodaceae and Asteraceae is seen in the Plio-Pleistocene Aquarius Well record (Hekel, 1972), and a steady increase in these two floristic groups is seen toward the Late Pliocene and Pleistocene in the ODP815 core (Martin & McMinn, 1993).

Two sites record the Plio-Pleistocene vertebrate record of central eastern Queensland (QML1384U and QML1420). This is due to the intermediate faunal similarity between the Early Pliocene rainforest faunal assemblage and the late Pleistocene faunal assemblage. QML1384U retains the distinct rainforest signal found in the Early Pliocene, however, there are a number of differences that may reflect a more seasonal climate. Additionally, QML1420, has a fauna that shows a more seasonal, open habitat.

*Frogs*. Only two frog species have been identified in the Plio-Pleistocene faunal assemblage, *Litoria* and *Kyarranus*. Although specimens are abundant at QML1384U, the presence of so few frog taxa may reflect a less complex vegetation and precipitation regime during this time. Neither taxon is specifically rainforest-dwelling, however, *Litoria* sp. indicates an arboreal environment and *Kyarranus* sp. indicates areas of permanent moisture.

*Squamates*. The presence of *Cyclodomorphus gerrardii* indicates a closed, wet, forest system.

*Mammals*. Although the mammal species are similar to those from the Early Pliocene, several taxa have been replaced by species with a broader environmental tolerance. *Antechinus flavipes* is present in the Plio-Pleistocene and possibly possesses a broader ecological range than that hypothesised for *Antechinus* sp. 1 and *Antechinus* sp. 2, which it replaces. *Sminthopsis macroura* also appears in Plio-Pleistocene, which may indicate a dry, open environment based on its present day distribution. Extant *Sminthopsis macroura* are commonly found in chenopod shrublands throughout central Australia

(Strahan, 1998), therefore the presence of chenopods in the Plio-Pleistocene pollen record could have provided suitable habitat for this species.

Arboreal possums continue to constitute a large portion of the QML1384U fauna, less so QML1420. Pseudocheirids are represented by three genera (*Pseudochirulus, Pseudocheirus* and *Petauroides*), petaurids with two genera (*Dactylopsila* and new genus), burramyids by *Cercartetus*, and phalangerids by *Strigocuscus*. The abundance of arboreal herbivores, insectivores and nectavores, indicates the retention of some rainforest and a dominance of angiosperms in the vicinity of Mt Etna.

Bandicoot diversity shows changes from the Early Pliocene with the appearance of two species of *Isoodon*. *Isoodon obesulus* possibly indicates a more mosaic vegetation structure (Strahan, 1998).

Macropod diversity remains high at QML1420, with a strong component of grazing macropodids, indicating the presence of more extensive grasslands at Marmor Quarry.

The mammal assemblage at QML1420 indicate a mosaic of environments present in the area, including open areas with grasses (*Macropus* spp, *Vombatus, Megalania prisca*, zygomaturine), closed forest (*Dendrolagus, Thylogale* sp. 2, *Trichosurus*, Petauroid new genus and *Melomys/Uromys*) and semi-aquatic (*Hydromys*).

### LATE PLEISTOCENE (ca. 149, 000 ybp)

*Dry, open arid-zone with closed 'refugial' forest.*

The pollen record for the late Pleistocene is absent at Aquarius Well and ODP815, demarcated by a hiatus of deposition and correlated with sea level fall (Hekel, 1972; Martin & McMinn, 1993). As an alternative, Lynch's Crater (Fig. 1A, 2), far north Queensland provides a better late Pleistocene record for Queensland (Kershaw, 1986). Kershaw (1986) estimates an annual precipitation rate which is 50% lower than the present day approximately 150,000 years ago. If it is hypothesised that the Mt. Etna area experienced a similar relative decrease in annual precipitation rate during this period of time, then the annual precipitation rate would have been less than 500mm (present day annual rainfall is between 800-1000mm, Data from Bureau of Meterology: www.bom.gov.au). An annual precipitation rate of below 500mm is equivalent to the precipitation rate currently recorded in central western Queensland, approximately 600kms to the west of Rockhampton. The late Pleistocene faunal assemblage reflects the very dry components of this ecology, however, it also records remnants of more mesic, probably refugial, environments.

*Frogs*. Frog diversity is low with only a single taxon so far positively identified and a complete absence of hylids (tree frogs).

*Squamates*. Squamate diversity is high, with most taxa identified, presently existing in the Australian arid zone. The squamates comprise, three agamids, all of which are currently restricted to the arid zone of central Australia; at least three species of skink; two large-sized varanids and several elapids. The absence of *Cyclodomorphus gerrardii* supports the contention for a very dry habitat.

*Mammals*. A distinct faunal change demarcates the late Pleistocene mammal assemblage from the older faunas of the same area. The small to large-sized dasyurids illustrate a diversity of insectivorous and carnivorous niches available within the ecology. There is retention of *Antechinus flavipes, Dasyurus hallucatus, Sminthopsis murina* and *Sminthopsis macroura* from older assemblages, with the addition of *Antechinus swainsonii, Dasyurus viverrinus, Planigale maculata* and *Phascogale topoatafa*. *Antechinus swainsonii* indicates the presence of closed wet environments, as do *Antechinus flavipes, Sminthopsis murina* and *Planigale maculata*. The remaining three new taxa lend evidence to the presence of dry sclerophyll in the region because all three extend into these environments today. Macropodines also indicate the presence of both open and closed environments with *Macropus* indicating grasses and *Thylogale* sp. 2 and *Dendrolagus* occupying closed forest. Possums are almost entirely absent with only two taxa present, *Trichosurus* sp. 1 and the new genus of petauroid.

*Perameles bougainville* appears in the record during the late Pleistocene, indicating the presence of dry open environments with shrubby, possibly chenopod-dominant ground cover. *Isoodon obesulus* remains in the faunal assemblage, supporting the mosaic nature of the palaeoenvironment. *Chaeropus ecaudatus* and *Macrotis lagotis* both strongly indicate a dry climate. Additionally, they illustrate the presence of grasses, possibly tussock grasses, in the area (Strahan, 1998). The rodent fauna also suggests a combination of distinctive dry and woodland species. The presence of species of *Notomys* and

*Leggadina* suggest an open environment, whilst *Conilurus* sp. suggests woodland.

On balance, the faunal assemblage indicates mosaic vegetation with areas of open grassland/chenopod shrubland, sclerophyll forest and a closed refugial forest. Such refugial forest is seen today in the semi-evergreen vine forest on Mount Etna, where the vine thickets are restricted to the wetter microclimates of limestone, whilst being surrounded by dry sclerophyll woodlands.

## CONCLUSION

Analysis of faunal and palaeoecological succession spanning the Early Pliocene to Holocene in central eastern Queensland is made possible by the long accumulation histories of cave and fissure systems in this region. As with the Wellington Caves of New South Wales (Dawson et al., 1999), Mount Etna provides a unique opportunity to document environmental change over ca. 4 million year period and the fauna associated with this change.

The Pliocene sites from Mount Etna are distinguished from all other sites in Australia of similar age by the presence of a distinct and dominant rainforest fauna, with the exception of the Hamilton Local Fauna. All other Pliocene sites in Australia differ from those at Mount Etna and Hamilton by possessing none or minor components of the fauna which are rainforest-adapted. In addition, the Mount Etna Fauna provides biogeographic links to Papua New Guinea and Irian Jaya by possessing taxa that are now restricted to these areas today or have only recently gone extinct there.

The mammalian fauna of the Early Pliocene at Mount Etna suggests biogeographic connectivity to Papua New Guinea and Irian Jaya during or just prior to this time. The murid fauna indicates a much earlier dispersal event of rainforest murids into Australia and questions the late Pleistocene or Holocene arrival previously suggested (Flannery, 1995; Winter, 1997). Combining an Early Pliocene record of rainforest specialist murids at Mount Etna with the incredibly diverse and endemic murid fauna from Rackham's Roost, Riversleigh, far north Queensland, substantially increases the probablility that murids entered Australia before the Early Pliocene and probably in the Late Miocene (Archer et. al., 1991; Long et al., 2002). The Pliocene possum and macropod faunas from Mount Etna illustrate connectivity between New Guinea and Australia also, by possessing taxa (or lineages) with affinities to taxa now extant or recently extinct in New Guinea.

Although the fossil record is patchy between the Early Pliocene and late Pleistocene, there is a distinct trend in the fauna to become arid-adapted, with an arid-adapted fauna by the late Pleistocene. The late Pleistocene fauna adds new records for the palaeodistribution of arid-adapted taxa, with several extant central Australian taxa being found extremely close to the eastern Australian coastline. Evenso, several mesic-adapted taxa persist into the late Pleistocene, probably existing in refugia offered by the limestone bluffs in the Mount Etna area, as is seen today.

The Mount Etna and surrounding fossil deposits offer a unique opportunity to document the evolution of the central Queensland environment over 4 million years of climate change, including the extinction of a diverse rainforest community, the expansion of the arid zone interior and the isolating affects on fauna utilising the refugial nature of limestone bluffs.

## ACKNOWLEDGEMENTS

Henk Godthelp is thanked for his assistance in rodent identifications. Jian-xin Zhoa is thanked for his provision of preliminary dating results. The following people and groups are acknowledged for their encouragement and assistance in developing this study: Aaron Sands, Alex Cook, Amy Sands, Aust. Skeptics, Ayla Tierney, Bernie Cooke, Chris White, Deb Lewis, Gilbert Price, Gregg Webb, Henk Godthelp, Jan Williams, Jeannette Sands, Jian-xin Zhao, Joanne Wilkinson, John Hocknull, John Walsh, Jonathan Cramb, Kristen Spring, Liz Reed, Lyndall Dawson, Mary Dettmann, Merv Barton, Michael Archer, Mina Bassarova, Morag Hocknull, Noel Sands, Paul Tierney, Peter Jell, Shona Marks, Steve Bourne, Sue Hand and numerous volunteers. This study (in part) has been assisted by funds provided by an Australian Research Council Linkage Grant LP0453664, with the following Industry Partners: Queensland Museum, Cement Australia, Central Queensland Speleological Society, Rockhampton Regional Development. Tourism Queensland is thanked for additional funding.

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| QML | 1311H | 1311CD | 1313 | 1385 | 1384L | 1384U | 1312 | 1284 | 1284a | 1420 | Olsens | Present |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Antechinus* sp. 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Antechinus* sp. 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Antechinus flavipes* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Antechinus swainsoni* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dasyurus hallucatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Dasyurus viverrinus* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Dasyurus* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phascogale* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Phascogale topoatafa* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Planigale maculata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Sarcophilus laniarius* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Sarcophilus harrisii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sminthopsis macroura* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Sminthopsis murina* | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| dasyurid (gen. et sp. nov.) | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Dendrolagus* spp. | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Thylogale* sp. 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Thylogale* sp. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Petrogale* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Pseudochirulus* sp. 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pseudochirulus* sp. 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pseudochirulus* sp. 3 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pseudocheirus* cf *peregrinus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Pseudocheirus* | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Petauroides* | 1 | 1 | 1 | 1 | 0 | 0 |  | 1 | 1 | 0 | 0 | 0 |
| *Pseudocheirops* sp. 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudocheirops* sp. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Pseudokoala* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| gen. et sp. nov. 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| gen. et sp. nov. 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Dactylopsila* sp. 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Dactylopsila* sp. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Incerti sedis gen. et sp. nov. | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Acrobates* sp | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Cercatetus* sp. | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Strigocuscus* | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichosurus* sp. 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Trichosurus* sp. 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Perameles* sp. 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Perameles* sp. 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Perameles bouganville* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Isoodon obesulus* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Isoodon* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Chaeropus ecaudatus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Macrotis lagotis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| perameloid gen. et sp. nov. 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |

| QML | 1311H | 1311CD | 1313 | 1385 | 1384L | 1384U | 1312 | 1284 | 1284a | 1420 | Olsens | Present |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| perameloid gen. et sp. nov. 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Notomys* sp. 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Notomys* sp. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Hydromys* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Pseudomys* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Rattus* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 |
| *Conilurus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Zyzomys* | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Leggadina* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Uromys/Melomys* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Pogonomys* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Mesembriomys* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| **Microchiropteran** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Macroderma gigas* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |

Appendix 1. Small-sized mammalian fauna data matrix. 0 = Absent, 1 = Present.

# A NEW SPECIES OF EARLY OLIGOCENE CETACEAN FROM PORT WILLUNGA, SOUTH AUSTRALIA

NEVILLE S. PLEDGE

Pledge, N. S. 2005 05 31. A new species of early Oligocene cetacean from Port Willunga, South Australia. *Memoirs of the Queensland Museum* **51**(1): 123-133. Brisbane. ISSN 0079-8835.

The partial skull of a small whale was found in a fallen block of cemented 'hardband', near the base of the cliff near the Aldinga Reef Marine Reserve, and derives from the Ruwarang Member of the Port Willunga Formation, of early Oligocene age. It shows distinctly primitive features, but is not an archaeocete. Comparison with descriptions of other species of similar age suggests that it represents an archaic mysticete close to *Chonecetus*, in the family Aetiocetidae, and is described as *Willungacetus aldingensis* gen. et sp. nov. ☐ *Oligocene, Cetacea, Mysticeti.*

*Neville S. Pledge, South Australian Museum, Adelaide, South Australia 5000; 1 August 2004.*

Fossil whale remains are rare in the early Tertiary marine sediments of Australia, and extremely so in South Australia. An unidentifiable tooth was described from the late Oligocene Ettrick Formation near Tailem Bend, Murray Basin, together with a cetacean radius from an indeterminate locality at Port Willunga (Pledge, 1994). The Oligocene is an important time in the evolution of whales, when modern suborders were beginning to differentiate (Fordyce & Barnes, 1994; Fordyce et al., 1994; Fordyce & Muizon 2001; Whitmore & Sanders, 1976).

Late in 1983 Murray Lindsay (South Australian Department of Mines & Energy) alerted the writer to possible whale bones in the cliff at Port Willunga. A nondescript limb-bone had been found in the area some years before (Pledge 1994), so the site was visited by the author. Two eroded specimens showing cancellous fabric were subsequently collected (19 December 1983) in boulders from the beach. However, these two nondescript pieces of rock were temporarily mislaid until 2001. These were prepared by dilute acetic acid dissolution of the limestone matrix. The first specimen disclosed unmistakeable bone, a sliver from the side of a battered vertebra, showing as a rectangular outline about 80mm long. (The other specimen, showing the form of a centrum with neural spine and transverse processes in cross-section, proved to be a fortuitously-shaped bryozoan colony.) Consequently, there was incentive, after 20 years, to revisit the site (Fig. 1).

In October, 2001, the writer and Jennifer Thurmer relocated the site, and found partly exposed, on the surface of a large fallen slab of hard cemented limestone, a ventrally planed-off cranial part of a skull showing occipital condyles, possible periotics and a squamosal. No other bone was seen in the area. The specimen was recovered with assistance from National Parks and Wildlife Service (NPWS), Onkaparinga City Council,journalists and TV news cameramen, and brought to the South Australian Museum for preparation.

## MATERIAL AND METHODS

Following substantial trimming, the specimen was CT-scanned to determine the extent and completeness of the bone, but no useful internal detail was apparent. Further paring unfortunately resulted in part of the occipital condyle being cut off and lost. Repairs were made using epoxy resin. Acid treatment of the block, (~5% acetic acid) was coupled with consolidation using. a dilute solution of 'Paraloid B-72'® (methyl acrylate/ethyl methacrylate copolymer) in acetone. Evidently much of the skull had originally protruded from the slab, but was lost to natural erosion, leaving a partial basicranium and the dorsal part of the braincase. Preburial damage resulted in loss of the rostrum. Nasals, premaxillae, maxillae and teeth are missing, but an edentulous fragment of the rostrum was found in the right temporal fossa. A second CT scan of the prepared specimen was made using a Toshiba Aquilion 4-slice scanner and program (Fig. 2). Still further acid treatment was undertaken, resulting in the skull parting along a natural sagittal break revealing the cranial cavity. A latex endocranial cast was made before the two halves

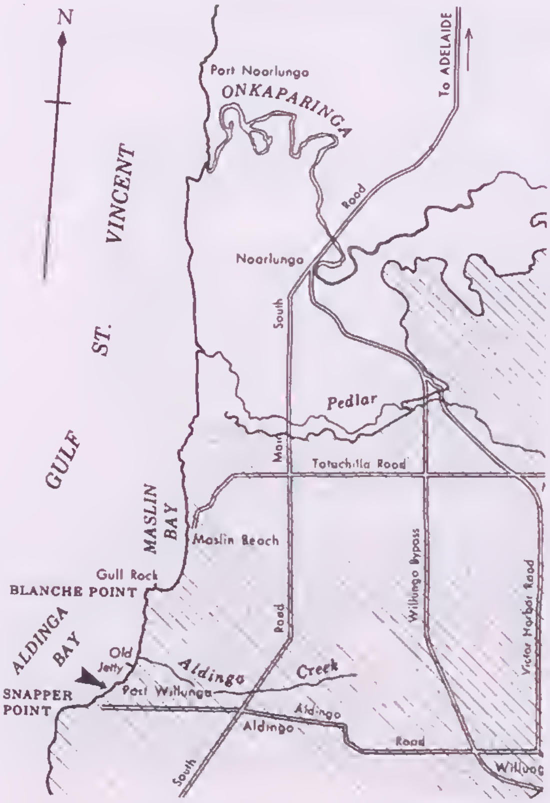

FIG. 1. Locality map: part of the Willunga Embayment (hatched), Gulf St Vincent, South Australia. After Cooper (1977).

were rejoined, incidentally removing the small distortion caused by the crack.

## RESULTS

The holotype, lodged in the Palaeontological Collections of the South Australian Museum (SAMP), comprises most of a cranium of a small cetacean split sagittally before or during burial, leaving a gap up to 5mm wide along the full length. Rostral bones separated or were broken off and were not preserved as recognisable pieces. A large sliver of such bone was found in the temporal fossa. In addition, the ventral side was truncated, at a slight angle, by erosion, possibly before full burial but certainly on exposure, as this was all that was showing in the slab of rock when found.

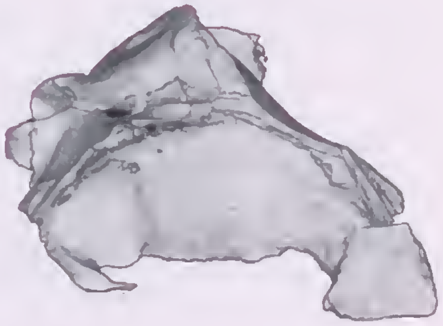

FIG. 2. *Willungacetus aldingensis* gen. et sp. nov., SAMP40034, holotype cranium, oblique right dorsolateral view, computer-assisted tomography synthesis. Image, Ross Harper.

## SYSTEMATIC PALAEONTOLOGY

### Order CETACEA Brisson, 1762
### Suborder MYSTICETI Flower, 1864
### ?Family AETIOCETIDAE Emlong, 1966

### **Willungacetus** gen. nov.

TYPE SPECIES. *Willungacetus aldingensis* sp. nov.

ETYMOLOGY. *Willunga*, for the locality, Port Willunga; *cetus* (Latin), whale.

DIAGNOSIS. As for species.

### **Willungacetus aldingensis** sp. nov.
(Figs 2-4)

MATERIAL. HOLOTYPE. SAMP40034, a partial cranium, from low cliff directly east of main 'reef', Port Willunga Marine Reserve, Port Willunga, midway between Aldinga Creek and Snapper Point in Aldinga Bay (Fig. 1), ~45 km south of Adelaide, South Australia, 34° 55' S, 138° 35'E; Ruwarung Member (Cooper, 1977, 1979) (a cherty limestone), Port Willunga Formation; Early Oligocene, Willungan Stage (Rupelian), planktonic zone P19 (Lindsay, 1967, 1985; Lindsay & Alley, 1995; McGowran et al., 2004: fig. 3). Referred specimens; SAM P40044, a longitudinal sliver of a vertebral centrum in a beach boulder several metres from holotype. SAMP10875, a damaged right(?) radius (Fordyce, pers. comm.; Pledge, 1994), precise locality unknown but from same cliff line.

ETYMOLOGY. From Aldinga Bay.

DIAGNOSIS. An ?aetiocetid (Barnes et al., 1994:396) differing from others in having longer intertemporal region with a sagittal crest, longer straighter lambdoid crests meeting at less than 90°, occipital shield more anteriorly inclined, almost circular foramen magnum; differs from *Aetiocetus* spp. in having sagittal crest, longer intertemporal region, narrower intertemporal constriction, frontals farther forward, basioccipital plate more inclined and less concave, smaller occipital condyles; differs from *Chonecetus spp. in having straight-sided lambdoid crest in dorsal view, cranium plan view outline more acute; differs from Ashorocetus* in having straighter and longer lambdoidal crests, less-concave occipital shield, relatively smaller and more protuberant occipital condyles; differs from *Morawanocetus* in having longer intertemporal region.

DESCRIPTION. A small ?aetiocetid whale, having a relatively long, narrow cranium, slightly longer than exoccipital width; long, wide, sulcate triangular supraoccipital, sloping forwards at low angle; prominent lambdoidal crest; long parietals forming slight sagittal crest; temporal constriction smoothly conical, slightly less than occipital condylar width, temporal fossa elongate oval; occipital condyles protuberant.

Skull not telescoped, truncated anteroventrally by syndepositional and/or post exhumation erosion, and therefore lacking definitely identifiable basicranial elements and all bones anterior of the parietals except for part of the right frontal and a displaced jaw-bone fragment possibly of the maxilla.

Broadly triangular in dorsal view, about 26cm wide across the squamosals, narrowing to about 8.5cm between the temporal fossae. Preserved length 32cm, the anteriormost is a partial supraorbital process of the right frontal. Braincase tapers forwards markedly but smoothly, without sharp constriction or angle. Temporal fossae long and ovate, broader anteriorly, merging into the squamosal fossa.

In dorsal view (Fig. 3A), skull dominated by the lambdoid (or nuchal) crest straight on the sides and angular, extending forwards medially into a faint sagittal crest (Fig. 2). In profile, sagittal crest with arbitrarily horizontal, the lambdoid crest rises steeply at nearly 70° before levelling to where it meets the vertex. In contrast, the midline of the supraoccipital is straight from condyle to vertex, making an angle of about 45° with the sagittal crest. Supraoccipital broadly sulcate triangular plate bounded by straight (in dorsal view) lambdoid crests, slightly convex laterally and depressed apically with a distinct median ridge (or external occipital crest) towards the vertex. Supraoccipital poorly preserved along the lambdoid suture with the parietals, with the thin edge broken away, but it shows a noticeable 'boss' about one third the distance from the apex, bounding the depression. The supraoccipital preserves a large fenestration roughly midway between these bosses, the foramen magnum and the skull apex, where the bone has thinned naturally to leave a smooth-edged, roughly elliptical hole 24mm wide and 20mm long. Occipital condyles have a slight 'neck' or condylar peduncle (Fig. 3A) which makes them prominent. Foramen magnum about 35mm wide, 30mm high, total span of condyles 89mm.

Parietals long, beginning up to 30mm behind the anterior edge of the temporal fossae, meeting dorsally at a slightly angulated junction extending 60mm along this sagittal 'crest' (Figs 2, 3A). Parietals smoothly curved with no temporal crest but in the centre of each, midway between the frontal and squamosal sutures, is a 'thumbprint' depression ahead of a small prominence which may be homologous with that crest. The temporal constriction is somewhat conical, narrow and deep as in archaeocetes, but not as abrupt as in modern whales, with a minimum diameter of about 85mm, about one third the overall width of the skull.

No posterolateral foramen is apparent. The suture with the frontal trends forwards away from the midline, at about 45°, before curving down into the temporal fossa and back posteriorly at the erosional edge of preservation (Fig. 3G). The suture with the squamosal (Figs 3 B, G) is approximately normal to the lambdoidal crest before curving forwards low-down some 30mm ahead of the zygoma root, into the missing truncated part of the skull. There is a small triangular bone on the left side, and a mosaic of smaller bones on the right side of the cranium, medial to the squamosals and between the supraoccipital and the parietals, associated with several small foramina on the suture lines. These bones are unidentified and the sutures may indicate the immature age of the animal.

The alisphenoid has barely survived the erosion of the ventral side of the skull. The ventral margin of the parietal appears to be marked by an indistinct suture about one centimetre above the eroded bottom surface on the left side (Fig. 3G): therefore, the alisphenoid makes a contribution to the wall of the temporal fossa, and possibly to the crest between temporal fossa and basicranium.

The temporal fossae (Fig. 3A, E) are elongate, up to 150mm long and an estimated 60+mm wide, narrowing posteriorly into the squamosal

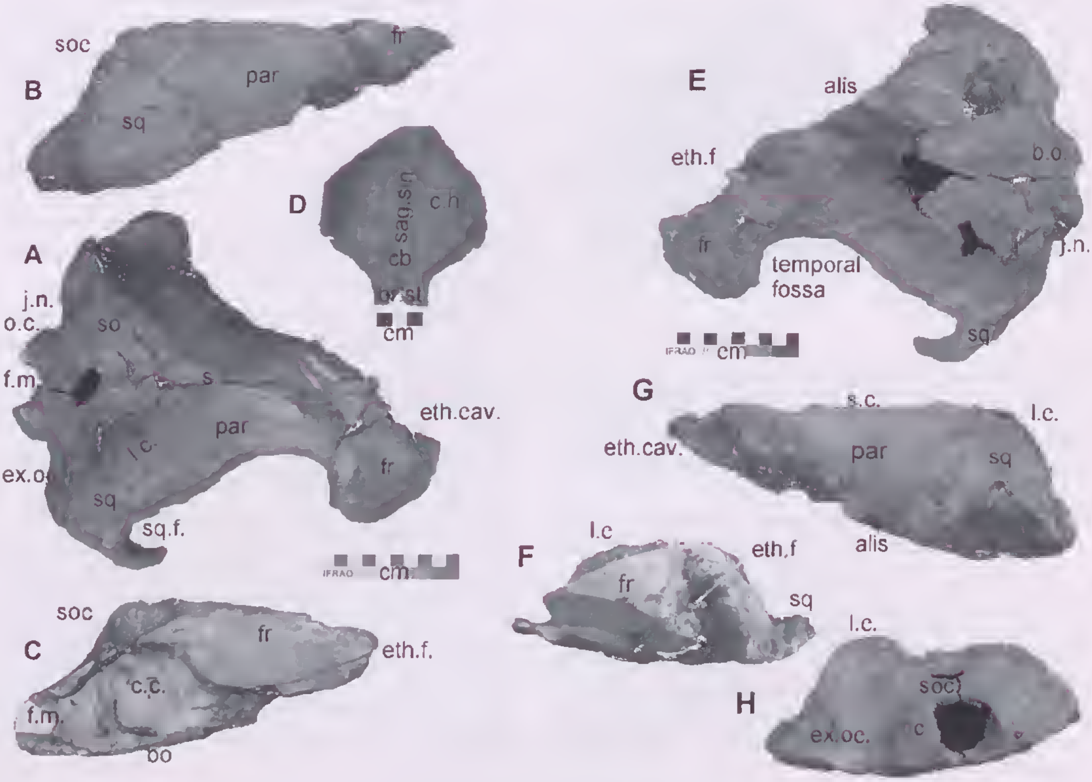

FIG. 3. *Willungacetus aldingensis* gen. et sp. nov., SAMP40034, holotype cranium. A, dorsal surface. B, right lateral. C, sagittal section, right lateral view. D, latex endocranial cast. E, ventral (truncated) surface. F, slightly lateral anterior view (canal arrowed). G, left lateral view showing ethmoturbinal cavity in frontal (at left). H, slightly lateral posterior view of supraoccipital. Scale in centimetres. Abbreviations: alis, alisphenoid; bo, basioccipital; br.st., brain-stem; cb, cerebellum; c.c. cranial cavity; c.h., cerebral hemisphere; eth. cav., ethmoid cavity; eth.f., ethmoid foramen; ex.oc., exoccipital; f.m., foramen magnum; fr, frontal; j.n., jugular notch; l.c., lambdoid crest; o.c., occipital condyle; par, parietal; sag.sin., sagittal sinus; s.c., sagittal crest; soc, supraoccipital; sq, squamosal; sq.f., squamosal fossa.

fossa. The point-to-point distance from the anterodorsal margin of the fossa (on the frontal) to the posteroventral margin (at the shelf of the squamosal) is 160mm, but this dimension has been distorted by the ventral truncation of the skull, and may not be that long. The squamosal fossa is narrow, up to 30mm wide, and longitudinal.

Squamosals are incomplete, each preserving a roughly triangular slightly convex cranial plate, approximately 60x70mm, and part of the zygomatic processes. The latter have been truncated ventrally by erosion (and also laterally on the right zygoma, suggesting some pre-burial damage), and there remain only the base of the process and a small part of the 'mastoid' region, the latter visible on the truncated ventral surface as very dense bone. The remnants suggest the zygomas were rather slender. There is no indication as to whether the zygomatic process would closely approach or meet a similar process (postorbital angle) from the frontal. Endocranially (Fig. 3C), the squamosal boundaries are unclear; the cranial endo-surface seems to be corroded, possibly by the action of scavengers before burial.

The frontal bone is poorly represented externally, and only as a small area at the lower medial side of the temporal fossa and an undistinguished mass of the right supraorbital process, with a somewhat roughened or eroded dorsal surface, at the anterior side of said space. Indistinct marks suggest the frontoparietal suture might extend back on the sagittal crest to within

60mm of the supraoccipital; this is weakly supported by the apparent line of the suture as seen internally in the sagittal section, where it seems to extend to a point level with the front of the cerebrum. The cranial part of the frontal is thick. In sagittal view, there is a deep, transversely-grooved, ethmoidal cavity (Fig. 3G), as much as 35mm long (anterovertically) and 20mm diameter, whose long axis in a parasagittal plane is at about 70° to the sagittal crest. It bears nine parallel grooves, formed by the ethmoturbinals, that flow into a median longitudinal canal (the ethmoidal foramen) about 1012mm wide and 4mm high that continues back into the brain cavity (Fig. 3C), apparently along the junction between the frontal and an unidentified bone (the vomer?). The postorbital process appears to have been quite thick, a primitive condition. The frontal is not preserved ventrally enough to show any sign of the orbit.

There are several small detached fragments of bone that became separated from the anterior extremity during the acid process; two of these, with surface preserved, seem to be symmetric about a longitudinal (sagittal) suture surface, and seem to roof the anterior end of the ethmoidal foramen, where it widens out into the ethmoidal cavity (Fig. 3F, G), lined with up to nine oblique grooves for the ethmoturbinals (or olfactory fossa, e.g. Breathnach, 1955, pl. 1).

Bones on the ventral side of the specimen (Fig. 3E) are eroded and difficult to delimit and identify. Regular and symmetrical variations in texture and density suggest some might be identifiable as the basioccipital, the bases of the pterygoids, the alisphenoids, the squamosals and the exoccipitals. Large holes in the eroded surface coincide roughly with the positions of erosionally-enlarged foramina ovales, or the 'cranial hiatus', and imply that the tympanic bullae are long since lost. On the sloping posterolateral side of the left-hand hole, between the putative squamosal and exoccipital, there are faint parallel suture-like grooves where the tympanic bulla might have articulated. Adjacent medially to the vacuities, a pair of thickenings of the basioccipital mark the former position of the lateral protuberances. The extent of development of the paroccipital process cannot be determined, and the external auditory meatus has likewise been planed off. A small hypoglossal foramen is seen on the dorsal side of the jugular notch

Brain cavity (Fig. 3D) broadly rhombic, roughly hemispherical, about 90mm long, 115mm wide and 60mm high (volume estimated at approximately 600 ml), partly divided by a dorsal longitudinal depression sinus, and with equally broad (about 40mm) anterior and posterior extensions for the (presumed) olfactory capsule and brain-stem respectively, although the anterior space has been enlarged by erosion. Endocasts of whale skulls are considered to be only approximations of the original brains, because of the mass of surrounding non-neural matter (e.g. Breathnach, 1955; Marples, 1949). Because of imperfect preservation of the internal surface of the cranial bones, and some damaged and missing portions, this endocranial cast is less than perfect, but some structures are nevertheless apparent. Sagittal sinus is broad and fairly deep, but the median tentorial depression is poorly defined, as is the lobus medius cerebelli, which is overlain by the cerebral hemispheres. The paraflocculus appears fairly well defined, but merges with the masses annexes, or spaces for non-neural matter, lower on each side of the endocast. The roots of the trigeminal nerve are obscure and uncertainly identified at the anterior edges of the latter.

A bone fragment (Fig. 4A, B), found obliquely within the right temporal fossa close to the frontal, is part of a smooth, broad, elongate bone that is considered to represent the maxilla, but could be a piece of dentary. As preserved, it is 63mm long, about 25mm wide, generally flat with a broadly curved edge on the smooth outer surface and corroded on the inner; it is obliquely truncated by erosion at one end; the other shows a preburial break. No trace of suture margins is present, but part of a small 6mm diameter tooth alveolus (and possibly the edge of another one slightly offset 34mm away and slightly diverging) lies on the curved edge (Fig. 4B). Another unidentifiable, smaller piece of bone was found in the left temporal opening.

Associated vertebral fragment, SAMP40044 (Fig. 4C preserves one side (imperfectly) and a segment of one epiphysis of the centrum, and was partially eroded before burial. The bulk of the bone was eroded away obliquely on the other side after its exposure and fall from the cliff (see below). The epiphysis appears to be slightly concave, with the margin faintly rounded. There is evidence for at least one longitudinal ridge along the centrum, which is probably lateral. It does not seem to be part of the neural arch. No foramina are preserved. The following dimensions are estimated, assuming the epiphysis was roughly circular and taking the intersection of lines normal to its circumference to be the centre. Diameter of centrum: up to 8cm, length of centrum: about 8cm, overall length of fragment: 9.5cm, width: 7cm.

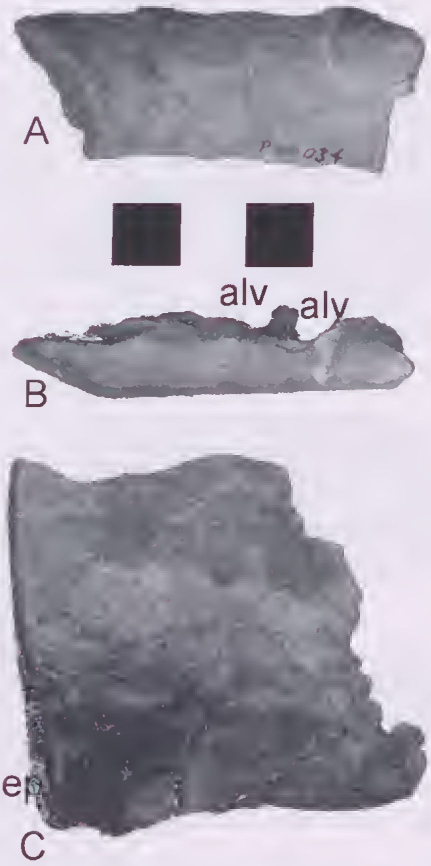

FIG. 4. *Willungacetus aldingensis* gen. et sp. nov., associated jaw fragment SAMP40034. A, lateral view. B, occlusal view, truncated end at right. C, SAMP40044, referred remnant of vertebral centrum, epiphysis at left. Scale in centimetres. Abbreviation: alv, alveolus; ep, epiphysis.

DISCUSSION. *Taphonomy.* No geopetal fabric or any other sedimentological structure could be discerned in the rock slab. It has therefore been assumed that the exposed surface of the slab as found at the cliff base was originally uppermost as it is the more common attitude of fossil cetacean skeletons (Fordyce et al., 1994).

Thus it appears that the whale's carcass came to rest piecemeal on the seafloor, the skull apparently separated from the backbone, itself disarticulated (e.g. Schäfer, 1972), and sank upside down into the soft sediment with its rostrum, being less dense, poking up at about 20° to the sediment surface, and the whole underside exposed to the actions of scavengers and erosion. The basicranial surface of the skull was therefore eroded, and the rostrum was separated with a couple fragments coming to rest in the temporal fossae. The cranial cavity shows evidence of some corrosion/erosion of the bone surface, probably by scavengers, with the patchy removal of the bone surface lamina exposing the diploe. The basicranial truncation also allowed sediment and scallop shell fragments to enter when sedimentation resumed; the shells were later weakly silicified, and survived the acid treatment. The period of erosion seems to have coincided with the formation of one of the 'hardgrounds', which are a feature of this part of the sequence of the Port Willunga Formation.

With recent exposure and erosion of the modern cliff, slabs of the cherty 'hardground' separate and fall only a few metres to the beach below, to become subject to further erosion. Considering the original size of the slab in question, it is unlikely to have moved far, nor to have been overturned by wave/tidal action. Therefore the surface seen on its discovery is probably little changed from the time it was originally buried.

*Comparisons.* Fossil whales of early Oligocene age are rare, and this would appear to be the first recorded for Australia. Because this is also the time when cetaceans were diversifying and dividing into the odontocete and mysticete lines (e.g. Fordyce et al., 1994; Fordyce & Muizon, 2001), it is important to attempt to categorise this species from Port Willunga. Therefore, it is compared with a number of other taxa from elsewhere around the world, mostly of late Oligocene age.

The skull is not noticeably telescoped, as in modern whales, and even less than in the late Oligocene *Agorophius pygmaeus* (Müller,1849) (e.g. Fordyce, 1981) and *Chonecetus sookensis* (Russell, 1968) which are useful bases for comparison, or the early Miocene cf. *Parietobalena* (SAMP63). Comparing it with Fordyce's Text-Fig. 2 (ibid.), the broadly sulcate triangular supraoccipital is like *Chonecetus* and *Ashorocetus* (Barnes et al., 1994) being bounded by straight (in dorsal view) lambdoid crests, slightly convex laterally and depressed apically but with a distinct median ridge (or external occipital crest) towards the vertex. The Willunga specimen is very incomplete, but is noticeably relatively longer, and is more like *Chonecetus*. Initial ideas of an archaeocete affinity such as *Dorudon* indicated by the rather archaic narrow cranium with elongate intertemporal region and strong supraoccipital crest, did not withstand scrutiny. The broad forwards-sloping supraoccipital, and the relatively broad, conical temporal constriction indicate a more advanced taxon.

The crest is more prominent than those of *Chonecetus* which are otherwise similar, and of the cetothere cf. *Parietobalaena* (SAMP63) (Bearlin, 1985; Glaessner, 1955) from the lower Miocene Morgan Limestone of South Australia. The supraoccipital differs from *Agorophius* where it is smoothly curved and possibly anteriorly extended, and from *Chonecetus sookensis* where it is semicircular. The lacuna in the supraoccipital does not appear to be the same as the (usually, symmetrically paired) fenestrations described by Pilleri et al. (1982) in various cranial bones of a diverse range of cetaceans, and those in *Chonecetus* (Russell, 1968).

Parietals also differ markedly from *Agorophius* (and *Parietobalaena*) in being relatively much longer. They are smoothly curved with no temporal crest as seen in *Agorophius*. The temporal constriction is conical as in *Chonecetus*, parallel-sided, narrow and deep as in archaeocetes, but not as abrupt as in modern whales. Unlike *Agorophius* (Fordyce, 1981), no posterolateral foramen is apparent. Large holes in the eroded ventral surface coincide roughly with the positions of erosionally-enlarged foramina ovales, or the 'cranial hiatus' seen in *Chonecetus* (Russell, 1968) and cetotheres such as *Parietobalaena*, and imply that the tympanic bullae are long since lost

There are not many characters (e.g. Barnes et al., 1994) preserved to enable subordinal assignment. However, apparent easy separation and loss of rostral bones (premaxillae, maxillae and nasals) from the skull of *Willungacetus* suggests it is referable to the mysticetes (Miller, 1923: 9, footnote), and this assignment is supported by the presence of ethmoturbinals, which are symplesiomorphic for archaeocetes and mysticetes but absent in odontocetes (Van Valen, 1968) (although they are present in early odontocetes, R.E. Fordyce, pers. comm. 2004).

The latest Eocene (or earliest Oligocene) species, *Llanocetus denticrenatus* Mitchell, 1989, from the La Meseta Formation of Seymour Island, Antarctic Peninsula, is considered to be the earliest known mysticete (ibid.), but only its jaw fragment and natural endocast could be compared, the skull being under study and not yet described (Barnes et al., 1994; Fordyce & Barnes, 1994). The jaw shows that the teeth were archaeocete-like but relatively small and two-rooted, which seems to be the case in *Willungacetus*. There are similarities between the two endocasts in the length:breadth proportions for instance, but some differences such as the development of the 'cerebellum' (apparently greater), and the form of the cerebral hemispheres (more divergent in *Willungacetus*) are apparent. The endocranial cast of *Llanocetus* is more than twice as big as the new species.

The bone fragment probably possesses the alveoli of a double-rooted tooth whose longitudinal axis is at a slight angle to the line of the jawbone, rather like the fragment of the much larger *Llanocetus* (Mitchell 1989)

The vertebral measurement estimates have been compared with those of the series of vertebrae of *Aetiocetus cotylalveus* (Emlong, 1966), with little success: there is approximate correspondence with the proportions of the 10th dorsal or the 2nd, 3rd or 4th caudals, but the assumptions are too many to make any inferences.

The Late Oligocene archaic cetacean, *Aetiocetus cotylalveus* (Emlong, 1966), from Oregon, differs significantly from the Port Willunga whale, notably in the short cranium, crescentic near-vertical supraoccipital, lack of sagittal crest, short diverging parietals and relatively short and wide temporal constriction. It retains some archaeocete characters, such as a near-vertical supraoccipital, not found in odontocetes, and was placed in a new family of archaeocetes, but is now referred to the Mysticeti (Van Valen, 1968). The new specimen resembles more the species *A. tomitai* Kimura & Barnes (Barnes et al., 1994) in the form of the supraoccipital and zygomas, the relatively long cranium and the presence of a sagittal crest.

*Chonecetus*, also of late Oligocene age, has been linked with *Aetiocetus* in the extinct archaic mysticete family Aetocetidae (Barnes, 1989; Barnes et al., 1995). Of the described species, *Willungacetus aldingensis* resembles *C. sookensis* (Russell, 1968) from Vancouver

Island, British Columbia, more than any other, notably in the shape of the cranium, extent of the parietals, the conical temporal constriction, and (less so) the shape of the supraoccipital, but not the unusual long twin parasagittal crests. However, the supraoccipital of *Chonecetus goedertorum* Barnes & Furusawa 1994 (Barnes et al. 1994) from Japan is more like that of the South Australian fossil, in being more triangular and with a median crest.

As far as can be determined, there is some resemblance to the partial cranium of *Ashorocetus eguchii* Barnes & Kimura (Barnes et al., 1994), also classed as an aetiocetid, but the Port Willunga specimen differs in having a much larger and more triangular supraoccipital.

The Late Oligocene *Agorophius pygmaeus*, a primitive odontocete from South Carolina, has a skull superficially similar to *Willungacetus*, so far as can be compared, but differs in much the same way as *Aetiocetus*, viz. short deep cranium, parabolic supraoccipital rising vertically at the base, short rounded parietal roof and short temporal constriction, and no sagittal crest. The process of cranial telescoping is well advanced in *Agorophius*, and is of odontocete style, but contrary to the situation in other toothed whales the supraoccipital has not extended forwards to meet the frontals (Miller, 1923). It is now regarded as an odontocete of uncertain position (Whitmore & Sanders, 1976; Fordyce, 1981) and can be eliminated from consideration.

Roughly contemporaneous with these is an unnamed specimen (USNM243979) from Oregon (Whitmore & Sanders, 1976, fig. 2a), which shows a disposition of the cranial bones similar to our new find. It has a 'triangular occiput…thrust forward in a manner reminiscent of the Mysticeti', a sagittal crest and strong temporal constriction, and a similar parietal-squamosal suture. It seems to differ from *Willungacetus* only in the degree of constriction (less), relative width of the supraoccipital (less), and sturdiness of the zygomatic processes of the squamosal (greater). It has been interpreted as a primitive non-squalodontoid odontocete (ibid.), and can also be eliminated from consideration.

The only described Australian specimen that might be directly relevant is the skull of *Mammalodon colliveri* Pritchard, 1939, from the Late Oligocene (Janjukian) of Torquay, Victoria. Unfortunately, Pritchard only described the partially prepared specimen, and the description and figure are quite inadequate. Fordyce has studied the subsequently prepared skull and given a better illustration (which shows a short rounded rostrum) and informal description (Fordyce, 1982, 1984; Fordyce & Muizon, 2001), but a full description is still awaited. Long et al., 2002: 202-204) give the best figure so far of the skull of this small whale, which Fordyce (ibid.) refered to the mysticetes on several lines of evidence, most of which are not applicable to the Willunga specimen. However, it can be seen immediately that the two are not the same species. Although similar in size — *Mammalodon* jugal width (scaled from Fig. 4E in Fordyce, 1984, where the jugals were speculatively reconstructed) is approximately 23cm; length from temporal constriction to condyle ~20cm; constriction diameter 6cm; *Willungacetus* skull approx. 28cm, 23cm and 8.5cm respectively — they have strikingly different supraoccipital bones, semicircular in dorsal view in *Mammalodon* and almost right-triangular in the South Australian specimen. There is also an age difference of 5 million years or more. Fordyce (1984) stresses the primitive features of *Mammalodon*, likening it to dorudontines. There is a slight possibility that, considering its even more primitive-looking cranium, *Willungacetus* is ancestral to the rather aberrant *Mammalodon*.

By contrast, the cetothere cf. *Parietobalaena* (e.g. "*Aglaocetus*?", SAMP63, Glaessner, 1955) shows only one point of similarity: the triangular shape of the supraoccipital. Otherwise, the cranium shows typical mysticete shortening; it is wider and shorter, the temporal constriction shorter, and the junction of the parietals much shorter (2cm) so that the longitudinally convex supraoccipital almost reaches the frontals.

It had been hoped that study of its endocranial cast might throw some light on the affinities of the specimen, since the shape and relative development of different parts of the brain reflect the different adaptations of the major groups (Jerison, 1973). Unfortunately the lack and obfuscation of detail by pre-burial erosion has prevented more than generalisations. In its rhombic outline, it approximates the endocranial cast of the modern mysticete *Megaptera* (e.g. Breathnach, 1955), but with much smaller cerebral hemispheres. There is also a resemblance to the larger of the natural endocasts described by Marples (1949) from the supposed Oligocene (but see reservations of Breathnach, 1955: 532) of New Zealand, as an odontocete, but apart from its overall smaller size the apices of

TABLE 1. Measurements in millimetres of crania of *Willungacetus* and other aetiocetids (after Barnes et al. 1994), and *Mammalodon colliveri*. Characters: 1, width across postorbital processes; 2, width of intertemporal region; 3, length of parietal on sagittal line; 4, length from anterior margin of temporal fossa/frontal to condyles; 5, zygomatic width; 6, exoccipital width; 7, greatest width across occipital condyles; 8, greatest height of occipital condyles; 9, greatest width of foramen magnum; 10, greatest height of foramen magnum. * Measurement obtained by doubling half-width; ( ) estimated measurement; # estimated from scaled figure; + measurement greater than indicated

| Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| *Willungacetus aldingensis* | (170+*) | 85 | 75 | 245 | 280 | 220 | 90 | 45+ | 37 | 32 |
| *Chonocetus sookensis* |  | 42 |  | 148# | 188 | 159 | 66 | 41 | 31 | 22 |
| *C. goedertorum* | 196 | 70 | 33 | 95# | 212 | 180 | 78 | 51 | 34 | 39 |
| *Ashorocetus eguchii* |  |  |  |  | 123+ | (230) | 88 | 46 | 43 | 22 |
| *Morawanocetus yabukii* | 212 | 81 | 26 | 77# | 290 | 228 | 89 | 42 | 49 | 20 |
| *Aetiocetus tomitai* | (230) | 86 | 42 | 102# | (240) | 210 | 93 | 45 | 39 | 23 |
| *A. cotylalveus* | 280* | 85 | 45 | 170# | 290* | 260* | 91 | 49 | 28 | 20 |
| *A. weltoni* | (273) | 68 |  |  | 292 | 254 | 99 | 61 | 31 | 35 |
| *A. polydentatus* | 254 | 68 | 66 | 177# | 272 | 236 | 91 | 60 | 25 | 28 |
| *Mammalodon colliveri* | 220*# | 60# | 95# | 235# | 230# | 130*# | 80# |  |  |  |

the cerebral hemispheres are much farther apart in the Willunga endocast, and the cerebellum seems relatively larger.

## SIGNIFICANCE

The early Oligocene was a critical time for the evolution of whales and saw the emergence of the two modern lines of cetaceans: the Mysticeti and the Odontoceti (Fordyce, 1992; Fordyce et al., 1994). However, there are few fossils to document the details of this event. Although it is incomplete, the Port Willunga specimen may go some way to elucidating the early evolution of the mysticetes.

The Eocene/Oligocene transition saw the final separation of the future Australian continent from the Antarctic remnant of Gondwana, and the establishment of the Circum-Polar Current, which forever changed the climatic history of the world into a series of worsening cold periods (e.g. Fordyce, 1977; Frakes et al., 1987; McGowran et al., 1992). It is therefore probable that the evolutionary and climatic events are linked (Barnes, 1977; Fordyce, 1992).

## SUMMARY AND CONCLUSION

*Willungacetus* dates from a time when cetaceans were differentiating into the modern suborders, and is therefore of some significance in understanding that process.

It is considered, on the characters preserved, such as the relative ease of loss of the rostral bones, the presence of ethmoturbinals, and of the form and style of the supraoccipital, that this important skull is a mysticete, although it is incomplete and has some traits, probably symplesiomorphic, that seem to point to odontocetes. It shares many primitive characters with members of the Family Aetiocetidae, such as apparently having teeth, but is more primitive in having a longer skull. Nevertheless, it is probably referable to the Aetiocetidae, and the greatest similarity seems to be with species of the late Oligocene *Chonecetus*. Some measureable characters are summarised and compared in Table 1. It is not a cetothere because of the plesiomorphic shape of the cranium and the lack of any apparent cranial shortening.

The referred right radius (SAMP10875) found in the vicinity of the skull appears to be intermediate between archaeocetes and cetotheres (Pledge, 1994) and offers some support for this interpretation.

The species therefore stands as a possible ancestor of the aetiocetids, and even of later mysticetes.

## ACKNOWLEDGEMENTS

I thank Dr J. Murray Lindsay (then of SADME) for alerting me to the potential of this locality, Ms Jennifer Thurmer for help in discovering the specimen and continued encouragement, Messrs Ben McHenry, Ben Kear, Jo Bain and Jim McNamara for help in the field or laboratory, and the South Australian National Parks and Wildlife Service and the Onkaparinga City Council for permissions and logistical support. Ben Kear organised for the CT-scans through Mr George

Kourlis, Royal Adelaide Hospital, Adelaide, and Mr Ross Harper, Lyell McEwin Hospital, Elizabeth. I thank also Dr R. E. Fordyce, University of Otago, for useful criticism of an early draft of this article, and help with obtaining references, and Dr B. McGowran for comments on the age of the specimen. I am grateful to Mr Robert Hamilton-Bruce for help with production of the images.

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# THE RIVERSLEIGH WYNYARDIIDS

NEVILLE S. PLEDGE

Pledge, N.S. 2005 05 31. The Riversleigh wynyardiids. *Memoirs of the Queensland Museum* **51**(1): 135-169. Brisbane. ISSN 0079-8835.

At least 18 different localities, mostly on D-Site Plateau, at Riversleigh have yielded wynyardiid material. Most of the 121 specimens examined are isolated teeth or small fragments of jaw. One almost perfect skull, an imperfect skull lacking basicranium, another crushed flat before burial, two partial skulls, 14 maxillae and 11 dentaries are recorded. These were studied metrically and morphologically and resolve into three distinct species described here: the more gracile *Namilamadeta albivenator* sp. nov. mainly from White Hunter site, *N. superior* sp. nov. from Upper Site, and the aberrant *N. crassirostrum* sp. nov. from other sites. Two isolated premolars from another site indicate a fourth taxon. Although dentally similar, the species are distinguishable from each other and from *N. suideri* of the Tarkarooloo Basin of South Australia, which provides, by correlation with the Lake Eyre Basin, the only independent age dating for this part of the extensive Riversleigh deposits. ❐

*Riversleigh, mid-Tertiary, Marsupialia, Diprotodonta, Wynyardiidae, Namilamadeta.*

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Wynyardiidae was established (Osgood, 1921) for a unique specimen found in the middle of the 19th Century, near the Tasmanian coastal town of Wynyard. It was a partial skeleton, including a damaged skull and mandible, buried in marine sediments of the Fossil Bluff Sandstone. First described in 1900 (Spencer, 1901), *Wynyardia bassiana* was for many years the oldest known Australian marsupial, although its age and affinities were often disputed (e.g. Gill, 1957; Ride, 1964). The age has been resolved as Longfordian, i.e. Early Miocene (e.g. Ludbrook, 1967, 1973; Quilty, 1966). Unfortunately, there were no teeth which would have facilitated assessment of relationship with other marsupials, and attention focussed on the basicranial region (e.g. Ride 1964, Aplin 1987).

This monopoly as the oldest Australian marsupial held until 1953, when Stirton (1954) discovered Tertiary mammals in the Lake Eyre Basin of northern South Australia. The recognised age of the oldest of these is considered to be late Oligocene (Woodburne et al., 1993), as Stirton had believed (Stirton et al., 1961), following a period where it was considered to be Mid-Miocene (e.g. Woodburne et al., 1985). In 1971, Tedford, examining similar sediments (Namba Formation; Callen & Tedford, 1976) near Lake Frome, 300km to the southeast of Stirton's sites, found mammal fossils correlative with those of the Etadunna Formation of the Lake Eyre Basin. In 1973, Tedford discovered two partial skeletons and some jaws of a rather unusual diprotodontan marsupial (Tedford et al., 1977). Pledge (2003) later described them as *Muramura pinpensis*. Features on some postcranial bones suggested to Tedford a relationship with *Wynyardia*, and a tooth was figured as '?Wynyardiidae QMAM 178'. This allowed Rich & Archer (1979) to refer their new species *Namilamadeta suideri* to the ?Wynyardiidae.

Discovery in 1983 of two complete skeletons of *Muramura williamsi* (Pledge, 1987), which have similar dentition to Tedford's material and to *Namilamadeta*, permitted comparison of the basicranial region (Aplin, 1987) and certain limb bones of *Wynyardia* with the new material (work in progress). This has strengthened the wynyardiid affinities of *Namilamadeta*.

The first specimens referable to *Namilamadeta* from the extensive Riversleigh limestone deposits (Archer et al., 1989, 1991, 1995, 1997) were recovered in 1986. Since then, about 120 specimens from 19 different localities have been obtained, and are the subject of this study.

## MATERIALS AND METHODS

Specimens are housed at the University of New South Wales, School of Biological Sciences, Vertebrate Palaeontology Laboratory, prefix 'AR', or the Queensland Museum Palaeontological collections, prefix 'QMF'. SAMP refers to specimens in the palaeontological collections of the South Australian Museum, and NMVP to those held by Museum Victoria.

Specimens were measured with vernier calipers or by a calibrated ocular scale in a Nikon SMZ-10 stereoscopic microscope. Measurements were subjected to graphical bivariate analysis on a locality-by-locality basis to ascertain uniformity of samples, and relationships between localities. Computer tomography X-ray scans were performed by Mr Ross Harper, Lyell McEwin Hospital, Elizabeth, South Australia, on two skulls of different *Namilamadeta* species, on a foam pad in a Toshiba Aquilion multislice spiral CT scanner using 0.5mm slice thickness, and reconstructed on both bone and soft tissue algorithms at 0.3mm slice spacing. Images were produced for each algorithm. All images were transferred in DICOM format to a high-end workstation running Voxar 3-D software. High resolution, multiplanar and 3-dimensional images were created. and captured as greyscale 2-D and colour-rendered 3-D sequences in both single image and movie format. Resultant images allowed both linear and volumetric measurement of various structures, including air-filled or matrix-filled cavities (R. Harper, pers. comm.).

Schematic morphology and terminology are given in Fig. 1. Although Archer's (1978) tooth homology system for marsupials is more pragmatic and practical (i.e. the first molariform tooth should be called the first molar), and was used in Pledge (1987), Australian authors have recently adopted, with varying degrees of reservation, Luckett's (1993) version of Flower's (1867) tooth notation, with Archer's M1 becoming dP3. This scheme is followed here in the interests of conformity.

Because of uncertainties of their relative ages, specimens from each Riversleigh locality were treated as a locality population sample for comparison with the other localities, and with the type specimen from Lake Tarkarooloo, South Australia. Paucity of comparable material often meant sample size was very small, and frequently only one specimen, with the result that any statistical treatment was pointless. However, some localities yielded numerous good jaw specimens so that samples of like teeth were of useable size. The collection included three fairly complete skulls (one crushed, another lacking the basicranium), two partial skulls, eight complete maxillae and eight dentaries (lacking only incisors in all but one, which is complete). These are all from Site D Plateau (Archer et al., 1991) and mostly from four sites; Wayne's Wok, Camel Sputum, White Hunter and Mike's Menagerie; except for one specimen from the 'Mesa' (Roo Site), of uncertain stratigraphic provenance.

Because the fossil localities are essentially isolated lenticular deposits, it has been difficult to arrange sites in relative stratigraphic order. Archer et al. (1989) separated sites into three 'systems', a practice criticised by Megirian (1992, 1994). Creaser (1997) examined individual geologies in an attempt to fit them into a sequence, but there seems to be contradiction between other authors when organising sites according to taxonomic and biostratigraphic characters. A recent summary, based upon the occurrences and relationships of fossil macropodoids, was given by Cooke (1997).

Riversleigh fossil faunas are very rich in the Australian context, and have been considered to represent a sub-tropical 'rainforest' environment (Archer et al., 1991), although unlike anything extant today. This is supported by Cooke's (1997) assessment based on the dental adaptations of the diverse and widespread macropodoid species. Megirian's (1992) interpretation, based on geological evidence, is for relatively dry, even semi-arid, conditions across a range of different depositional environments, with any rainforest being riparian along perennial streams, separated by mesic habitats. In the modern tropical situation, marsupial diversity is high, yet in any particular guild, related species can be differentiated readily by size or (tooth) morphology or both, as well as preferred environment. It is therefore assumed, for parsimony, that each site contains only one species, since tooth-size measurements form fairly discrete clusters (except possibly in the case of Dirk's Towers) and on inspection this appears to be the case. Initial collecting separated the several Tower sites, which were later amalgamated. However, it seems here that Towers sites may represent different time periods in a shifting depositional environment, or a mixed fauna of species from two or more different habitats. The ages of these sites are uncertain for some authors (e.g. Cooke, 1997), being indicated as either System A or B.

There is little or no indication in the teeth themselves for any sexual dimorphism, although it should be expected if modern kangaroos are any guide (Bartholomai, 1971) (however, data in Crowcroft (1967) for *Lasiorhinus latifrons* is equivocal with respect to dentition), but there is a suggestion of dimorphism in the robustness of one or two dentaries which are noticeably larger

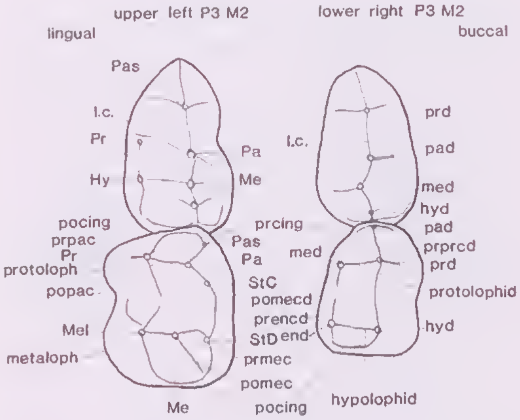

FIG. 1. Schematic diagram of upper and lower premolars and molars ($M^1$) to show morphology and terminology.

than others in their samples and therefore possibly represent 'alpha-males' (e.g. QMF 12461 from Camel Sputum).

Initially, only isolated teeth and jaw fragments were available. Each cheek-tooth was measured for three parameters; length, anterior width and posterior width (see Appendix 1). In an effort to discriminate between localities (= populations), various graphical treatments were given to these data. By trial and error, individual bivariate scatter diagrams of length vs posterior width of upper and lower premolars ($P^3$, $P_3$) and molars ($M^1$, $M_1$) gave an indication that certain localities could be grouped together whilst others were distinct. These separations were confirmed by plots of premolar length vs M1 length for associated teeth in jaws. Sample sizes for associated teeth were noticeably reduced when P3 and M1 were both required, but each locality sample separated distinctly from all other localities (Fig. 2). By associating isolated teeth on the basis of preservation, degree of wear and handedness, sample sizes were slightly enlarged for White Hunter and Camel Sputum upper teeth. This slightly enlarged their respective fields to the extent that the Camel Sputum sample could be extended to overlap with the diffuse Wayne's Wok sample. The Wayne's Wok site is rather extensive (tens of metres) compared with others. Similarly, the White Hunter sample could be affiliated meristically with Dirk's Towers 6, which has no lower jaw representatives. (The Dirk's Towers collections, initially numbered and treated separately, were also spread over several metres, and could represent a moving depocentre if the faunal content can be shown to vary from one number to another.)

Plotting length vs width, length vs length/ posterior width (e.g. Fig. 3), premolar length vs molar length, and P3 vs M1 length/ posterior width ratios produced similar separations.

Six or seven complete or partial skulls were recovered from several localities showing two distinct morphotypes, based on the morphology of the snout (with a hint of gradation between localities at one extreme), which partly coincide with the separations based on dental criteria.

The teeth from various wynyardiid localities can be grouped or subgrouped on P3 and M1 meristic grounds:

1.White Hunter, Quantum Leap, Upper Site: 1a. Dirk's Towers 6;1b. LSO Site

2. Camel Sputum, Neville's Garden, Dirk's Towers 5: 2a. Wayne's Wok; 2b. Mikes Menagerie; 2c. Hiatus Site, Roo Site(no premolar-molar association preserved)

The skulls group as follows:

1. (tapering snout, plesiomorphic) Upper Site, White Hunter, *N. snideri*
2. (bulbous snout, apomorphic)
2a. Wayne's Wok
2b. Camel Sputum (slightly less apomorphic)

The *Namilamadeta snideri* tooth hypodigm overlaps the dimensions fields of the Dirk's Towers 6 and Camel Sputum samples. However, morphological differences can be found to separate the South Australian species from them. The Upper Site skull also stands alone, as does the LSO dentary. The remaining sites; Outasite, Judy's Jumping Joint, RSO, Sticky Beak, and Dirk's Towers 4, have not provided appropriate material for this analysis.

For the premolar and first molar teeth only, the White Hunter complex is distinct in most tooth measurements from the Camel Sputum complex which is closer to the type species *Namilamadeta snideri*. The latter, however, does not display the inflated rostrum of the larger group. The Camel Sputum complex could be considered to be in a cline with Wayne's Wok and Mike's Menagerie at the upper extreme; and if $P^3$ only is considered, then Outasite is even farther to the extreme and could represent a fifth group. At the same time, it must be said that the White Hunter sample of $M^1$ falls within the field of the *Namilamadeta snideri* type series, for which there is some variation e.g. length 8.9-9.6, posterior width 7.4-8.2, n = 3 (cf.

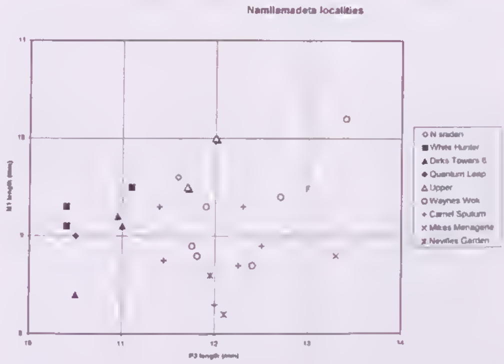

FIG. 2. Bivariate scatter diagram of lengths of upper premolars ($P^3$) vs associated upper molars ($M^1$) of *Namilamadeta* spp. from different Riversleigh sites, and for *N. snideri*.

White Hunter length 9.1-9.55, posterior width 7.3-8.2, n = 4. See Appendix 1). The fields of $P^3$ overlap: *N. snideri* length 11-11.3, n = 2; width 7.05-7.15, n = 2; cf. White Hunter length 10.4-11.3, n = 4; width 6.5-7.3, n = 4.

Combining the above groupings gives us the following breakdown in which several sites cannot be allocated for lack of characters:

1.small teeth, tapering snout: White Hunter, (Quantum Leap, Dirk's Towers 6, LSO Site)
2.large teeth, tapering snout: Upper Site
3.large teeth, bulbous snout: Camel Sputum
4.large teeth, very bulbous snout: Wayne's Wok
5.very large premolars: Outasite
6.unallocated, large teeth: Neville's Garden, Dirk's Towers 5, Mike's Menagerie, Hiatus, Roo Site.

The last have been referred to the combined group 3+4 on the basis of measurement similarities, and in some cases (Neville's Garden, Dirk's Towers 5, Judy's Jumping Joint) the orientation of the anterior mental foramen.

White Hunter sample (group 1) is considered here as a separate taxon, close to but different from the type species *N. snideri*. Apart from morphological differences, part of the rationale for this is geographic separation between the sites, uncertainty of contemporaneity, and the rather poor state of preservation (and hence inadequate description) of *N. snideri*. Upper Site (group 2) also represents a separate taxon, while the Camel Sputum and Wayne's Wok samples (groups 3 and 4) may be related at a subspecific level or as a third new species. The Outasite sample is considered too small to characterise a new species.

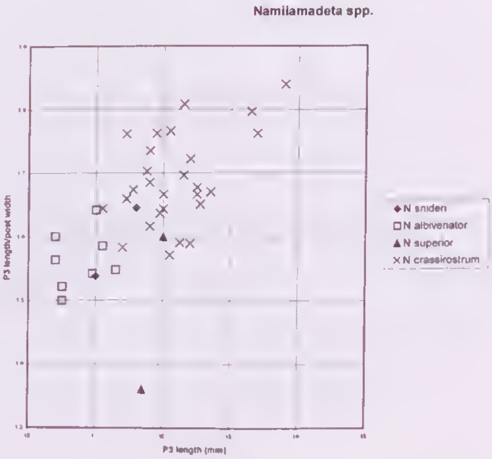

FIG. 3. Bivariate scatter diagram of upper premolar ($P^3$) lengths vs. the ratio of length:posterior width, according to perceived species. Compare with Fig 2.

In approximate descending stratigraphic order, the Riversleigh sites represented by species of *Namilamadeta* are (after Cooke, 1997; Creaser 1997): Judy's Jumping Joint; Neville's Garden, (Roo Site?); Upper; Dirk's Towers (part); Mike's Menagerie; Camel Sputum; Outasite, RSO; Wayne's Wok; Quantum Leap; Dirk's Towers (part); Sticky Beak; White Hunter; LSO(?); Hiatus.

The Wayne's Wok assemblage is considered to correlate (e.g. Cooke, 1997) with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation of the Lake Eyre Basin, while White Hunter equates with the Ngama local fauna, zone D of the Etadunna Formation at Lake Palankarinna (Myers & Archer, 1997; Woodburne et al., 1993).

## SYSTEMATIC PALAEONTOLOGY

MARSUPIALIA (Illiger, 1811)
DIPROTODONTIA Owen, 1866
VOMBATIFORMES Woodburne, 1984
VOMBATOMORPHIA Aplin & Archer, 1987
Family WYNYARDIIDAE Osgood, 1921

**Namilamadeta** Rich & Archer, 1979

**Namilamadeta albivenator** sp. nov.
(Figs 5-7)

MATERIAL. HOLOTYPE. QMF23834 partial skull - right maxilla $M^{34}$; $P^3$ $M^{12}$ (AR 16775); left and right

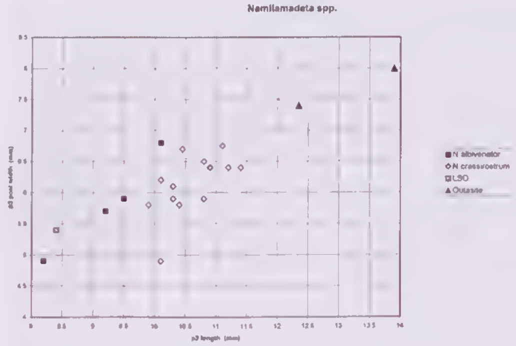

FIG. 4 Bivariate scatter diagram of lower premolar (P3) lengths vs posterior widths. Compare with Fig. 3.

premaxillae, left maxilla, fragmented palate and rostrum (AR 17188) (Fig. 5) from. White Hunter site, Hal's Hill, D Site Plateau (Archer et al., 1991), considered to be a lower assemblage in System B, Oligo-Miocene (Archer et al., 1989). This assemblage is also equated with the Ngama local fauna (latest Oligocene) of the Lake Eyre Basin (Myers & Archer, 1997; Woodburne et al., 1993).. PARATYPE. QMF 40278, right dentary with $I_1$ $P_3$ $M_{14}$ (Fig. 6). REFERRED SPECIMENS. White Hunter: QMF 51337, left and right nasals, premaxillae (no teeth), left maxilla $P^3$ $M^{12}$, right maxilla fragment, $P^3$ (Fig. 7C, D); QMF 51338, left $P^3$; QMF 51339, left $M^1$; QMF 51340, dentary fragment with $M_3$; QMF 51341, juvenile left dentary with $P_2$ $M_{13}$; QMF 51342, juvenile right dentary ($M_3$ missing); QMF 51343, left dentary, all teeth; QMF 51344 right lower incisor; QMF 23499 right $M_{3?}$; QMF 30700, complete right dentary split longitudinally through the teeth. Dirk's Towers 6: QMF 13093, left maxilla; QMF 20035, a right maxilla; QMF 20037, right maxilla; QMF 23494, left premaxilla; QMF 30506, left dentary fragment with $P_3M_1$ (locality unspecified, but referred here because its size and morphology match topotypic material), QMF 36343, right $M^4$. Quantum Leap: QMF 24138, a left maxilla with $P^3M^{13}$. LSO: QMF 36348, right $M^1$; QMF 36349, right $M^3$; QMF 36350, left $M^1$; QMF 40251, a perfect right dentary.

ETYMOLOGY. *Albus* (Latin): white, *venator* (Latin) hunter; thus named for the locality.

DIAGNOSIS. Small, having relatively broad premolars combined with narrow molars. Skull lightly built with tapering snout.

DESCRIPTION. Holotype comprises the anterior part of the skull, lacking the cranium. QMF51337 preserves the anterior part of the rostrum, including the nasal passage. Nasals are long and slender, each with, on the inner surface, a hemicylindrical dorsolateral groove 34mm across that together form a distinct longitudinal canal along the roof of the nasal passage, which is circular in cross-section (excluding the canal), with a diameter of about 15mm at the posterior edge of the premaxilla. Narial opening retracted almost to the level of the front of the canine (missing), at which the premaxilla is narrowest; width of 11.5mm. Anterior mental foramen opens just ahead of the level of the $P^3$; directed backwards and slightly downwards. Lachrymal bone roughly semicircular on the face, with foramen near edge of the orbital rim.

*Upper Incisors*. $LI^1$ preserved; long, open-ended, curved tooth, slightly smaller than that of *N. snideri*. Slight tapering is discernible; apparent size difference may be a matter of age of the animal. Alveoli indicate incisors $I^2$ and $I^3$ of the same order of size as in *N. snideri*.

*Canine*. $RC^1$ small, smaller than $I^3$ judging from alveoli, and slightly smaller than that of *N. snideri*. Bilaterally compressed and bladed, and with a rounded apex in profile.

*Upper Premolars*. Relatively short (only slightly longer than $M^1$) and rectangular (i.e. of fairly uniform width) in occlusal view with a right-angled anterior point. Slight midway constriction labially. Longitudinal crest strongly developed and slightly labial of the midline; extending from the anterior-most point through a high parastyle at the first quarter mark, to an elongate parametacone at roughly the two-thirds mark, and on to the postcingulum. Lingual and labial crests extend equally and strongly from the parastyle, almost to the base of the enamel. A strong crest extends slightly anterolabially from the paracone which is slightly labial of the longitudinal crest, and another extends slightly posterolabially, thus making a broad labial buttress. A weak crest extends anterolingually to a small discrete protocone about midway along the lingual side of the tooth. (Protocone not developed in QMF51338.) A lingual crest from the metacone goes to the base of a strong hypocone. Postcingulum extends labially from the end of the longitudinal crest, to the base of the paracone buttress and more strongly lingually to the hypocone.

*Upper Molars*. $M^1$ is the characteristic tooth of the genus (and indeed family, *vide* Tedford et al., 1977), being distinguished by a well-developed anterobuccal preparacrista linking to a prominent stylar cusp B or parastyle (see Rich and Archer, 1979: 201). In *N. albivenator*, this tooth is smaller and narrower than in *N. snideri*. As with *N.*

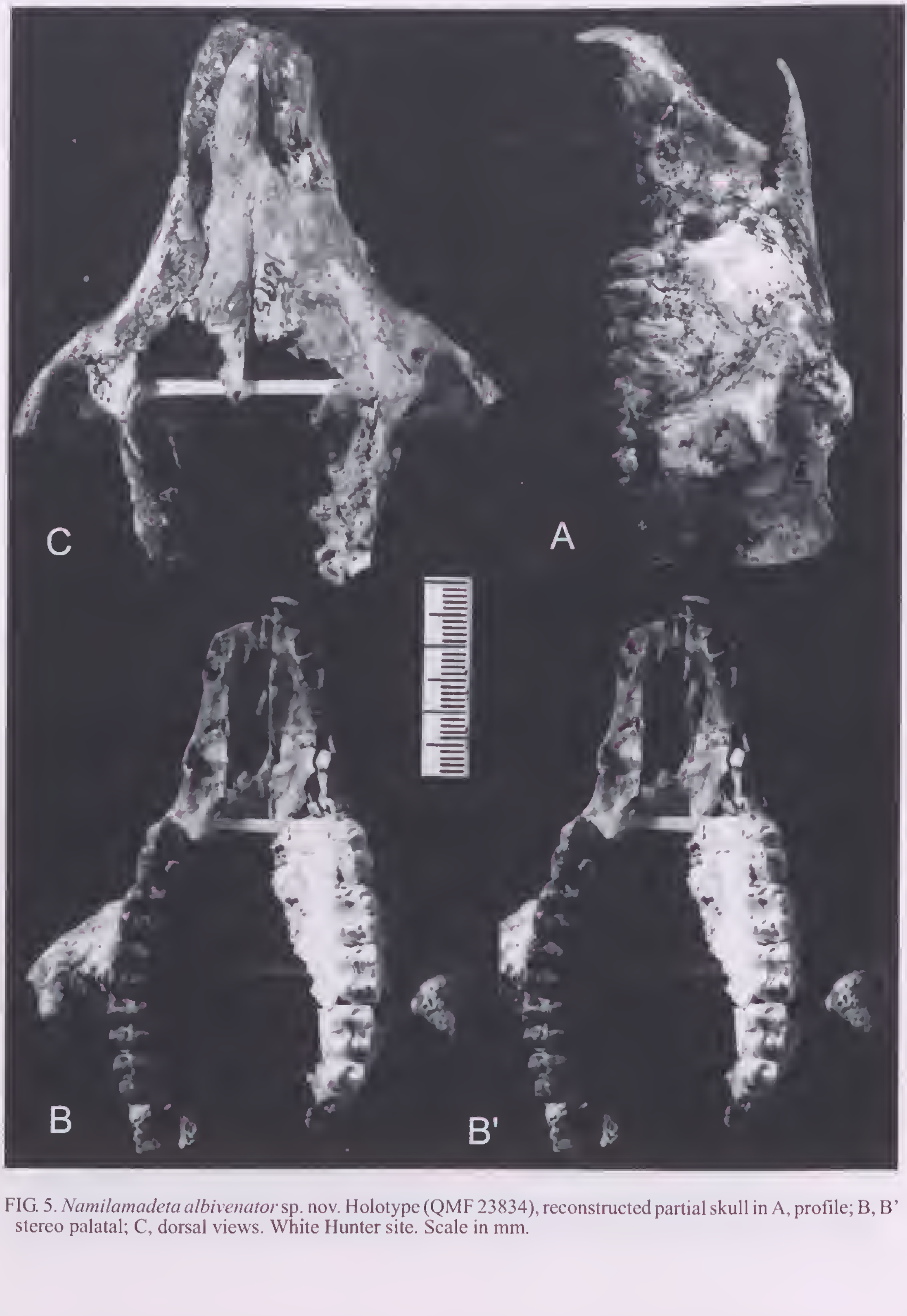

FIG. 5. *Namilamadeta albivenator* sp. nov. Holotype (QMF 23834), reconstructed partial skull in A, profile; B, B' stereo palatal; C, dorsal views. White Hunter site. Scale in mm.

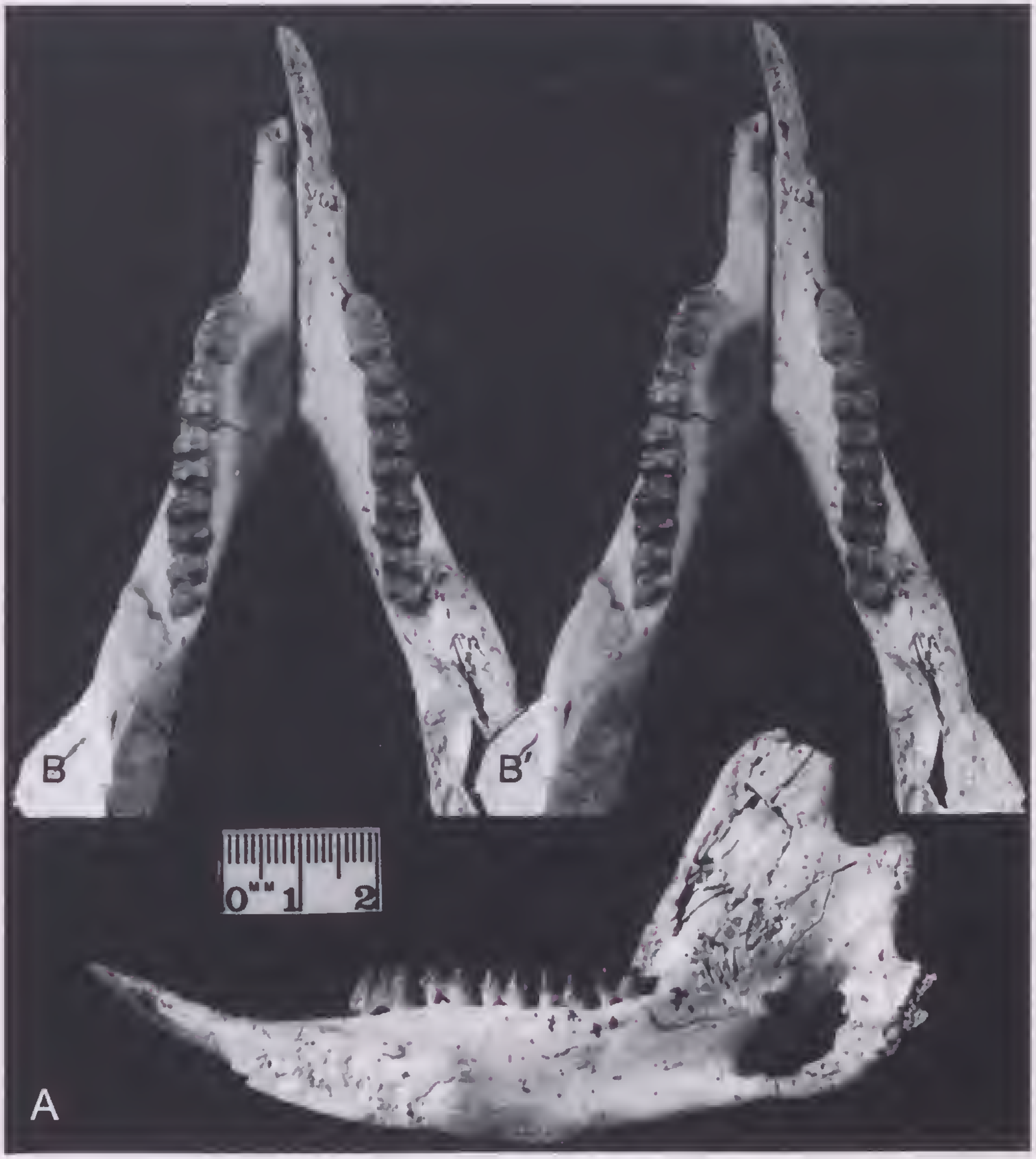

FIG. 6. *Namilamadeta albivenator* sp. nov. Paratype (QMF40278), dentary in A, medial & B, B' stereo occlusal views. White Hunter site.

*superior* the tooth is more quadrate, with the posterolingual corner being more angular. The postparacrista is deflected only slightly from the line of the protoloph, possibly a little more than in *N. snideri*, and is approximately at right angles to the preparacrista, slightly more than *N. snideri* and less than *N superior* (below). The parastyle is more like *N. snideri* (NMV 48993) than *N. superior* but the parastylar spur is not as marked.

M$^2$: The several examples of this tooth are better preserved and less worn than in the *N. snideri* series, but are similar to them in all respects except overall proportions and possibly the parastylar corner where the parastyle is

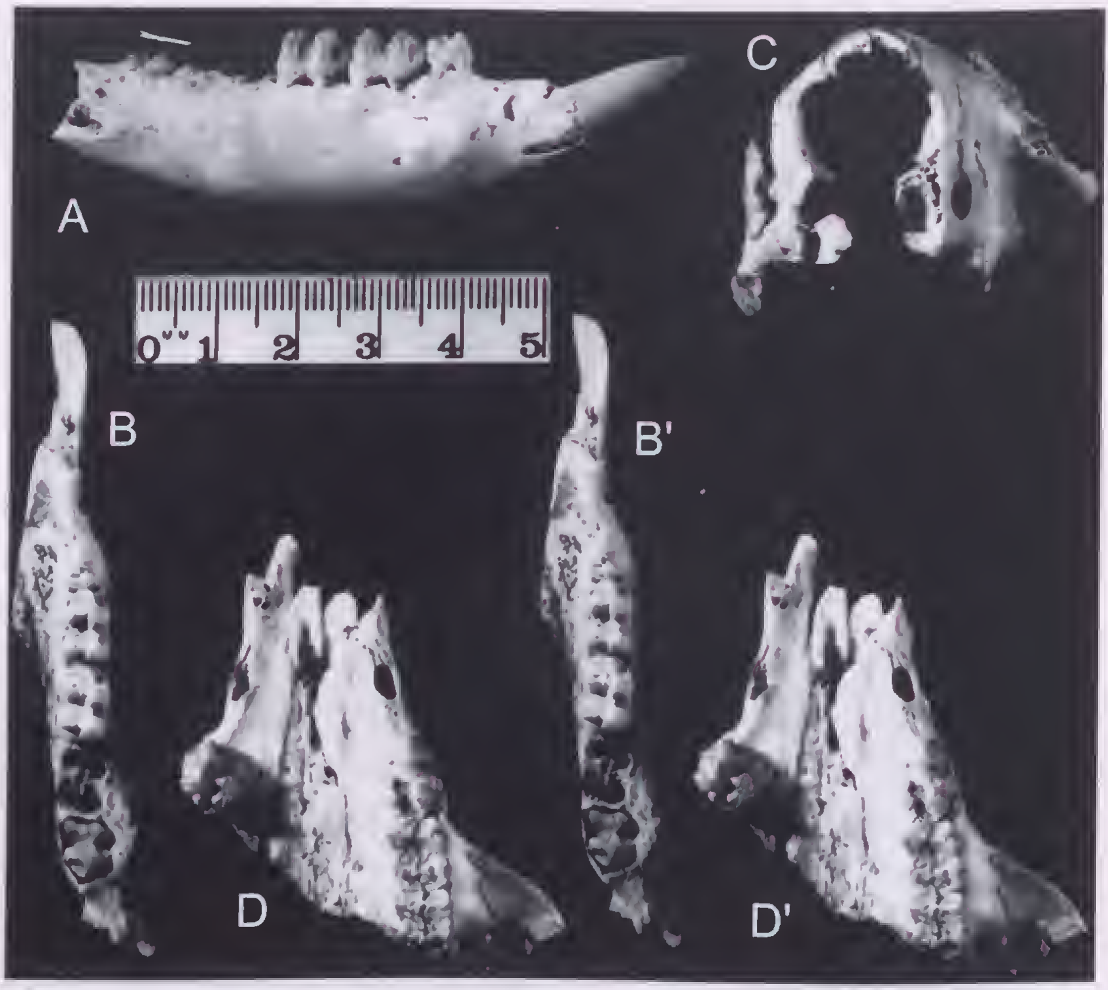

FIG. 7. *Namilamadeta albivenator* sp. nov. Referred specimens: juvenile dentary (QMF51342) in A, lateral; B, B' stereo occlusal view; snout (QMF51337) in C, anterior; D, D' stereo palatal views. White Hunter site.

slightly inside the line of the buccal face of the tooth. The precingulum of *N. albivenator* may be slightly wider transversely than *N. snideri* and the postcingulum narrower. Features of this tooth are better seen in *N. superior*.

$M^3$ in *N. snideri* damaged posterolingually and quite worn. Protoloph in *N. albivenator* shows only the slightest thickening in the position of the paracone, no more than in *N. superior* (QMF 51348). Stylar cusp B is reduced to insignificance at the end of the precingulum. Metacone considerably reduced, compared to $M^2$, more obvious than the paracone. Tooth effectively bilophodont.

$M^4$ is known only from the right side (fragment QMF23834) of the holotype. It is slightly narrower in the protoloph and hence less triangular than that of *N. snideri*. Anterior half of the tooth is similar to that of $M^2$ and $M^3$, but the posterior part is laterally compressed. Postmetaconulecrista is reduced compared with *N. superior* but more apparent than in *N. snideri*. The postcingulum is also poorly expressed compared with *N. snideri*.

*Dentary*. There are two young adult dentaries, which are probably a pair; Paratype QMF40278 (AR12793) (right) and QMF51343 (left), and two incomplete juvenile jaws; QMF51341 (left) and QMF51342 (right, Fig. 7A, B) of different ontogenetic ages. The adult jaws do not occlude neatly with either skull specimen.

TABLE 1. Cranial dimensions of *Namilamadeta* spp., *Muramura williamsi* and *Wynyardia bassiana* type specimens. * = second values from QMF 51337.

| Cranial Dimension | *N. snideri* | *N. albivenator** | *N. superior* | *N. crassirostrum* | *M. williamsi* | *W. bassiana* |
|---|---|---|---|---|---|---|
| Total length | | | 148 | >128 | 140.4 | >105 |
| Zygomatic width | >>60 | ~76 (e) | 85 | >76 | 80 | 67 |
| Max. height | >47 | | 57 | 46 | 47.5 | >35 |
| Rostral length | ~49 | 43 | 45 | 47 | 44 | >20 |
| Rostral width | >32 | 22.5; 33 | 39 | 37 | 32 | ~24 |
| Rostral height | ~41 | 29; 32 | 33 | 35 | 29 | >18 |
| P3 M4 length | 44 | 41.5 | 44.5 | 43.6 | 35.9 | |
| Width between P3 | ~22 | 19;21 | 26.3 | 22.9 | 19.8 | |
| Width between M2 | 24 | >22 | 27.8 | 23.1 | 20.0 | |
| Width between M4 | | 21 | 25.4 | 22.1 | 21.2 | |
| Length before P3 | 30 | 30 | 36 | 32 | 34.5 | |
| Length I3 C1 | 10.5 | 10.5 | 12.5 | 15.4 | 13.5 | |
| Length C1 P3 | 8.9 | 7 | 8 | 3.5 | 9.0 | |
| Palate length to palatal vacuity. | ~52 | ~49 | 54.8 | 56 | 55 | |
| Width suboccipital | | | 58 | | 61 | |
| Width occiput | | | 44 | >42 | ~46 | |

Dentaries are slender and gracile, shallower than those of *N. crassirostrum* (e.g. QMF51363, Camel Sputum) with a shallower, less sharply bounded masseteric fossa. These differences could be due to sexual or developmental age differences. (The dentary from LSO site, QMF40251, is slightly, but not significantly, smaller overall.) Ventral edge not keeled as in QMF51363, although it has the same curved profile. The incisor follows and extends this gentle curvature.

Left and right rami not fused. The symphyseal surface is rough and extends to the posterior end of the premolar and there is a further bulge to the end of $M_1$ caused by the incisor root. Diastema is about 10mm long and the exposed incisor another 24mm dorsally (26mm ventrally). Anterior mental foramen opens about 4mm anterior of and below the premolar. Horizontal ramus is deepest below $M_2$, about 18mm. Buccinator groove absent on the lateral surface, only a slight depression below $M_1$. Ascending ramus has a broad base, nearly 39mm level with the toothline, tapers slightly. Anterior edge reclines at about 70° to the molar occlusal surface, and the coronoid process reaches a height of about 32mm above it. Articulating condyle about 17mm above the occlusal surface of the molars. Total dentary length is about 112mm, bone length 95mm, total height 57mm, and width normal to the symphyseal midline 37mm.

*Lower Incisor*. Five known: QMF40278, QMF51343 (tip broken off), QMF51342, QMF-51344 (an isolated tooth in a fragment of dentary), and QMF40251.

Incisors are deep and open-rooted, tapering gently towards the tip. Curved ventral profile and a straighter dorsal profile accentuated by occlusal wear to produce a chisel point (best seen on the juvenile QMF51342). Unless there is postmortem torsion due to, say, differential shrinkage between enamel and dentine, all teeth show a marked inward curvature of the tips across the midline of the jaw, to the extent that the dentaries could not have fused without greatly affecting the incisors. Little or no sign of interdental appression is seen on the medial surface of the teeth, indicating some degree of ligamental padding in the symphyseal region.

Enamel is restricted to the convex ventrolateral surface of the incisor and a strip nearly 2mm wide on the ventral edge of the median face. Dorso-laterally the enamel forms a raised edge above the dorsal surface. This is truncated anteriorly by the occlusal bevelled surface which is at, or just below, the occlusal surface of the molar teeth. In cross-section, the incisor is slightly more than a quarter circle.

*Premolars*. The deciduous premolar $dP_2$ is known from QMF51341 and QMF51342, and in both cases is underlain by $P_3$. Tooth is molariform, being elongate triangular with three distinct cusps: the relatively large (and tallest) anterior cusp (protoconid), a smaller more slender lingual cusp midway along the tooth (hypoconid) and a broader posterior cusp (hypoconulid). The three cusps approximate the relationships and spacing of the posterior cusps on $P_3$ (e.g. in QMF40278). The first and third cusps are on the midline of the tooth, and align with the preprotocristid and protoconid of $M_1$.

$P_3$. The permanent premolar is present but unerupted in both juvenile jaws. It has not been excavated from its crypt in QMF51342, but has been freed in the less ossified, younger QMF 51341, where the enamel crown of $P_3$ has barely started to form; only the four cusps are preserved. The $P_3$ is better exemplified in QMF40278, QMF 51343 and QMF40251.

This tooth is relatively short compared with *N. crassirostrum*, being only a little longer than $M_1$. It is slightly wider posteriorly, tapering gently forwards to the level of the anterior cuspid where both sides converge sharply towards the extremity of the median crest. The anterior cuspid (protoconid?) is on the midline at about the one-quarter point and supports symmetrical buccal and lingual crests. The largest cuspid is just behind the midpoint; being on the median, longitudinal crest, it is slightly bladed. There is a broad buccal buttress to this cuspid, the paraconid. The metaconid is displaced slightly lingually and is separated from the paraconid by a shallow dip in the median crest which returns to the midline and drops away to the small hypoconid. Descending on either side of the hypoconid are the buccal and lingual branches of a very weak postcingulum which curve forwards and disappear.

*Lower Molars*. $M_1$ is best seen, in its unworn state, in QMF51342. It is marginally the longest of the lower molars but its anterior width is less than that of the succeeding $M_2$ and $M_3$, although its posterior width may equal or exceed that of $M_2$. Thus, the tooth has a slight anterior taper.

The tooth is bilophodont, with the lophids considerably narrower at their crests than at their bases, and with the protolophid narrower than the hypolophid. The hypolophid is transverse, normal to the tooth row and lingual face of the tooth. The protolophid is directed slightly posterolingually, so as to converge eventually with the hypolophid. Both lophids have a shallow notch about halfway across. The protoconid is about on the midline of the tooth, the hypoconid just buccal of it. Metaconid and entoconid are right at the lingual face of the tooth.

A longitudinal crest starts at the paraconid on the precingulum, at the anterior end of the midline, and continues unbroken through the protoconid and hypoconid before curving slightly lingual and joining the posterior cingulum. A shallow basin is defined buccally by the preprotocristid and the precingulum and a deeper one lingually. The latter renders the metaconid as a very slender cusp compared with the other cusps. There is no distinct premetacristid, but a weak postmetacristid joins a stronger pre-entocristid at the bottom of the transverse median valley. The postcingulum forms a small deep pocket on the posterior face of the tooth.

$M_2$ differs from $M_1$ in being slightly shorter and more rectangular and the protoconid and hypoconid more buccally placed. The precingulum is broader on the lingual side of the longitudinal crest, the lophids are transverse and parallel, there is a median bulge on the protolophid, and a bulge on the cristid obliqua near the bottom of the transverse valley. The metaconid is slightly stouter than in $M_1$.

In contrast to QMF 51342, $M_2$ of QMF 40278 shows a distinct postmetacristid-pre-entocristid.

$M_1$ and $M_2$ of QMF 51342 are noticeably longer than their equivalents in the more mature, adult QMF 40278. This may in part be by reduction of the latter by interdental appression, but the distance between protoconid and hypoconid is also greater in QMF 51342.

Looking now at the paratype QMF 40278, $M_3$ resembles $M_2$ except that the protolophid is slightly broader now than the hypolophid, and the postcingulum is straighter.

$M_4$ resembles $M_3$ except for being smaller, and its postcingulum forms a relatively large pocket behind the reduced hypolophid.

REMARKS. Differs from *N. snideri* in having smaller (shorter), narrower premolar P3 with small but distinct protocone. Differs from *N. superior* sp. nov. in having a cylindrical nasal passage, a larger $I^1$; smaller, more rectangular $P^3$ with a distinct separate lingual cusp (protocone) anterior of the enlarged separate hypocone;

smaller molars; $M^2$ without crest between paracone and parastyle. Differs from *N. crassirostrum* sp. nov. in having a tapering snout with narrower nasal passage, anterior mental foramen directed more longitudinally at about 10° to the axis of the skull rather than 50-60°; smaller more rectangular $P^3$, smaller molars. Lower premolars more tapered anteriorly, i.e. relatively broader posteriorly, and shorter; second and third cuspids more closely united, third cuspid less offset lingually; $M_1$ narrower anteriorly (paraconid closer to metaconid); dentary more gracile; shorter tooth row. Differs from Outasite taxon in having much smaller upper premolars.

### **Namilamadeta** sp. cf. **N. albivenator**

REFERRED MATERIAL. LSO Site (Lee Sye's Outlook), northern D-Site Plateau. Low in the Verdon Creek Sequence, probably System A (Creaser 1997). QMF 40251, right dentary, QMF 36348 unerupted, damaged l$M^1$, QMF 36349 right maxilla fragment with $M^3$, QMF 36350 r$M^1$.

DESCRIPTION. *Upper Molars*. The few upper molars referred to this species are virtually indistinguishable from those of *N. albivenator*.

*Dentary*. The dentary is lightly built, less deep than that of *N. albivenator*, and thinner in the corpus of the ramus. Viewed from below, it is slightly convex buccally (*N. albivenator* is almost straight), and the angular shelf is wider. From behind, the notch between the angular process and the neck of the condyle is deeper, the neck is slimmer and the condyle transversely narrower and abruptly expanded from the ascending ramus. The ascending ramus has a steeper leading edge (67° vs 62° to the occlusal plane), is lower, shorter longitudinally, and the coronoid process is also shorter. The mandibular foramen opens into both the pterygoid and the masseteric fossae. The mental foramen opens level with the front edge of the premolar rather than 2–3mm ahead of it as in *N. albivenator*. The diastema is short (11mm vs 13mm) and the incisor is robust and less procumbent, being inclined at 40° vs 35°.

*Lower Incisor*. The incisor is quite a robust tooth: thicker (4.5mm vs 4.1mm), deeper and straighter than that of *N. albivenator*. Its occlusal facet is also more obtuse, in keeping with the steeper angle of the tooth.

*Lower Premolar*. The $P_3$ is one of the most distinctive features of this taxon. It is short with roughly parallel sides until level with the paraconid, when the buccal face abruptly turns across to the anterior point of the tooth. A sharp cristid rises from this point up to the apex of the paraconid, which is well separated from the protoconid, and continues longitudinally through the protoconid to a small cuspid on the posterior cingulum. About midway along this half of the cristid, the metaconid is a distinct cusp well separated on the lingual side of the ridge, with no obvious link to it.

REMARKS. Differs from *N. crassirostrum* in having a much slighter dentary with smaller teeth overall, shallower masseteric fossa, anterior mental foramen level with the beginning of $P_3$ rather than ahead of it, premolar shorter and less parallel-sided, its longitudinal crest more inturned anteriorly and metaconid displaced more lingually, first molar narrower anteriorly.

Differs from typical *N. albivenator* in having a more gracile dentary with steeper leading edge of the ascending ramus, narrower coronoid process, more abrupt articular condyle, deeper masseteric fossa, anterior mental foramen level with the beginning of $P_3$ rather than 23mm ahead of it, $M_1$ more rectangular with protolophid and hypolophid almost equal, much shorter $P_3$ with the metaconid markedly displaced lingually, shorter diastema, and a shorter, straighter and thicker lower incisor.

### **Namilamadeta superior** sp. nov.
(Fig. 8)

MATERIAL. HOLOTYPE. QMF40276, a near complete skull, lacking only left and right $I^3$ and $C^1$, with right $I^1$, $I^2$ and $M^2$ damaged; from Upper Site, Godthelp Hill, eastern end of D Site Plateau (Archer et al., 1991), considered to be an upper assemblage in System B: early Miocene (Archer et al., 1989), and has been correlated with the Kutjamarpu local fauna of the Lake Eyre Basin (Godthelp et al., 1989).

ETYMOLOGY. *Superior* (Latin): upper, higher - referring to the type locality name and generally to the perceived higher stratigraphic position within System B.

DIAGNOSIS. Skull similar in size to that of *N. snideri* but slightly more gracile; masseteric processes up to 50% larger and broader, malar fossa deeper, infraorbital foramen smaller and directed more posteroventrally.

DESCRIPTION. *Skull*. To be described in detail elsewhere. Skull 148mm long parallel to the occlusal plane, and 85mm across zygomatic arches. Slender, but rather high and short tapered rostrum expands smoothly into a relatively broad 'face' at the orbits. Nasal opening about 17mm high (excluding the dorsal channel), 14mm wide, widening to become more equidimensional

FIG. 8. *Namilamadeta superior* sp. nov. Holotype (QMF 20476), skull in A, lateral; B, B' stereo palatal.

farther in. Nasals long and slender, expanding at the frontal suture to twice anterior width but not extending as far forward as in *Muramura williamsi* (Pledge, 1987), only to about halfway between the beginnings of I$^1$ and P$^3$, but farther than in *N. crassirostrum* (q.v.). In anterior view they are hemicylindrical, forming a small (~5mm diameter) channel on the dorsal side of the nasal passage. This feature is more strongly developed than in other species. Narial opening is retracted almost to the level of the P$^3$, at which point the premaxilla is a minimum 9mm wide. "Forehead' is only slightly 'dished' in the naso-frontal area, unlike the marked depression seen in profile in *N. crassirostrum*, see below.

Orbits directed anterodorsally and a little laterally. Lachrymal bone roughly semicircular, with a fairly large foramen well forwards on the dorsal surface, about 5mm anterior of the orbit. Jugal border of orbit thickened and accentuates the depression of the malar fossa ('masseteric fossa' of Pledge (1987)). Ventrally from this, the maxilla extends a solid masseteric process about 13mm, some 6mm below the occlusal plane of molars. Cheek-tooth rows noticeably convex buccally, unlike those of *Muramura* where they are straight and very slightly divergent posteriorly, and the congeneric *N. crassirostrum*, where they are also straight and parallel. Jugals fairly deep, with a simple interdigitation with the squamosals, and form an almost square cheek outline in dorsal view (i.e. the width is approximately equal to the length between the front of the orbit and the posterior root of the squamosal part of the cheek bone, about 79 x 75mm). The upper part of this squamosal wing curves medially. Frontals are unfortunately damaged, but the highest point of the skull is about at the frontal-parietal suture, where weak lateral crests converge before forming the more prominent sagittal crest. The lambdoidal crest overhangs the supraoccipital bone and its condyles. Strongly developed basioccipital process, larger and straighter than in *Muramura*, and similar to that in *Macropus*. Auditory region well preserved on the left side, less so on the right, and is similar to Aplin's description (1987) of *Wynyardia*. This supports assignment of *Namilamadeta* to the Wynyardiidae. Briefly, a squamosal tympanic wing (SQW) roofs the anterior tympanic cavity, there is no tympanic process of the squamosal (SQP), nor an epitympanic sinus of the squamosal (SQS), but there is an alisphenoid lamina on the tympanic process (details to be published elsewhere).

*Upper Incisors*. Only the first two are preserved in the skull. I$^1$ has an occlusal surface not much larger than I$^2$, which already shows considerable wear. It is noticeably smaller than I$^1$ of *N. snideri* and *N. albivenator*, but larger than in *N. crassirostrum*. However, I$^1$ is much 'higher' and seems to increase in diameter slightly as it emerges. It is apparently rootless, like the I$^1$ of wombats and of *Diprotodon*, but this may simply be a manifestation of its relative youth, since Rich and Archer (1979) found in *N. snideri* that the root itself had a slight taper suggesting eventual closure.

The relative size of I$^1$ with respect to I$^2$ and I$^3$ differs markedly from the situation in *N. snideri* and *N. albivenator* QMF23834, and in QMF-23494 from Dirk's Towers 6, the only other Riversleigh I$^1$ specimen, which closely resembles *N. snideri*.

I$^2$ is relatively low crowned, with the enamel fully exposed and the root just visible between it and the bone of the premaxilla. To judge from the alveoli, I$^3$ could be approximately the same size as I$^2$ and the canine. Both preserved incisors are heavily worn, in contrast to the cheek teeth, where the enamel is barely breached on the highest cusps of M$^1$.

*Upper Premolars*. P$^3$. The premolars of the skull are somewhat figure-of-eight shaped, with a noticeable midway constriction. The longitudinal crest is almost straight, extending from the rounded angular anterior extremity of the tooth, along the midline through the protocone and paracone, then a slight lingual dog-leg to the metacone and returning to a small cusp on the blunt posterior cingulum. There is a buccal rib transverse from the protocone, stronger than that going lingually. A lingual crest that meets the longitudinal crest midway between protocone and paracone forms the anterior border of a pocket created by the strong hypocone and the crest joining it to the metacone.

*Upper Molars*. In this species, M$^1$ is very similar to that of *N. snideri* in both size and morphology. The differences are (comparing with the least worn example of the latter, NMV P48993): 1) the tooth is more quadrate because the posterolingual corner is squarer and less rounded; 2) the postparacrista is directed more posteriorly, i.e. it is less aligned with the protoloph, thus being more symmetrical with the preparacrista and enclosing a more obtuse angle; 3) the parastyle is virtually on the precingulum, and not connected to it by a short but distinct curved crest; 4) the metacone is closer to stylar cusp D; 5) the precingulum almost equals the postcingulum instead of being three quarters the transverse width; 6) the parastylar 'spur' of Rich and Archer (1979) is reduced.

$M^2$. In *N. snideri* this tooth is, like the rest of the tooth row, considerably worn and shows no stylar cusp B nor the linking preparacrista (Rich & Archer, 1979). The type of *N. superior* does show such features, although muted by wear. There is a well-developed preparacrista going anterobuccally to a small but distinct parastyle at the buccal end of the precingulum; it is almost symmetrical with the postparacrista that links to stylar cusp C, which is almost as high as the paracone. Unlike the situation in $M^1$ where these crests enclose an obtuse angle, estimated c. 100-110°, in $M^2$ the angle is acute, c. 70-80°. There is no parastylar 'spur'. In other respects $M^2$ is similar to $M^1$.

$M^3$. This tooth shows increasing lophodonty, unrelated to wear. In the skull, QMF 40276, the protoloph is defined by the protocone and stylar cusp C, with the paracone being a barely noticeable irregularity. Stylar cusp B is a minute enlargement at the buccal end of the precingulum and is unconnected to the paracone. Instead it is joined to stylar cusp C by a low crest. On the metaloph, the metacone is still distinct but greatly reduced.

$M^4$. This tooth is greatly compressed in the posterior moiety. Anteriorly it is similar to $M^3$, with only slight thickening on the protoloph at the site of the paracone. On the metaloph, the metacone and stylar cusp D have fused into a rather broad low cusp, separate from the metaconule, and a loph strictly does not exist.

Dentary. No dentary is known from Upper Site, nor any isolated lower teeth, to allow comparison with other sites.

REMARKS. Differs from (reconstructed) skull of *N. albivenator* in having a more pointed, tapering rostrum and higher profile, and laterally compressed nasal passage. Differs from skull of *N. crassirostrum* in lacking inflated rostrum caused by large sinuses within maxillae, and having laterally compressed nasal passage. $I^1$ about half the diameter of *N. snideri*, but canine possibly larger than in that species.

Upper premolars mostly longer and wider than *N. snideri*, with the hypocone not linked to the buccal crest (parametacone). Upper molars closely similar to *N. snideri*, noticeably shorter than premolar.

Upper premolars differ from *N. albivenator*, and many *N. crassirostrum* specimens, in being longer with an anterior taper, less rectangular and narrower in the anterior moiety, and in having no or only very small accessory cusp on the lingual cingulum anterior of the hypocone. They are slightly wider than most of those of *N. crassirostrum*, about the same length as those from Camel Sputum and Neville's Garden sites, and shorter than most from Wayne's Wok and Mike's Menagerie. Upper molar $M^1$ differs from *N. albivenator* and *N. snideri* in having a crest between paracone and parastyle.

### **Namilamadeta crassirostrum** sp. nov.
(Figs 9-11)

MATERIAL. HOLOTYPE. QMF31462, incomplete skull lacking the nasals, occiput, basicranium, and zygomatic arches (Fig. 9). Wayne's Wok Site. PARATYPE. QMF51375, right dentary (Fig. 10). Wayne's Wok site. REFERRED MATERIAL. Wayne's Wok Site; QMF51345 left maxillary fragment, QMF51346 left maxilla, QMF51347 right maxillary fragment, QMF51348 juvenile right maxilla, (which possibly goes with) QMF51349 juvenile left maxilla, QMF51350 r$P^3$, QMF51351 left maxilla fragment $P^3M^{12}$, QMF31480 right premaxilla and maxilla, QMF30836 right dentary fragment, QMF51352 l$M_2$; numerous isolated teeth. Dirk's Towers 4; QMF51353 r$P^2$, QMF51354 l$P^3$, QMF36342 l$P^3$, QMF51355 l$M^2$. Dirk's Towers 5; QMF51356 r$M^1$, QMF24218 left dentary. Camel Sputum; QMF40279 a partial skull including full palate and left side of face back to frontal bone but no incisors, QMF51357 right maxilla fragment with $P^{2-3}$, QMF51358 r$P^2$, QMF51359 right maxilla fragment r$M^{14}$, QMF51360 r$M^{24}$, QMF20497 r$M^{14}$, QMF20498 r$M^{23}$, QMF20574 left maxilla, QMF30303 palate with premaxillae, QMF 30534 maxilla fragment, QMF 12461 right dentary, QMF 51361 dentary fragment r$M_{24}$, QMF 51362 left dentary, QMF 51363 left dentary; numerous isolated teeth. Mike's Menagerie; QMF 51364 right maxillary fragment $P^3M^{12}$, QMF 51365 left dentary $P_3M_{14}$; numerous isolated teeth. Roo Site; QMF 51366 juvenile dentary; Sticky Beak; QMF 51367 left $I_1$. Judy's Jumping Joint; QMF 51372 left $P^3$, QMF 51376 right $P^3$.

TYPE LOCALITY AND STRATIGRAPHIC POSITION. Wayne's Wok site, Hal's Hill, D Site Plateau (Archer et al., 1991). System B, 3-4 metres below Upper Site (Archer et al., 1989). The Wayne's Wok faunal assemblage contains a number of species in common with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation, Lake Eyre Basin (e.g. Godthelp et al., 1989, Archer 1994, Cooke 1997).

ETYMOLOGY. Crassus (Latin): thick, rostrum: beak, snout - in reference to the bulbous snout shown in the skull.

DIAGNOSIS. Skull with inflated rostrum. Anterior of anterior mental foramina (AMF) parallel; lateral sides of premaxillae converge

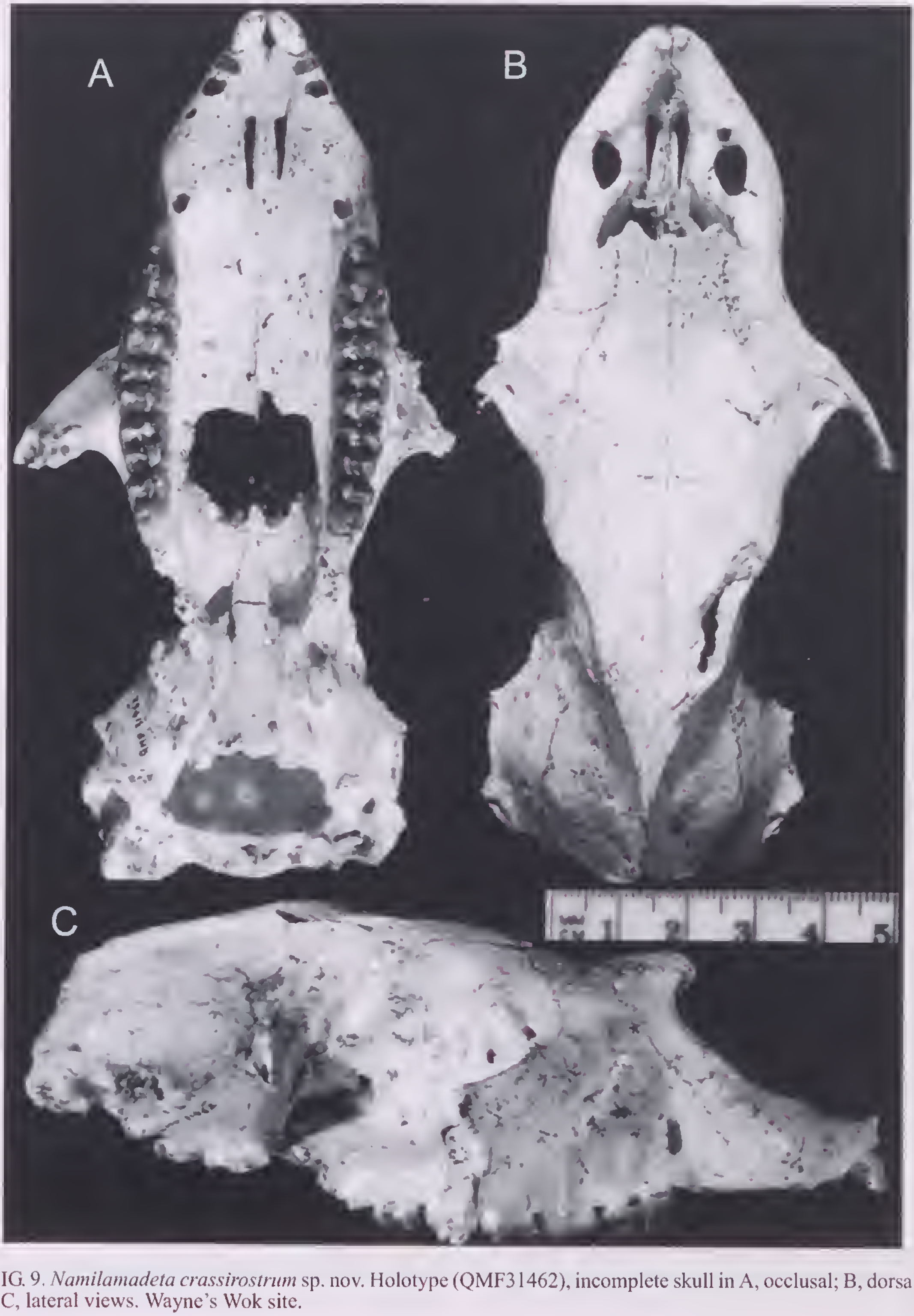

FIG. 9. *Namilamadeta crassirostrum* sp. nov. Holotype (QMF31462), incomplete skull in A, occlusal; B, dorsal; C, lateral views. Wayne's Wok site.

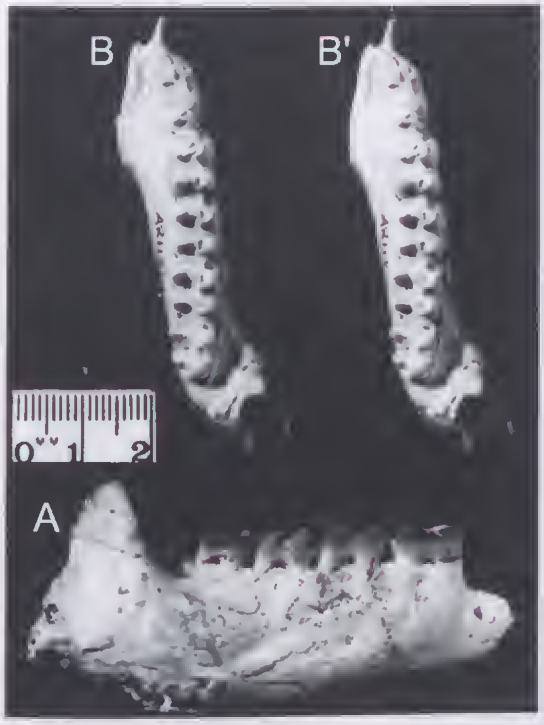

FIG. 10. *Namilamadeta crassirostrum* sp. nov. Paratype (QMF51375), dentary in A, lateral; B, B' stereo-occlusal views. Wayne's Wok site.

strongly at 60°. Lower border of naris greatly thickened by large sinus developed mainly in premaxilla and opening vertically upwards. Posterior border of naris almost level with AMF rather than canine. Nasals apparently short, extending only 1cm beyond $P^3$. AMF a near-vertical slot entering almost transversely (at about 60° to midline), rather than an ovate hole entering almost longitudinally. Canine closer to premolar. Cheek-tooth rows almost straight and parallel rather than convex buccally.

DESCRIPTION. *Skull*. Occiput, basicranium and zygomatic arches unavailable. About the same size as the skull of *N. superior* (Table 1), with a preserved length of 129mm (QMF31462), with inflated snout. Nasal opening almost circular (diameter 2.53cm) in anterior view, compared with a tall, narrow opening in *N. superior*. Rostrum parallel-sided in posterior half, the same width at the level of the premolars as at a point about midway along the premaxilla, at which point, it tapers sharply forwards to produce a V-shaped incisor arcade, instead of the elliptical ones in other *Namilamadeta*. This is the result of a pair of large inflated sinuses developed mainly in the premaxillae but extending back into the portion of the maxillae in front of the anterior mental foramina. Sinuses each have a large (up to 5mm diameter) ovate dorsal opening in what would otherwise have been the lower narial edge of the premaxilla; the openings have a smooth regular margin with no sign of the roughness associated with a pathological condition (C. Pardoe, pers. comm.). The feature is therefore considered real, especially as it is seen almost identically in all premaxillary specimens from the Wayne's Wok and Camel Sputum sites. (It appears slightly less developed in the Camel Sputum specimen; none of the other sites referred to this species have yielded premaxillae.)

Possibly associated with this feature is the slight posterior displacement and reorientation of the AMF, now directed, initially, inwards at about 60° to the midline (CT scans show the canal turns abruptly to the posterior, about 3mm inside the bone). This diagnostic character enables even small fragments of maxilla to be identified, e.g. QMF51372, a $P^3$ in a fragment showing the foramen and a trace of the sinus, from Judy's Jumping Joint. In addition, the naris is retracted as far as the premolar, instead of level with the canine in *N. superior*, *N. albivenator* and *N. snideri*. The nasal bone appears to be tilted slightly upwards at the front (giving a 'dished' appearance in profile), the tip being broken off just ahead of its suture with the premaxilla, and its maximum width (at the fronto-lachrimal junction) is less than in *N. superior*. The dorsal wing of the premaxilla is narrower and thicker than in the other species, and the dorsal wing of the maxilla is much narrower, but the malar fossa is slightly shallower. Masseteric process of jugal broken off, so it is not possible to compare it with the deep ones of *N. albivenator* and *N. superior*. So far as can be compared, the posterior part of the skull is similar to the other species.

*Upper Incisors*. Only first incisors are present in the holotype; and are smaller than in *N. superior*. Very worn second and third incisors occur in the Camel Sputum specimen QMF30303, but appear also to be smaller. From the alveoli, the incisor arcade of the holotype is V-shaped, as compared to being more U-shaped in *N. superior*.

*Upper Canine*. One damaged representative; small, alveoli vary from 3–4mm in diameter, about the same as in *N. superior*.

*Upper Premolars*. $DP^2$ is known from a tooth associated with an unerupted $P^3$ (QMF51357) and another (QMF51358) from Camel Sputum

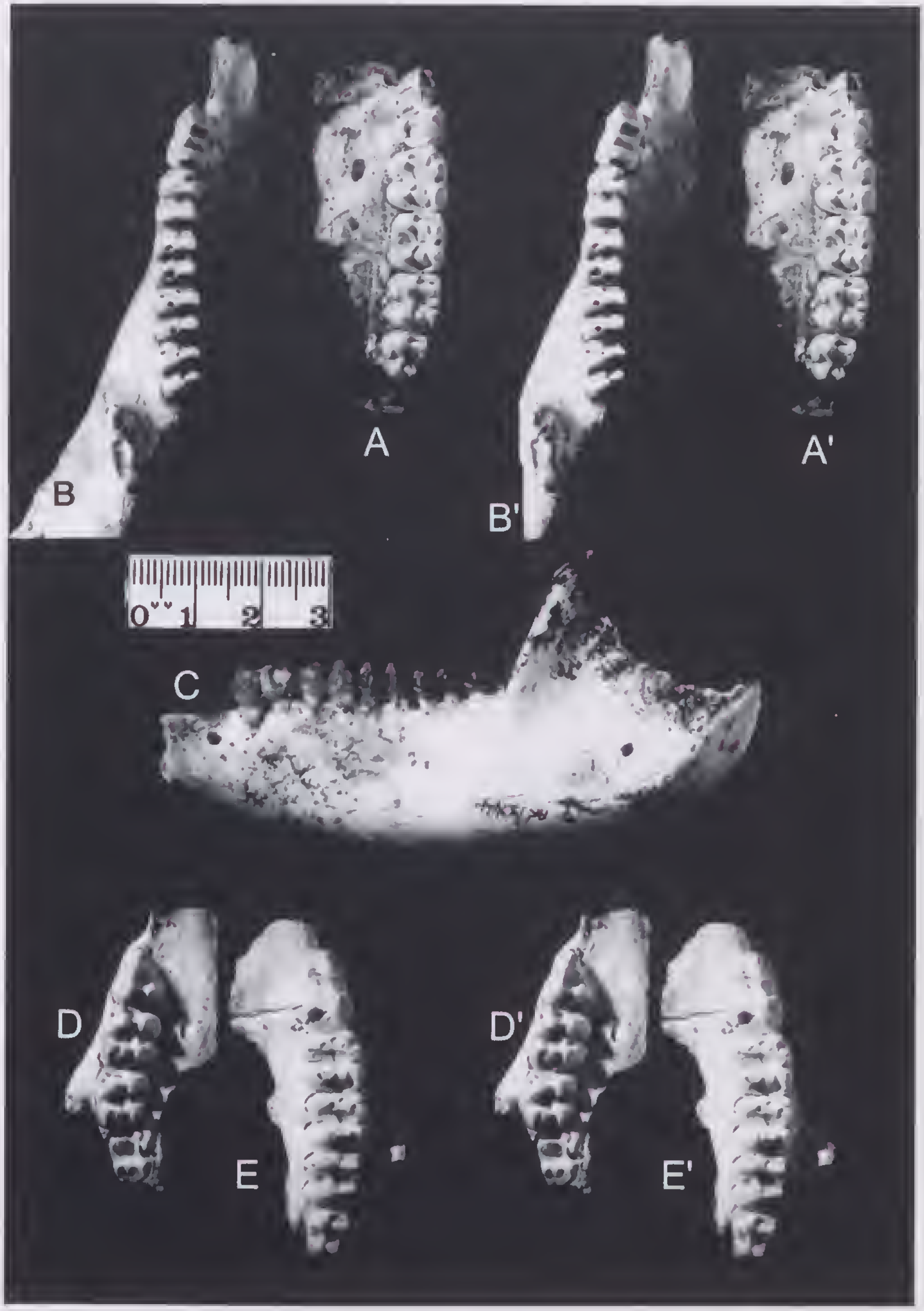

FIG. 11. *Namilamadeta crassirostrum* sp. nov. Referred specimens: A, A' left maxilla QMF 20574 (Camel Sputum site); B, B' left dentary QMF51363, (Camel Sputum site); C, QMF51363 in lateral view; D, D' juvenile right maxilla QMF51348 (Wayne's Wok site); E, E' adult left maxilla QMF51346 (Wayne's Wok site, all in stereo-occlusal view.

site and three, each associated with $M^1$ and $M^2$, from Wayne's Wok (QMF51347, QMF 51348 and QMF51349). Teeth are roughly equilateral-triangular, slightly longer than wide and blunt posteriorly. Buccal crest with a distinct protocone in the anterior moiety, about equally as high as the anterior-most of the two close cusps (paracone) on the posterior moiety. Hypocone distinct near the lingual corner, having only a slight link with the paracone. These teeth differ from a $DP^2$ (QMF51353) from Dirk's Towers 4, which is slightly smaller, has a more trenchant buccal crest and lacks a distinct metacone.

$P^3$. Two site-related morphs are apparent. Shorter ones (Camel Sputum and Neville's Garden) are wider posteriorly, taper more than the longer ones (Wayne's Wok), and have a small cingular cusp anterior of the hypocone. Two specimens from Wayne's Wok (QMF51350, QMF51351 probably the same individual) and one from Mike's Menagerie (QMF51364) have exceptionally long $P^3$s and are wider anteriorly relative to others of this species.

*Upper Molars*. Similar in size and form to those of *N. superior*. $M^1$ : In unworn examples from Wayne's Wok (QMF51347, 51348, 51349) $M^1$ has stylar cusp C more developed and stylar cusp B expanded buccally to form a distinct anterobuccal pocket on the outside of the preparacrista. These features are quickly obliterated with wear. Of the Camel Sputum specimens, QMF51359 is too worn for detailed comparison, but QMF20574, scarcely worn, shows slightly more resemblance (in disposition of pre- and post-paracristae) to *N. snideri*, although its degree of ornamentation and cusp development on $P^3$ is much stronger.

$M^2$. Second molar slightly shorter than first and about the same width. It differs in the reduction of stylar cusp B to a variably distinct cuspule at the junction of the preparacrista and precingulum, e.g. clear in QMF51346 and QMF51348 from Wayne's Wok but obscure in QMF20574 from Camel Sputum; this may indicate a subspecific difference between two localities. The paracone is quite distinct at about the outer third point on the protoloph and equal to stylar cusp C in size, while the metacone is midway between the metaconule and stylar cusp D. Thus, it is quite similar in form to the $M^1$, but quite different to the $M^2$ of *N. albivenator*.

$M^3$. Parastyle further reduced and paracone no longer distinguishable, although the metacone is still apparent. This resembles the $M^2$ of *N. albivenator*. The metacone of $M^3$ is slightly larger in *N. crassirostrum* from Camel Sputum (QMF20574) and the unworn QMF51348 from Wayne's Wok than that of *N. superior*.

$M^4$. The simplification process has continued in this tooth, with the posterior narrowing of the crown and reduction in size of the metacone.

*Dentary*. Relatively lightly built, fairly deep (more than in *N. albivenator*) slightly deeper posteriorly. Ventral margin slightly convex in profile, more so in QMF12461 from Camel Sputum, also noticeably deeper. In paratype QMF40277 and QMF12461 the ventral margin is rounded, but in QMF51363, (Camel Sputum), it bears a distinctly angular keel. In the paratype, the cheek-tooth row is 45.7mm long; depth of dentary at $P_3M_1$ is 20.6mm, at $M_3M_4$ is 22.3mm. Anterior mental foramen situated just in front of the premolar at about one-third depth. Dentaries are not fused; symphysis extends level with posterior end of premolar. The ascending ramus (QMF51363) rises steeply at some 70° to the occlusal surface. It is broad with a deep, sharply-bounded masseteric fossa, pierced externally by a small masseteric foramen. Internally is the larger opening of the mandibular foramen, farther back and just below the level of the teeth. A shallow buccinator groove extends diagonally on the outer face from just below the posterior root of the premolar to well below $M_3$. Post-alveolar shelf is short. The diastema anterior of the premolar is short, about 12mm in QMF51363. Incisive alveolus large, oval in cross-section, slightly narrower ventrally, and at this point the dentary is 6mm wide.

*Lower Incisor*. Two are known: QMF51366 with associated left $P_2$ and molars, from Roo Site, and a well-worn isolated left incisor QMF51367 from Sticky Beak Site. QMF51366 is barely worn at the tip, but is broken at the base, so its full length is unknown. Preserved enamel length is about 34mm. Tooth slightly curved, ventrally convex, and towards tip shows increasing curvature medially. Towards the base, the dorso-ventral diameter reaches 6.7mm, with a transverse diameter of 3.8mm. In cross-section the incisor is roughly elliptical, but with a dorso-medial bulge, with a concomitant shallow groove ventromedially just above the medial edge of enamel, and a sharp dorso-lateral edge of the lateral side of the enamel. Dorso-medial bulge is enamel-free. Enamel distribution extends down from the dorso-lateral edge, around and up about 1.5mm on the medial side of the tooth.

*Lower Premolars*. $P_2$ is known only from the Roo Site specimen QMF51366. It is elongate and triangular bearing three cuspids: an isolated protoconid with a straight crest extending to the anterior corner, an equally tall but more lingual hypoconid and a smaller posterobuccal hypoconulid joined to it by a crest. A weak postcingulum forms a shallow basin on the posterolingual side of the hypoconid.

$P_3$ generally almost parallel-sided, with a rather pointed anterior end and a blunt posterior (e.g. QM 40277 (WW), QMF51363 (CS), QMF51365 (MM)), but others show a little more taper (e.g. QMF51362, QMF12461 (CS)) being slightly wider posteriorly.

A longitudinal crest is almost central, interrupted at about the one-third point by the protoconid, from which buccal and lingual crests extend, and at the two-thirds point by the metaconid on the buccal side of midline giving rise to a slight buccal crest. Halfway between the metaconid and the posterior end of the tooth, and slightly lingual to the midline is the hypoconid with a lingual crest. Longitudinal crest continues to a small cusp on postcingulum, which extends equally on either side to form shallow basins on the flanks of the metaconid and hypoconid. On unworn teeth (QMF51362), the longitudinal crest therefore appears as a widely-open zigzag. Protoconid and metaconid are equally high, with the hypoconid slightly lower. There is a minute cusp at the halfway point, ahead of the metaconid, that scarcely interrupts the longitudinal crest, and the posterior-most cusp on the postcingulum is the lowest.

*Lower Molars*. $M_1$. Longest and, generally, the widest of the lower molars, although its anterior width is often less than that of the succeeding $M_2$ and $M_3$. Thus, it tapers noticeably forwards. In the unworn specimen from Roo Site (QMF51366), $M_1$ is bilophodont. Its protolophid is narrower than the hypolophid and bears cusps only at its buccal and lingual extremities. The protolophid is normal to the lingual face of the tooth, unlike the hypolophid which trends anterolingually, thus converging with it. Both lophids are notched about half-way across.

Protoconid and hypoconid are just buccal of the midline, and are highpoints on a longitudinal crest that starts at the paraconid (?) on the extremity of the precingulum, continues back along aligned pre- and postprotocristids and cristid obliqua, then curves lingually as the post-hypocristid, and merges into the postcingulum. The precingulum defines shallow basins on either side of the preprotocristid. There is no premetacristid, but a weak postmetacristid parallels the longitudinal crest and crosses the transverse valley to meet the entoconid about half-way up. A weaker postentocristid joins the postcingulum low down on the back of the tooth. With a little wear, the weaker crests are obliterated, as in QMF51375.

$M_2$-$M_4$. Posterior molars are essentially identical, with minor proportional changes, a possibly widening precingulum, and a narrower hypolophid on $M_4$. Development of the postcingular basin may vary. In the deep-jawed (Alpha-male?) QMF12461, the postcingulum forms a particularly well-defined and deep fossette, particularly on $M_4$, that is considerably deeper than on other specimens. One isolated tooth, QMF51352 from Wayne's Wok, presumably a left $M_2$, has the barest suggestion of a medial neomorphic cuspid on the protolophid, just lingual of the notch.

REMARKS. First upper molar smaller in lateral diameter than in other species except perhaps *N.* cf. *albivenator*, much smaller than in *N. snideri*. Upper premolars parallel, not converging anteriorly, more rectangular than in other species. Upper molars similar to those of *N. superior.* $M^1$ differs from both *N. albivenator* and *N. snideri* in having a crest between paracone and parastyle. Lower premolars differ from those of *N. albivenator* in being more rectangular, with anterior width only slightly less than posterior width, in being absolutely longer and larger relative to $M_1$, and in having second and third cuspids on the longitudinal crest separated, with third cuspid noticeably displaced lingually.

### **Namilamadeta** sp. indet.

MATERIAL. QMF51368, $lM^2$; QMF51369, $lP_3$; QMF51370, $lP_3$; QMF51371, left dentary fragment with $M_{2-4}$. Outasite, Godthelp Hill. Low (basal?) in System B (Archer et al., 1989,1991; Cooke 1997; Creaser 1997).

DESCRIPTION. The small sample from this site makes it difficult to characterise the taxon with any certainty. However, several features are noteworthy if all the specimens are conspecific: a) the upper premolar $P_3$ of QMF51370 is longer and wider than in any other species or specimen (e.g. Fig. 4), $M^2$ is more equidimensional than in *N. albivenator*, but similar in size and proportion to *N. superior*, and the lower molars are similar in size to *N. crassirostrum*.

TABLE 2. Comparison of character states of some features of upper teeth of *Namilamadeta* spp., using *Muramura* as an outgroup.

| Character | *Muramura* | *N. snideri* | *N. albivenator* | *N superior* | *N. crassirostrum* |
|---|---|---|---|---|---|
| I1 size | slightly broader than I2 | large, approximately equal to N. albivenator | large, slightly smaller than N. snideri | little more than half breadth of N. snideri | small, converging |
| I2-3 | slightly smaller than I1 | small relative to I1 | small relative to I1 | moderately large relative to I1 | slightly smaller than I1 |
| P3 size | small, > length of M1 | larger than M1 (~20% more) | slightly larger than M1 (~10%) | larger than M1 (20%) | larger than M1 |
| protocone | very slight bump | no | small but distinct cusp | minute cusp | |
| hypocone | well developed | well developed | relatively large | relatively large | relatively large |
| shape | rectangular | rectangular - larger than N. albivenator | roughly rectangular | roughly triangular, broader posteriorly, constricted medially | roughly rectangular, about size of N. snideri |
| M1 shape | rectangular | roundly quadrate | quadrate | quadrate | quadrate |
| postero-lingual corner | rounded | round | sub-rounded | sub-angular | sub-rounded |
| angle between pre- & post paracristae | n.a. | <90° | approx 90° | >90° | >90° |
| parastyle | preparacrista crest curves lingually at end | crest curves lingually at end | like N. snideri | on cingulum, at junction with straight crest | like N. snideri |
| parastylar spur | insignificant | marked | less than N. snideri | insignificant | |
| M2 preparacrista | strong, goes to ectocrista | strong | absent | weak | strong |
| parastyle | at corner of tooth | at corner of tooth | slightly lingual of corner | at corner of tooth | lingual of corner |
| stylar cusp C | absent | indistinct | distinct | insignificant | distinct |
| paracone | strong, midway between Pr and StB | indistinct, closer to StB | indistinct | closer to StB | distinct, closer to StB |
| metacone | closer to metaconule | closer to StD | midway | ~ midway | closer to StD |
| M3 paracone | strong, midway | not apparent | slight thickening | slight thickening | slight thickening |
| StB | distinct | weak | weak | distinct | indistinct |
| metacone | strong, midway | distinct, close to StD | distinct, midway | distinct, closer to StD | closer to StD |
| M4 shape | elongate, triangular | broad, triangular | rounded, triangular | triangular | tapering rectangular |
| postmetaconule-crista | moderate | insignificant | distinct | strong | Strong |

## DISCUSSION

*Age*. In South Australia, the vertebrate fossil-bearing beds of the Lake Eyre Basin are well-defined stratigraphically at and near Lake Palankarinna, the type locality of the Etadunna Formation and Ngapakaldi Fauna (Stirton et al., 1961, 1968), and superposition can be clearly demonstrated (Woodburne et al., 1993). Species correlation, both vertebrate and microfossil, between different basins, including marine sequences, has helped to establish the ages of the sediments. Stirton's early assessment of an Oligocene age for these formations and faunas (Stirton et al., 1961) was initially based on the stage of evolution he perceived in diprotodontoids (Stirton, Woodburne & Plane 1967), and palynological assessment (Balme, 1963; pp. 89-104 in Johns & Ludbrook, 1963), and current thinking has returned to this point of view (Woodburne et al., 1993) as a result of new information, which is admittedly still only tentative, with a Late Oligocene age (24-26 million years old) based on foraminifers, isotopic dating of sedimentary illite, and magnetostratigraphy (Woodburne et al., 1993).

In contrast, one of the problems of the numerous Riversleigh fossil assemblages is the uncertainty of their relative ages because of the type of sedimentary environment that has preserved them. Intercontinental correlation of bat species (Sigé, Hand & Archer, 1982) has helped define the age of some localities at least, and some taxa have allowed correlation with geological units of the Lake Eyre Basin. Tentative stratigraphies have been worked out (e.g. Archer et al., 1989, 1991, see Megirian 1994 for alternative) based primarily on faunal content of the different localities and perceived stage of evolution of various taxa within them (e.g. Cooke, 1997). Wayne's Wok assemblage is considered (e.g. Cooke, 1997) to correlate with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation of the Lake Eyre Basin, while White Hunter equates with the Ngama local fauna, zone D of the Etadunna Formation at Lake Palankarinna (Myers & Archer, 1997, Woodburne et al., 1993).

*Namilamadeta snideri* is from the Namba Formation at Lake Tarkarooloo (Rich & Archer, 1979) in the Tarkarooloo Basin (Callen, 1977) some 300km SE of Lake Palankarinna. The Namba Formation is correlated on lithological and faunal grounds with the Etadunna Formation. Pledge (1986) suggested that the Tarkarooloo Local Fauna was slightly older than the Ngama Local Fauna (Zone D of Woodburne et al., 1993) at Lake Palankarinna. A single specimen (SAMP24648) from the Ngama Local Fauna closely resembles the posterior three-quarters of $rM_4$ of *N. crassirostrum*, e.g. QMF12461 from Camel Sputum, rather than the supposedly contemporaneous *N. albivenator*, from White Hunter.

Overall, *N. snideri* may be approximately the same age as *N. albivenator*. It appears to be older than *N. crassirostrum*, which seems to have had a longer time range. The relative position of *N. superior* is uncertain. The oldest of all seems to be the Hiatus material. A simple explanation may be to assume two more-or-less contemporaneous but ecologically mutually exclusive lines, with *N. snideri* giving rise to *N. albivenator* and then *N. superior*, while a *N. crassirostrum*-like form appeared in Ngama time and continued in north Queensland until mid-System B time.

*Relationships*. Comparison of character states of various features on upper teeth of *Namilamadeta* spp., using *Muramura* sp. as a demonstrably older outgroup (Table 2), gives no clear species polarity. While the species are distinct, they are too close in age to be separated by this method. (Only upper dentitions were considered here because lower teeth are unknown for *N. snideri*, which is critical for extra-regional correlations, and for *N. superior*.)

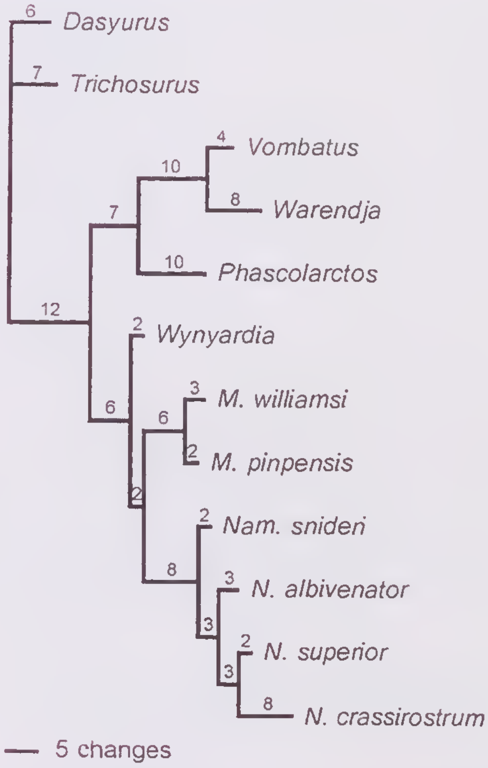

FIG. 12. Phylogram showing relationships of *Namilamadeta* spp. relative to *Muramura*, *Wynyardia*, *Phascolarctos*, *Warendja*, *Vombatus*, *Trichosurus*, and *Dasyurus*; from matrix, Table 4.

A broader cladistic analysis was attempted, using PAUP* 4.0b10 (Swofford, 2000), on 62 cranial and dental characters, and twelve taxa (Tables 3-4) with *Dasyurus* as the outgroup, but with little clear result except grouping the species of *Muramura* and *Namilamadeta* as two sister genera related to *Wynyardia* (Fig. 12). Koalas and wombats form a sister group to the wynyardiids. This tree (tree length 114) implies a closer relationship of these genera to koalas than wombats, and *Wynyardia* is a sister group to the Vombatiformes. This rather unexpected result may be because no postcranial characteristics could be used, due to the lack of recognised bones for *Namilamadeta*, and the lack of dental information for *Wynyardia*. The best consensus tree (tree length 62) for wynyardiids was that produced by analysis of eight taxa (*Trichosurus* as outgroup) and 22 informative characters, and is similar to that in Fig. 12.. The relationships implied are: *Wynyardia* ((*Muramura williamsi*,

TABLE 3. Score of character states of vombatiformes and outgroup marsupials

| Charac | *Dasyu* | *Trich* | *Phasc* | *Vomb* | *Waren* | *Wyn.b* | *M.will* | *M.pin* | *N.snid* | *N.albi* | *N.sup* | *N.cras* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3 | 1.64 | 1.58 | 1.68 | 1.23 | 3.22 | 1.69 | 1.69 | | | | 1.76 | 1.73 |
| 4 | 3.4 | 2.64 | 2.65 | 2.67 | 3.35 | 2.33 | 2.59 | | | | 2.58 | 2.83 |
| 5 | 0.92 | 0.75 | 1.05 | 0.92 | 1.0 | (0.55) | 1.08 | | (1.32) | 1.55 | 0.93 | 0.98 |
| 6 | X | X | X | X | X | X | X | X | X | X | X | + |
| 7 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | b |
| 8 | 1 | 1 | + | X | ? | ? | -? | | ? | 1 | + | + |
| 9 | x | X | X | X | X | X | X | X | X | X | X | 1 |
| 10 | long | long | long | long | long | long | long | | long | long | long | trans |
| 11 | 0 | 0 | 0 | 1 | 1 | | 0 | | 0 | 1 | | 1 |
| 12 | 0 | 0 | 1 | 1 | 1 | | 1 | 1 | 1 | 1 | | 1 |
| 13 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 15 | X | X | + | X | 1 | X | X | | + | 1 | + | X |
| 16 | curv | curv | straight | curv | curv | curv | straight | ? | ? | curv | curv | straight |
| 17 | taper | taper | parallel | taper | taper | taper | parallel | ? | ? | taper | taper | ? |
| 18 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | | | 0 | 0 | 0 |
| 19 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | | | | 1 | 1 |
| 20 | 0 | 0 | 1 | 1 | 1 | 0 | ? | | | | 0 | |
| 21 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | | | | 0 | |
| 22 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | | | | 1 | |
| 23 | 0 | 0 | 1 | 1 | 1 | | 1 | | | | | |
| 24 | 0 | 0 | 1 | 1 | | | 0 | | | | | |
| 25 | 0 | 0 | 0 | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 |
| 26 | 2.0 | 1.67 | 1.6 | na | na | | 1.83 | | 1.67 | 1.83 | | |
| 27 | 0 | 0 | 0 | 1 | 1 | | 0 | | 0 | 0 | 0 | 0 |
| 28 | 0 | 0 | 1 | 1 | 1 | | | | | 0 | | 0 |
| 29 | str | str | str | str | str | | str | curv | ?curv | curv | curv | str |
| 30 | na | tri | triangul | tri | triang | | rect | rect | rect | rect | rect | rect |
| 31 | - | 1 | 1 | 0 | | | 1 | 1 | 1 | 1 | 1 | 1 |
| 32 | 0 | 0 | 1 | 0 | | | 0 | 0 | 1 | 1 | 1 | 1 |
| 33 | 1.6 | 1.25 | 1.2 | 1.27 | 1.3 | | 1.29 | 1.25 | 1.76 | 1.57 | 1.6 | 1.76 |
| 34 | 0.67 | 0.8 | 0.875 | 0.74 | 0.75 | | 1.1 | 1.18 | 1.2 | 1.1 | 1.2 | 1.41 |
| 35 | 0.625 | 0.72 | 0.97 | 0.625 | 0.77 | | 0.84 | 0.88 | 0.82 | 0.89 | 0.85 | 0.87 |
| 36 | - | 0 | 1 | 1 | | | 0 | 1 | 0 | 1 | 1 | 1 |
| 37 | - | - | 0 | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 |
| 38 | 0 | 1 | 1 | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 0 |
| 39 | 0 | - | 0 | 0 | 0 | | 1 | 1 | 1 | 1 | 1 | 1 |
| 40 | 0 | 1 | 0 | 1 | 1 | | 0 | 0 | 0 | 0 | 0 | 0 |
| 41 | 0 | 0 | 1 | | | | 0 | 0 | 0 | 1 | 0 | 1 |
| 42 | 0 | 1 | 0 | 1 | | | 0 | 0 | 0 | 0 | 0 | 0 |
| 43 | na | 0.92 | 1.11 | 1.0 | 0.92 | | 1.03 | 1.03 | 0.97 | 1.04 | 1.01 | 1.0 |
| 44 | na | 1.35 | 1.08 | 1.2 | 1.21 | | 1.23 | 1.16 | 1.51 | 1.33 | 1.33 | 1.38 |
| 45 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | | 1 | | 1 |
| 46 | 70 | 70 | 75 | 75 | 57 | | 70 | 70 | | 60 | | 65 |
| 47 | 0 | 0 | 0 | 1 | 1 | | 0 | 0 | | 0 | | 0 |
| 48 | 20 | 20 | 30 | 15 | 18 | | 30 | | | 25 | (25) | 25 |
| 49 | deep | deep | m-shall | deep | shallow | | med | med? | | shall | | deep |

| Charac | *Dasyu* | *Trich* | *Phasc* | *Vomb* | *Waren* | *Wyn.b* | *M.will* | *M.pin* | *N.snid* | *N.albi* | *N.sup* | *N.cras* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 50 | 0 | 0 | 1 | 0 | 0 | | 0 | 0 | | 0 | | 0 |
| 51 | 0 | 0 | 1 | 1 | 1 | | 1 | | | 1 | | 1 |
| 52 | str | str | str | str | str | | str | str | | str | | curv |
| 53 | 1.86 | 1.51 | 1.5 | 1.25 | 1.71 | | 1.15 | 1.37 | | 1.73 | | 1.67 |
| 54 | 0.83 | 0.96 | 0.83 | 0.625 | 0.72 | | 0.83 | 0.88 | | 1.16 | | 1.08 |
| 55 | 0.86 | 0.97 | 0.77 | 0.8 | 0.61 | | 0.95 | 0.87 | | 0.95 | | 0.92 |
| 56 | 0.52 | 0.65 | 0.69 | 0.625 | 0.69 | | 0.77 | 0.74 | | 0.71 | | 0.69 |
| 57 | 0.78 | 0.98 | 1.00 | 1.0 | 1.00 | | 1.23 | 1.10 | | 1.00 | | 1.06 |
| 58 | 0.73 | 0.92 | 1.00 | 1.0 | 0.93 | | 1.04 | 1.04 | | 1.04 | | 1.00 |
| 59 | 0.25 | 0.28 | 0.26 | 0.25 | 0.26 | 0.19 | 0.31 | ? | ? | ? | 0.30 | 0.37 |
| 60 | na | 0.66 | 0.56 | 0.78 | 1.0 | ? | 0.73 | 0.44 | ? | ? | 0.52 | 0.51 |
| 61 | 3.78 | 3.95 | 3.75 | 3.5 | 4.7 | ? | 3.9 | ? | ? | ? | 3.17 | 2.9 |
| 62 | 0.59 | 0.75 | 0.59 | 0.27 | 0.67 | ? | 0.56 | 0.59 | 0.55 | 0.53 | 0.58 | 0.73 |

*M. pinpensis*)(*Namilamadeta snideri* (*N. albivenator* (*N. superior*, *N. crassirostrum*))).

*Morphology*. Distinctive rostral morphology in *N. crassirostrum*, although different in detail, invites comparison with some macropodid species, e.g. *Sthenurus stirlingi* Wells & Tedford, 1995; *Sthenurus baileyi* Prideaux & Wells, 1998; *Congruus congruus* McNamara, 1994, and to a lesser extent, *Macropus rufus* and *M. antilopinus*, where the nasal expansion has been considered to be an adaptation for a hot, dry climate. In some *Macropus* spp., e.g. *M. robustus*, this has been interpreted as sexual dimorphism, particularly for an Alpha male (M. Archer, pers. comm.). It is felt that sexual dimorphism in this character can be ruled out because it appears to be site specific, the two never co-occur. The expanded nasal cavity of *N. crassirostrum* may therefore indicate drier conditions for this species. Similarly the primitive zygomaturine *Silvabestius johnnilandi* (Black & Archer, 1997) from VIP Site (coeval with Wayne's Wok; Creaser, 1997), which differs from its older congener *S. michaelbirti* (from Hiatus Site) in having a swollen rostrum.

These macropodids, however, show nothing similar or analogous to the sinus in *N. crassirostrum*. No osseous structure like this appears to occur in other marsupials, although it has been suggested that it may be equivalent to the nasovomerine organ, otherwise known as Jacobson's Organ. This is known in a variety of marsupials (Broom, 1896), but is enclosed in cartilage and opens ventrally into the oral cavity. In our situation, the sinus is blind except for a large ovate opening on the dorsal edge of the thickened premaxilla; there is no natural connection with the mouth directly or through the anterior palatal foramen. It is possible the fossa was lined with nasal mucosa, perhaps to concentrate scents or to moisten incoming air (P. Murray, pers. comm.). The feature appears to be unique: the only analogy might be the paired pits for the nasal diverticula in *Equus*, *Tapirus* and *Onohippidium* (Gregory, 1951: figs. 21.43B, 21.70A, B1); these, however, are outside the nasal cavity.

The other distinctive feature of the rostrum is the retracted premaxillary margin. While this is not as extreme as in tapirs or palorchestids (but note the similarity to the mid-Miocene *Propalorchestes novaculacephalus* Murray, 1986, as reconstructed in Fig. 3A of Murray, 1991), it suggests that *N. crassirostrum* possessed a mobile snout.

## WYNYARDIID CHARACTER STATES

1. carnivorous/omnivorous (0), vs herbivorous (1)
2. teeth tritubercular (0): diprotodontan (1)
3. skull slender, length: width less than 1.7 (0)
4. skull low, length: height less than 2.6 (1)
5. rostral height: width just anterior to jugal root less than1.0 (0)
6. presence (1) or absence of large paired sinuses in upper surface of premaxillae (0)
7. snout tapering (0) or bulbous (1)
8. nasals projecting (1)
9. premaxilla edge retracted (1) to level of P3 or not (0)
10. infraorbital foramen in maxilla oriented longitudinally (0) or transversely (1)
11. infraorbital foramen close to premax/maxillar suture (1), i.e. expansion of premax at expense of maxilla
12. presence of malar fossa (or depression) (1)
13. development of masseteric processes (1)

14. enlargement of masseteric processes (1)
15. great expansion of anterior interorbital area (1)
16. zygomatic arches angular, straight (1) or curved (0)
17. zygomatic arches parallel (1) or tapering forwards (0)
18. sagittal crest present (0)
19. auditory capsule roofed by alisphenoid (0) or squamosal (SQW) (1)
20. no squamosal process (SQP) (0)
21. no squamosal sinus (SQS) (0)
22. alisphenoid component to tympanic process (0)
23. tail long (0), short (1)
24. tail very short (1)
25. incisor I1 greatly enlarged (1)
26. incisor I1 diameter >1.7 times greater than I3 (1) or less (0)
27. upper canine present (0) or lost (1)
28. P2 present (0) or lost (1)
29. upper tooth-rows straight (0) or curved (1)
30. premolar P3 rather triangular, small, sectorial (0), rectangular, large (1)
31. P3 has longitudinal crest (1)
32. P3 has strong lingual crest for hypocone (1)
33. P3 length: width greater (1) or less (0) than 1.3
34. P3:M1 length greater (1) or less than 1.2 (0)
35. P3:M1 width greater (1) or less than 0.85 (0)
36. upper molars selenodont (1)
37. selenodonty reduced (1)
38. presence of stylar cusps on upper molars (0)
39. stylar cusps enlarged (1)
40. stylar shelf lost (1)
41. parastyle on M1 reduced (1)
42. primary cusps on upper molars labial (1) or midway on lophs (0)
43. M1 anterior width less than posterior width (0) or equal or greater (1)
44. M4 rectangular or triangular; metaloph slightly shorter (0) or much shorter than protoloph (1) (prl:mel<1.3>)
45. dentary shallow (0) or deep (1)
46. anterior border of ascending ramus more (1) or less than 65o (0)
47. coronoid process wide (0) or narrow(1)
48. articular condyle on (<25o ) (0) or above molar occlusal plane (1)
49. masseteric fossa shallow (0) or deep (1)
50. angular process very reduced (1)
51. I2 present (0) or lost (1)
52. lower cheek tooth-row straight (0) or curved (1)
53. P3 length: width greater (1) or less than 1.5 (0)
54. P3:M1 length greater (1) or less than 1.0 (0)
55. P3:M1 width greater (1) or less than 0.9 (0)
56. M1 width: length more (1) or less than 0.7 (0)
57. length M1 : M2 more (1) or less (0) than 1.0
58. width M1 : M2 more (1) or less (0) than 1.0
59. rostral:total skull length less than 0.3 (0)
60. I3 P3 diastema: cheek-tooth row length more than 0.7 (0)
61. skull: cheek-tooth row length greater than 4 (0)
62. palatal width: cheek-tooth row length less than 0.6 (0) 0 plesiomorphic; 1 apomorphic

## CONCLUSIONS

Metric and morphological examination of 121 specimens from 18 Riversleigh localities demonstrates at least three distinct taxa are

TABLE 4. Matrix of scores for PAUP 4.0b1 analysis

```
MATRIX
[                               10        20        30        40        50        60 ]
[                                .         .         .         .         .         . ]

Dasyurus                000100000000000000000100010000-0100--00000--010010001000000-10
Trichosurus             010100010000100000101100000000100000-1-10101010010001010000111
Vombatus                1101000110110000011110111-11000000011001?110111010100000110010
Warendja                1111000?001100100011101?1-1100??100?1001??00101000101000100001
Phascolarctos           11011000000110111111111100010011001101001010110101101000110110
Wynyardia               1100000??0??1100001001??????????????????????0?????????????0???
M._williamsi            1101100100011101101?0110110?0110000010100010110110100011111000
M._pinpensis            11???001?0?111??????????1?????1110001110100010110?10?0000111?1?0
Nam._snideri            11??10010001111?????????100?1111110010100001?????????????????0
N._albivenator          11??10010011111000??????1100111110111010101110010010111111???0
N._superior             1111000100??1110001001?100?1111111111010?011???1??????????1110
N._crassirostrum        1111011111111101?0??????1?00011111111010101110011011111011111 1
```

present. *N. albivenator,* primarily from White Hunter site, (plus DT6 and LSO), is noticeably smaller than the almost unique specimen *N. superior* from Upper Site and the *N. crassirostrum* complex from the remaining sites. While *N. snideri* is morphologically closer to *N. albivenator*, it seems closer in size to *N. superior*. Thus, no conclusion can be reached about their relative ages, although *N. snideri* seems on other evidence to be slightly older or about the same age as *N. albivenator*.

In general, the Riversleigh *Namilamadeta* spp. support a correlation of 'System B' sites with the upper part of the Etadunna Formation of the Lake Eyre Basin, and therefore a late Oligocene to earliest Miocene age. Physiologieal considerations of the skull morphology of *N. crassirostrum* suggest an adaptation to hotter/drier conditions during some period of the early Miocene. Structure of the auditory region in *N. superior* supports assignment to the Family Wynyardiidae, as originally suggested by Rich & Archer (1979).

## ACKNOWLEDGEMENTS

I thank M. Archer for access to material obtained by fieldwork supported by the Australian Research Grant Scheme, University of New South Wales, National Estate Grant Scheme (Queensland), Commonwealth Department of Environment, Sports and Territories, Queensland National Parks and Wildlife Service, Commonwealth World Heritage Unit, ICI Australia, Australian Geographic Society, Riversleigh Society, and the Australian Museum, and assistance from Henk Godthelp, Anna Gillespie and the late Stephan Williams (all University of New South Wales), amongst others. Computer tomographic X-ray scans and syntheses were performed by Ross Harper, Lyell McEwin Hospital, Elizabeth, South Australia. The first draft of this manuscript was initially typed by Ms D. Churches. Ben McHenry helped with statistical treatment in an early stage, and Mike Lee with adviee on cladistic analysis.

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## APPENDIX 1.

Measurements of considered teeth of *Namilamadeta* spp. All measurements in millimetres.

*Namilamadeta snideri* Rich & Archer 1979

| Tom O's Quarry | | | |
|---|---|---|---|
| SAM P19951 | holotype - partial palate and rostrum | | |
| tooth | length | ant. width | post. width |
| rI1 | 6.2 | 4.5 | |
| lI1 | 6.3 | 4.5 | |
| lI2 | >4.5 | 4.5 | |
| lI3 | 4.5 | 3.3 | |
| lC1 | 3.2 | 2.0 | |
| rP3 | 11.0 | 5.7 | 7.15 |
| lP3 | 11.6 | 5.95 | 7.05 |
| lM1 | 9.6 | 8.2 | 8.5 |
| lM2 | 9.2 | 8.5 | 8.3 |
| lM3 | 8.6 | 7.8 | 7.1 |
| lM4 | 7.2 | 6.5 | 4.3 |
| NMV P8993 | | | |
| rM1 | 8.55 | 7.3 | 7.3 |
| NMV P8994 | | | |
| rM1 | 9.6 | 7.95 | 8.2 |
| rM2 | 9.1 | 8.0 | 7.7 |
| rM3 | 8.7 | 7.1 | 6.5 |

*Namilamadeta albivenator* sp. nov.

| White Hunter - Riversleigh | | | |
|---|---|---|---|
| AR 16775 | (joins to QMF 23834, AR 17188) Holotype | | |
| rP3 | 10.4 | 5.8 | 6.65 |
| rM1 | 9.3 | 7.2 | 7.3 |
| rM2 | 8.9 | 7.7 | 7.4 |
| QMF 51337 | | | |
| rP3 | | 6.15 | |
| lP3 | 11.1 | 6.2 | 7.0 |
| lM1 | 9.5 | 7.6 | 7.7 |
| lM2 | 8.7 | 7.55 | 7.3 |
| AR 17188 | (joins to AR 16775, QMF 23834) maxilla | | |
| lI1 | 5.6 | 3.7 | |
| rC1 | 2.5 | 2.0 | |
| lP3 | 10.4 | 5.8 | 6.5 |
| lM1 | 9.1 | 7.5 | 7.7 |
| lM2 | 8.95 | 7.45 | 7.1 |
| lM3 | 8.9 | 6.7 | 6.0 |
| lM4 | | 6.2 | |
| QMF 51338 | premaxilla | | |
| lP3 | 11.3 | 6.3 | 7.3 |
| QMF 51339 | | | |
| lM1 | 9.55 | 7.9 | 8.2 |
| QMF 23834 | (joins to AR 16775, and AR 17188) maxilla | | |
| rM3 | 8.3 | 6.95 | 5.7 |
| rM4 | 7.2 | 5.8 | 4.4 |
| QMF 51340 | dentary fragment broken tooth | | |
| rM3 | ~1 | 6.5 | |
| QMF 51341 | left juvenile dentary with P2, M1, and M2-3 in crypt | | |
| lP2 | 6.3 | 2.9c | 4.3 |
| lM1 | 9.7 | 5.9 | 5.5 |
| lM2 | 9.4e | 5.8e | in crypt |
| lM3 | in crypt | | |
| QMF 40278 | right dentary, almost perfect (paratype) | | |
| rI1 | 6.5 | 4.2 | >25 |
| rP3 | 9.2 | 4.5 | 5.7 |
| rM1 | 8.3 | 5.4 | 6.2 |
| rM2 | 8.2 | 5.9 | 6.1 |
| rM3 | 8.2 | 6.0 | 5.9 |
| rM4 | 7.7 | 5.4 | 5.0 |
| QMF 51342 | r. dentary, juvenile, rM3 missing, rM4 unerupted | | |
| rI1 | >6.4 | | 4.25 |
| rP2 | 6.0 | 3.0 | 4.4 |
| rM1 | 9.5 | 5.6 | 6.0 |
| rM2 | 9.3 | 5.8 | 6.1 |
| QMF 51343 | dentary, fractured. I1 broken (pair to AR 12793?) | | |
| lI1 | >6.2 | | >4 |
| lP3 | 9.5 | 4.8 | 5.9 |
| lM1 | 8.5 | 5.6 | 6.2 |
| lM2 | 8.2 | 6.0 | 6.2 |
| lM3 | 8.2 | 5.9 | 5.8 |
| lM4 | 7.7 | 5.3 | 4.8 |
| QMF 51344 | lower | | |
| rI1 | 6.7 | 4.8 | |
| QM F23499 | lower | | |
| rM3? | 8.8 | 5.9 | 5.9 (cf. QMF 51342) |
| QM F30700 | right dentary, split lengthwise through teeth | | |
| rI1 | 5.7 | 3.75 | |
| rP3 | 10.1 | 5.5 | 6.8 |
| rM1 | 8.7 | 6.3 | 7.0 |
| rM2 | 8.3 | 6.75 | 6.8 |
| rM3 | 7.9 | 6.5 | 6.0 |
| rM4 | 7.8 | 5.9 | 5.7 |
| Dirk's Towers - DT6 | | | |
| QMF 13093 | left maxilla, dark preservation cf. QMF 23494 | | |
| lP3 | 10.5 | 5.7 | 7.0 |
| lM1 | 8.4 | 8.0 | 7.5 |

| | | | |
|---|---|---|---|
| lM2 | 8.7 | 7.8 | 7.3 |
| lM3 | | | 6.2 |
| lM4 | 6.8 | 5.8 | 4.3 |
| QMF 20035 | right maxilla, light preservation | | |
| rP3 | 11.0 | 5.5 | 6.7 |
| rM1 | 9.1 | 8.2 | 8.7 |
| rM2 | 8.2 | 7.9 | 7.4 |
| rM3 | 8.2 | 7.1 | 6.3 |
| rM4 | 7.5 | 5.8 | 4.7 |
| QMF 20037 | (2 pieces) maxilla | | |
| rP3 | 10.95 | 5.75 | 7.1 |
| rM1 | 9.2 | 8.0 | 7.6 |
| rM2 | 8.5 | 7.5 | 7.0 |
| rM3 | 8.2 | 6.75 | 6.2 |
| QMF 23494 | left premaxilla, (cf. QMF 13093, also N. snideri) | | |
| lI1 | 6.5 | 4.9 | |
| lI2 | 3.3 | 4.1 | |
| lI3 | 3.1 | 3.2 | |
| QMF 36343 | | | |
| rM4 | 6.5 | 6.1 | 5.2 |
| QMF 30506 | left dentary fragment (locality unspecified) | | |
| lP3 | 8.2 | 4.3 | 4.9 |
| lM1 | 9.0 | 5.0 | 5.3 |
| Quantum Leap | | | |
| QMF 24138 - | left maxilla,P3-M3 | | |
| P3 | 10.5 | 5.9 | 6.9 |
| M1 | 9.0 | 7.6 | 8.4 |
| M2 | 8.5 | 7.9 | 7.8 |
| M3 | 8.2 | 6.9 | 6.5 |
| L.S.O. | | | |
| QMF 36348 | upper | | |
| rM1 | >8.9 | | 8.6 |
| QMF 36349 | right maxilla fragment | | |
| rM3 | 7.9 | 6.4 | 5.8 |
| QMF 36350 | | | |
| lM1 | 8.8 | 7.9 | 7.8 |
| QMF 40251 | right dentary | | |
| rI1 | 6.2 | 4.2 | |
| rP3 | 8.4 | 5.0 | 5.4 |
| rM1 | 9.0 | 5.0 | 5.3 |
| rM2 | 8.9 | 5.6 | 5.3 |
| rM3 | 8.3 | 5.9 | 5.4 |
| rM4 | 7.8 | 5.3 | 4.9 |

*N. superior* sp. nov.

| Upper Site | | | |
|---|---|---|---|
| AR15875 | upper | | |
| rM2 | 8.6 | 8.2 | 7.4 |
| AR15876 | upper | | |
| lM3 | 8.3 | 7.75 | 7.3 |
| AR16127 | lower | | |
| lMx (damag.) | 8.75 | ~6.7 | |
| AR12884 | upper | | |
| rM2? | 8.8 | 7.7 | 7.5 |
| QMF 40276 | skull (holotype) N. superior | | |
| lI1 | 4.9 | 3.9 | |
| lI2 | 5.1 | 4.1 | |
| I3 and C1 | missing | | |
| lP3 | 12.0 | 6.3 | 7.5 |
| lM1 | 10.0 | 8.9 | 8.8 |
| lM2 | 8.5 | 8.8 | 8.1 |
| lM3 | 8.4 | 7.7 | 6.5 |
| lM4 | 7.6 | 6.4 | 4.8 |
| rI1 damaged | | | |
| rI2 | 4.9e | 4.6e | damaged |
| rP3 split | 11.7 | ~6.9 | ~8.6 |
| rM1 split | 9.5 | ~9.5 | ~8.8 |
| rM2 | 8.5 | | 8.0 |
| rM3 | 8.5 | 7.7 | 6.3 |
| rM4 | 7.8 | 6.4 | 4.8 |

*N. crassirostrum* sp. nov.

| Waynes Wok | | | |
|---|---|---|---|
| QMF 51346 | left maxilla | | |
| lP3 | 12.4 | 6.25 | 7.8 |
| lM1 | 8.7 | 8.8 | 9.0 |
| lM2 | 8.75 | 8.6 | 8.1 |
| lM3 | 8.65 | 7.8 | 7.15 |
| lM4 | (7.3) | (6.1) | (5.1) |
| QMF 51348 | juvenile right maxilla | | |
| rP2 | 8.7 | (4.5) | 6.7 |
| rM1 | 9.0 | 8.4 | 8.4 |
| rM2 | 8.9 | 7.8 | 7.3 partly erupted |
| rM3 | unerupted | | |
| QMF 51349 | juvenile left maxilla | | |
| lP2 | 8.45 | (4.4) | 6.5 |
| lP3 | 11.9 | 5.5 | 6.75 (ex crypt) |
| lM1 | 9.3 | 8.5 | 8.4 |
| lM2 | 8.7 | 7.8 | 7.9 |
| QMF 51351 | mature left maxilla fragment (cf. QMF 51350) | | |
| lP3 | 13.4 | 6.8 | 7.6 |
| lM1 | 10.2 | 9.3 | 9.2 |

| | | | |
|---|---|---|---|
| lM2 | 9.0 | 8.95 | 8.4 |
| QMF 51350 | (cf. QMF 51351) upper | | |
| rP3 | 13.8 | 6.7 | 7.5 |
| QMF 51345 | upper | | |
| lP3 | 12.8e | | |
| lM1 | 9.2 | 9.3e | 8.9 |
| lM2 | 8.9 | 8.7 | 8.4 |
| lM3 | 8.4 | 7.6 | 7.05 |
| QMF 51347 | upper | | |
| rP2 | 8.0 | 4.2 | 6.6 |
| rM1 | 9.2 | 8.2 | 8.3 |
| rM2 | 8.4 | 7.7e | (7.2) unerupted |
| AR 9820 | isolated crowns, upper | | |
| ?lM2 | >8.8 | ~8 | 7.4 damaged |
| ?lM3 | 8.3 | 7.4 | 7.0 |
| AR 12858 | worn | | |
| lM1 | 9.3 | 9.5 | 9.4 |
| lM2 | 8.6 | 8.2 | 7.8 |
| QMF 51375 | mature worn right dentary (paratype) | | |
| rP3 | 11.4 | 5.7 | 6.4 |
| rM1 | 10.3 | 6.8 | 7.0 |
| rM2 | 9.4 | 7.1 | 6.5 |
| rM3 | 9.0 | 6.9 | 6.2 |
| rM4 | 9.0 | 6.1 | 5.4 |
| AR 9711 | left dentary fragment | | |
| P3 | 10.1 | 5.3 | 6.2 |
| AR 10789 | lower | | |
| rP3 | 10.9 | 5.4 | 6.4 |
| AR 10639 | lower | | |
| lP3 | 10.4 | 5.2 | 5.8 |
| AR 10638 | lower | | |
| rP3 | 9.9 | 5.1 | 5.8 |
| AR 10565 | lower | | |
| lM2 | 8.9 | 6.4 | 6.1 |
| AR 11866 | lower | | |
| lP3 | 10.3 | 5.0 | 5.9 |
| AR 12860 | lower | | |
| lM2? | 9.7 | 6.7 | 7.1 |
| QMF 51352 | lower | | |
| lM2 | 9.2 | 6.5 | 6.5 |
| QMF 24507 | lower | | |
| lM1 | 9.9 | 6.2 | 6.9 |
| QMF 30755 | upper | | |
| lM4 | 7.9 | 6.75 | 5.0 |
| QMF 30756 | upper | | |
| rP3 | 12.1 | 6.2 | 7.7 |
| QMF 30757 | upper | | |
| rM1 | 9.0 | 9.1 | 8.8 |
| QMF 30758 | upper | | |
| rM1? | 9.0 | 8.7 | 8.2 |

| | | | |
|---|---|---|---|
| QMF 30759 | upper | | |
| rM4 | 7.6 | 6.5 | 5.3 |
| QMF 30760 | upper | | |
| rM2 | 8.6 | 7.6 | 7.3 |
| QMF 30762 | lower | | |
| rM1 | 9.3 | 5.9 | 6.1 |
| QMF 30836 | right dentary fragment | | |
| rP3 | >9.3 | | 5.6 |
| rM1 | 9.1 | 6.3 | 6.7 |
| QMF 31462 | imperfect skull swollen snout (holotype) | | |
| rI1 | 4.4 | 3.6 | |
| lI1 | 4.5 | 3.6 | |
| rP3 | 11.8 | 6.1 | 7.0 |
| lP3 | 11.75 | 6.1 | 6.9 |
| rM1 | 8.8 | 8.4 | 8.5 |
| lM1 | 8.9 | 8.6 | 8.7 |
| rM2 | 8.6 | 7.6 | 7.6 |
| lM2 | 8.7 | 7.8 | 7.8 |
| rM3 | 8.2 | 7.1 | 6.6 |
| lM3 | 8.3 | 7.0 | 6.4 |
| rM4 | 7.3 | 6.1 | 5.0 |
| lM4 | 7.0 | 6.25 | 5.15 |
| QMF 31480 | right premaxilla and maxilla | | |
| rP3 | 12.7 | 6.45 | 7.6 |
| rM1 | 9.4 | 8.8 | 8.7 |
| Camel Sputum | | | |
| AR 8686 | upper | | |
| P3 | 11.45 | 5.9 | 6.9 |
| M1 | 8.75 | 8.0 | 8.0 |
| AR 10038 | upper | | |
| lM1? damaged | 9.2 | >8.0 | ~7.9e |
| lM2? | 9.0 | 8.7 | 8.2 |
| AR 11840 | upper | | |
| lM2 | 8.5 | 8.5 | 8.2 |
| lM3 | 8.3 | 7.7 | 7.0 |
| lM4 alveolus | | | |
| AR 12881 | upper | | |
| rP2 | 8.8 | | 7.0 |
| QMF 51357 | upper | | |
| rP2 | 8.5 | | 7.0 |
| rP3 unerupted | 12.55 | 6.3 | 7.6 |
| QMF 51358 | upper | | |
| rP2 | 8.4 | | 7.8 |
| QMF 51359 | upper | | |
| rM1 | 8.55 | 7.9 | 8.0 |
| rM2 | 8.3 | 7.7 | 7.4 |
| rM3 | 7.9 | 7.1 | 6.7 |
| rM4 | smashed | | |
| QMF 51360 | upper | | |
| rM2 | 9.0e | 9e | 8.2 |

| | | | |
|---|---|---|---|
| rM3 | 8.7 | 8.2 | 7.5 |
| rM4 | 7.5 | 6.7 | 4.7 |
| QMF 20497 | upper | | |
| rM1 | 9.7 | 9.1 | 9.2 |
| rM2 | 8.9 | 8.6 | 8.6 |
| rM3 | 8.6 | 7.9 | 6.9 |
| rM4 | 7.7 | 6.6 | 4.9 |
| QMF 20498 | upper | | |
| rM2 | 8.25 | 8.1 | 7.9 |
| rM3 | 8.3 | 7.15 | 6.8 |
| QMF 20574 | maxilla | | |
| lP3 | 11.4e | ~6.2 | 7.2e |
| lM1 | 9.3 | 8.8 | 9.1 |
| lM2 | 8.9 | 8.4 | 8.7 |
| lM3 | 8.8 | 7.7 | 7.3 |
| lM4 | 7.7 | 6.5 | 4.95 |
| QMF 40279 | partial skull left side damaged | | |
| lP3 | 12.3 | >5.4 | 6.8 |
| rP3 | 12.0 | 6.0 | 7.3 |
| lM1 | 9.3 | | |
| rM1 | 8.3 | 8.0 | 7.9 |
| lM2 | 7.7 | 7.3 | 7.5 |
| rM2 | 7.4 | 7.4 | 7.3 |
| lM3 | 8.2 | 6.6 | <7.1 |
| rM3 | 8.0 | 6.7 | 6.4 |
| lM4 | 7.7 | <6.3 | <4.8 |
| rM4 | 7.8 | 6.1 | 4.2 |
| QMF 30303 | mature palate, with premaxillae | | |
| lI2 very worn | 3.9 | 4.1 | |
| lI3 very worn | 3.7 | 3.3 | |
| lC1 damaged | | | |
| lP3 | 12.25 | 6.2 | 7.7 |
| rP3 | 12.5 | damaged | damaged |
| lM1 | 8.7 | 8.5 | 8.3 |
| rM1 | 8.9 | 8.1 | 8.3 |
| lM2 | 8.6 | 8.1 | 7.8 |
| rM2 | 8.2 | 7.9 | 7.6 |
| lM3 | 7.9 | 7.2 | 6.4 |
| rM3 | 7.7 | 7.4 | 6.6 |
| lM4 | 7.5 | 6.3 | 5.7 |
| rM4 | 7.3 | 6.2 | 4.8 |
| QMF 30534 | right maxilla, fragment | | |
| rM1? | | | 8.1 |
| rM2? | 8.8 | 8.1 | 7.8 |
| AR 12946 | upper | | |
| rP3 | 12.5 | 6.1 | 7.45 |
| AR 13374 | upper | | |
| lP3 | 11.8 | 5.9 | 7.3 |
| AR 16838 | upper | | |
| rP3 | 12.3 | 6.1 | 7.25 |

| | | | |
|---|---|---|---|
| AR 10691 | upper | | |
| lM2 | 9.4 | 8.9 | 8.8 |
| AR 10686 | upper | | |
| rM2 | 8.6 | 8.2 | 7.7 |
| AR 16839 | upper | | |
| lM3? | 8.8 | 7.9 | 6.9 |
| QMF 23490 | upper | | |
| lM2 | 8.9 | 8.6 | 8.6 |
| QMF 51361 | right dentary fragment | | |
| rM2 | 9.1 | 6.7 | 6.7 |
| rM3 | 8.7 | 6.6 | 6.2 |
| rM4 | 8.3 | 6.1 | 5.7 |
| QMF 51362 | left dentary, venter missing | | |
| lP3 | 10.8 | 5.4 | 6.5 |
| lM1 | 9.5 | 5.8 | 6.9 |
| lM2 | 9.0 | 6.8 | 6.8 |
| lM3 | 8.6 | 6.6 | 6.2 |
| lM4 | 8.6 | 6.3 | 5.7 |
| QMF 51363 | left dentary, L 90.5mm, D at M2 23.3mm | | |
| lP3 | 10.3 | 5.6 | 6.1 |
| lM1 | 8.7 | 6.3 | 6.7 |
| lM2 | 8.5 | 6.6 | 6.3 |
| lM3 | 8.3 | 6.6 | 5.9 |
| lM4 | 8.6 | 6.1 | 5.4 |
| AR 13898 | dentary fragment with split M1 unmeasurable | | |
| AR 17073 | lower | | |
| rM4 | 8.1 | 6.4 | 5.1 |
| QMF 12461 | right dentary | | |
| rP3 | 10.8 | 5.1 | 5.9 |
| rM1 | 9.0 | 6.1 | 6.7 |
| rM2 | 8.8 | 6.6 | 6.5 |
| rM3 | 8.7 | 6.5 | 6.0 |
| rM4 | 8.4 | 6.2 | 5.6 |
| Mike's Menagerie | | | |
| QMF 51364 | right maxilla | | |
| rP3 | 13.3 | 6.75 | 7.4 |
| rM1 | 8.8 | 8.4 | 8.5 |
| rM2 | 8.2e | 7.9 | 7.8 |
| AR 12868 | upper | | |
| rP3 unerupted | 11.45 | 5.1 | 6.5 |
| AR 9744 | abraded, eroded, unmeasurable | | |
| AR 9745 | upper | | |
| lM2 | 8.7 | 8.3 | 9.0 |
| AR 9762 | upper | | |
| rM3 | 8.6 | 8.05 | 7.6 |
| AR 9913 | upper | | |
| rM3? | 8.8 | 8.3 | 8.0 |
| AR 12871 | upper | | |
| rM2? | 8.9 | 8.3 | 8.5 |
| QMF 51365 | left dentary fragment | | |

| | | | |
|---|---|---|---|
| lP3 | 11.2 | 5.7 | 6.4 |
| lM1 | 10.0 | >6.8 | >6.9 |
| lM2 | 9.2 | >7.2 | >6.8 |
| lM3 | 8.8 | 7.1 | 6.4 |
| lM4 | 8.7 | 6.3 | 5.6 |
| AR 10703 | fragment, right dentary alveoli for P3, M2 3 | | |
| rM1 | 8.9 | 6.1 | 6.6 |
| AR 9742 | lower | | |
| lP3 | 10.1 | 4.5 | 4.9 unerupted |
| AR 9743 | lower | | |
| lM1 | 9.9 | 6.4 | 6.7 |
| AR 9915 | lower | | |
| rM1 | 10.0 | 6.2 | 6.5 |
| AR 12869 | lower | | |
| lM1 | 9.7 | 6.5 | 6.7 |
| AR 12870 | (fits AR10703) | lower | |
| rM2? | 8.8 | 6.6 | 6.5 |
| AR 16961 | lower | | |
| rM2? or 1 | 9.4 | 6.0 | 6.6 |
| Dirk's Towers DT4 | | | |
| QMF 51353 | upper | | |
| rP2 | >7.9 | (5.4) | >6.8 damaged |
| QMF 51354 | upper | | |
| lP3 | 11.8 | 5.7 | 6.8 |
| QMF 51355 | upper | | |
| lM2 | 9.05 | 7.7 | 7.6 |
| QMF 36342 | (site unspecified) upper | | |
| lP3 | 12.0 | 5.9 | 7.2 |
| Dirk's Towers DT5 | | | |
| QMF 51356 | upper | | |
| rM1 | 8.7 | 8.4 | 7.9 |
| QMF 24218 | left dentary, with P3 M4 | | |
| P3 | 10.45 | 5.6 | 6.7 |
| M1 | 8.8 | 6.5 | 6.8 |
| M2 | 8.7 | 6.7 | 6.5 |
| M3 | 8.5 | 6.8 | 6.3 |
| M4 | >8.0 | >6.1 | >6.1 |
| Sticky Beak | | | |
| QMF 51367 | | | |
| lI1 | 6.5 | 3.8 | |
| QMF 51373 | | | |
| rP3 | 11.1 | 5.25 | 6.75 |
| Roo Site | | | |
| QMF 51366 | juvenile dentary remnants | | |
| lI1 | ~11.7 | 3.8 | |
| lP2 | 8.9 | | 5.3 |
| lP3 unerupted | incomplete | | |
| lM1 | 9.4 | 5.8 | 6.7 |
| lM2 | 8.6 | 6.5 | 5.9 |
| lM3 incomplete | - | 6.4 | - |

Unallocated:

cf. *N. crassirostrum*

| | | | |
|---|---|---|---|
| Neville's Garden | | | |
| QMF 51374 | upper | | |
| rP3 | 11.55 | 5.8 | 6.9 |
| QMF 23014 | maxillae | | |
| rP3 | 11.95 | 5.9 | 7.3 |
| rM1 | 8.6 | 7.5 | 7.95 |
| rM2 | 8.2 | 7.8 | 7.25 |
| rM3 | 8.1 | 6.9 | 6.4 |
| rM4 | >6.4 | 5.6 | 4.5 |
| QMF 23201 | left maxilla fragment | | |
| lP3 | 12.1 | 6.1 | 6.85 |
| lM1 | >8.2 | >8.4 | >8 crown missing |
| Outasite | | | |
| QMF 51368 | upper | | |
| lM2 | 8.1 | 8.0 | 7.8 |
| QMF 51369 | lower | | |
| lP3 | 12.35 | 6.0 | 7.4 |
| QMF 51370 | lower | | |
| lP3 | 13.9 | 6.6 | 8.0 |
| QMF 51371 | left dentary fragment | | |
| LM2 | 9.4 | 7.2 | 6.8 |
| lM3 | 8.8 | 6.9 | 6.3 |
| lM4 | 8.5 | 6.5 | 5.4 |

cf. *N. crassirostrum*

| | | | |
|---|---|---|---|
| Judy's Jumping Joint | | | |
| QMF 51372 | | | |
| lP3 | 12.4 | 6.0 | 7.2 |
| QMF 51376 | | | |
| rP3 | 12.5 | 5.8 | 7.5 |
| RSO | | | |
| AR 11109 | lower | | |
| rM2 | 9.1 | 5.9 | 6.0 |
| J.H. | | | |
| QMF 30724 | | | |
| lP3 | >12.6 | 7.1 | 8.5 |

Isolated teeth

| | | | |
|---|---|---|---|
| Bone Reef | | | |
| AR17590 | lower | | |
| rM2 | 9.0 | 6.1 | 6.1 |
| rM3 | 8.8 | 6.2 | 5.6 |
| rM4 | 8.2 | 5.8 | 5.25 |

cf. *N. crassirostrum* crushed skull lacking rostrum

| Hiatus | | | |
|---|---|---|---|
| QMF 23216 | | | |
| lM1 | 8.6 | 8.0 | 7.8 |
| rM1 | | | 8.2 |
| lM2 | 8.0 | 7.2 | 7.0 |
| rM2 | 8.2 | 7.5 | 7.5 |
| lM3 | 7.6 | 6.4 | 6.2 |
| rM3 | 7.6 | 6.7 | 6.1 |
| lM4 | 6.7 | 5.4 | 4.0 |
| rM4 | 6.6 | 5.5 | 3.9 |

APPENDIX 2. Mean values for *Namilamadeta* spp. tooth dimensions, various localities.

| Tooth | Length | Anterior Width | Posterior Width | N |
|---|---|---|---|---|
| Tom O's Quarry | *N. snideri* | | | |
| $P^3$ | 11.3 | 5.83 | 7.1 | 2 |
| $M^1$ | 9.25 | 7.82 | 8 | 2 |
| $M^2$ | 9.15 | 8.25 | 7.8 | 2 |
| $M^3$ | 8.65 | 7.45 | 6.8 | 2 |
| White Hunter | *N. albivenator* | | | |
| $P^3$ | 10.8 | 6.03 | 6.86 | 4 |
| $M^1$ | 9.36 | 7.55 | 7.73 | 4 |
| $M^2$ | 8.85 | 7.57 | 7.27 | 3 |
| $M^3$ | 8.6 | 6.83 | 5.85 | 2 |
| $M^4$ | -7.2 | 6 | -4.4 | 2(1) |
| $P_3$ | 9.35 | 4.65 | 5.8 | 2 |
| $M_1$ | 8.77 | 5.53 | 6.13 | 3 |
| $M_2$ | 8.56 | 5.9 | 6.13 | 3 |
| $M_3$ | 8.4 | 5.93 | 5.87 | 3 |
| $M_4$ | 7.7 | 5.35 | 4.9 | 2 |
| Dirk's Towers DT6 | *N. albivenator* | | | |
| $P^3$ | 10.82 | 5.65 | 6.93 | 3 |
| $M^1$ | 8.9 | 8.07 | 7.93 | 3 |
| $M^2$ | 8.47 | 7.73 | 7.23 | 3 |
| $M^3$ | 8.2 | 6.93 | -6.23 | 2(3) |
| $M^4$ | 7.15 | 5.8 | 4.5 | 2 |
| Upper Site | *N. superior* | | | |
| $P^3$ | 11.85 | 6.6 | 8.15 | 2 |
| $M^1$ | 9.75 | 9.2 | 8.8 | 2 |
| $M^2$ | 8.6 | -8.23 | 7.75 | 4(3) |
| $M^3$ | 8.4 | 7.72 | 6.7 | 3 |
| $M^4$ | 7.7 | 6.4 | 4.8 | 2 |
| Waynes Wok | *N. crassirostrum* | | | |
| $P^3$ | -12.52 | 6.26 | 7.36 | 8(9) |
| $M^3$ | 9.16 | 8.8 | 8.71 | 12 |
| $M^2$ | 8.73 | 8.07 | 7.74 | 11 |
| $M^3$ | 8.37 | 7.38 | 6.84 | 5 |
| $M^4$ | 7.42 | 6.34 | 5.11 | 5 |
| $P_3$ | 10.33 | -5.28 | 6.01 | 7(6) |
| $M_1$ | 9.65 | 6.05 | 6.68 | 4 |
| $M_2$ | 9.3 | 6.68 | 6.55 | 4 |
| $M_3$ | 9 | 6.9 | 6.2 | 1 |
| $M_4$ | 9 | 6.1 | 5.4 | 1 |
| Camel Sputum | *N. crassirostrum* | | | |
| $P^3$ | 12 | 6.08 | 7.28 | 6 |
| $M^1$ | 9.1 | 8.36 | 8.44 | 5 |
| $M^2$ | 8.77 | 8.47 | 8.23 | 10 |
| $M^3$ | 8.49 | 7.66 | 7.01 | 7 |
| $M^4$ | 7.63 | 6.6 | 4.85 | 3 |
| $P_3$ | 10.63 | 5.37 | 6.17 | 3 |
| $M_3$ | 9.07 | 6.07 | 6.77 | 3 |
| $M_2$ | 8.73 | 6.67 | 6.57 | 4 |
| $M_3$ | 8.57 | 6.57 | 6.07 | 4 |
| $M_4$ | 8.4 | 6.22 | 5.5 | 5 |
| Mike's Menagerie | cf. *N. crassirostrum* | | | |
| $P_3$ | 12.38 | 5.93 | 6.95 | 2 |
| $M_1$ | 8.75 | 8.35 | 8.75 | 2 |
| $M_2$ | 8.55 | 8.1 | 8.15 | 2 |
| $M_3$ | 8.7 | 8.18 | 7.8 | 2 |
| LSO | cf. *N. albivenator* | | | |
| $M^1$ | 8.85 | -7.9 | 8.2 | 2(1) |
| $P_3$ | 8.4 | 5 | 5.4 | 1 |
| $M_1$ | 9 | 5 | 5.3 | 1 |
| $M_2$ | 8.9 | 5.6 | 5.3 | 1 |
| $M_3$ | 8.3 | 5.9 | 5.4 | 1 |
| $M_1$ | 7.8 | 5.3 | 4.9 | 1 |
| Neville's Garden | *N.* sp. | | | |
| $P^3$ | 11.87 | 5.93 | 7.02 | 3 |
| $M^1$ | 8.4 | 7.95 | 8 | 2 |
| | | | | |
| Outasite | *N.* sp. | | | |
| $P^3$ | 13.13 | 6.3 | 7.7 | 2 |
| Judys Jumping Joint | cf. *N. crassirostrum* | | | |
| $P^3$ | 12.45 | 5.9 | 7.35 | 2 |
| Hiatus (skull) | *N.* sp. | | | |
| $M^1$ | 8.6 | 8 | -8 | 1(2) |
| $M^2$ | 8.1 | 7.35 | 7.25 | 2 |
| $M^3$ | 7.6 | 6.55 | 6.15 | 2 |
| $M^4$ | 6.65 | 5.45 | 3.95 | 2 |

APPENDIX 3 . Data for bivariate analyses of P3, M1

| Specimen no. | Locality | lP3 | wP3 | lM1 | aM1 | pM1 | P3 l/pw | M1 l/pw |
|---|---|---|---|---|---|---|---|---|
| SAMP19951 | *N. snideri* | 11 | 7.15 | | | | 1.54 | |
| SAMP19951 | type | 11.6 | 7.05 | 9.6 | 8.2 | 8.5 | 1.65 | 1.13 |
| NMV8993 | | | | 8.55 | 7.3 | 7.3 | | 1.17 |
| NMV8994 | | | | 9.6 | 7.95 | 8.2 | | 1.17 |
| AR16775 | White Hunter | 10.4 | 6.65 | 9.3 | 7.2 | 7.3 | 1.56 | 1.27 |
| QMF51337 | | 11.1 | 7 | 9.5 | 7.6 | 7.7 | 1.59 | 1.23 |
| AR17188 | | 10.4 | 6.5 | 9.1 | 7.5 | 7.7 | 1.60 | 1.18 |
| QMF51338 | | 11.3 | 7.3 | | | | 1.55 | |
| QMF51339 | | | | 9.55 | 7.9 | 8.2 | | 1.16 |
| QMF13093 | Dirks Towers | 10.5 | 7 | 8.4 | 8 | 7.5 | 1.50 | 1.12 |
| QMF20035 | | 11 | 6.7 | 9.1 | 8.2 | 8.7 | 1.64 | 1.05 |
| QMF20037 | | 10.95 | 7.1 | 9.2 | 8 | 7.6 | 1.54 | 1.21 |
| QMF24138 | Quantum Leap | 10.5 | 6.9 | 9 | 7.6 | 8.4 | 1.52 | 1.07 |
| QMF40276 | Upper site | 12 | 7.5 | 10 | 8.9 | 8.8 | 1.60 | 1.14 |
| QMF40276* | type | 11.7 | 8.6 | 9.5 | 9.5 | 8.8 | 1.36 | 1.08 |
| QMF51346 | Waynes Wok | 12.4 | 7.8 | 8.7 | 8.8 | 9 | 1.59 | 0.97 |
| QMF51348 | | | | 9 | 8.4 | 8.4 | | 1.07 |
| QMF51349 | | 11.9 | 6.75 | 9.3 | 8.5 | 8.4 | 1.76 | 1.11 |
| QMF51351 | | 13.4 | 7.6 | 10.2 | 9.3 | 9.2 | 1.76 | 1.11 |
| QMF51350 | | 13.8 | 7.5 | | | | 1.84 | |
| QMF51345 | | | | 9.2 | 9.3 | 8.9 | | 1.03 |
| QMF51347 | | | | 9.2 | 8.2 | 8.3 | | 1.11 |
| AR12858 | | | | 9.3 | 9.5 | 9.4 | | 0.99 |
| QMF30756 | | 12.1 | 7.7 | | | | 1.57 | |
| QMF30757 | | | | 9 | 9.1 | 8.8 | | 1.02 |
| QMF30758 | | | | 9 | 8.7 | 8.2 | | 1.10 |
| QMF31462r | type | 11.8 | 7 | 8.8 | 8.4 | 8.5 | 1.69 | 1.04 |
| QMF31462l | | 11.75 | 6.9 | 8.9 | 8.6 | 8.7 | 1.70 | 1.02 |
| QMF31480 | | 12.7 | 7.6 | 9.4 | 8.8 | 8.7 | 1.67 | 1.08 |
| AR8686 | Camel Sputum | 11.45 | 6.9 | 8.75 | 8 | 8 | 1.66 | 1.09 |
| QMF51357 | | 12.55 | 7.6 | | | | 1.65 | |
| QMF51359 | | | | 8.55 | 7.9 | 8 | | 1.07 |
| QMF20497 | | | | 9.7 | 9.1 | 9.2 | | 1.05 |
| QMF20574 | | 11.4 | 7.2 | 9.3 | 8.8 | 9.1 | 1.58 | 1.02 |
| QMF40279l | | 12.3 | 6.8 | 9.3 | | | 1.81 | |
| QMF40279r | | 12 | 7.3 | 8.3 | 8 | 7.9 | 1.64 | 1.05 |
| QMF30303l | | 12.25 | 7.7 | 8.7 | 8.5 | 8.3 | 1.59 | 1.05 |
| QMF30303r | | 12.5 | | 8.9 | 8.1 | 8.3 | | 1.07 |
| AR12946 | | 12.5 | 7.45 | | | | 1.68 | |
| AR13374 | | 11.8 | 7.3 | | | | 1.62 | |
| AR16838 | | 12.3 | 7.25 | | | | 1.70 | |
| QMF51364 | Mikes Menagerie | 13.3 | 7.4 | 8.8 | 8.4 | 8.5 | 1.80 | 1.04 |
| AR12868 | | 11.45 | 6.5 | | | | 1.76 | |
| QMF51354 | DT | 11.8 | 6.8 | | | | 1.74 | |
| QMF36342 | | 12 | 7.2 | | | | 1.67 | |
| QMF51356 | | | | 8.7 | 8.4 | 7.9 | | 1.10 |
| QMF51373 | | 11.1 | 6.75 | | | | 1.64 | |

| Specimen no. | Locality | lP3 | wP3 | lM1 | aM1 | pM1 | P3 l/pw | M1 l/pw |
|---|---|---|---|---|---|---|---|---|
| QMF36350 | DT | | | 8.8 | 7.9 | 7.8 | | 1.13 |
| QMF51374 | Nev Garden | 11.55 | 6.9 | | | | 1.67 | |
| QMF23014 | | 11.95 | 7.3 | 8.6 | 7.5 | 7.95 | 1.64 | 1.08 |
| QMF23201* | | 12.1 | 6.85 | 8.2 | 8.4 | 8 | 1.77 | 1.03 |
| QMF51372 | Judys JJ | 12.4 | 7.2 | | | | 1.72 | |
| QMF51376 | | 12.5 | 7.5 | | | | 1.67 | |
| QMF30724* | JH | >12.6 | 8.5 | | | | | |
| QMF23216+ AR91 | Hiatus | | | 8.6 | 8 | 7.8 | | 1.10 |
| no. | | lp3 | pwp3 | lm1 | awm1 | pwm1 | p3 l/pw | m1 l/pw |
| QMF40278 | paratype | 9.2 | 5.7 | 8.3 | 5.4 | 6.3 | 1.61 | 1.32 |
| QMF51342 | White Hunter | | | 9.5 | 5.6 | 6 | | |
| QMF51343 | | 9.5 | 5.9 | 8.5 | 5.6 | 6.2 | 1.61 | 1.37 |
| QMF30700 | | 10.1 | 6.8 | 8.7 | 6.3 | 7 | 1.49 | 1.24 |
| QMF30506 | D6 | 8.2 | 4.9 | 9 | 5 | 5.3 | 1.67 | 1.70 |
| QMF51375 | paratype | 11.4 | 6.4 | 10.3 | 6.8 | 7 | 1.78 | 1.47 |
| AR9711 | Waynes Wok | 10.1 | 6.2 | | | | 1.63 | |
| AR10789 | | 10.9 | 6.4 | | | | 1.70 | |
| AR10639 | | 10.4 | 5.8 | | | | 1.70 | |
| AR10638 | | 9.9 | 5.8 | | | | 1.71 | |
| AR11866 | | 10.3 | 5.9 | | | | 1.75 | |
| QMF24507 | | | | 9.9 | 6.2 | 6.9 | | 1.43 |
| QMF30762 | | | | 9.3 | 5.9 | 6.1 | | 1.52 |
| QMF30836 | | | 5.6 | 9.1 | 6.3 | 6.7 | | 1.36 |
| QMF51362 | Camel Sputum | 10.8 | 6.5 | 9.5 | 5.8 | 6.9 | 1.66 | 1.38 |
| QMF51363 | | 10.3 | 6.1 | 8.7 | 6.3 | 6.7 | 1.69 | 1.30 |
| QMF12461 | | 10.8 | 5.9 | 9 | 6.1 | 6.7 | 1.83 | 1.34 |
| QMF51365 | Mikes Menagerie | 11.2 | 6.4 | 10 | 6.8 | 6.9 | 1.75 | 1.45 |
| AR10703 | | | | 8.9 | 6.1 | 6.6 | | 1.35 |
| AR9742 | | 10.1 | 4.9 | | | | 2.06 | |
| AR9743 | | | | 9.9 | 6.4 | 6.7 | | 1.48 |
| AR9915 | | | | 10 | 6.2 | 6.5 | | 1.54 |
| AR12869 | | | | 9.7 | 6.5 | 6.7 | | 1.45 |
| QMF24218 | D5 | 10.45 | 6.7 | 8.8 | 6.5 | 6.8 | 1.56 | 1.29 |
| QMF51373 | StickyBeak | 11.1 | 6.75 | | | | 1.64 | |
| QMF51366 | Roo | | | 9.4 | 5.8 | 6.7 | | 1.40 |
| QMF40251 | LSO | 8.4 | 5.4 | 9 | 5 | 5.3 | 1.56 | 1.70 |
| QMF40281 | Outasite | 12.35 | 7.4 | | | | 1.67 | |
| QMF40282 | | 13.9 | 8 | | | | 1.74 | |

# PLEISTOCENE PALAEOECOLOGY AND ENVIRONMENTAL CHANGE ON THE DARLING DOWNS, SOUTHEASTERN QUEENSLAND, AUSTRALIA.

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Price, G.J. & Sobbe, I.H. 2005 05 31: Pleistocene palaeoecology and environmental change on the Darling Downs, southeastern Queensland, Australia. *Memoirs of the Queensland Museum* **51**(1): 171-201. Brisbane. ISSN 0079-8835.

A diverse Pleistocene fossil assemblage was recovered from a site (QML1396) exposed in the southern banks of Kings Creek, Darling Downs, southeastern Queensland. The site includes both high-energy lateral channel deposits and low-energy vertical accretion deposits. The basal fossil-bearing unit is laterally extensive, fines upward and its geometry and sedimentary structures suggest deposition within a main channel. The coarse channel fill passes upward into overbank levee deposits made up of lenticular sandy-shelly strata alternating with muds. Several taphonomic biases relating to preservation of different faunal groups and skeletal elements was discerned. Biases may be related to fluvial sorting of the assemblage, but causes for differences between the preservation and accumulation of mammal versus non-mammal terrestrial vertebrates remain unclear. In general, the vertebrate material was accumulated and transported into the deposit from the surrounding proximal floodplain. The assemblage is composed of 44 species including molluscs, teleosts, anurans, chelids, squamates, and small and large-sized mammals. Palaeoenvironmental analysis suggests that a mosaic of habitats, including vine thickets, scrublands, open sclerophyllous woodlands interspersed with sparse grassy understories, and open grasslands, were present on the floodplain during the late Pleistocene. From sedimentological and ecological data, it is evident that increasing aridity during the late Pleistocene led to woodland and vine thicket habitat contraction, and grassland expansion on the floodplain. At present, there is no evidence to support the suggestion that the retraction of late Pleistocene Darling Downs habitats was due to anthropogenic factors. ❐*Pleistocene, Darling Downs, Kings Creek catchment, taphonomy, sedimentology, habitat change, megafauna.*

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The Darling Downs, southeastern Queensland, contains some of the most extensive and significant Pleistocene megafauna deposits in Australia. Molnar & Kurz (1997) recognised more than 50 specific Darling Downs localities where fossil material has been collected. Species lists are dominated by large-sized taxa such as *Diprotodon* spp., *Macropus titan*, and *Protemnodon* spp. (Bartholomai, 1976; Molnar & Kurz, 1997). More recently, Roberts et al. (2001a) suggested that some Darling Downs fossil deposits are among the youngest deposits known to contain megafauna remains. As Pleistocene fossils have been known from the Darling Downs since the 1840's (Owen, 1877a), it is generally assumed that the palaeoenvironmental record is well established. Darling Downs palaeoenvironments have been interpreted as consisting of vast grasslands and woodlands, as indicated by an abundant and diverse range of grazing and browsing megafauna species preserved in the deposits (Bartholomai, 1973; 1976; Archer, 1978; Molnar & Kurz, 1997). However, Molnar & Kurz (1997) recognised a collecting bias towards large-sized species suggested that smaller-sized taxa have generally been overlooked. Additionally, there have been few attempts to document sedimentologic and stratigraphic aspects of the Pleistocene deposits of the region. Macintosh (1967), Gill (1978), and Sobbe (1990) provided limited stratigraphies for sections along creeks from the southern Darling Downs, introducing the terms 'Toolburra silt', 'Talgai pedoderm' and 'Ellinthorpe clay'. However, those names have not seen subsequent use and are not considered valid stratigraphic units (Molnar & Kurz, 1997). Taphonomic aspects of the deposits are also largely unknown. Molnar et al. (1999) reported a deposit that contained articulated remains of

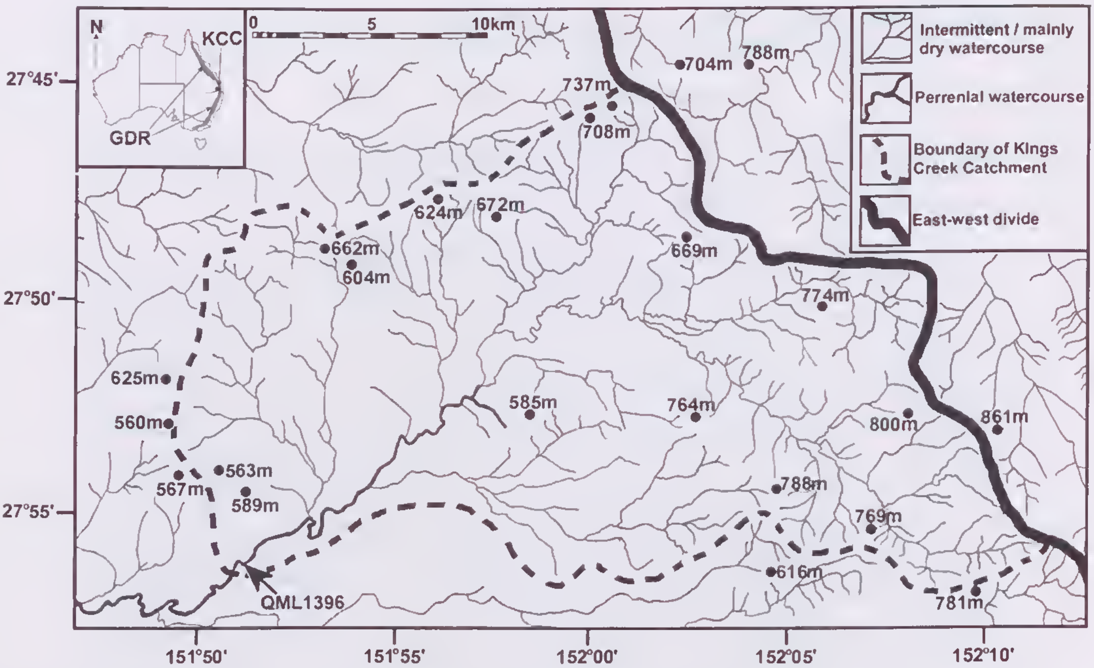

FIG. 1. Modern Kings Creek Catchment with heights (metres) of surrounding peaks, and the current study area, QML1396 (GDR: Great Dividing Range; KCC: Kings Creek Catchment).

megafauna taxa, but noted that articulation of fossil skeletal material was relatively uncommon in the region. Collectively, palaeonvironmental interpretations of the region are limited owing to the poor understanding of stratigraphic, sedimentologic and taphonomic aspects of the deposits, as well as past collecting biases that have focused on the recovery of large-sized taxa.

Recent systematic collecting of a deposit (site QML1396) from the Darling Downs targeted the recovery of both large and small-sized taxa. Consequently, a comprehensive faunal assemblage has been uncovered. Typical Darling Downs megafauna taxa are represented, as well as an extensive small-sized fauna that includes a diverse range of molluscs, teleosts, anurans, chelids, squamates, and small and large-sized mammals. Such assemblages are beginning to demonstrate that Pleistocene Darling Downs palaeoenvironments were much more complex than previously thought (Price, 2002; Price, 2004; Price et al., in press). The aim of the present paper is to describe a multidisciplinary approach integrating sedimentologic and taphonomic information, as well as ecological information obtained from mammals and non-mammals that occur in the deposit. The combined data sets allow a better understanding of Pleistocene palaeoenvironments and possible climate change in the region. In light of the ongoing debate over the causes and timing of Australian megafauna Pleistocene extinctions (e.g. Field & Fullager, 2001; Roberts et al. 2001a, b; Brook & Bowman, 2002; 2004; Barnosky et al., 2004; Johnson & Prideaux, 2004; Wroe, 2004), studies of Pleistocene palaeoenvironments may provide important information that could aid in elucidating the causes of faunal change.

## SETTING

The Darling Downs, southeastern Queensland, encompasses low rolling hills and plains west of the Great Dividing Range. Fluvial sediments of the region consist of clays, silts and sands that are generally derived from the erosion of Mesozoic sandstones (Gill, 1978) and Miocene basalts of the Great Dividing Range (Woods, 1966). Site QML1396 is exposed laterally over 70 metres in the southern bank of Kings Creek, southern Darling Downs (Fig. 1). The modern Kings Creek catchment, bounded to the north, east and south by the Great Dividing Range, is fed by several mainly dry or intermittent watercourses (Fig. 1), resulting in a relatively small geographic sampling area. Considering relatively low rates of erosion and uplift since the late Pleistocene, it is unlikely that the Pleistocene Kings Creek catchment was markedly larger than present (Price, 2004). Therefore, it is unlikely that material from QML1396 was subjected to long distance fluvial transport from a significantly larger catchment.

## METHODS

SEDIMENTOLOGY. A section was measured representing the entire depositional sequence exposed in the creek bank. Stratigraphic horizons were distinguished on the basis of lithological criteria. Sediment samples were collected from each stratigraphic horizon for the purpose of grain size analysis. The sediment samples were disaggregated by applying alternating cycles of bleach and detergent. Disaggregated sediments were dried and sieved according to Wentworth size classes (-2 to +4 phi; Wentworth, 1922). Differentiation and identification of calcrete followed Arakel (1982).

One unit (Horizon D; Fig. 2) contained abundant lenses of the freshwater gastropod, *Thiara (Plotiopsis) balonnensis*. The orientations of 100 gastropods from one such lense were measured to determine whether fluvial transport acted on the gastropods in influencing their final orientations. The angle was measured between north and the spire of the shell (long direction).

TAPHONOMY. Cranial and post-cranial elements from horizons B and D formed the basis for the taphonomic study. The units of element representation were NISP (number of identified specimens), MNI (minimum number of individuals- as determined by counting the most abundant element referable to a particular species represented in the sample), and MNE (minimum number of elements) (following Andrews, 1990). For vertebrates, calculation of MNI was based on maxillary and dentary remains, except in the case of fish, frogs, turtles and some squamates where vertebrae, pelvi, shell fragments and osteoderms were used respectively.

Several indices were used to characterise and describe the taphonomic features of the assemblage based on the skeletal remains of large and small mammals, as well as squamates.

*Relative abundance.* Relative abundance of each skeletal element was calculated following the equation:

$$Ri = Ni \times 100/(MNI)Ei \qquad (1)$$

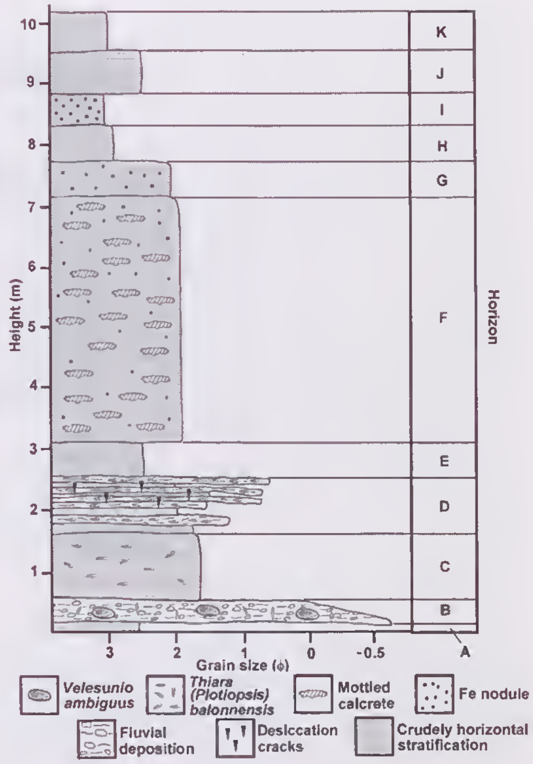

FIG. 2. Measured section of QML1396.

following Andrews (1990), where R = relative abundance of element i, n= minimum number of element i, MNI = minimum number of individuals, and E = expected number of element i in the skeleton. The relative abundance equation allows the comparison of different skeletal elements that occur in varied proportions in mammal or squamate skeletons. Determination of E was based on modern comparative skeletons for mammals and follows Greer (1989) for squamates.

*% Post-crania to crania.* The percentage of post-crania to crania follows Andrews (1990). The number of post cranial elements (femur, tibia, humerus, radius and ulna [n=10]) are compared to cranial elements (dentary, maxilla and molars [n=16 for murids, 20 for marsupials, 4 for squamates]). As the ratio of post crania to crania is not 1:1, the post crania and crania are corrected by 10/16 for murids, 10/20 for marsupials, and 10/4 for squamates, to match numbers of skeletal elements.

*% Distal element loss.* Distal element loss was measured by comparing the number of distal limbs (tibia and radii) to proximal limbs (femura and humeri). The ratio measures preferential loss of distal limbs.

*% Fore limb element loss.* Limb element loss was measured by comparing the number of fore limb bones (humeri and radii) to hind limb bones (femora and tibiae). The ratio measures any preferential loss of fore limbs.

*% Molar tooth loss.* Molar tooth loss was measured by comparing the number of isolated molars in the sample to the number of available alveoli spaces in the dentaries or maxillae. Values >100% indicates the loss or destruction of dentaries or maxillae (Andrews, 1990).

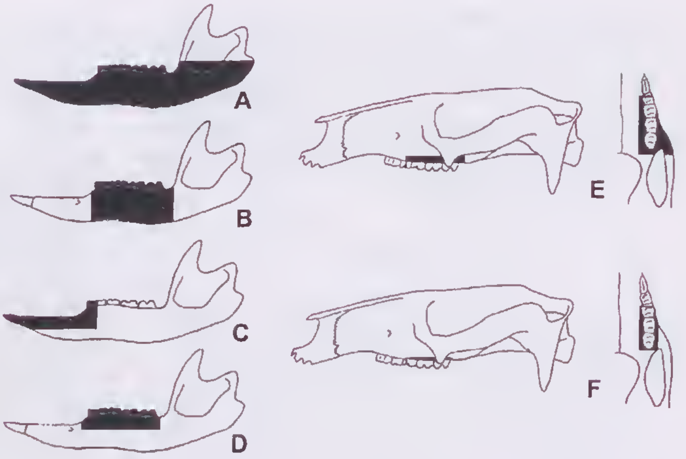

FIG. 3. Mammal cranial breakage categories from the QML1396 assemblage (shaded areas indicates the preserved portions). Refer to table 5 for definition of the breakage categories.

*% Relative loss of molar tooth sites.* Relative loss of molar tooth sites was calculated by comparing the actual number of tooth sites in the sample (regardless of whether they contain teeth or not) to the theoretical number of molar tooth sites assuming that there was no breakage. Relative loss of molar tooth sites was used as an independent check for cranial breakage (Kos, 2003).

*Cranial modifications.* The cranial breakage patterns of squamates and mammals were identified within the deposit following Andrews (1990; Figs 3 & 4). The percentage of representation of each pattern was calculated to attempt to distinguish any differences between large and small-sized mammals, as well as between agamid and scincid lizards.

*Breakage of post-crania.* Identification of breakage patterns of major post-cranial limb bones (humeri, femora, ulnae and tibiae) follows Andrews (1990). Broken limb bones were scored as to whether the represented proximal, shaft, or distal portions.

*Comparison to "Voorhies Groups".* The experimental work of Voorhies (1969) and Dodson (1973), on hydraulic dispersive mechanisms for mammal bones, forms a comparative framework for explaining the dispersal of skeletal elements in the fossil record. Their studies documented transportability of different skeletal elements at constant rates of water flow, and concluded that different skeletal elements disperse at different rates in relation to stream flow velocity. Differences in the dispersal potential of skeletal elements reflect the density and shape of the elements. Relative abundance of elements from the QML1396 assemblage were compared to the published results for skeletal element transportability in hydraulic systems.

FAUNA. Fossils were recovered by in situ collecting and sieving of sediment specifically to target smaller specimens. Fossil material was generally restricted to Horizons B and D (Fig. 2). All fossil material collected was labeled according to the stratigraphic horizon where it was collected. Sediments were washed using graded sieves of 10mm to 1mm. Approximately 700kgs of sediment were processed from Horizon D, and 200kgs of sediment were processed from Horizon B. The disparity in collecting efforts between Horizons D and B reflects the position of Horizon B below the present water table. Collecting of Horizon B was generally possible only during drought conditions. Most material was collected from Horizon B in November and December 2002.

Descriptions of the fossil fauna have been limited to diagnostic features in most cases. Molluscan shell terminology follows Smith and Kershaw (1979). Squamate cranial morphology terminology follows Withers and O'Shea (1993). Marsupial dental nomenclature follows Luckett (1993), where the adult unreduced cheek tooth

TABLE 1. Description of stratigraphic horizons at QML1396.

| Horizon (height) | Fill type | Mean $\phi$ | Characteristics | Notes |
|---|---|---|---|---|
| A (0-0.2m) | Fine montmorillonite clay | 2.65 | crudely horizontal bedding; poorly sorted, srtrongly fine skewed grains | pebbles to 20mm rare; shelly marterial rare; vertebrate material rare |
| B(0.2-0.6m) | coarse grain fill bed | -0.78-0.19 | fining upwards sequence; poorly sorted; finely skewed grains | Freshwater molluscs abundant; vertebrate material abundant; rounded basalt, calcrete and sandstone pebbles and cobbles abundant |
| C(0.6-1.7m) | brown-grey clay | 1.7 | crudely horizontal bedding, poorly to very poorly sorted; strongly finely skewed grains | Mollusc shell rare; vertebrate material rare |
| D (1.7-2.6m) | coarse to fine-sized quartz sand beds | 0.6-2.0 | Sand beds 3cm to 10cm thick overlain by laterally discontinuous horizontal and sloping shelly lenses 2-10cm thick; shell beds with desiccation cracks, in filled by fine clays; very poorly sorted, fine skewed grains | Freshwater gastropods and small bivalves common, large-sized bivalves rare; polymodal orientation of *Thiara* (*Plotiopsis*) *balonnensis* gastropods (Fig. 5); vertebrate material abundant; shell and vertebrate fossil material commonly cemented by calcrete |
| E (2.6-3.1m) | brown clay | 2.53 | Crudely horizontal bedding; poorly sorted, strongly fine skewed grains | Mollusc shell rare; vertebrate material rare |
| F (3.1-7.2m) | brown clay | 1.88 | Crudely horizontal bedding; in-situ, mottled, grey-white calcrete; iron nodules to 5mm diameter present; poorly sorted, strongly fine skewed grains | Mollusc shell rare; vertebrate material rare |
| G (7.2-7.7m) | black clay | 2.0 | Crudely horizontal bedding; iron oxides to 5mm diameter present; poorly sorted, strongly fine skewed grains | Organic rich clay; mollusc shell rare; vertebrate material rare |
| H (7.7-8.3m) | grey-white clay | 2.8 | Crudely horizontal bedding; poorly sorted, strongly fine skewed grains | Mollusc shell rare; vertebrate material rare |
| I (8.3-8.8mm) | grey-white clay | 3.0 | Crudely horizontal bedding; iron oxides to 5mm diameter present; poorly sorted, strongly fine skewed grains | Mollusc shell rare; vertebrate material rare |
| J (8.8-9.5m) | grey clay | 2.4 | Crudely horizontal bedding; poorly sorted, strongly fine skewed grains | Mollusc shell rare; vertebrate material rare |
| K (9.5-10.2m) | black clay | 2.98 | Moderately sorted, strongly fine skewed grains | Organic rich, likely altered by modern agriculture |

formula is P1-3 and M1-4 in both upper and lower dentitions. Marsupial dental morphology follows Archer (1976). Higher systematics follows Beesley et al. (1998) for molluscs, Glasby et al. (1993) for amphibians and reptiles, and Aplin and Archer (1987) for mammals. All material is deposited at the Queensland Museum (QMF: Queensland Museum Fossil; QML: Queensland Museum Locality).

DATING. Samples of charcoal and freshwater bivalves (*Velesunio ambiguus*) were submitted to ANSTO (Australia Nuclear Science and Technology Organisation; Lawson et al., 2000) for the purpose of AMS$^{14}$C dating. Only complete, conjoined bivalves were submitted for dating. Con-joined, apparently well-preserved bivalves are unlikely to have been reworked in comparison to disarticulated or fragmentary shell remains.

## RESULTS

SEDIMENTOLOGY. The entire deposit is characterised by a fining-upwards sequence (Fig. 2). The section is comprised of: 1) grey-white to black clays; 2) in-situ mottled calcretes; 3) iron nodules; 4) quartz sand in channel fills; 5) basalt, calcrete and sandstone pebbles and cobbles (predominantly in coarser fills); and 6) invertebrate and vertebrate fossils (Table 1). Freshwater bivalves (*Velesunio ambiguus* and *Corbicula (Corbiculina) australis*) and thiarid gastropods (*Thiaria (Plotiopsis) balonnensis*) are more abundant in coarser-grained horizons such as Horizon B and D, than fine-grained horizons. Vertebrate fossil material is generally restricted to Horizons B and D.

Horizon B exhibits the largest grain sizes (Fig. 2, Table 1). The horizon is laterally extensive, being recorded over approximately 70 metres. The majority of the lower portion of Horizon B is

TABLE 2. Species NISP and MNI for Horizons D and B at QML1396 (* Extinct on Darling Downs; ** Totally extinct).

| | Horizon D | | Horizon B | |
|---|---|---|---|---|
| Species | NISP | MNI | NISP | MNI |
| *Velesunio ambiguus* | 10+ | 5+ | 20+ | 10+ |
| *Corbicula (Cobiculina) australis* | 100+ | 100+ | 50+ | 50+ |
| *Thiara (Plotiopsis) balonnensis* | 1000+ | 1000+ | 50+ | 50+ |
| *Gyraulus gilberti** | 249 | 249 | 0 | 0 |
| *Coencharopa* sp.* | 9 | 9 | 0 | 0 |
| *Gyrocochlea* sp. 1* | 35 | 35 | 0 | 0 |
| *Gyrocochlea* sp. 2* | 5 | 5 | 0 | 0 |
| *Austrocuccinea* sp.* | 1 | 1 | 0 | 0 |
| *Xanthomelon pachystylum** | 1 | 1 | 0 | 0 |
| *Strangesta* sp.* | 1 | 1 | 0 | 0 |
| *Saladelos* sp.* | 1 | 1 | 0 | 0 |
| Teleost | 89 | 1 | 0 | 0 |
| *Limnodynastes tasmaniensis* | 8 | 8 | 0 | 0 |
| *L.* sp. cf. *L. dumerili* | 3 | 3 | 0 | 0 |
| ?*Limnodynastes* | 1 | 1 | 0 | 0 |
| *Neobatrachus sudelli* | 2 | 2 | 0 | 0 |
| *Kyarranus* sp.* | 1 | 1 | 0 | 0 |
| chelid | 4 | 1 | 0 | 0 |
| *Tympanocryptis "lineata"** | 15 | 4 | 0 | 0 |
| "*Sphenomorphus* group" sp. 1 | 19 | 13 | 0 | 0 |
| "*Sphenomorphus* group" sp. 2 | 6 | 2 | 0 | 0 |
| *Tiliqua rugosa** | 6 | 1 | 0 | 0 |
| *Cyclodomorphus* sp.* | 1 | 1 | 0 | 0 |
| *Varanus* sp. | 1 | 1 | 0 | 0 |
| *Megalania prisca*** | 4 | 1 | 0 | 0 |
| elapid | 14 | 1 | 0 | 0 |
| *Sminthopsis* sp. | 1 | 1 | 0 | 0 |
| *Dasyurus* sp. | 1 | 1 | 0 | 0 |
| *Sarcophilus* sp.* | 0 | 0 | 1 | 1 |
| *Thylacinus cynocephalus*** | 0 | 0 | 1 | 1 |
| *Perameles bougainville** | 1 | 1 | 0 | 0 |
| *Pe. nasuta* | 1 | 1 | 0 | 0 |
| *Diprotodon* sp.** | 0 | 0 | 1 | 1 |
| *Thylacoleo carnifex*** | 0 | 0 | 1 | 1 |
| *Aepyprymnus* sp. | 1 | 1 | 0 | 0 |
| *Troposodon minor*** | 0 | 0 | 2 | 2 |
| *Macropus agilis siva*** | 5 | 2 | 1 | 1 |
| *M. titan*** | 1 | 1 | 5 | 2 |
| *Protemnodon anak*** | 2 | 1 | 3 | 1 |
| *Pr. brehus*** | 2 | 1 | 1 | 1 |
| *Pseudomys* sp.* | 4 | 2 | 0 | 0 |
| *Rattus* sp. | 2 | 1 | 0 | 0 |
| unidentified murid | 182 | 26 | 0 | 0 |

TABLE 3. MNE and expected relative abundance of skeltal elements recovered from Horizons D & B at QML1396.

| | Horizon D | | | | | | Horizon B | |
|---|---|---|---|---|---|---|---|---|
| | <5kg mammals | | <5kg squamates | | >5kg mammals | | >5kg mammals | |
| skeletal element | n | % | n | % | n | % | n | % |
| dentary | 7 | 10.6 | 29 | 72.5 | 1 | 8.3 | 6 | 30 |
| maxilla | 7 | 10.6 | 17 | 42.5 | 4 | 33.3 | 0 | 0 |
| incisor | 101 | 76.5 | na | na | 2 | 8.3 | 4 | 20 |
| molar | 97 | 19 | na | na | 23 | 24 | 19 | 11.9 |
| femur | 11 | 16.7 | 0 | 0 | 0 | 0 | 0 | 0 |
| tibia | 18 | 27.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| pelvis | 2 | 3 | 0 | 0 | 1 | 8.3 | 0 | 0 |
| calcaneum | 10 | 15.2 | 0 | 0 | 1 | 8.3 | 0 | 0 |
| humerus | 4 | 6.1 | 2 | 5 | 0 | 0 | 0 | 0 |
| radius | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| ulna | 8 | 12.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| ribs | 6 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 |
| vertebra | 57 | 3.9 | 196 | 12.6 | 20 | 7.6 | 0 | 0 |
| phalange | 53 | 3.5 | 2 | 0.2 | 1 | 0.4 | 2 | 0.4 |

below the modern watertable. Large-sized bivalves (*Velesunio ambiguus*) are more abundant in Horizon B than in Horizon D.

Horizon D is represented by a series of coarse to fine quartz sand beds that are overlain by laterally discontinuous horizontal and sloping shelly lenses (Fig. 2, Table 1). Desiccation cracks within the shelly lenses are filled with fine clay. A rose diagram plot of the orientations of freshwater gastropods (*Thiaria (Plotiopsis) balonnensis*) indicates a polymodal distribution (Fig. 5).

In-situ, non-reworked mottled calcretes occur in Horizon F. Iron oxide nodules were also present within that horizon, as well as Horizons G and I. Few sedimentary structures other than crudely horizontal bedding were observed within other stratigraphic horizons (Fig. 2, Table 1).

TAPHONOMY. Vertebrate fossil material was generally restricted to Horizons B and D. Fossil material from other horizons is poorly preserved. Hence, the following taphonomic observations are based on fossil material from Horizons B and D. Additionally, a large number of unidentifiable bone fragments were collected from the main fossiliferous horizons. Few meaningful data could be obtained from those fragments, hence, the taphonomic component was based solely on identifiable elements.

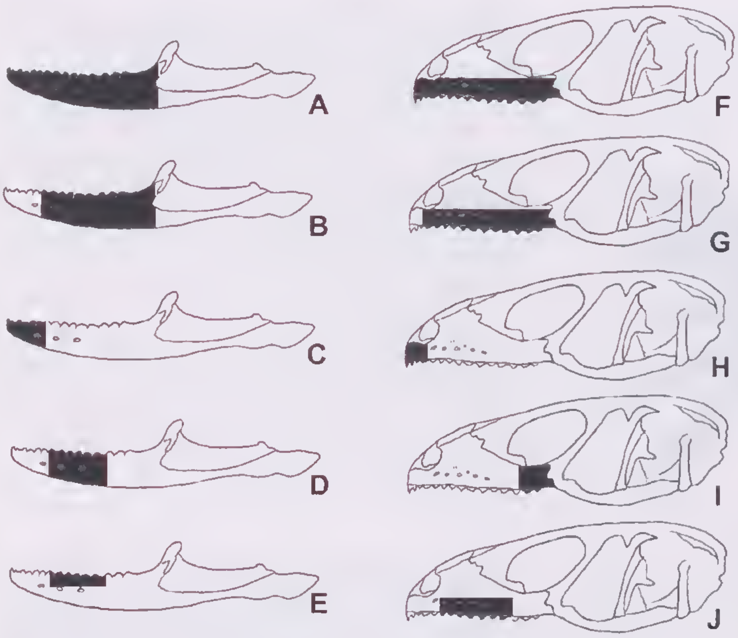

FIG. 4. Squamate cranial breakage categories from the QML1396 assemblage (shaded areas indicates the preserved portions). Refer to table 6 for definition of the breakage categories.

*Species representation.* In terms of diversity, land snails, frogs, squamates and small mammals dominated the terrestrial faunal component represented in the Horizon D assemblage (Fig. 6, Table 2). Large mammals were the least represented size group in Horizon D, and the only represented terrestrial group in Horizon B (Fig. 6).

*Skeletal relative abundance.* Skeletal relative abundance was calculated for large and small mammals, as well as squamates (Table 3). In terms of relative abundance, cranial elements of squamates are the most well represented element for the three major groups of terrestrial animals in Horizon D. However, overall, the relative abundance of all skeletal elements suggests that they are underrepresented. Incisors are the most abundant cranial element recovered for small mammals in Horizon D, but that may reflect a processing bias as incisors are among the most easily identifiable small mammal remains (Andrews, 1990). The dentary is a relatively robust element and that may account for the higher proportion of skeletal elements for squamates and mammals in both horizons. There is a greater loss of squamate post-cranial remains in comparison to mammals in Horizon D. Small-sized terrestrial vertebrates were not recovered from Horizon B.

*Skeletal modifications.* Indices of skeletal modifications (Table 4) indicate that there is significant loss of post-cranial elements in each horizon. Horizon B is completely devoid of large-sized mammal limb bone elements. For Horizon D mammals there was a slight loss of proximal limbs (femora and humeri) in comparison to distal limbs (tibiae and radii). Additionally, there was a significant loss of forelimb elements in comparison to hind limbs. Reasons for the loss of different limb elements remain unclear, but may simply be the result of using statistically small numbers for comparison. Indices for the loss of molar teeth and molar tooth sites indicate the loss or destruction of dentaries or maxillae for mammals within each main fossiliferous horizons (Table 4).

*Breakage of crania.* There were no complete mammal skulls or dentaries recovered from the deposit (Table 5). Mammal dentary breakage appears slightly greater for Horizon D than Horizon B. A high proportion of broken maxillae retained only a small portion of the zygomatic arch in Horizon D.

TABLE 4. Skeletal modifications for arbitary faunal groups from QML1396

| skeletal modification | Horizon D | | | Horizon B |
|---|---|---|---|---|
| | <5kg mammals | < 5kg squamates | >5kg mammals | >5kg mammals |
| % post-crania to crania | 24.2 | 17 | 0 | 0 |
| % distal element loss | 133.3 | 0 | 0 | 0 |
| % fore limb loss | 41.4 | 0 | 0 | 0 |
| % molar tooth loss | 741 | na | no available tooth spaces | 150 |
| % relative loss of molar tooth sites | 275 | na | 160 | 109 |

FIG. 5. Orientations of *Thiara (Plotiopsis) balonnensis* gastropods (n: 100) from a single shelly lense within Horizon D at QML1396.

TABLE 5. Mammal cranial modifications from QML1396 (following breakage patterns Fig. 3)

| Breakage pattern | Horizon D | | Horizon B |
|---|---|---|---|
| | <5kg mammals | > 5kg mammals | <5kg mammals |
| % dentary with ascending ramus mostly absent (Fig. 3A) | 0 | - | 17 |
| % dentary with ascending and anterior ramus mostly absent (Fig. 3B) | 33 | - | 50 |
| % dentary with anterior ramus only, lacking inferior border(Fig. 3C) | 67 | - | 0 |
| % dentray with horizontal ramus only lacking inferior border (Fig. 3D) | 0 | - | 33 |
| % maxilla with most of zygomatic missing (Fig. 3E) | 100 | 75 | - |
| % maxilla alveoli or tooth row only (Fig. 3F) | 0 | 25 | - |

There also were no complete squamate skulls or dentaries preserved (Table 6). Reasonably complete dentaries are equally abundant in both agamids and scincids. However, particular breakage patterns appear to be exclusive to each squamate family (Table 6). For agamids, the central portion of the dentary and central to anterior portions of the maxilla are preserved; for skinks, the majority of the dentary and central to posterior portions of the maxilla are preserved. Overall, scincid dentaries are more completely preserved than those of agamids. However, a reverse trend exists for the maxillae, where a greater portion are preserved in agamids than scincids (Table 6).

*Breakage of post crania.* There were no complete major limb bones (i.e. humeri, ulnae, femora, tibiae) preserved in the deposit (Table 7). Additionally, major limb bones were mostly restricted to small-sized mammals from Horizon D. Most broken limb bones have transverse fractures perpendicular to the bone surface and indicate post-mortem fracturing of dry or fossilised bone (Johnston, 1985). Additionally, the broken ends of the limb bones do not appear to be significantly rounded or abraded, suggesting minimal reworking or transport of fossil material. Squamates were represented by only two proximal humeri from Horizon D. However, high numbers of unidentifiable limb element shafts from small-sized animals (n~120) could equally be referable to either squamates or mammal post-cranial limb bones.

*Comparison to "Voorhies Groups".* For Horizon D small-sized mammals, the majority of the skeletal elements comprise those that would disperse in the middle to late categories of dispersal (Table 8). Additionally, the high number of limb bone shafts (see earlier discussion) would presumably fit within that category of stream transportability. There was no clear trend for small-sized squamates from

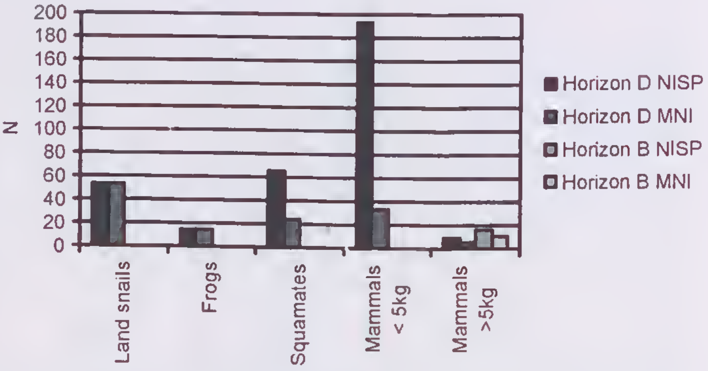

FIG. 6. Comparison of MNI and NISP of terrestrial taxa from Horizons B and D at QML1396.

TABLE 6. Squamate cranial modifications from Horzon D, QML1396

| Breakage pattern | agamids | skinkids |
|---|---|---|
| % dentary mostly complete (Fig. 4A) | 38 | 43 |
| % posterior portion of dentary only (Fig. 4B) | 0 | 33 |
| % anterior portion of dentary only (Fig. 4C) | 0 | 24 |
| % central portion of dentary only (Fig. 4D) | 38 | 0 |
| % central portion of dentary only, lacking inferior border (Fig. 4E) | 25 | 0 |
| % premaxilla and maxilla mostly complete (Fig. 4F) | 22 | 0 |
| % maxilla mostly complete, lacking premaxilla (Fig. 4G) | 67 | 0 |
| % premaxilla only (Fig. 4H) | 11 | 0 |
| % posterior portion of maxilla only(Fig. 4I) | 0 | 25 |
| % central portion of maxilla only (Fig. 4J) | 0 | 75 |

TABLE 7. Breakage patterns of major post cranial limb bones from Horizon D, QML1396.

| | <5kg mammals | | <5kg squamates | |
|---|---|---|---|---|
| Limb bone | n | % | n | % |
| *humerus* | | | | |
| complete | 0 | 0 | 0 | 0 |
| proximal | 1 | 17 | 2 | 100 |
| shaft | 4 | 66 | 0 | 0 |
| distal | 1 | 17 | 0 | 0 |
| *femur* | | | | |
| complete | 0 | 0 | 0 | 0 |
| proximal | 7 | 39 | 0 | 0 |
| shaft | 0 | 0 | 0 | 0 |
| distal | 11 | 61 | 0 | 0 |
| *ulna* | | | | |
| complete | 0 | 0 | 0 | 0 |
| proximal | 8 | 73 | 0 | 0 |
| shaft | 2 | 18 | 0 | 0 |
| distal | 1 | 9 | 0 | 0 |
| *tibia* | | | | |
| complete | 0 | 0 | 0 | 0 |
| proximal | 0 | 0 | 0 | 0 |
| shaft | 3 | 15 | 0 | 0 |
| distal | 18 | 85 | 0 | 0 |

Horizon D. For large-sized mammals from Horizon D, the majority of elements comprised those that are progressively the last to be transported in flowing water. Horizon B is dominated by middle-late transported elements (i.e. dentaries; Table 8).

## SYSTEMATIC PALAEONTOLOGY

A much abbreviated treatment of the systematic palaeontology is given in order to document the specific material for which taxa are assigned. The fundamental purpose of the taxonomic work was to facilitate ecologic and assemblage information. Thus, only the diagnostic features of the material are provided, as all faunal elements are well known fossil or extant taxa. At the end of each description the primary authority used for identification is given in closed brackets. Two other publications deal with the amphibians (Price et al., in press) and the bandicoots (Price, 2004).

### Phylum MOLLUSCA Linnaeus, 1758
### Class BIVALVIA Linnaeus, 1758
### Family HYRIIDAE Ortmann, 1910

**Velesunio** Iredale 1934
**Velesunio ambiguus** (Philippi, 1847) (Fig. 7A)

REFERRED MATERIAL. QMF44633; QMF44651; QMF44653.

DESCRIPTION. Equivalved, length to 110mm, moderately to well inflated; shell thin to very thick; weak ridge runs posteriorly from umbone; pallial line well developed; pallial sinus absent; anterior and posterior adductor muscle scars well developed; teeth lamellar, cardinal teeth absent; hinge moderately developed; beak cavity moderately developed. [Lamprell & Healy, 1998]

### Family CORBICULIDAE Gray, 1847

**Corbicula** Mühfeld, 1811
**Corbicula (Corbiculina)** Dall, 1903
**Corbicula (Corbiculina) australis** (Deshayes, 1830)
(Fig. 7B)

REFERRED MATERIAL. QMF44628-30.

DESCRIPTION. Equivalved, length to 20mm, slightly inflated; pallial line entire but weak; anterior and posterior adductor muscle scars weakly defined; anterior and posterior pedal retractor muscle scars hidden by overhang of anterior and posterior teeth respectively; three cardinal teeth, and anterior and posterior lateral teeth well developed; beak cavity very deep; hinge line narrow. [Lamprell & Healy, 1998]

TABLE 8. Skeletal element transportability for small mammals (Dodson, 1973) and large mammals (Voorhies, 1969) compared to the relative abundance of skeletal elements from Horizons B and D at QML1396 (listed in decreasing abundance). Elements higher in the Dodson (1973) and Voorhies (1969) columns were the last to be transported by moving water in flume experiments.

| Relative movement | Dodson (1973) small mammals | Voorhies (1969) large mammals | Horizon D | | | Horizon B |
|---|---|---|---|---|---|---|
| | | | <5kg mammals | < 5kg squamates | >5kg mammals | >5kg mammals |
| late | mandible | skull, maxilla | tibia<br>femur,<br>calcania,<br>ulna,<br>dentary<br>maxilla<br>humerus,<br>vertebrae<br>radius | dentary,<br>maxilla,<br>vertebae<br>humerus | maxilla<br>dentary<br>pelvi<br>vertebrae | dentary |
| middle-late | calcania, radius, ulna | mandible | | | | |
| middle | skull<br>tibia-fibula,<br>femur,<br>hunerus | femur,<br>tibia<br>humerus<br>pelvis<br>radius | | | | |
| early-middle | pelvis, cervical and caudal vert. | ulna | | | | |
| early | thoracic vert<br>maxilla | vertebra | | | | |

### Class GASTROPODA Cuvier, 1797
### Order SORBEOCONCHA Fischer, 1884
### Family THIARIDAE Troschel, 1857

### **Thiara (Plotiopsis)** Brot 1874
### **Thiara (Plotiopsis) balonnensis** (Conrad, 1850)
(Fig. 7C)

REFERRED MATERIAL. QMF44631-32.

DESCRIPTION. *Shell.* Elongate, dextrally coiled, robust, turreted, length to 30mm; 6-7 whorls, carinate, spiral ridges complemented with nodules; ovoid shaped aperture; inner lip thickened, outer lip thin. [Smith and Kershaw 1979]

### Order PULMONATA Cuvier, 1817
### Family PLANORBIDAE Rafinesque, 1815

### **Gyraulus** Charpentier,1837
### **Gyraulus gilberti** (Dunker, 1848)
(Fig. 7D).

REFERRED MATERIAL. QMF44574-79.

DESCRIPTION. *Shell.* Planispiral, diameter to 6.29mm; 4 whorls; spire sunken; umbilicus wide; last whorl with a peripheral keel; shell sculpture consists of fine transverse ridges; aperture keeled elongate; outer lip relatively thin and straight. [Brown, 1981]

### Family RHYTIDIDAE Pilsbry, 1895

### **Saladelos** Iredale, 1933
### **Saladelos** sp.
(Fig. 7E)

REFERRED MATERIAL. QMF44956.

DESCRIPTION. Shell planispiral, diameter to 3mm; whorl count reduced, 2-3 whorls, last whorl capacious; spire slightly depressed; shell sculpture of fine radial ribs; umbilicus narrow; aperture ovate-lunate; lip simple. [Iredale ,1933]

### **Strangesta** Iredale, 1933
### **Strangesta** sp.
(Fig. 7F)

REFERRED MATERIAL. QMF44582-83.

DESCRIPTION. *Shell.* Planispiral, diameter to 6.82mm; 3-4 whorls; slightly depressed spire; apical sculpture of fine to medium coiled radial ribs; umbilicus narrow; aperture wide, ovate-lunate; lip simple. [Smith and Kershaw,1979]

### Family CHAROPIDAE Hutton, 1884.

### **Coenocharopa** Stanisic, 1990
### **Coenocharopa** sp.
(Fig. 7G)

REFERRED MATERIAL. QMF44584-89.

DESCRIPTION. *Shell.* Planispiral, diameter to 4.5mm; whorls coiled, last descending; apex and spire slightly elevated; apical sculpture of prominent coiled radial ribs; post-nuclear

FIG. 7. A. *Velesunio ambiguus*; B. *Corbicula (Corbiculina) australis*; C. *Thiara (Plotiopsis) balonnensis* ; D. *Gyraulus gilberti*; E. *Saladelos* sp.; F. *Strangesta* sp.; G. *Coenocharopa* sp.; H. *Gyrococlea* sp.; I. *Austrosuccinea* sp.; J. *Xanthomelon pachystylum*.

sculpture moderately spaced; umbilicus wide and U-shaped; aperture ovate-lunate; lip simple. [Stanisic, 1990]

**Gyrocochlea** Hedley, 1924
**Gyrocochlea** sp. 1 and 2
(Fig. 7H)

REFERRED MATERIAL. Sp. 1: QMF44590-95; Sp. 2: QMF44598-602.

DESCRIPTION. Shell planispiral, diameter to 4mm; moderately tightly coiled whorls, last descending more rapidly; apex slightly concave; apical sculpture of fine crowded spiral cords and weakly curved radial ribs; umbilicus wide and U-shaped; aperture ovately lunate; lip simple. [Stanisic 1990]

REMARKS. *Gyrococlea* sp. 1 differs from *Gyrococlea* sp. 2 by a smoother shell sculpture, and possessing a more closed umbilicus.

Family SUCCINEIDAE Beck, 1837

**Austrosuccinea** Iredale, 1937
**Austrosuccinea** sp.
(Fig. 7I)

REFERRED MATERIAL. QMF44580.

DESCRIPTION. Shell elongate, dextrally coiled; shell height 10.65mm; 4 whorls present, last whorl large; spire short; fine growth lines on shell; aperture ovate; inner lip relatively straight, outer lip thin and straight. [Smith & Kershaw, 1979]

Family CAMAENIDAE Pilsbry, 1895

**Xanthomelon** Martens, 1861
**Xanthomelon pachystylum** (Pfeiffer, 1845)
(Fig. 7J)

REFERRED MATERIAL. QMF44581.

DESCRIPTION. Shell subglobose, diameter to 18.7mm; 4 whorls present, body whorl large; spire slightly elevated; shell sculpture relatively smooth; anomphalous; aperture ovate lunate; outer and inner lip simple, thin. [Solem,1979]

Phylum CHORDATA Linnaeus, 1758
Class REPTILIA Laurenti, 1768
Order SQUAMATA Oppel, 1811
Family AGAMIDAE Hardwicke & Gray, 1827.

**Tympanocryptis** Peters, 1863
**Tympanocryptis "lineata"** Peters, 1863
(Fig. 8H)

REFERRED MATERIAL. QMF44198-202, maxillary fragments; QMF44619, dentary.

DESCRIPTION. *Maxilla*. 4 foramen present; pleurodont teeth 2, acrodont teeth 12; 1st pleurodont tooth oritentated mesiobuccally; 2nd pleurodont tooth caniniform; maxillary suture

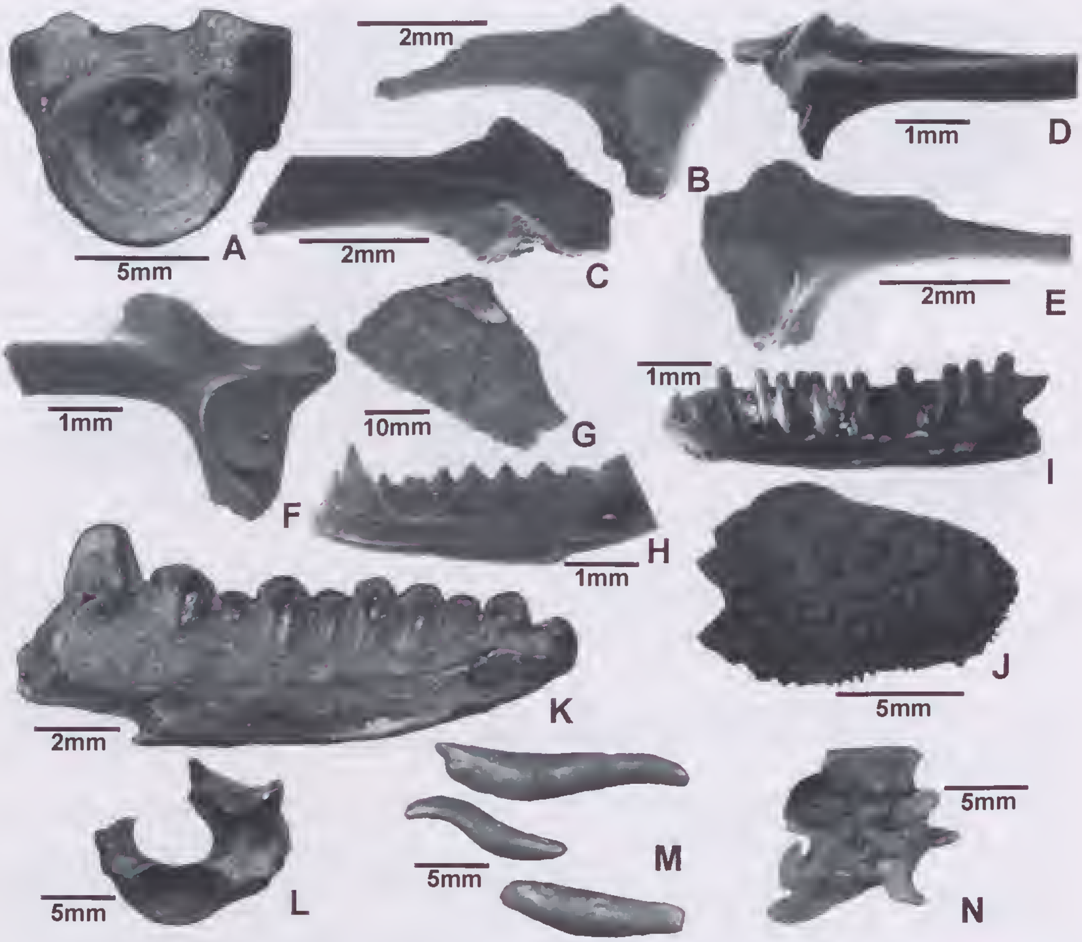

FIG. 8. A. Fish vertebra; B. *Limnodynastes tasmaniensis*, left ilium; C. *L.* sp. cf. *L. dumerili*, left ilium; D. ?*Limnodynastes* sp., right ilium; E. *Neobatrachus sudelli*, right ilium; F. *Kyarranus* sp.; G. Chelid plastron fragment; H. *Tympanocryptis* "*lineata*", right dentary. I. "*Sphenomorphus* Group" sp., right dentary; J. *Tiliqua rugosa*, osteoderm; K. *Cyclodomorphus* sp., left dentary; L. *Varanus* sp. vertebra; M. *Megalania prisca*, osteoderms; N. Elapid vertebra.

anterodorsal to pleurodont teeth; dorsal maxillary process narrow.

*Dentary*. Short; 3 mental foramina present; pleurodont teeth 2, acrodont teeth 12; pleurodont teeth closely positioned, 2nd pleurodont twice the size of the 1st; acrodont teeth sub-triangular with indistinct anterior and posterior conids; Meckel's groove parallel to dental sulcus, narrowed anteriorly. [Hocknull, 2002]

REMARKS. *Tympanocryptis lineata* is distinguished from other members of the genus by a combination of features including: 1) its larger size, 2) 1st pleurodont tooth orientated mesiolabially, and 3) lower anterior hook.

### Family SCINCIDAE Oppel, 1811

Skinks are the largest and most diverse squamate group in Australia (Greer, 1979; Hutchinson, 1993). Within the Scincidae, three distinct monophyletic groups are informally recognised: the *Egernia* group, *Eugongylus* group, and *Sphenomorphus* group (Greer, 1979, Hutchinson, 1993). Members allied to the *Sphenomorphous* Group and *Egernia* group are represented in the deposit.

### “**Sphenomorphus** Group” sp. 1 and 2 (sensu Greer, 1979)
(Fig. 8I)

REFERRED MATERIAL. Sp. 1: QMF44620-22, QMF44654, dentaries; Sp. 2: QMF44623-25, maxillae.

DESCRIPTION. *Dentary*. Tooth row bears up to 17 teeth or tooth loci; Meckel’s groove widely open along ventrolingual margin; internal septum poorly developed; up to 6 mental foramina present, last one postitioned about the level of the 12th tooth; tooth crowns not flared or thickened; lingual face of each crown vertical. [Greer, 1979]

REMARKS. *Sphenomorphus* Group members are distinguished from the *Egernia* and *Eugongylus* Groups by possessing a Meckel’s groove that remains open along the length of the ventrolingual margin of the dentary (Hutchinson, 1993). Two distinct size classes of members representing the *Sphenomorphus* group were identified within the deposit. Hutchinson (1993) recognised that while sexual dimorphism is common in skinks, it is only subtle. The large size difference between the two size classes is considered here to represent distinct species.

Until the taxonomy of those two species is better known, their significance in Pleistocene Darling Downs will remain unclear.

### “*Egernia* group” (sensu Greer, 1979)

### **Tiliqua** Gray 1825a
### **Tiliqua rugosa** (Gray, 1825a)
(Fig. 8J)

REFERRED MATERIAL. QMF44603-605, osteoderms.

DESCRIPTION. *Osteoderms*. Up to 10mm in diameter; thick, coarsely pitted; rugose surface.

REMARKS. The osteoderms of *Tilqua rugosa* differ from all other *Tiliqua* as they are generally thicker and more coarsely pitted, functioning to form an armoured shield (Hutchinson, 1993). [Smith, 1976]

### **Cyclodomorphus** Fitzinger, 1843
### **Cyclodomorphus** sp.
(Fig. 8K)

REFERRED MATERIAL. QMF44639, dentary.

DESCRIPTION. *Dentary*. Near complete with large hemispherical teeth and closed Meckel’s groove; ventral symphysal crest extends to third tooth; ten teeth present in dentary with tenth tooth markedly larger than all anterior teeth; teeth variable in size, with acutely conical crowns; specimen is adult as dental sulcus well defined, and dentary indicates cycles of tooth replacement.

REMARKS. *Cyclodomorphus* spp. are similar in size to *Tiliqua* spp., but are distinguished by a markedly larger tenth tooth in the dentary (Hutchinson, 1993). The fragmentary nature of the fossil remains precludes a full comparison to other members of the genus. [Shea ,1990]

### Family VARANIDAE Hardwicke & Gray, 1827.

### **Varanus** Merrem 1820
### **Varanus** sp.
(Fig. 8L)

REFERRED MATERIAL. QMF48166, vertebra.

DESCRIPTION. Vertebra broken dorsally; condyle overhanging, oblique articulation; cotyle oblique; centrum broad; neural canal round.

REMARKS. The fragmentary nature of the vertebra, particularly the lack of neural spine, precludes a full comparison to other *Varanus* spp. [Smith,1976].

### **Megalania** Owen, 1860
### **Megalania prisca** (Owen, 1860)
(Fig. 8M)

REFERRED MATERIAL. QMF44615-17, osteoderms.

DESCRIPTION. Small, worm shaped osteoderms to 8mm in length, 3mm in diameter; growth lines evident.

REMARKS. *Megalania prisca* osteoderms grow in the snout and nape regions of the lizard (Erickson et al., 2003). Growth lines present on the osteoderms may reflect the age of the individual (Erickson et al., 2003). [Hecht, 1975]

### Family ELAPIDAE Boie, 1827
### gen. et sp. indet.
(Fig. 8N)

REFERRED MATERIAL. QMF44606-08, vertebrae.

DESCRIPTION. Vertebrae with long, acute accessory processes; hypapophysis arises near lip of cotyle, extends posteriorly for half the length of centrum, then deepens to taper into a sharp point; parapophysial processes rounded anteriorly; neural spine low, laterally compressed, does not extend posteriorly; four pairs of foramina present.

FIG. 9. A. *Sminthopsis* sp., left dentary; B. *Dasyurus* sp., $M^4$; C. *Sarcophilus* sp., $C_1$; D. *Thylacinus cynocephalus*, $I_1$; E. *Perameles bougainville*, $M_1$; F. *P. nasuta*, $M_3$.

REMARKS. Elapid vertebrae considered here are comparable in size to extant forms currently found on the Darling Downs today, such *Pseudechis australis* and *P. porphyriacus*. [Smith,1976]. However, the fragmentary nature of the fossil material precludes a full comparison to other members of the family.

Class MAMMALIA Linneus, 1758
Order MARSUPIALIA Cuvier, 1817
Family DASYURIDAE Goldfuss, 1820; sensu Waterhouse, 1838

**Sminthopsis** Thomas, 1887
**Sminthopsis** sp.
(Fig. 9A)

REFERRED MATERIAL. QMF44637, dentary.

DESCRIPTION. *Dentary*. Small, gracile, deepest below $M_1$; mental foramen posteroventral to root of $M_1$. $P_3$ ovoid in occlusal outline; anterior cuspid reduced, lingual to midline, forming anterior margin; central cuspid massive, positioned one third from anterior margin; blade-like crest runs posteriorly to a small posterior cuspid. $M_1$ anterior one-third triangular, remainder sub-rectangular in occlusal outline; talonid wider than trigonid; protoconid tallest cusp on crown, followed by metaconid, hypoconid, paraconid and entoconid; paraconid forms anterior margin slightly lingual to midline; protoconid posterobuccal to paraconid; metaconid transverse and slightly posterior to protoconid; hypoconid posterobuccal to protoconid; entoconid most posterior cusp forming posterolingual corner of crown; anterior and posterior cingula small but distinct; metacristids and hypocristids transverse to long axis.

REMARKS. Identification to specific level is not possible due to insufficient preservation of diagnostic features. [Archer,1981]

**Dasyurus** Geoffroy, 1796
**Dasyurus** sp.
(Fig. 9B)

REFERRED MATERIAL. QMF44597, $M^4$.

DESCRIPTION. $M^4$. Ovoid in occlusal outline; paracone tallest cusp on crown followed in descending order by stylar cusp B, metacone and protocone; paracone most anterior cusp, positioned in midline of crown; Stylar cusp B posterobuccal to paracone; metacone posterolingual to paracone; anterior cingulum absent.

REMARKS. $M^4$ described above is much larger than the corresponding tooth in all species of *Dasyurus* excepting *D. maculatus*. It is well within the size range of extant *D. maculatus*, although differs in that: 1) it is not anteriorly concave in occlusal outline, 2) the metacone is positioned more lingually, and 3) the anterior cingulum is absent. [Ride,1964].

**Sarcophilus** Cuvier, 1837
**Sarcophilus** sp.
(Fig. 9C)

REFERRED MATERIAL. QMF44640, $C_1$.

DESCRIPTION. $C_1$. Enamel constricted to anterior one-quarter of tooth; curved slightly in occlusal view and is deepest one-third from

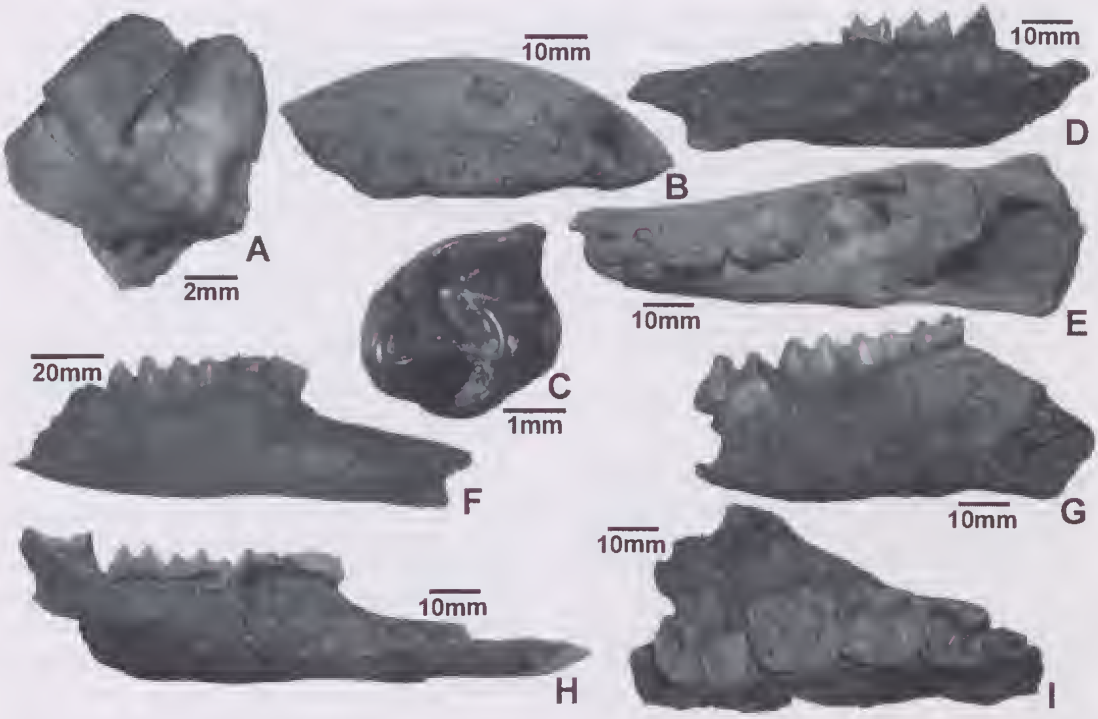

FIG. 10. A. *Diprotodon* sp., $P_3$; B. *Thylacoleo carnifex*, $I^1$; C. *Aepyprymnus* sp., $M^3$; D. *Troposodon minor*, right dentary; E. *Procoptodon pusio*, left dentary; F. *Macropus agilis siva*, right dentary; G. *M. titan*, right dentary; H. *Protemnodon anak*, left dentary; I. *P. brehus*, right maxilla.

enamelised tip of tooth; root laterally compressed tapering to a blunt point.

REMARKS. QMF44640 compares well to the corresponding tooth of recent *Sarcophilus harissi* although is slightly larger and may represent the Pleistocene *S. laniarius*. [Ride, 1964]

Family THYLACINIDAE Bonaparte, 1838

**Thylacinus** Temminck 1824
**Thylacinus cynocephalus** (Harris, 1808)
(Fig. 9D)

REFERRED MATERIAL. QMF44643, $I_1$.

DESCRIPTION. $I_1$. Markedly curved in lateral and occlusal view; enamel constricted to the anterior one-quarter of tooth and tapers to an acute point; deepest and broadest half way along length of entire tooth; root laterally compressed, deep, with posterior half tapering to an acute point.

REMARKS. QMF44643 is morphologically similar to the corresponding tooth of recent *Thylacinus cynocephalus*. [Ride,1964]

Family DIPROTODONTIDAE Gill, 1872

**Diprotodon** Owen, 1838
**Diprotodon** sp.
(Fig. 10A)

REFERRED MATERIAL. QMF44649, $P_3$.

DESCRIPTION. $P_3$. Sub-rectangular in occlusal outline; bilophid with lophs connected by a high lingual crest; anterior lophid markedly larger than posterior lophid; enamel thick with a worm-eaten puncate appearance.

REMARKS. *Diprotodon* sp. is distinguished from other diprotodontids by possessing a bilophodont lower premolar, with thick, punctated enamel. [Archer,1977]

Family THYLACOLEONIDAE Gill, 1872

**Thylacoleo** Owen 1858
**Thylacoleo carnifex** Owen, 1858
(Fig. 10B)

REFERRED MATERIAL. QMF44642, $I^1$.

DESCRIPTION. *$I^1$*. markedly curved in occlusal view with enamel confined to anterior and lateral surface in a U shape; occlusal wear surface concave; root deep and laterally compressed.

REMARKS. *Thylacoleo carnifex* is distinguished from other members of the genus by its significantly larger size. [Wells et al., 1982]

### Family POTOROIDAE Gray, 1821; sensu Archer & Bartholomai, 1978

**Aepyprymnus** Garrod, 1875
**Aepyprymnus** sp.
(Fig. 10C)

REFERRED MATERIAL. QMF44652, $M^3$.

DESCRIPTION. *$M^3$*. metalophid low and very thin, but distinct; postmetacrista connects to posterior cingulum to form a very large and fairly deep pocket-like structure on posterior margin of tooth; premetacrisa well defined.

REMARKS. Fragmentary material precludes a full comparison to *Aepyprymnus rufescens*, the only the only known member of the genus. [Tate, 1948]

### Family MACROPODIDAE Gray, 1821
### Subfamily STHENURINAE Glauert, 1926

**Procoptodon** Owen 1874
**Procoptodon pusio** (Owen, 1874)
(Fig. 10E)

REFERRED MATERIAL. QMF44648, dentary.

REMARKS. *Dentary.* Short, deep and robust; buccal groove on ramus well defined.

*Lower molars.* Sub-rectangular in occlusal outline, with slight constriction in midvalley; base of molars swollen and lophids high, convex anteriorly; enamel crenulated, though smooth on lingual and buccal lateral surfaces; anterior cingulid is high, angled slightly lingually.

REMARKS. *Propcoptodon pusio* is distinguished from other members of the genus by a combination of characters including: 1) its slightly smaller size, 2) lacking a distinct posthypocristid, and 3) less extensive transverse anterior portion of paracristid (Prideaux, 2004). The horizon from which the *P. pusio* material was collected is unknown. *Procoptodon* is restricted to Pleistocene deposits, though may have had its origins in the late Tertiary (Bartholomai, 1970; Prideaux, 2004). [Prideaux, 2004]

### Subfamily MACROPODINAE Gray, 1821

**Troposodon** Bartholomai 1967
**Troposodon minor** (Owen, 1877b)
(Fig. 10D)

REFERRED MATERIAL. QMF44646-47, dentaries.

DESCRIPTION. *Dentary.* Shallow and gracile; symphysis elongate with ventral surface markedly lower than ventral surface of ramus. *Lower molars.* Subrectangular in occlusal outline, with slight kink in midvalley; lophs low, angled slightly lingually, and slightly concave anteriorly; preparacristid links to anterior cingulid; premetacristid descends anterolingually from metaconid to fuse with preparacristid.

REMARKS. *Troposodon minor* is placed within Macropodinae rather than Sthenurinae following Prideaux (2004). *T. minor* is easily distinguished from other members of the genus by being intermediate in size between the larger *T. kenti* and smaller *T. bowensis*. [Flannery and Archer, 1983]

**Macropus** Shaw 1790
**Macropus agilis siva** (De Vis, 1895)
(Fig. 10F)

REFERRED MATERIAL. QMF44638, $I_1$; QMF44655, dentary; QMF44656-7, maxillary fragments.

DESCRIPTION. *Dentary.* Gracile, with groove on ventral surface of ramus extending from posterior of symphysis to below posterior root of $M_2$; symphysis elongated and diastema long. $I_1$. Elongated and deeply rooted; slightly curved in both lateral and occlusal views. $P_3$. Elongated, blade-like; small ridges descend lingually and buccally from apex of longitudinal ridge.

*Lower molars.* Increase in size from $M_{1-3}$; sub-rectangular in occlusal outline, with slight constriction in midvalley; hypolophid wider than protolophid; lophids high; cristid obliqua high; posterior cingulid absent. $DP^2$ elongated, broad posteriorly; small ridges descend main crest; posterolingual fossette shallow. $DP^3$ molariform; subrectangular in occlusal outline with slight constriction in midvalley; lophs low; metaloph wider than protoloph; posterior fossette moderately developed. $M^1$ sub-rectangular in occlusal outline, with slight constriction in midvalley; high lophs; metaloph broader than protoloph; midlink moderately high; posterior fossette well developed.

REMARKS. *Macropus agilis siva* is distinguished from other members of the genus by possessing a combination of features including: 1) elongate diastema, 2) $P_3$ as long as $M_1$, 3) lower molars high crowned, with high links, and lacking posterior cingula, 4) elongate upper premolars, and 5) upper molars elongated with high crowns, slight forelink and moderate midlink. [Bartholomai,1975]

### **Macropus titan** Owen, 1838
(Fig. 10G)

REFERRED MATERIAL. QMF44645, dentary.

DESCRIPTION. *Dentary.* moderately deep, the base of symphysis slightly lower than the base of horizontal ramus.

*Lower molars.* Sub-rectangular in occlusal outline, slightly constricted across talonid basin; lophids high and curved slightly anteriorly; forelink high, curving anteriorly to meet a high anterior cingulid; posterior fossette present on posterior loph.

REMARKS. *Macropus titan* is distinguished from other members of the genus by a combination of features including: 1) its large size, 2) elongate diastema, 3) high crowned, elongated lower molars with slightly curved lophids, high links and high anterior cingulum (Bartholomai, 1975). An additional dentary fragment, QMF44644, is referred to *M.* sp. cf. *M. titan*. The molars are within the size range of *M. titan*, however it differs in that: 1) the dentary is markedly more robust and deep, 2) forelink is slightly lower, 3) anterior cingulid broader, and 4) cristid obliqua is higher. [Bartholomai,1975]

### **Protemnodon** Owen 1874
### **Protemnodon anak** (Owen, 1874)
(Fig. 10H)

REFERRED MATERIAL. QMF44650, skull; QMF44658, dentary.

DESCRIPTION. *Dentary.* Moderately shallow, with elongated symphysis ascending anteriorly at low angle; mental foramen oval shaped, close to diastemal crest. $P_3$. Elongated, blade-like; exceeds length of $M_1$.

*Lower molars.* Sub-rectangular in occlusal view with slight constriction in midvalley; lophids high, concave anteriorly with high forelink; posterior cingulid small $P^3$. Elongate; crown concave buccally; high longitudinal crest, slightly concave buccally; transected by four vertical blades.

*Upper molars.* Sub-rectangular in occlusal outline, slightly constricted across mid valleys; midlink strong; forelink absent; anterior cingulum slightly swollen.

REMARKS. *Protemndon anak* is distinguished from other Pleistocene members of the genus by a combination of characters including: 1) small size, 2) $P^3$ elongate, concave bucally, with high longitudinal crest, and longer than $M^4$, 3) $M^3$ and $M^4$ lacking cuspules in the lingual portion of the midvalley. [Bartholomai,1973]

### **Protemnodon brehus** (Owen, 1874)
(Fig. 10I)

REFERRED MATERIAL. QMF44627, maxilla.

DESCRIPTION. *Upper molars.* Sub-rectangular in occlusal outline, slightly constricted across midvalley; anterior cingula broad; forelink absent; strong ridge curves from paracone into crista obliqua.

REMARKS. *Protemnodon brehus* is distinguished from other members of the genus by: 1) its large size, and 2) lacking a lingual cuspule in the midvalley of $M^{3-4}$. [Bartholomai,1973]

## Order RODENTIA Bowdich, 1821.
## Family MURIDAE Illiger, 1811

### **Pseudomys** Gray 1832
### **Pseudomys** sp. 1 & 2
(Fig. 11A)

REFERRED MATERIAL. Sp. 1: QMF44609-10, maxillae; Sp.2: QMF48168, maxilla.

DESCRIPTION. *Maxilla.* Anterior portion of zygomatic arch not broadened; molar alveoli pattern $3(M^1)$ $3(M^2)$ $3(M^3)$. $M^1$. Relatively elongate; T7 absent; three rooted, with one lingual root.

REMARKS. *Pseudomys* sp. 1 and 2 could not be identified to specific level considering the nature of the fragmentary remains. *Pseudomys* sp. 1 fits within the size class of extant *P. australis*. *Pseudomys* sp. 2 is smaller, approximating the size of extant *P. delicatulus*. [Jones & Baynes,1989]

### **Rattus** sp. (Fischer, 1803)
(Fig. 11B)

REFERRED MATERIAL. QMF44611-12, isolated molars; QMF44613-14, maxillae.

DESCRIPTION. *$M^1$*. Cusps rounded in occlusal outline; two lingual cusps; five rooted, with two

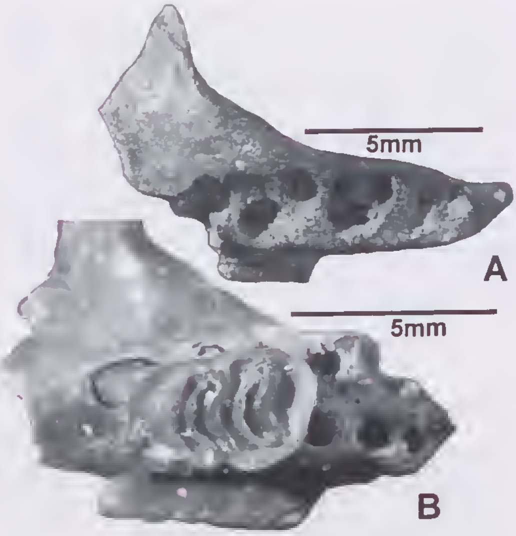

FIG. 11. A. *Pseudomys* sp. 1, left maxilla; *Rattus* sp., left maxilla.

lingual alveoli. $M^2$. Four rooted, arranged in a square pattern.

REMARKS. *Rattus* spp. are distinguished from other murid genera by possessing an $M^2$ that has four roots, arranged in a square pattern (Knox, 1976). [Jones & Baynes,1989]

## MATERIAL ASSIGNED TO OTHER TAXA

Teleostei fam. gen. et sp. indet. (Fig. 8A); QMF44634-36, vertebrae.

**Limnodynastes tasmaniensis** (Gnther, 1858) (Fig. 8B);. QMF43978-43985, ilia.

**L.** sp. cf. **L. dumerili** (Peters, 1863) (Fig. 8C); QMF43995-43997, ilia.

**?Limnodynastes** (Fitzinger, 1843)(Fig. 8D); QMF44000, ilium.

**Neobatrachus sudelli** (Lamb, 1911) (Fig. 8E); QMF44001-44002, ilia.

**Kyarranus** sp. (Fig. 8F); QMF44003, ilium.

Chelidae gen. et sp. indet. (Fig. 8G); QMF44626; QMF44641, carapace fragments.

**Perameles bougainville** (Quoy & Gaimard, 1824) (Fig. 9E); QMF44549, $RM_1$,.

**Perameles nasuta** (Geoffroy, 1804) (Fig. 9F); QMF44566, $LM_3$.

## ECOLOGICAL REMARKS

Elements of the fauna are here listed with minor pertinent ecological comments as appropriate.

MOLLUSCS. The invertebrate fauna is rich and diverse. Four families of land snails are represented, comprising seven species, as well as two families of freshwater snails, containing two species (J. Stanisic, pers. comm.). Freshwater bivalves are also common throughout the main fossiliferous units.

**Velesunio ambiguus** (Philippi, 1847): This most common species of the Australian Unioniodea, occurs in coastal and interior rivers throughout South Australia, Victoria, New South Wales and Queensland (Lamprell & Healy, 1998). *Velesunio ambiguus* is a typical floodplain species commonly found in billabongs and creeks; it rarely occurs in large rivers, except in the vicinity of impoundments (Sheldon & Walker, 1989). The exclusion of *V. ambiguus* from larger rivers probably reflects its weak anchorage (Sheldon & Walker, 1989).

Extant populations of *Velesunio ambiguus* are common throughout the creeks and tributaries of the Darling Downs. Additionally, *V. ambiguus* has been recorded from the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

**Corbicula (Corbiculina) australis** (Deshayes, 1830): *C. (C.) australis* occurs in coastal and inland rivers and streams. It is a hermaphroditic species that has a benthic crawling larva that makes it possible for *C. (C.) australis* to spread rapidly (Britton & Morton, 1982).

Extant *C. (C.) australis* are common throughout water courses of the Darling Downs. Additionally, *C. (C.) australis* has been reported from the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

**Thiara (Plotiopsis) balonnensis** (Conrad, 1850): *T. (P.) balonnensis* was the most common identifiable species recovered from the deposit. It was collected in-situ from shell beds up to 10cm thick. It is the most widespread of the Australian thiraids, common throughout the Murray-Darling River system.

Extant populations commonly occur in ponds, dams and rivers (Smith & Kershaw, 1979). Extant populations of *Thiara (Plotiopsis) balonnensis* are present on the Darling Downs. *Thiara (P.)* sp. has been reported from the fossil record of the Pleistocene Darling Downs (Gill, 1978; Sobbe, 1990).

**Gyraulus gilberti** (Dunker, 1848): Planorbids are a common Australian family of freshwater snails. The Planorbidae are confined to waters with low salinity and are generally associated with macrophytes or algae. *Gyraulus* has been reported in the Tertiary fossil record of northern Australia (McMichael, 1968).

**Saladelos** sp.: *Saladelos* sp. commonly occur in closed to open forest to vine thicketed habitats (J. Stanisic pers. comm.).

**Strangesta** sp.: *Strangesta* sp. commonly occur under dry, dense ground cover in dry forest to woodland scrub, and vine thickets (Smith & Kershaw, 1979; J. Stanisic pers. comm.).

**Coenocharopa** sp.: *Coenocharopa* sp. are generally found in warmer temperate forest thickets to cool, dry, sub-tropical notophyll vine forests from the central to north eastern coast of the Australian continent (Stanisic, 1990).

**Gyrocochlea** sp. 1 and 2: Members of *Gyrocochlea* typically inhabit dry to humid sub-tropical vine forests and prefer to live under logs (Stanisic, 1990). Like most charopids, *Gyrocochlea* sp. are common throughout central eastern Australia (Stanisic, 1990).

**Austrosuccinea** sp.: *Austrosuccinea* are land snails that are found in a variety of habitats ranging from marches and swampy environments, to sand dunes and seasonally dry stream basins (Solem, 1993).

**Xanthomelon pachystylum** (Pfeiffer, 1845): Camaenids are among the most diverse of Australian land snails. The Australian camaenid fossil record is scant with only a few known records (Ludbrook, 1978, 1984; McMichael, 1968; Kear et al., 2003). *X. pachystylum* is a herbivorous species associated with dense vine thickets (J. Stanisic, pers. comm.).

## AMPHIBIANS

**Limnodynastes tasmaniensis** (Gnther, 1858): Extant *L. tasmaniensis* populations are common over much of eastern Australia and have been recorded in a range of habitats ranging from wet coastal environments to dry, arid regions (Cogger, 2000).

Extant populations of *L. tasmaniensis* have been recorded from the Darling Downs (Ingram & Longmore, 1991).

**L.** sp. cf. **L. dumerili** (Peters, 1863): Extant populations have been recorded in most habitats, with the exception of alpine areas, rainforest, and extremely arid zones (Cogger, 2000).

Extant populations of *L. dumerili* have been recorded from the Darling Downs (Ingram & Longmore, 1991).

**Neobatrachus sudelli** (Lamb, 1911)

Extant populations of *Neobatrachus sudelli* occur throughout southeastern Australia, commonly occurring in open woodlands with grassy understories (Cogger, 2000).

**Kyarranus** sp.

Extant *Kyarranus* populations occur in areas of dense ground cover and thickets in isolated montane forest patches on the Great Dividing Range in southeastern Queensland and northeastern New South Wales (Tyler, 1991).

## REPTILES

**Tympanocryptis "lineata"** (Peters, 1863): Extant *T. lineata* populations occur in a variety of semi-arid to arid environments in central Australia. *T. lineata* commonly occur in earth cracks, grass or ground litter on desert sandhills, to black soil plains (Cogger, 2000).

Extant *T. lineata* populations have been recorded from the Darling Downs (Covacevich & Couper, 1991). Additionally, agamids have previously been recognised in the Darling Downs fossil record (Bennett, 1876; Lydekker, 1888; Molnar & Kurz, 1997).

"**Sphenomorphus** Group" sp. 1 and 2: The ecology of extant members of the *Sphenomorphus* group is varied and includes taxa that burrow in soil, burrow under leaf litter, have semi-amphibious lifestyles and others that are found in rocky arid environments (Cogger, 2000).

**Tiliqua rugosa** (Gray, 1825a): Extant populations of *T. rugosa* are found in a range of habitats including coastal heaths, dry sclerophyll forest, woodlands, mallee, and arid *Acacia* and eucalypt scrublands. *T. rugosa* shelters under fallen timber and leaf litter spinifex when inactive (Cogger, 2000).

**Cyclodomorphus** sp.: *Cyclodomorphus* spp. are ground dwelling skinks, although commonly climbs on low growing vegetation. Extant *Cyclodomorpus* populations have been recorded from wet to dry sclerophyll forest, commonly found under leaf litter or areas with low ground cover (Cogger, 2000).

**Varanus** sp.: Extant *Varanus* sp. populations have been recorded in a wide range of habitats from deserts to rainforest, and may have semi-aquatic, terrestrial, or arboreal locomotive strategies.

Extant *Varanus* populations have been recorded from the Darling Downs (Covacevich & Cooper, 1991). Additionally, *Varanus* sp. has been recorded from the Pleistocene Darling Downs (Wilkinson, 1995).

**Megalania prisca** (Owen, 1860): Molnar (1990) suggested that *M. prisca* was unlikely to have been arboreal, though it may have had a semi-aquatic life style.

*Megalania prisca* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997).

**Other elements:** Indeterminate chelid and elapid remains have been found in the deposit.

MARSUPIALS

**Sminthopsis** sp.: Extant *Sminthopsis* spp. populations occur in open to closed habitats (Strahan, 1995).

Extant populations of *S. murina* have been recorded on the Darling Downs (Van Dyck & Longmore, 1991).

**Dasyurus** sp.: *Dasyurus maculatus* is the largest extant native mammalian carnivore on the mainland of Australia. *Dasyurus* spp. are partly arboreal and occur on the eastern margin of the continent and Tasmania in a wide range of wooded habitats including rainforests, open forests, woodlands, and riparian forest. Den sites commonly include caves, rock crevices and hollow logs.

**Sarcophilus** sp.: Once common over the central and eastern portions of the Australian continent, *Sarcophilus* is now restricted to Tasmania where it is abundant in dry sclerophyll forest and woodlands that are interspersed with grasslands (Jones, 1995).

**Thylacinus cynocephalus** (Harris, 1808): Prior to European arrival in Australia, extant *T. cynocephalus* was restricted to Tasmania before over hunting led to its subsequent extinction. *T. cynocephalus* was once common in open forest and woodland (Dixon, 1989).

**Perameles bougainville** (Quoy & Gaimard, 1824): Extant populations of *P. bougainville* are restricted to Bernier and Dorre Islands, Shark Bay, Western Australia, although once occurred over much of semi-arid Australia (Friend & Burbidge, 1995). Extinction on the mainland has been attributed to the effects of habitat disturbance and introduction of non-native predators by Europeans. *P. bougainville* was once common on the mainland in a range of habitats including dense scrub thickets, open saltbush plains and stoney ridges bordering scrubland (Friend & Burbidge, 1995).

**Perameles nasuta** (Geoffroy, 1804): Extant *Perameles nasuta* populations occur in a wide range of habitats including rainforests, wet to dry woodlands, and areas with very little ground cover (Stoddart, 1995). It is a common and widely distributed species with a wide range of habitat tolerances, and its presence in the fossil record is of little palaeoenvironmental significance.

Extant *Perameles nasuta* populations are common on the Darling Downs.

**Diprotodon** sp.: *Diprotodon* spp. are generally regarded browsers of shrubs and forbs and probably occupied an open woodland to savanna habitat (Murray, 1984).

**Thylacoleo carnifex** (Owen, 1858) : *T. carnifex* may have occupied an open forest habitat (Murray, 1984). *T. carnifex* filled the 'large cat' niche of the Australian Pleistocene, and may have had the ability to kill *Diprotodon*-sized animals (Wroe. et al., 1999). The lower incisor functioned as a stabbing or piercing tooth that occludes with the upper incisors where it acts as an anvil against which food is restrained (Wells et al. 1982).

*T. carnifex* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997).

**Aepyprymnus** sp.: Extant *A. rufescens* populations occur in a variety of habitats ranging from wet sclerophyll to dry open woodlands, but only occupy areas with sparse grassy understories commonly adjacent to areas of dense undergrowth (Dennis & Johnston, 1995).

**Procoptodon pusio** (Owen, 1874): *Procoptodon* spp. were adapted for a diet of highly fibrous vegetation (Prideaux, 2004).

*P. pusio* has been recorded from several fossil localities on the Darling Downs (Molnar & Kurz, 1997; Prideaux, 2004).

**Troposodon minor** (Owen, 1877b): *Troposodon minor* is generally regarded as a semi-browser (Bartholomai, 1967). Flannery & Archer (1983) suggested that at least two species of *Troposodon* occurred sympatrically at most Plio-Pleistocene localities. However, *T. minor* remains the only member of the genus recorded at QML1396.

*Troposodon* minor is relatively common in Pleistocene Darling Downs deposits (Molnar & Kurz, 1997).

**Macropus agilis siva** (De Vis, 1895): Extant *Macropus agilis* populations favour savannah woodland or open forest habitats (Bell, 1973).

*M. a. siva* was common and widespread on the Pleistocene Darling Downs (Molnar & Kurz, 1997).

**Macropus titan** (Owen, 1838): The high crowned molars *M. titan* are typical of grazing species (Bartholomai, 1975).

*M. titan* was one of the most common and widespread megafauna species on the Darling Downs, being recorded from 21 fossil deposits (Molnar & Kurz, 1997).

**Protemnodon anak** (Owen, 1874),

**Protemnodon brehus** (Owen, 1874): *Protemnodon* spp. are regarded as grazers (Bartholomai, 1973).

*P. anak* and *P. brehus* have been recorded from over 30 fossil localities on the Darling Downs (Molnar & Kurz, 1997).

## RODENTS

**Pseudomys** sp. 1 & 2: Extant *Pseudomys* spp. populations occur in a wide variety of habitats from sparsely vegetated deserts to closed sclerophyll forests (Strahan, 1995). Until the taxonomy of the Pleistocene Darling Downs *Pseudomys* spp. is better known, their palaeoenvironmental significance will remain unclear.

*Pseudomys* spp. have been recorded from the Pleistocene Darling Downs (Archer & Hand, 1984).

**Rattus** sp.: In terms of abundance and diversity, *Rattus* is the most diverse extant murid genus in Queensland. Extant *Rattus* populations are found in a number of habitats including rainforests, woodlands, and savanna grasslands.

Extant *Rattus* spp. populations (native and introduced) have been recorded from the Darling Downs (Covacevich & Easton, 1974). Additionally, *Rattus* sp. has been reported from the Pleistocene Darling Downs (Archer & Hand, 1984).

## DATING.

The AMS$^{14}$C dating results of freshwater bivalves and charcoal indicate that deposition of Horizon B occurred 44300± 2200 to >49900 and Horizon D at 45150±2400 (Table 9). However, those results should be considered as minimum ages only considering the fact that the QML1396 assemblage appears to be close the limits of the AMS$^{14}$C dating technique. Owing to the importance associated with dating late Pleistocene megafauna extinction and climate change, it is desirable to further test the dating results presented here.

TABLE 9. AMS $^{14}$C dating results of charcoal and *Velesunio ambiguus* samples from QML1396. Ages quoted are radiocarbon ages, not calendar ages. Ages rounded according to Stuiver & Polach (1977)

| ANSTO code | sample | horizon | conventional $^{14}$C age ± 2σ error |
|---|---|---|---|
| OZG855 | charcoal | D | 45150 ± 2400 |
| OZG547 | bivalve | B | >49900 |
| OZG548 | bivalve | B | 44300 ± 2200 |

## DISCUSSION

SEDIMENTOLOGY. The deposit represents both high velocity lateral channel deposition and low velocity vertical accretion. The lower fossiliferous unit, Horizon B, represents the most significant input of sandy deposits in the sedimentary environment. Horizon B is laterally continuous for more than 70 metres. However, the horizon is largely unexposed and positioned below the modern water table, therefore the precise lateral extent of Horizon B is unknown. Horizon B is characterised by: 1) abundant freshwater mollusc fossils, including large-sized bivalves; 2) vertebrate fossils; 3) fluvially transported sediments (including rounded basalt, calcrete and sandstone pebbles and cobbles); and 4) upwardly fining grain size. The geometry of Horizon B and the interpreted sedimentary processes suggest that deposition took place in the main channel. Horizon B accumulated under higher velocity deposition than Horizon D considering the significantly larger grain sizes and preponderance of larger-sized bivalves (Fig. 2, Table 1).

The fine brown-grey clay unit, Horizon C, suggests a period of low velocity deposition. Mollusc shells are rare, however, freshwater gastropods (*Thiara* (*Plotiopsis) balonnensis*) are slightly more common than freshwater bivalves. The presence of freshwater molluscs in the horizon are consistent with the proximity to the channel.

Horizon D is laterally continuous for approximately 30 metres. Horizon D is characterised by: 1) discontinuous lenticular sandy and shelly beds; 2) mud cracks in-filled with fine clays; 3) vertebrate fossils; and 4) fluvially transported sediments (including rounded basalt, calcrete and sandstone pebbles). The facies association of lenticular shelly beds overlies the low velocity brown-grey clay unit (in continuity with the channel deposit). Freshwater gastropods in Horizon D show polymodal current directions indicating that they were not deposited as traction load in flowing water. The data suggest that deposition occurred as overbank deposits on the floodplain adjacent to the channel belt. A succession of several small overbank depositional events created superposed shelly lenses up to 100mm thick. The depositional setting of Horizon D is interpreted as representing a series of small crevasse splays and subsequent drying pools in the overbank that resulted from minor flood events. It is hypothesised that as the pools evaporated, stranded gastropods moved into the deeper parts of the pools (hence showing polymodal orientations) eventually dying when the pools evaporated.

Overlying fine-grained deposits of the upper units represent vertical accretion on the floodplain (Fig. 2, Table 1). The occurrence of iron nodule formation in the upper units of the profile reflect alternating periods of oxidation and reducing conditions due to watertable fluctuations. Additionally, in-situ, white to brownish-grey mottled calcrete formation in the upper units is related to similar watertable fluctuations. Mottled calcretes are chemically precipitated in the freshwater phreatic zone of the watertable, and are primarily related to the lateral movement and percolation of alkaline waters in the soil profile (Arakel & McConchie, 1982). The close association of the formation of in-situ mottled calcretes and ferruginous oxides are indicative of a response to an increasingly arid environment, subsequent to deposition of the major fossiliferous horizons.

## TAPHONOMIC HISTORY OF BONES.

Numerous unidentifiable bone fragments recovered from the deposit exhibited a range of abrasion and weathering characteristics. However, the following taphonomic conclusions are largely based on identifiable vertebrate remains horizons B and D. Better preserved specimens may yield more accurate palaeobiological and palaeoecological information than unidentifiable fragments. However, it is recognised that some components of the assemblage may have had different taphonomic pathways leading to their final deposition.

It is unlikely that acidic ground waters have played a role in the diagenesis of fossil material from either horizon, considering the high degree and diagentically unaltered preservation of calcareous material (i.e. mollusc shell and calcrete) that has been identified in the deposit. Additionally, root etching of vertebrate fossil material was not observed. Few of the identifiable specimens indicate any significant pre-burial weathering (sensu Behrensmeyer, 1978).

There were several biases in the preservation of different faunal groups and skeletal elements observed in the deposit. For squamates, there was a noticeable lack of post-cranial material preserved in the deposit in comparison to mammals. Similar biases between terrestrial non-mammals and mammals have been identified within fossil deposits of the Koobi Fora Formation of Kenya (Behrensmeyer, 1975). Additionally, within the Agamidae and Scincidae, differences were observed in the preservability of cranial and dental elements. The differences may be related to minor differences in bone density or structure. However, few previous studies have addressed the causes of such preservational biases, focusing predominantly on the accumulation of fossil mammals. In the absence of comparative data on squamate transportability and preservability in fluvial systems, it is difficult to explain such biases in the fossil record.

Large-sized mammals are better preserved in Horizon B than Horizon D, but small-sized taxa are generally absent from Horizon B. Bones and shells act as sedimentary particles in fluvial systems and may have settling velocities that are related to equivalent-sized spherical quartz grains (Behrensmeyer, 1975). Therefore, if the size of bone and shells are relative to the size of the surrounding grains, then coarse-grained units such as Horizon B would be expected to contain larger-sized skeletal elements or species than finer-grained units such as Horizon D. That hypothesis may equally explain: 1) why large-sized bivalves are more common in Horizon B than Horizon D; 2) why the Horizon B assemblage is dominated by large-sized vertebrates, and Horizon D by small-sized vertebrates; and 3) the differences between the relative abundance of skeletal elements of large and small mammals within Horizon D.

Assemblages of both horizons are generally characterised by: 1) low levels of post-crania; 2) high degrees of bone breakage; 3) low degrees of abrasion; and 4) low degrees of weathering. A comparison of the abundance of skeletal elements to experimental data of skeletal element transportability in fluvial systems indicates that both units contain elements that are among the last to be transported in flowing water. That suggests that horizons B and D represent bone lag deposits. The high degree of breakage of skeletal elements suggests that the vertebrate remains were subjected to considerable forces. Additionally, the loss of limb bone ends may reflect a density mediated destruction of lower-density bone (distal and proximal ends) and that the higher-density bone shafts were not destroyed (Rapson, 1990). The low degree of bone abrasion and low degree of pre-burial weathering indicate that the vertebrates died within close proximity to the final point of deposition and were probably buried rapidly after death. Additionally, no elements were recovered that show the effects of digestion, polishing or gnawing that may be attributable to predator accumulation (sensu Andrews, 1990; Sobbe, 1990). Collectively, the data indicate that the vertebrate material was accumulated and fluvially transported into the deposit from the surrounding proximal floodplain.

## PALAEOENVIRONMENTAL INTERPRETATION

Megafauna species are less abundant and less well preserved in Horizon D (low-energy overbank deposition) than Horizon B (high-energy channel deposition), and all vertebrate taxa smaller than *Sarcophilus* sp. (~8 kg) are absent from Horizon B (Figure 6). Three hypotheses could explain the faunal differences: 1) Megafauna went locally extinct progressively between the time of deposition of Horizons B and D (the age of the two QML1396 assemblages may bracket the terminal extinction event of the Australian megafauna [~46ka; Roberts et al., 2001a]); 2) Sampling by the creek system was biased towards the collection of small-sized species in Horizon D; or 3) Larger-sized bones may not have been able to be transported into overbank deposits from flood events (large bones in the overbank deposits may be derived directly from the proximal floodplain rather than from fluvial transport). Additionally, a third of the large-sized taxa that are present in Horizon B, but absent from Horizon D, are carnivorous species (*Sarcophilus* sp., *Thylacinus cynocephalus* & *Thylacoleo carnifex*; Table 2). Hence, the rarity of carnivorous taxa in the Pleistocene Darling Downs might be assumed regardless. However, considering the taphonomic sampling biases of the Pleistocene channel, it is difficult to accurately compare habitat and species differences between the Horizon D and B assemblages, and hence, directly demonstrate the extinction of megafauna temporally based on data from QML1396.

TABLE 10. Preferred and inferred habitat types of extant and fossil taxa recorded from Horizon B. (* Extinct on Darling Downs; ** Totally extinct).

| Species | freshwater | open woodland | open grassland |
|---|---|---|---|
| *Velesunio ambiguus* | x | | |
| *Corbicula (Cobiculina) australis* | x | | |
| *Thiara (Plotiopsis) balonnensis* | x | | |
| *Sarcophilus* sp.* | | x | |
| *Thylacinus cynocephalus*** | | x | |
| *Diprotodon* sp.** | | x | x |
| *Thylacoleo carnifex*** | | x | |
| *Troposodon minor*** | | x | |
| *Macropus agilis siva*** | | x | |
| *M. titan*** | | x | x |
| *Protemnodon anak*** | | x | x |
| *P. brehus*** | | x | x |

Large-sized taxa previously used to make interpretations about Darling Downs Pleistocene palaeoenvironments are present in the Horizon B assemblage, thus in agreement with previous broad interpretations of a woodland and open grassland Pleistocene habitat (Table 10). All of the mammals recorded from Horizon B are either locally or totally extinct.

The Horizon D assemblage consists of large and small-sized taxa that are extant, locally or totally extinct. The small-sized faunas have revealed a series of increasingly complex terrestrial habitats, some that have not previously been documented in the Pleistocene Darling Downs. It appears that at the time of deposition of Horizon D, a suite of habitats existed that consisted of grasslands, open woodlands with grassy understories, and scrubby vine-thicketed habitats (Table 11). A scrubby vine thicketed habitat is indicated predominantly by the diverse land snail fauna. That interpretation is additionally supported by the presence of *Kyarranus*, a frog genus whose extant members are restricted to dense understories and thickets. Vine thickets are common on the Great Dividing

TABLE 11. Preferred and inferred habitat types of extant and fossil taxa from Horizon D. (* Extinct on Darling Downs; ** totally extinct).

| species | freshwater | vine-thicket | scrubland | colsed woodland | open woodland | open/ grassland |
|---|---|---|---|---|---|---|
| *Velesunio ambiguus* | X | | | | | |
| *Corbicula (Cobiculina) australis* | X | | | | | |
| *Thiara (Plotiopsis) balonnensis* | X | | | | | |
| *Gyraulus gilberti** | X | | | | | |
| *Coencharopa* sp.* | | X | | | | |
| *Gyrocochlea* sp. 1* | | X | | | | |
| *Gyrocochlea* sp. 2* | | X | | | | |
| *Austrocuccinea* sp.* | X | | | | X | X |
| *Xanthomelon pachystylum** | | X | | | | |
| *Strangesta* sp.* | | X | X | | | |
| *Saladelos* sp.* | | X | | | | |
| Teleost | X | | | | | |
| *Limnodynastes tasmaniensis* | | X | X | X | X | X |
| *L.* sp. cf. *L. dumerili* | | X | X | X | X | X |
| *?Limnodynastes* | | X | X | X | X | X |
| *Neobatrachus sudelli** | | | | | X | X |
| *Kyarranus* sp.* | | X | | X | | |
| Chelid | X | | | | | |
| *Tympanocryptis "lineata"** | | | | | | X |
| "*Sphenomorphus* Group" sp. 1 | | X | X | X | X | X |
| "*Sphenomorphus* Group" sp. 2 | | X | X | X | X | X |
| *Tiliqua rugosa** | | | X | | X | X |
| *Cyclodomorphus* sp.* | | X | X | X | X | |
| *Varanus* sp. | X | X | X | X | X | X |
| *Megalania prisca*** | X | | | | X | X |
| Elapid | X | X | X | X | X | X |
| *Sminthopsis* sp. | | X | X | X | X | X |
| *Dasyurus* sp. | | | | X | X | |
| *Perameles bougainville** | | X | X | | | |
| *Pe. nasuta* | | X | X | X | X | X |
| *Aepyprymnus* sp | | | | | X | |
| *Macropus agilis siva*** | | | | | X | |
| *M. titan*** | | | | | X | X |
| *Protemnodon anak*** | | | | | X | X |
| *Pr. brehus*** | | | | | X | X |
| *Pseudomys* sp.* | | X | X | X | X | X |
| *Rattus* sp. | | X | X | X | X | X |

Range today and support a similar land snail fauna (J. Stanisic, pers. comm.). Additionally, scrubby and closed habitats have previously been suggested for late Pleistocene deposits of the Kings Creek catchment (Price, 2004; Price et al., in press). Woodlands were likely to have been open sclerophyll, interspersed with sparse grassy understories. That interpretation is highlighted by the presence of taxa such as *Austrocuccinea* sp., *Neobatrachus sudelli*, *Aepyprymnus* sp., and *Macropus agilis siva*. Grasslands were likely dominated by large browsing macropods including *Macropus titan* and *Protemnodon* spp. Small agamid lizards such as *Tympanocryptis lineata* probably occupied a similar open habitat, utilizing the earth cracks within black soils.

There are few modern analogues to explain the high habitat diversity indicated by the fauna represented in the Horizon D assemblage. However, considering the relatively constrained sampling area of the Kings Creek palaeo-catchment, it is unlikely that the diverse QML1396 assemblage resulted from the sampling of wide geographic areas outside the immediate catchment area (i.e. by long distance fluvial transport). Additionally, taphonomic data indicates that while the assemblage was hydraulically transported, the components were unlikely to have been transported over long distances. Collectively, those data suggest that a mosaic of grassland, sclerophyllous woodlands, and scrubby vine-thicketed habitats were present within the geographically small Pleistocene Kings Creek catchment. Non-analogue associations of taxa (sensu Lundelius, 1989, as 'disharmonious' associations) from other sites in the Kings Creek catchment (e.g. bandicoots from QML796) support the hypothesis that a vegetative mosaic of habitats was present during the late Pleistocene (Price, 2004).

Comparison of such Pleistocene habitats to those of the modern Kings Creek catchment is difficult considering extensive pastoral activities which have altered natural vegetation in the region since the early 1840's. Even where natural remnant vegetation survives, its current structure and floristics do not necessarily reflect its pre-settlement character. However, a review of over 5,000 land surveys from periods of the initial settlement of the Darling Downs indicates that the region surrounding the immediate area of deposition of QML1396 was dominated by grasslands, with *Eucalyptus orgadophila* woodlands with grassy or shrubby understories being found closer to the range (Fensham & Fairfax, 1997). Based solely on the numbers of different species representing the interpreted Pleistocene habitats of QML1396, it is evident that taxa indicating open grassland habitats are the minority, and that species favouring woodlands and scrubby, vine thicketed habitats dominate the assemblage (Tables 10 & 11). It is hypothesised that the immediate area surrounding the Pleistocene watercourse was dominated by woodlands, scrublands and vine thickets, and that open grasslands were situated farther away from the creek. That interpretation suggests that there must have been significant environmental change between the time of deposition of QML1396 and present, and that would have reflected contraction of woodlands and vine thickets closer to the range, and expansion of grasslands in the catchment area.

Deposition of the QML1396 assemblage occurred around the time of the extinction of the Australian megafauna, i.e. ~46ka (Roberts et al., 2001a). Hence, it is an extremely important Pleistocene assemblage as it provides detailed information about habitats and environments during a critical period for Australian megafauna. The two major hypotheses surrounding the extinction of Australian megafauna are: 1) a naturally driven climate change that coincided with the last glacial maximum, and reduced viable habitats for megafauna, and 2) anthropogenic overkill of megafauna or modification of habitats during initial colonisation of the continent during the late Pleistocene (Martin & Klein, 1984; Diamond, 2001, Roberts et al., 2001a; Brook & Bowman, 2004; Barnosky et al., 2004; Wroe et al., 2004). While there are numerous examples documenting increasing aridity and less fertile habitats during the late Pleistocene (Ayliffe et al., 1998; Bowler et al., 2001; Field et al., 2002; Pack et al., 2003), there are very few examples linking early human artifacts directly to megafauna (Roberts et al., 2001a). One source of confusion has been that important archaeological sites such as Lake Mungo and Koonalda Cave have yielded meager faunal data. Cuddie Springs, New South Wales, is the only site in Australia that shows evidence of a dated association between human technology and megafauna (Dodson et al., 1993). Fossil bone exhibiting human processing marks were dated to 36-27 ka (Field & Dodson, 1999). However, the association between the artifacts and megafauna remains was questioned by Roberts et al. (2001a) who suggested: 1) that sediment mixing and re-deposition of bones from older to younger units had occurred, and 2) the cut marks on the bones relate to an extant species of kangaroo. Although there is little systematic evidence to suggest an anthropogenic component to Australian megafauna extinction, Flannery (1990) argued that because of the rapid nature of an overkill 'blitzkrieg' extinction, kill sites are unlikely to be found. Additionally, timing the arrival of the first humans and extinction of the megafauna has been impeded by a lack of reliable dates (Baynes, 1999; Diamond, 2001; O'Connell & Allen, 2004). On the Darling Downs, there is no evidence of human occupancy prior to 12ka (Gill, 1978). From sedimentological and ecological data, it is evident that increasing aridity on the Darling Downs during the late Pleistocene may have led to woodland and vine thicket habitat contraction, and grassland expansion on the floodplain. Such habitat change was likely detrimental to the persistence of megafauna species on the Darling Downs during the late Pleistocene. However, at present there is no direct evidence to support a hypothesis of an anthropogenic component relating to the retraction of habitats on the Darling Downs between the Pleistocene and present.

## CONCLUSIONS

Systematic collecting targeting both large and small-sized species has facilitated the recovery of a wide variety of fossil taxa, many previously unknown in the Darling Downs fossil record. First Pleistocene Darling Downs records include: pulmonates (7 terrestrial species, 1 aquatic species), *Tympanocryptis "lineata"*, scincids (4 species), and *Sminthopsis* sp. Additionally, several of those new records indicate Pleistocene geographic range extensions.

It has been assumed that the Pleistocene Darling Downs represents a single local fauna with no faunal regionalisation (Molnar & Kurz, 1997). That may appear to be true for larger megafauna taxa, but the small-sized fossil faunas are poorly known at most sites owing to the lack of systematic treatment. Hence, additional systematically collected and dated sites are required to test the hypothesis proposed by Molnar and Kurz (1997), that the Darling Downs represents a single local fauna.

The habitats deduced for the time of deposition of Horizon D appear to be more floristically complex than that of Horizon B. However, analysis of the Pleistocene channel deposits have revealed several taphonomic biases relating to the preservation of large- and small-sized taxa within and between those horizons. Such biases limit palaeoenvironmental comparisons between those two units.

It is evident that there was major habitat change in the Kings Creek floodplain post-deposition of the two major fossiliferous horizons at QML1396. That habitat change likely reflected the contraction of woodlands, vine thickets and scrublands, and expansion of grasslands on the floodplain. Sedimentological and ecological data suggest that that habitat change was climatically driven and occurred irrespective of potential human occupation of the region during the late Pleistocene.

## ACKNOWLEDGMENTS

We thank Gregg Webb, Alex Cook, Liz Reed and Troy Myers for valuable comments and discussion on earlier drafts of this manuscript. Bernie Cooke, Scott Hocknull, Liz Reed and Brendan Brooke are thanked for helpful discussions and comments on various aspects of Darling Downs palaeoenvironments. Matthew Ng, Ricky Bell, Philip Colquhon, Luke Shipton, Kristin Spring, Trevor Sutton, Diane and Amy Sobbe, and Desmond and Jennifer Price, provided much needed support and assistance in the collection and preparation of fossil material. John Stanisic and Scott Hocknull provided identifications for the molluscs and agamids respectively. The AMS$^{14}$C dating component of the study at ANSTO was supported by grants from AINSE (Grant no's. 02-013 & 03-123). This work was funded in part by both the Queensland University of Technology and the Queensland Museum.

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# A SMALL ADULT *PALORCHESTES* (MARSUPIALIA, PALORCHESTIDAE) FROM THE PLEISTOCENE OF THE DARLING DOWNS, SOUTHEAST QUEENSLAND.

*Memoirs of the Queensland Museum 51(1): 202.*

*Palorchestes* is a rare component of the Australian fossil record with late Tertiary origins (Black, 1997). Several species have been described, including; *P. painei* Woodburne 1967 (Late Miocene); *P. anulus* Black 1997 (Late Miocene); *P. selestiae* Mackness 1995 (early Pliocene); *P. parvus* De Vis 1895 (Plio-Pleistocene); and *P. azael* Owen 1874 (Pleistocene). Recent collecting from a late Pleistocene deposit on the eastern Darling Downs, SEQ, recovered a small dentary not referable to those species of *Palorchestes* where the dentary is known.

Family PALORCHESTIDAE Tate, 1948

**Palorchestes** Owen 1873

**Palorchestes** sp. (Fig. 1)

**Material.** QMF49455, edentulous right dentary. QML796, Kings Creek, near Clifton, eastern Darling Downs; late Pleistocene (see Price, 2004).

**Description.** Dentary broken anteriorly at $I_1$ alveolus, posteriorly below $M_3$ anterior alveolus; edentulous (excepting for in situ, broken, heavily worn protolophid of $M_2$); gracile, tapering anteriorly; anterior portion flared buccally; symphysis elongate, ankylosed; mental foramen anteroventral to $P_3$; diastemal ridge well defined, lingually offset, concave lingually. Alveoli measurements in mm: $P_3$: 16.3L × 12.7W, $M_1$: 18.6L × 10.9W; $M_2$: 20.5L × 13.6W.

**Remarks.** The dentary is referred to *Palorchestes* based on the combination of its large size; presence of lophids; long and narrow symphysial region; gently tapered anterior; and buccally flared diastema. The ankylosed symphysis, heavily worn protolophid of $M_2$ and presence of $P_3$ alveoli indicates that the individual was an adult. Therefore, morphological differences between QMF49455 and other *Palorchestes* species are unlikely to be ontogenetic. Measurements of alveoli suggest that the teeth were similar in size to *P. parvus*. However, QMF49455 differs from *P. parvus*, *P. azael* and *P. painei* by being more gracile with an anterior margin more buccally flared; diastemal ridge better defined and lingually concave; and diastema proportionately shorter. Comparison to *P. selestiae* and *P. anulus* is not possible as those species are known only from the $M^1$. Black (1997) shows *P. selestiae* to be markedly larger and *P. anulus* to be smaller than *P. parvus*. Hence, QMF49455 may represent an undescribed, small species of *Palorchestes* or sexual dimorphism within small-sized *Palorchestes* spp.

*Palorchestes* spp. generally occur allopatrically showing a trend of increased body size from the mid Tertiary to the late Pleistocene (Murray, 1991). QMF49455 is unusual in being a small adult *Palorchestes* from the late Pleistocene. A second species of *Palorchestes*, also recovered from QML796 and represented by a $RI_1$, is referable to *P. azael* (QMF33024). Sympatry in *Palorchestes* spp. has been noted by Davis & Archer (1997), however, those occurrences may be due to temporally mixed faunas. Here we confirm sympatry of two *Palorchestes* species during the late Pleistocene.

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FIG. 1. QMF49455, *Palorchestes* sp. right dentary. A, occlusal view. B, lateral view.

# FIRST RECORD OF A GIANT VARANID (*MEGALANIA*, SQUAMATA) FROM THE PLEISTOCENE OF NARACOORTE, SOUTH AUSTRALIA

ELIZABETH REED AND MARK N. HUTCHINSON

Reed, E.H. & Hutchinson, M.N. 2005 05 31: First record of a giant varanid (Megalania, Squamata) from the Pleistocene of Naracoorte, South Australia. *Memoirs of the Queensland Museum* **51**(1): 203-213. Brisbane. ISSN 0079-8835.

A humerus attributable to the giant varanid *Megalania prisca* Owen, 1859, from a newly discovered Pleistocene cave site near Naracoorte, South Australia extends the distribution of giant varanids south of any previous record. Unlike the only other known humerus (QM F865 from the eastern Darling Downs), the new specimen represents an immature animal (epiphyses unfused) and allows insight into the pattern of growth of *Megalania*. Both *Megalania* humeri are massively built with the distal width being much broader than the proximal width (proximal is slightly greater than distal in all living varanids). The immature specimen from Naracoorte is within the range of lengths seen in large extant varanids but is far more robust than any living species. Estimates of the size and proportions of *Megalania* have been based on *Varanus komodoensis*, the largest living varanid. However, based on our examination of humeri from 19 living varanid species, the humeri of even large *V. komodoensis* retain the proportions of smaller varanids and do not suggest the remodelling evident in *Megalania*. Rather than being a scaled-up *Varanus*, *Megalania* as represented by the humeri, appears to have been a massively built animal throughout its life, its proportions not matched by those of any living *Varanus*. Size estimates for *Megalania* based on the length of bones in living varanids may well be in error, and the larger estimates are probably overestimates. ❑ *Pleistocene, Naracoorte, varanid, Megalania, humerus, caves.*

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Fossil remains of giant Pliocene to Pleistocene varanids, currently attributed for convenience to *Megalania prisca* Owen, 1859, are known from widely scattered localities in northern and eastern Australia (Fig. 1) (Longman, 1924; Hecht, 1975; McNamara, 1990; Mackness & Hutchinson, 2000). The earliest record of Australian giant varanids comes from the Miocene of the Northern Territory (Murray & Megirian, 1992). Many parts of the skeleton of *Megalania* are represented by fossils, but these stem from only one or two fragmentary skeletons together with numerous isolated bones, mostly vertebrae (Rich & Hall, 1979). Remains have been considered too scanty, with few elements known from multiple examples, to determine whether the remains are attributable to one species or several. Several workers have questioned whether the genus *Megalania* is distinct from *Varanus* (Estes, 1983; Lee, 1996; Hutchinson & Mackness, 2002), given that the differences between the two genera are mostly thought to be due to expansion and robustness associated with large body size. Hecht (1975), Rich & Hall (1979) and Wroe (2002) have discussed the overall size and proportions of *Megalania*, and Erickson et al., (2003) made estimates of growth rates and time to maturity. In the absence of adequate associated remains, reconstructions of *Megalania*'s appearance depend heavily on extrapolations from living varanid lizards. Similarly, reconstructions of its palaeoecology are limited by knowledge of its distribution.

The caves of Naracoorte, South Australia contain some of the richest Pleistocene fossil deposits in Australia and have yielded a diverse array of vertebrate species (Reed & Bourne, 2000), yet fossils attributable to *Megalania* have never been found there. This paper describes a specimen from a Naracoorte cave site that is recognisable as belonging to a giant varanid such as *Megalania*. The Naracoorte specimen is a humerus of an immature individual and allows some insight into the pattern of growth. Comparison between humeral proportions for the fossil varanids and extant species is also presented in this paper.

## METHODS

The site of the discovery of the new specimen is Crawford's Cornucopia Cave, located 11km

FIG. 1. Map showing the location of Naracoorte (indicated by arrow) and other localities where remains of *Megalania* have been found.

south of the township of Naracoorte in the SE of South Australia (Fig. 1). The cave was discovered during vineyard preparation in 1999, and contains bone-rich sediment cone deposits. Preliminary excavations have been conducted by one of the authors (ER) and S. Bourne. Dating samples are yet to be processed; however associated fauna indicate a Pleistocene age (Reed & Bourne, 2000). The Naracoorte specimen is registered in the palaeontology collection of the South Australian Museum, and has been assigned the registration number SAMP40102. To assess the proportions of the Naracoorte fossil the following measurements were taken (see Fig. 2): length, proximal width, distal width, maximum and minimum diameter of the diaphysis. Comparative data were taken from a cast of the sole humerus attributed to *Megalania prisca* (QMF865), housed in the Queensland Museum and first described by De Vis (1885); see also Anderson (1930) and Hecht (1972, 1975). Anatomical terms used in this paper for describing lizard humeri follow Lécuru (1969).

To make comparisons between the fossils and living varanids, we obtained a series of measurements for humeral proportions from 19 extant species. These measurements were taken in the same manner as for the fossils (Fig. 2). Data for modern varanid species were obtained from skeletons in the collection of several major institutions. Table 1 provides a full list of specimens used in this study, the measurements obtained and details regarding the institutions in which they are housed.

To compare the relative robustness of the two 'giant' varanid humeri with extant species, we used the method of Lécuru (1969) to calculate the ratio of robustness (length / maximum diaphysis diameter) and the ratio of the extremities (proximal width / distal width). The proportions of humeri are presented as bivariate scatter plots, showing humerus length plotted against snout-vent length, humerus proximal and distal width against humerus length, and distal width against proximal width. The snout-vent length of the specimens supplying the humeri was obtained from the museum or, where lacking, was estimated from the skeletal specimens. We estimate that such approximated SVL measurements of larger varanids are likely to be within 10cm of the true value.

## RESULTS

DESCRIPTION. SAMP40102 (Fig. 3A-B, Fig 4A-B) is a left humerus with a preserved length of 105.3 mm. It is short, stout and robust with pronounced torsion (~40°) of the distal extremity relative to the proximal. Missing epiphysial caps are unfused indicating an immature individual. Distinct ectepicondylar foramen, prominent ectepicondylar crest, weak entepicondylar crest, deep olecranon fossa and a shallow, oval-shaped muscle scar (for insertion of the *latissimus dorsi)* on the dorsal surface at the base of the proximal head. The proximal head is damaged, with the top of the deltopectoral crest missing.

The proximal width is 47.1mm and distal width is 73.3mm. Maximum and minimum diameter of the diaphysis at its mid-point are 22.4mm and 19.7mm, respectively. Estimating the size and proportions of the epiphyses using the mature humerus attributed to *Megalania* (QMF865) as a model gives values of ~123mm for maximum length, ~48mm for proximal width and ~75mm for distal width (Fig. 4C-D).

REMARKS. The specimen is clearly a lizard. Presence of an ectepicondylar foramen, absence

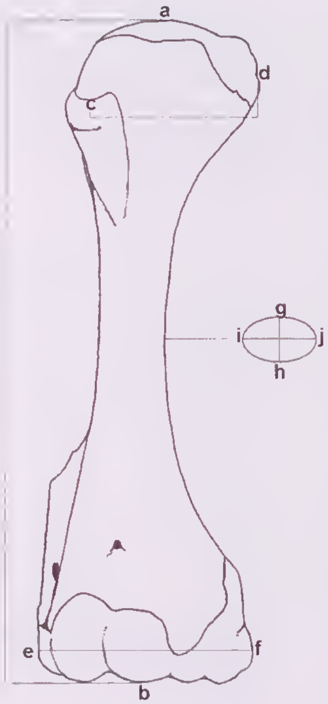

FIG. 2. Measurements taken for varanid humeri. a to b = length, c to d = proximal width, e to f = distal width, g to h = minimum diaphysis diameter, i to j = maximum diaphysis diameter.

of an entepicondylar foramen, and the position of the deltopectoral crest adjacent to the head of the humerus rule out a marsupial. Monotreme humeri (*Tachyglossus* and *Megalibgwilia*) are also eliminated by their extreme modifications to the proximal and distal extremities. Absence of an enlarged medial process opposite the deltopectoral crest eliminates a turtle. The denseness of the bone evident in broken surfaces eliminates a bird as a possibility.

While identification as a lizard is well founded, the general morphology is much more robust than is usual in lizards (see Lécuru, 1969). Relative proportions and general morphology compare favourably with the sole humerus (QMF865) attributed to *Megalania prisca* (see De Vis, 1885 for description of this specimen).

COMPARISON WITH EXTANT VARANIDS. When compared to the humeri of extant varanids, both fossils are more massively built, with particularly short and stout diaphyses (compare Figs 2 and 3). There are clear differences between *Megalania* and extant varanids in the relative proportions of the humerus, and both fossil specimens are far more robust than any living species (Fig. 5, Table 2).

In the extant species studied, there is a general trend for increase in length of the humerus with snout-vent length (Fig. 6). The fossil humeri attributable to *Megalania* are not extraordinary in terms of length when compared to the living varanids (Table 1). The Queensland fossil is only 4% longer than the largest *Varanus komodoensis* specimen studied, and the immature Naracoorte specimen falls within the range of lengths seen in large living varanids (Table 1).

When humeral length is compared with proximal width, all species in this study (including *Megalania*) fall within a similar range (Fig. 5A). However, when distal width is plotted against humeral length (Fig. 5B) and proximal width (Fig. 5C), *Megalania* clearly differs from the pattern displayed by living species in that the distal extremity is much broader than the proximal. In the living species the width of the proximal extremity is equal to or slightly greater than the distal. As the immature fossil shows the same pattern as the adult, it suggests that *Megalania* had a different pattern of growth from any living varanid.

These relationships are further illustrated by the ratios presented in Table 2. The ratio of robustness (ie. the ratio of diaphysis length to maximum diameter) for the *Megalania* humeri indicate they are approximately 1.45 times as robust as the extant species studied. The ratio of the extremities (proximal width to distal width), indicates that the *Megalania* humeri are considerably broader distally.

## DISCUSSION

The Naracoorte specimen extends the distribution of giant varanids well south of any previous record indicating a wider geographic range than previously thought. This is important as *Megalania* has previously been described as rare with a limited geographic range, largely restricted to sub-tropical and tropical regions (see Wroe, 2002). The discovery of remains attributable to *Megalania* at Naracoorte shows that giant goannas ranged into temperate as well as tropical latitudes. This is not necessarily surprising as at least one living varanid species, *Varanus gouldii*, has a continent-wide range, while others, notably the relatively large *V. varius*, occur from tropical to temperate latitudes (Cogger, 2000).

TABLE 1. Measurements (mm) of varanid humeri used in study. L = length, PW = proximal width, DW = distal width, D-Min = minimum width of diaphysis, D-Max = maximum width of the diaphysis, est. = estimated to include epiphyses. Unreg. = unregistered specimen. * indicates epiphyses absent. QM = Queensland Museum; SAM P = South Australian Museum palaeontology collection; SAM R = South Australian Museum reptile collection; FU = Flinders University; AMNH = American Museum of Natural History; NHM = Natural History Museum, London ; YPM = Yale Peabody Museum of Natural History; SMF = Senckenberg Museum, Frankfurt; CSIRO R = Commonwealth Scientific and Industrial Research Organisation Canberra, Reptile collection; AZ = Adelaide Zoo; SBLR = comparative collection of the author (ER); LACM = Los Angeles County Museum; NHRM = Naturhistorische Museum, Leiden.

| Species | Reg. Number | L (mm) | PW (mm) | DW (mm) | D-Min (mm) | D-Max (mm) |
|---|---|---|---|---|---|---|
| *Megalania prisca* | QM F865 | 174.23 | 73.58 | 105.28 | 32.13 | 35.08 |
| | | | 78.98 est. | | | |
| *Megalania* (Naracoorte) | SAM P40102 | *105.25 | 47.10 | 73.30 | 19.70 | 22.40 |
| | | 123.5 est. | 48.00 est. | 75.50 est. | | |
| *Varanus* sp (fossil) | FU10640 | *64.18 | 25.82 | 24.63 | 7.16 | 7.95 |
| | FU10668 | *68.33 | 28.39 | 25.16 | 7.26 | 8.62 |
| | FU10158 | *53.19 | 20.34 | 19.51 | 5.87 | 6.94 |
| *Varanus* sp | AMNH139671 | 67.20 | 25.90 | 26.90 | 6.90 | 7.80 |
| | AMNH123313 | 69.80 | 27.80 | 26.00 | 6.40 | 7.90 |
| *Varanus albigularis* | NHM RR1961.1760 | 54.00 | 24.10 | 21.10 | 5.20 | 6.10 |
| *Varanus beccarrii* | YPM11899 | 41.76 | 9.40 | 8.50 | 2.79 | 2.85 |
| *Varanus bengalensis* | YPM11028 | 33.00 | 11.00 | 11.50 | 3.00 | 3.50 |
| | YPM11202 | 48.50 | 16.00 | 16.00 | 4.00 | 5.00 |
| | SMF60428 | 70.60 | 33.70 | 32.60 | 9.40 | 10.30 |
| | AMNH29932 | 64.20 | 23.80 | 22.50 | 5.00 | 6.60 |
| *Varanus dumerilli* | YPM11038 | 37.91 | 12.21 | 12.04 | 3.30 | 3.79 |
| | YPM11203 | 44.00 | 16.00 | 15.00 | 4.00 | 5.50 |
| *Varanus exanthematicus* | YPM11141 | 27.00 | 10.00 | 9.00 | 2.00 | 3.00 |
| | AMNH137238 | 29.50 | 11.30 | 10.60 | 2.50 | 3.10 |
| | AMNH137237 | 32.60 | 13.10 | 12.20 | 3.00 | 3.80 |
| | AMNH140804 | 48.60 | 21.50 | 19.00 | 5.40 | 6.20 |
| | AMNH140803 | 22.40 | 8.70 | 8.10 | 1.80 | 2.30 |
| *Varanus giganteus* | SAM R33352 | 76.80 | 34.00 | 30.40 | 7.30 | 9.00 |
| *Varanus gouldii* | CSIROR01278 | 61.30 | 25.50 | 23.80 | 6.10 | 8.40 |
| | CSIROR01278 | 61.00 | 25.10 | 23.60 | 6.00 | 7.60 |
| | CSIROR05080 | 33.70 | 12.30 | 12.10 | 2.70 | 3.50 |
| | CSIROR05080 | 33.80 | 12.20 | 12.20 | 2.90 | 3.50 |
| | CSIROR05085 | 45.00 | 15.80 | 15.00 | 3.80 | 5.20 |
| | CSIROR05085 | 41.50 | 15.70 | 15.10 | 3.90 | 4.90 |
| | CSIROR - unreg. | 46.00 | 16.40 | 15.90 | 3.70 | 4.90 |
| | CSIROR - unreg. | 45.90 | 16.30 | 14.10 | 3.80 | 4.60 |
| *Varanus griseus* | YPM14332 | 62.60 | 26.64 | 22.62 | 5.50 | 8.08 |
| | YPM 10383 | 40.00 | 14.50 | 12.00 | 3.50 | 4.00 |
| *Varanus komodoensis* | LACM 121971 | 137.80 | 69.60 | 64.30 | 17.40 | 18.30 |
| | LACM 121971 | 138.30 | 69.10 | 64.60 | 17.60 | 18.40 |
| | YPM10881 | 132.04 | 59.64 | 60.27 | 17.92 | 19.95 |
| | NHM 1934.9.2.2 | 130.30 | 62.60 | 57.40 | 16.20 | 20.40 |
| | NHRM 19.7.26 | 160.00 | 81.10 | 73.00 | 21.40 | 22.00 |
| | NHRM 17497 | 127.00 | 63.60 | 58.40 | 15.20 | 18.00 |
| | NHRM 21.11.38 | 150.00 | 74.40 | 66.70 | 18.00 | 20.00 |
| | NHRM 17504 | 143.00 | 73.30 | 66.30 | 19.50 | 20.20 |
| | SMF37209 | 140.00 | 73.80 | 62.50 | 18.30 | 20.30 |
| | SMF57555 | 140.00 | 65.70 | 64.50 | 18.00 | 20.90 |

| Species | Reg. Number | L (mm) | PW (mm) | DW (mm) | D-Min (mm) | D-Max (mm) |
|---|---|---|---|---|---|---|
| *Varanus komodoensis* | SMF68133 | 102.20 | 47.80 | 41.40 | 14.70 | 15.50 |
| | AMNH37912 | 137.30 | 65.30 | 62.30 | 16.10 | 18.20 |
| | AMNH37909 | 155.00 | 77.90 | 69.90 | 21.00 | 21.80 |
| | AMNH37900 | 112.30 | 54.00 | 49.40 | 11.70 | 13.90 |
| | AMNH37908 | 82.30 | 35.20 | 33.60 | 8.10 | 10.20 |
| | AMNH74606 | 138.60 | 67.50 | 62.70 | 16.9 | 18.40 |
| | AMNH37911 | 132.10 | 64.60 | 60.10 | 15.7 | 16.60 |
| | AMNH37913 | 129.10 | 62.80 | 58.00 | 13.9 | 15.00 |
| *Varanus melinus* | YPM11202 | 48.50 | 16.00 | 16.00 | 4.00 | 5.00 |
| *Varanus niloticus* | YPM10880 | 68.00 | 26.00 | 24.00 | 4.00 | 5.00 |
| | YPM10879 | 61.00 | 23.00 | 20.00 | 3.00 | 5.00 |
| | YPM10877 | 56.00 | 20.00 | 19.00 | 4.00 | 5.00 |
| | YPM14333 | 70.32 | 29.11 | 25.89 | 6.90 | 7.19 |
| | NHM 1975.994 | 86.50 | 37.00 | 31.80 | 8.20 | 9.70 |
| | NHM 1970.1983 | 53.40 | 19.10 | 18.40 | 4.20 | 5.30 |
| | NHRM - unreg. | 75.80 | 30.50 | 29.60 | 7.50 | 8.40 |
| | AMNH137116 | 96.30 | 42.50 | 43.50 | 9.80 | 12.00 |
| | AMNH88635 | 53.90 | 20.60 | 18.30 | 4.20 | 5.60 |
| | AMNH140805 | 34.00 | 11.40 | 10.90 | 2.40 | 3.30 |
| | AMNH10085 | 66.30 | 25.40 | 24.10 | 5.70 | 6.80 |
| *Varanus rosenbergi* | SBLR002 | 32.07 | 10.76 | 10.69 | 2.50 | 3.31 |
| | SBLR002 | 32.42 | 10.67 | 10.59 | 2.43 | 3.33 |
| *Varanus rudicolis* | YPM12234 | 44.88 | 15.78 | 16.03 | 3.69 | 4.58 |
| | YPM12235 | 64.41 | 25.75 | 23.82 | 5.63 | 7.50 |
| | SMF59216 | 73.70 | 28.40 | 26.70 | 6.80 | 7.10 |
| *Varanus salvadori* | SMF58064 | 104.70 | 36.4 | 32.50 | 8.90 | 9.50 |
| *Varanus salvator* | YPM 10834 | 92.00 | 37.00 | 34.00 | 8.00 | 9.00 |
| | YPM 11022 | 15.00 | 4.00 | 4.00 | 1.00 | 1.50 |
| | YPM 12723 | 93.11 | 39.91 | 36.55 | 10.97 | 11.54 |
| | NHM - unreg. | 92.60 | 40.90 | 38.90 | 9.40 | 11.60 |
| | NHM1961.1761 | 43.10 | 15.60 | 12.80 | 3.20 | 3.40 |
| | NHRM 9.5.1906 | 115.20 | 45.60 | 42.50 | 11.10 | 12.50 |
| | NHM 1972.2162 | 77.40 | 29.20 | 29.50 | 6.80 | 8.40 |
| | SMF40175 | 86.70 | 34.70 | 32.90 | 7.50 | 9.50 |
| | AMNH57765 | 83.10 | 30.10 | 30.80 | 7.40 | 9.30 |
| | AMNH141148 | 36.90 | 12.10 | 12.00 | 3.30 | 4.20 |
| | AMNH141155 | 36.60 | 13.00 | 13.30 | 3.30 | 4.20 |
| | AMNH49230 | 82.40 | 31.90 | 32.90 | 6.70 | 9.30 |
| *Varanus storri* | YPM11042 | 24.04 | 7.22 | 6.68 | 1.89 | 2.10 |
| *Varanus tristis* | YPM11175 | 19.00 | 6.00 | 6.00 | 1.00 | 2.00 |
| *Varanus varius* | SAM R33351 | 55.30 | 20.20 | 18.80 | 4.80 | 5.20 |
| | SAM R33351 | *49.80 | 18.50 | 17.10 | 4.80 | 5.20 |
| | SAM display | 86.10 | 39.10 | 37.00 | 11.70 | 12.80 |
| | SAM display | 86.10 | 38.60 | 35.70 | 10.90 | 12.80 |
| | CSIROR05081 | 62.00 | 25.20 | 21.60 | 6.80 | 7.20 |
| | CSIROR05081 | 61.90 | 25.50 | 21.10 | 6.60 | 6.90 |
| | CSIROR05832 | 72.90 | 31.00 | 23.90 | 6.90 | 8.00 |
| | CSIROR05832 | 73.40 | 31.00 | 26.80 | 7.30 | 8.00 |
| | AZ display | 87.50 | 39.08 | 38.00 | 10.30 | 12.00 |
| | AZ display | 87.00 | 41.09 | 36.41 | 10.19 | 11.81 |
| | SBLR001 | 61.22 | 24.68 | 21.19 | 5.97 | 6.75 |
| | SBLR001 | 61.20 | 24.89 | 21.27 | 5.99 | 6.76 |
| *Varanus yuwonoi* | YPM12495 | 44.30 | 14.63 | 14.40 | 3.40 | 4.24 |

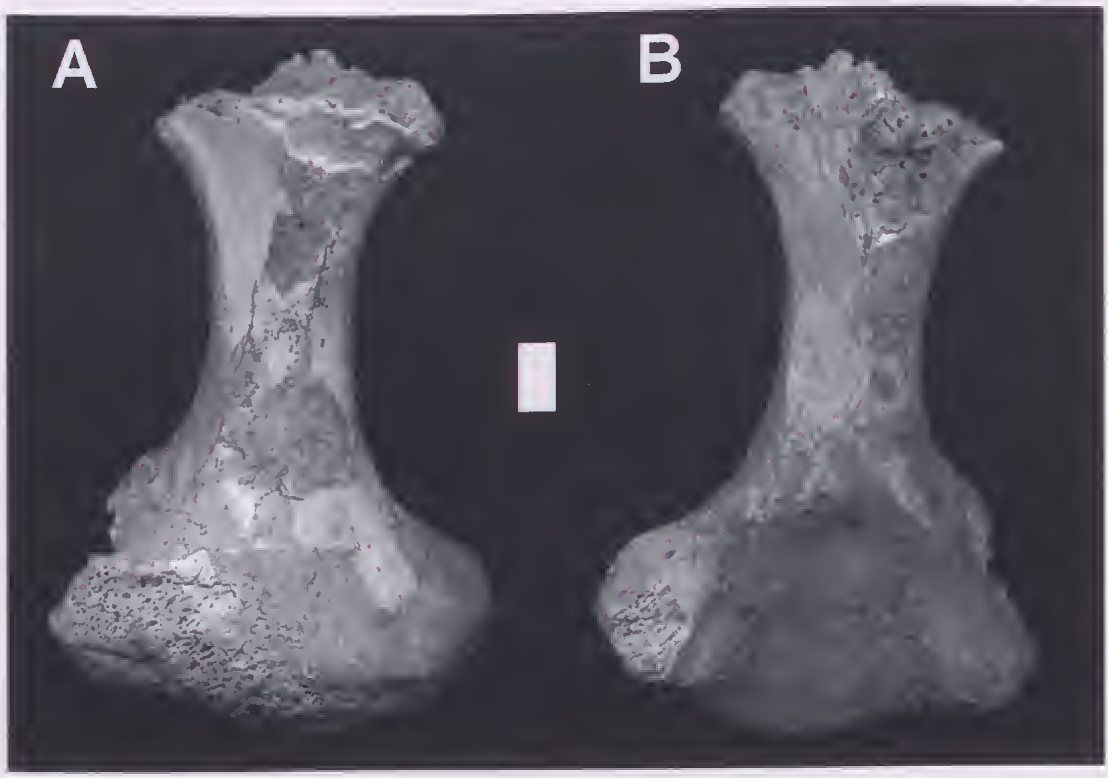

FIG. 3. SAMP40102, left humerus of a giant varanid from Naracoorte. A. Postero-dorsal view. B. Antero-ventral view. Scale = 5cm.

Wroe (2002) favoured the interpretation that the apparent low abundance of *Megalania* in Pliocene to Pleistocene fossil deposits reflected its actual rarity in the palaeofaunas, but acknowledged that some "unkown taphonomic phenomena" may have influenced its representation in fossil deposits. The mode of accumulation would have a strong influence over whether large reptiles would become accumulated in deposits. The site of discovery of the Naracoorte fossil is one of only two sites in the region with evidence of being a carnivore lair, while the majority of other sites are pitfall deposits (Reed & Bourne, 2000). The fact that this is the only site to have yielded evidence of *Megalania* after 30 years of collecting suggests that *Megalania* may not have been vulnerable to pitfall entrapment. Worthy & Holdaway (1996) have made the important point that when attempting palaeoecological reconstructions a range of sites of varying taphonomies should be investigated to eliminate biases produced by single modes of accumulation.

Previous writings on the possible ecological significance of *Megalania* have sometimes been coloured by an apparent lack of knowledge of the growth, distribution and abundance of living large Australian reptile carnivores. Wroe (2002: 18) stated "it is clear for taxa of indeterminate growth in particular, maximum dimensions are likely to represent gross deviations from the mean and do not provide reasonable grounds for predicting ecology". This statement overlooks what is now known of squamate patterns of growth. Estes (1983), Estes et al., (1988) and more recently Maisano (2001, 2002) point out that lizards have determinate growth, with relatively short juvenile periods and adult size rapidly approaching an asymptote following sexual maturity. In the case of the Queensland humerus, the complete epiphysial fusion would indicate an individual within 20% of the maximum size achieved by the species (Maisano, 2002). Thus many populations of extant lizards that live for more than a few years are composed mainly of animals at or near statistically normal adult size.

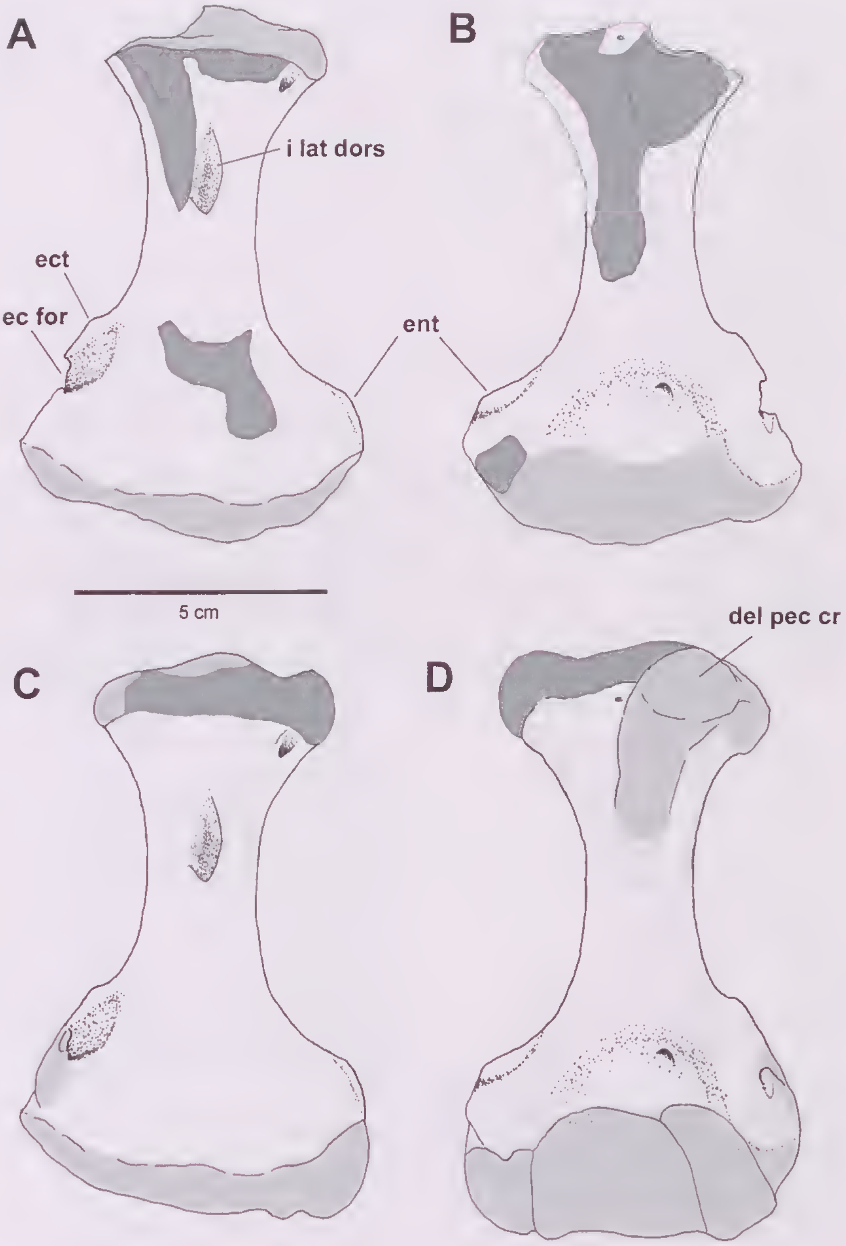

FIG. 4. A, B, diagram of *Megalania* humerus as recovered. Pale grey indicates unfinished bone, dark grey broken bone surface. C, D, restored humerus. Pale grey shading indicates distal joint surfaces and massive pectoral crest restored based on adult humerus (QM F865) and dark grey the surface of the proximal articulation (mostly missing in QMF865) extrapolated from extant varanids. Abbreviations: del pec cr, deltopectoral crest, ect, ectepicondyle, ec for ectepicondylar foramen, ent, entepicondyle, I lat dors, insertion for *m. latissimus dorsi*. Scale bar = 4cm.

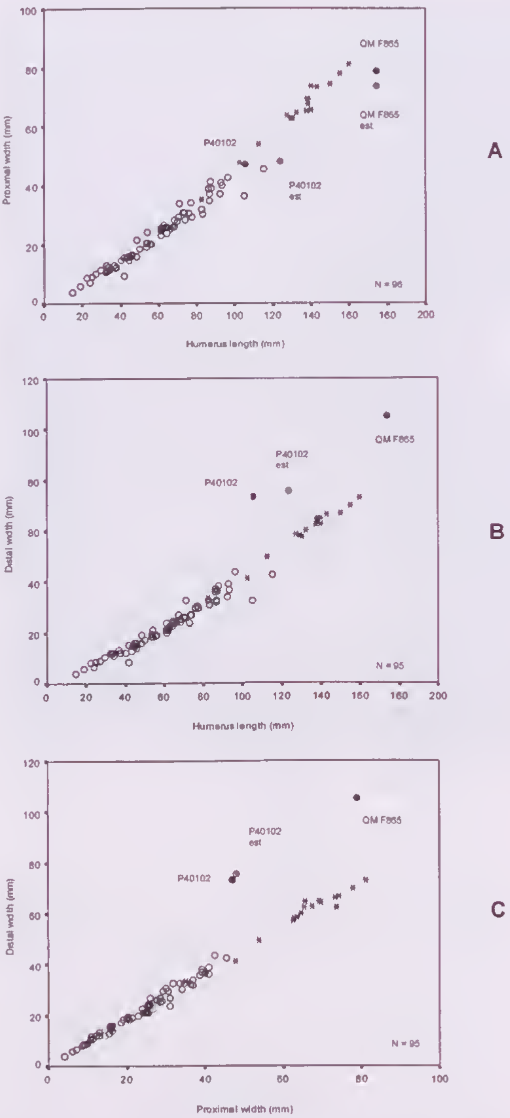

FIG. 5. Scatter plots of measurements taken for humeri of *Megalania* and extant varanids. A, Length vs proximal width. B, Length vs distal width. C, Proximal width vs distal width (see Fig. 2 for measurements taken). All measurements are in millimetres. The fossil specimens are indicated by their registration numbers. * = *Varanus komodoensis*, °= all other species. N = 96 for A. N = 95 individual specimens for B & C.

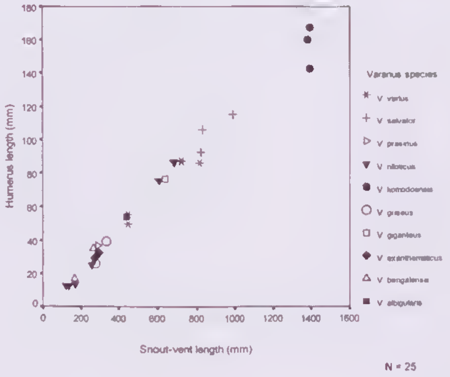

FIG. 6. Scatter plot showing snout-vent length vs humerus length for 10 extant *Varanus* species.

Erickson et al., (2003) estimated growth rates for *Megalania*, based on an associated femur and dermal bones, and suggested that *Megalania* grew to its large size by maintaining high, juvenile-like growth rates longer than large living varanids. Their data were based on a specimen that had not stopped growing (unfused femoral epiphyses), and they made their sizes estimates based on a published study of living varanids that correlated femur length with snout-vent length. Extrapolating from the living species, Erickson et al., (2003) obtained an estimated snout-vent length for this 'young adult' specimen as about 2m. Most of the recent published mentions of the size of *Megalania* are based on the less explicit review of Hecht (1975), which gave a variety of estimated body sizes, depending on the bone chosen for comparison. Most bones gave an estimate of 2-3 metres for snout-vent length, with one outlying, maximum of 4.5m based on an ungual phalanx and the minimum adult size estimate from the humerus (1.5 m SVL). In all cases, the estimates assume that the overall proportions of *Megalania*, as in *V. komodoensis* (Auffenberg 1981), were simple increments beyond those of living varanids. Few writers (De Vis, 1885; Anderson, 1930) have considered the idea that *Megalania*, throughout its growth, was different in its proportions from any living varanid.

Molnar (1990), in describing the frontal and parietal, also based his conclusions on extrapolation from living large varanids (*V. salvadorii* and *V. varius*), but his data indicate that the frontal region of the skull was thicker than expected from size alone and exaggerated via a sagittal crest. Molnar's conclusion was that these bones showed *Megalania* was qualitatively different from living *Varanus* in frontal thickness and in the bony contacts between the frontal and

TABLE 2. Ratio of robustness (RR) and ratio of the extremities (RE) for the specimens measured for this study. Ratios calculated following the method of Lécuru (1969). Institutional abbreviations follow Table 1.

| Species | Reg. Number | RR (L/D-Max) | RE (PW/DW) |
|---|---|---|---|
| *Megalania prisca* | QM F865 | 4.97 | 0.75 |
| *Megalania* (Naracoorte) | P40102 | 4.69 | 0.64 |
| *Varanus* sp (fossil) | FU10640 | 8.07 | 1.05 |
| | FU10668 | 7.93 | 1.13 |
| | FU10158 | 7.66 | 1.04 |
| *Varanus* sp | AMNH139671 | 8.62 | 0.96 |
| | AMNH123313 | 8.84 | 1.07 |
| *Varanus albigularis* | NHM RR1961.1760 | 8.85 | 1.14 |
| *Varanus beccarrii* | YPM11899 | 14.65 | 1.11 |
| *Varanus bengalensis* | YPM11028 | 9.43 | 0.96 |
| | YPM11202 | 9.70 | 1.00 |
| | SMF60428 | 6.85 | 1.03 |
| | AMNH29932 | 9.72 | 1.06 |
| *Varanus dumerilli* | YPM11038 | 10.00 | 1.01 |
| | YPM11203 | 8.00 | 1.07 |
| *Varanus exanthematicus* | YPM11141 | 9.00 | 1.11 |
| | AMNH137238 | 9.52 | 1.07 |
| | AMNH137237 | 8.58 | 1.07 |
| | AMNH140804 | 7.84 | 1.13 |
| | AMNH140803 | 9.74 | 1.07 |
| *Varanus giganteus* | SAM R33352 | 8.53 | 1.12 |
| *Varanus gouldii* | CSIROR01278 | 7.30 | 1.07 |
| | CSIROR01278 | 8.02 | 1.06 |
| | CSIROR05080 | 9.69 | 1.02 |
| | CSIROR05080 | 9.66 | 1.00 |
| | CSIROR05085 | 8.65 | 1.05 |
| | CSIROR05085 | 8.47 | 1.04 |
| | CSIROR - unreg. | 9.39 | 1.03 |
| | CSIROR - unreg. | 9.99 | 1.16 |
| *Varanus griseus* | YPM14332 | 7.75 | 0.92 |
| | YPM 10383 | 10.00 | 1.18 |
| | Lécuru (1969) | 11.73 | 1.13 |
| *Varanus komodoensis* | LACM 121971 | 7.53 | 1.08 |
| | LACM 121971 | 7.52 | 1.07 |
| | YPM10881 | 6.62 | 0.99 |
| | NHM 1934.9.2.2 | 6.39 | 1.09 |
| | NHRM 19.7.26 | 7.27 | 1.11 |
| | NHRM 17497 | 7.05 | 1.09 |
| | NHRM 21.11.38 | 7.50 | 1.12 |
| | NHRM 17504 | 7.08 | 1.11 |
| | SMF37209 | 6.90 | 1.18 |
| | SMF57555 | 6.70 | 1.02 |
| | SMF68133 | 6.61 | 1.15 |
| | AMNH37912 | 7.54 | 1.05 |
| | AMNH37909 | 7.11 | 1.11 |
| | AMNH37900 | 8.08 | 1.09 |
| | AMNH37908 | 8.07 | 1.05 |
| | AMNH74606 | 7.53 | 1.08 |
| *Varanus komodoensis* | AMNH37911 | 7.96 | 1.07 |
| | AMNH37913 | 8.61 | 1.08 |
| *Varanus melinus* | YPM11202 | 9.70 | 1.00 |
| *Varanus niloticus* | YPM10880 | 13.60 | 1.08 |
| | YPM10879 | 12.20 | 1.15 |
| | YPM10877 | 11.20 | 1.05 |
| | YPM14333 | 9.78 | 1.12 |
| | NHM 1975.994 | 8.92 | 1.16 |
| | NHM 1970.1983 | 10.07 | 1.04 |
| | NHRM - unreg. | 9.02 | 1.03 |
| | AMNH137116 | 8.03 | 0.98 |
| | AMNH88635 | 9.63 | 1.13 |
| | AMNH140805 | 10.30 | 1.05 |
| | AMNH110085 | 9.75 | 1.05 |
| | Lécuru (1969) | 9.44 | 0.99 |
| *Varanus rosenbergi* | SBLR002 | 9.69 | 1.01 |
| | SBLR002 | 9.73 | 1.01 |
| *Varanus rudicolis* | YPM12234 | 9.80 | 0.98 |
| | YPM12235 | 8.59 | 1.08 |
| | SMF59216 | 10.38 | 1.06 |
| *Varanus salvadori* | SMF58064 | 11.02 | 1.12 |
| *Varanus salvator* | YPM 10834 | 10.22 | 1.09 |
| | YPM 11022 | 10.00 | 1.00 |
| | YPM 12723 | 8.07 | 1.09 |
| | NHM - unreg. | 7.98 | 1.05 |
| | NHM1961.1761 | 12.68 | 1.22 |
| | NHRM 9.5.1906 | 9.22 | 1.07 |
| | NHM 1972.2162 | 9.21 | 0.99 |
| | SMF40175 | 9.13 | 1.05 |
| | AMNH57765 | 8.94 | 0.98 |
| | AMNH141148 | 8.79 | 1.01 |
| | AMNH141155 | 8.71 | 0.98 |
| | AMNH49230 | 8.86 | 0.97 |
| | Lécuru (1969) | 10.60 | 1.02 |
| *Varanus storri* | YPM11042 | 11.45 | 1.08 |
| *Varanus tristis* | YPM11175 | 9.50 | 1.00 |
| *Varanus varius* | SAM R33351 | 10.63 | 1.07 |
| | SAM R33351 | 9.58 | 1.08 |
| | SAM display | 6.73 | 1.06 |
| | SAM display | 6.73 | 1.08 |
| | CSIROR05081 | 8.61 | 1.17 |
| | CSIROR05081 | 8.97 | 1.21 |
| | CSIROR05832 | 9.11 | 1.30 |
| | CSIROR05832 | 9.18 | 1.16 |
| | AZ display | 7.29 | 1.03 |
| | AZ display | 7.37 | 1.13 |
| | SBLR001 | 9.06 | 1.16 |
| | SBLR001 | 9.05 | 1.17 |
| *Varanus yuwonoi* | YPM12495 | 10.45 | 1.02 |

postorbitofrontal. Hecht's (1975) earlier summary pointed out further character states that appeared to be unique to *Megalania*, not just the simple consequence of scaling up a *Varanus*. These include a vertically oriented supraoccipital as well as the unusually short humeral shaft.

Lécuru's (1969) summary of intrafamilial variation in varanid humeri reported little of significance across the small sample of living species. Our larger sample confirms this pattern. As large *Varanus* species reach their maximum size, the proximal and distal regions expand laterally, but distal expansion is only slightly greater than proximal even in *V. komodoensis*. The most obvious proportional difference between humeri of large and small living varanids is expressed by Lécuru's 'Ratio of Robustness' (humerus length to mid-diaphysial diameter; Table 2), with the value of the ratio falling as the bone becomes stouter in larger animals. The humerus of *Megalania*, as represented by the two known specimens, was far more robust (even in immature animals) than is the case for any living varanid, and yet disproportionately short if *Megalania* is reconstructed as an extension of the growth patterns shown by living *Varanus*. The developmental pattern and body proportions do not seem to be merely an extrapolation from living varanid development. *Megalania* appears to have been a very stocky and heavily built animal well before it matured, perhaps with the head, neck and fore-body relatively more robust than living species of *Varanus*. If its proportions did not match those of any living *Varanus*, body size estimates based solely on length of individual bones may well be misleading.

## ACKNOWLEDGEMENTS

We thank Steve Donnellen (South Australian Museum) who made many of the measurements presented here during a tour of the major museums, and we acknowledge the helpfulness of the curators of those collections (Leiden, Frankfurt, London and New York). We also thank Steven Bourne for excavation, preparation and cataloguing of specimens from the cave; H. Crawford and P. Bird for ensuring protection of and allowing access to the excavation site, and G. Bradford for his assistance. We are indebted to the following people for supplying measurements or allowing access to skeletal material from their collections: Kent Beaman (Natural History Museum of Los Angeles County), Tom Rich and Dianne Bray (Museum Victoria), Scott Hocknull (Queensland Museum), Terry Morley (Adelaide Zoo), Robert Palmer (CSIRO Canberra) and Gregory Watkins-Colwell (Yale Peabody Museum of Natural History).

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# AUSTRALIA'S OLDEST KNOWN SNAKES: *PATAGONIOPHIS*, *ALAMITOPHIS*, AND CF. *MADTSOIA* (SQUAMATA: MADTSOIIDAE) FROM THE EOCENE OF QUEENSLAND

JOHN D. SCANLON

Scanlon, J.D. 2005 05 31: Australia's oldest known snakes: *Patagoniophis*, *Alamitophis*, and cf. *Madtsoia* (Squamata: Madtsoiidae) from the Eocene of Queensland. *Memoirs of the Queensland Museum* **51**(1): 215-235. Brisbane. ISSN 0079-8835.

Small madtsoiid snakes referred to *Patagoniophis* and *Alamitophis* are represented by specimens of all major regions of the vertebral column from the Tingamarra Local Fauna (Early Eocene; Murgon, Queensland, Australia), and are diagnosed as distinct from members of the same genera from the Late Cretaceous (Campanian - ?Maastrichtian) of Patagonia, Argentina. The Tingamarra deposit has also produced ribs and dentary bones of two distinct morphotypes, which are provisionally assigned to the same two taxa. A single rib fragment represents a larger form comparable to South American *Madtsoia* spp., although not positively identifiable as a madtsoiid. It is inferred that two (and probably three) madtsoiid lineages had Antarctic-spanning distributions during the Late Cretaceous and/or Paleocene, with implications for their biology and that of their Neogene and Quaternary descendants. ❒ *Ophidia, Madtsoiidae, Patagoniophis australiensis sp. nov., Alamitophis tingamarra sp. nov., vertebrae, mandible, historical biogeography.*

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The oldest snakes known from Australia occur in the Tingamarra Local Fauna, recovered from the Early Eocene (Ypresian, Godthelp et al., 1992; Scanlon, 1993) Boat Mountain deposit, near Murgon in SE Queensland (26°S, 152°E). The fauna also includes earliest known remains of marsupial and placental mammals (including bats) from Australia, birds (including the world's oldest passerines), trionychid turtles, mekosuchine crocodiles, frogs, lungfish, and teleosts (Godthelp et al., 1992, 1999; Tyler & Godthelp, 1993; Archer et al., 1993; Willis et al. 1993; Boles et al. 1994; Hand et al., 1994; Salisbury & Willis, 1996; Boles 1995, 1997, 1999; White, 2001). Scanlon (1993) reported isolated but well-preserved vertebrae represent two snake taxa, small members of the extinct family Madtsoiidae similar to (respectively) *Patagoniophis parvus* and *Alamitophis argentinus*, from the Late Cretaceous of Patagonia, Argentina (Albino, 1986).

Differences from the Patagonian type material previously appeared consistent with intracolumnar and individual variation within each taxon, so that recognition of new species was not justified at the time. Another species of *Alamitophis* has subsequently been described from Patagonia (*A. elongatus* Albino, 1994), additional diagnostic material has been identified from Tingamarra (Scanlon, 1996, and this work), and other species of small madtsoiids have been described from younger Australian deposits (*Nanowana* spp., Scanlon, 1997). A full taxonomic treatment of the Tingamarra snake material is therefore now warranted.

## MATERIALS AND METHODS

All fossil specimens described here are from the MP1 horizon in the sequence of lacustrine clays exposed at Tingamarra, Boat Mountain, near Murgon, south-east Queensland (possibly a member of the Oakdale Sandstone Formation, see Salisbury & Willis, 1996), and were collected by Henk Godthelp, Michael Archer, volunteers, and students from the School of Biological Sciences, University of New South Wales, Sydney, in the mid-1980's to early 1990's. The age of 54.6 Ma was obtained by K/Ar on authigenic illites (Godthelp et al., 1992), and this early Eocene date is corroborated by the stage of evolution of the fauna (Hand et al., 1994; Boles, 1999; Godthelp et al., 1999: 293; contra the opinion of Woodburne & Case, 1996, based on a single doubtfully interpreted mammal tooth).

Small specimens, including all snake material, were obtained by wet-sieving, initial reduction of clay sediments being carried out in the field and the remainder by Syp Praesouthsouk and Anna Gillespie in the Vertebrate Palaeontology Laboratory, School of Biological Sciences, University of New South Wales. Specimens were drawn using a binocular microscope and camera lucida, and measured using a Wild MM235 digital length-measuring set. Scanning electron micrographs were made at Westfield Hospital, Sydney, with the assistance of Coral Gilkeson (Westmead Dental Clinic) and Jeanette Muirhead (UNSW School of Biological Sciences). Specimens with QMF prefix are deposited in the Queensland Museum, Brisbane.

All Murgon snake remains are disarticulated and no association among elements can be demonstrated, so identification of some elements is indirect, based on relative frequency and size of morphotypes; such specimens are listed as 'referred' rather than type material. All vertebrae from the Murgon deposit complete enough for comparison are consistent with adult rather than juvenile snakes, and all are either trunk vertebrae (with paradiapophyses for rib articulation; posterior to the axis, anterior to the cloacal series) or caudals (postcloacal vertebrae bearing fixed, unforked pleurapophyses). Descriptive terminology and criteria for inferring ontogenetic stage and intracolumnar position of snake vertebrae are discussed in numerous works including Simpson (1933), Auffenberg (1963), Hoffstetter & Gasc (1969), Rage (1984), Szyndlar (1984), and LaDuke (1991); serial variation has also been studied by the author in associated partial skeletons of Australian madtsoiids (Scanlon, 1992, 1996, 1997; Scanlon & Lee, 2000; and unpublished data) as well as other extant and fossil squamates (Scanlon, 2001; Scanlon & Mackness, 2002; Lee & Scanlon, 2002; Scanlon et al., 2003). In the absence of a shoulder girdle, the posterior limit of the neck of snakes is indefinite and its extent therefore contentious, but this does not justify restriction of the term 'cervical' to just the atlas and axis, or the atlas alone (LaDuke, 1991: 5; Caldwell, 2000: 731-2; see also Cohn & Tickle, 1999: Fig. 1; Polly et al., 2001). Tooth or alveolar positions are referred to using cardinal or ordinal numerals, counting from the anterior (mesial) end of the tooth row on the element concerned. Categorical ranks are not used for taxa above that of genus.

## SYSTEMATIC PALAEONTOLOGY

### SQUAMATA Oppel, 1811

### OPHIDIA Brongniart, 1800

### Family MADTSOIIDAE Hoffstetter, 1961

DIAGNOSIS (modified from Rage, 1998). Snakes of small to very large size; hypapophyses present only in anterior trunk; middle and posterior trunk vertebrae with moderately or well developed haemal keel (except a few near the cloacal region), often with short laterally paired projections on the posterior part of the keel. All trunk and caudal vertebrae with a parazygantral foramen (or sometimes several foramina) in a more or less distinct fossa lateral to each zygantral facet; prezygapophyseal processes absent; paracotylar foramina present; diapophyses relatively wide, exceeding width across prezygapophyses at least in posterior trunk vertebrae.

REMARKS. Whereas Serpentes Linnaeus, 1758 comprises Scolecophidia and Alethinophidia and includes all extant snakes, Scanlon & Lee (2000; see also Lee & Scanlon, 2002; Scanlon, 2003) presented evidence that Madtsoiidae lies outside this clade but within the more broadly defined Ophidia (sensu Lee, 1998). Taxa included in Madtsoiidae, all extinct, are listed by Rage (1998) and Rage & Werner (1999). While few of the included taxa are known from cranial remains, monophyly of this group is here accepted provisionally on the basis of vertebral characters (Scanlon, 1992; Rage, 1998), although paraphyly with respect to modern snakes cannot be ruled out (Scanlon, 2003).

Presence of haemal keels throughout the middle and posterior trunk is shared with most snakes, but derived relative to other squamates; absence of posterior hypapophyses is plesiomorphic (cf. Underwood, 1967; Hoffstetter, 1968).

Laterally paired projections of the haemal keel are variable in form and not represented in all described madtsoiids, but not reported in any other snakes and hence a distinctive apomorphy of some or all of this group (Scanlon, 1992; Albino, 1996); the term 'paired hypapophyses' (Simpson, 1933) is taken simply to mean 'paired inferior processes' of the haemal keel and does not imply (serial) homology with 'true' median hypapophyses, since both kinds of structures occur together on some vertebrae.

Presence of parazygantral foramina is usually considered autapomorphic for Madtsoiidae, but they are also present in *Simoliophis* (Hoffstetter, 1955: fig. 22), some palaeophiid-like aquatic lineages such as *Tuscahomaophis* (Holman & Case, 1992), and some Colubroidea (e.g. hydrophiine elapids; Scanlon et al., 2003). Some vertebrae referred to *Madtsoia* sp. (e.g. Albino, 1986) and most vertebrae of large Australian madtsoiids (*Wonambi naracoortensis* Smith, 1976, and *Yurlunggur* spp.; Scanlon, 1992, 1996) have the parazygantral foramina divided into two or three on each side, rather than the single foramen usual or constant in non-Australian and small Australian taxa, but (contrary to Rieppel et al., 2002) there is no longer any reason to doubt the structures are homologous across the group (as did Rage, 1984, 1987; but not Rage, 1998).

Lack of prezygapophyseal processes is considered plesiomorphic, as they are absent in limbed terrestrial squamates, marine varanoids, and a number of early fossil snakes (*Simoliophis*, *Pachyrhachis*, *Eupodophis*, *Haasiophis*, *Lapparentophis*, *Pouitella*, and unnamed forms of similar grades; Hoffstetter, 1959; Rage, 1988; Cuny et al., 1990; Lee & Caldwell, 1998; Rage & Escuillié, 2000, 2002; Rieppel et al., 2003), while slightly developed in *Dinilysia* (Hecht, 1982; Rage & Albino, 1989) and generally present in Scolecophidia and Alethinophidia (secondarily absent in some Boinae; Underwood, 1976).

Occurrence of paracotylar foramina is variable among varanoid lizards (e.g. present in some *Varanus* and *Megalania*, pers. obs.) and within *Dinilysia* (Rage & Albino, 1989) and Alethinophidia (Hoffstetter & Gasc, 1969; Underwood, 1976), as well as among early fossil snake lineages, so polarity is uncertain.

Unlike most vertebrae of modern snakes, in madtsoiids the surfaces for rib articulation (paradiapophyses, or synapophyses) are borne on more or less distinctly projecting transverse processes. Having the diapophyses extending as far as or further laterally than the zygapophyses in middle and posterior trunk vertebrae is more plesiomorphic (more similar to limbed varanoids and the early fossil snakes mentioned above) than Scolecophidia and Alethinophidia (McDowell, 1987); however, the relative width of these processes varies considerably among madtsoiids, and the extreme seen in South American *Madtsoia* spp. (Simpson, 1933; Rage, 1998) is probably apomorphic.

A median anterior indentation of the zygosphene is present in most madtsoiids and presumed to be plesiomorphic (shared with the early fossil snake taxa listed above, and approaching the deeply notched condition of the zygosphene where present in lizards), but replaced by a straight margin or median prominence (as in most Scolecophidia and Alethinophidia) in some small madtsoiids (Scanlon, 1993, 1997; Albino 1994, 1996; Rage, 1996), and hence this character is omitted from the diagnosis. Presence of true chevrons on caudal vertebrae has been observed directly only in *Wonambi naracoortensis* (Scanlon & Lee, 2000), so this plesiomorphic feature is also omitted from the diagnosis although varanid-like pedicels for articulation of (probable) chevrons are known in several other madtsoiid taxa (e.g. *Alamitophis*, see below). All modern snakes (Serpentes) have caudal haemal arches modified or absent, not forming chevrons or articulated to the centrum (Hoffstetter & Gasc, 1969; Lee & Scanlon, 2002: characters 204-206).

### **Patagoniophis** Albino, 1986

TYPE SPECIES. *Patagoniophis parvus* Albino, 1986.

DIAGNOSIS (modified from Albino, 1986, 1987; Scanlon, 1993). Very small madtsoiids (vertebrae usually less than 5mm wide), centrum relatively long and narrow. Neural spine low, long and thin, neural arch low, zygosphene shallow. Haemal keel in middle and posterior trunk defined laterally by distinct but shallow grooves.

The smallest known madtsoiids, somewhat smaller than species of *Alamitophis*, *Nanowana*, and *Herensugea*, and much smaller than the remaining taxa. Further distinguished from all except *Herensugea caristiorum* by the low neural spine, and lack of several probable apomorphies of the latter species: in *Patagoniophis* the zygapophyses are inclined above horizontal, zygosphene concave anteriorly, subcentral grooves shallow, neural arch smooth dorsally or with only faint bulges flanking the neural spine.

### **Patagoniophis australiensis** sp. nov.
(Figs 1-3, 4A-B, 5)

*Patagoniophis* sp. cf. *P. parvus* Albino, 1986: Scanlon, 1993: p. 4-5, Figs 1, 3A

DIAGNOSIS. Distinguished from *P. parvus* by the subcentral ridges being strongly concave behind the transverse processes in ventral view, becoming approximately parallel on the posterior part of the vertebra, rather than straight or weakly curved throughout; more depressed neural arch; broader, less strongly arched zygosphene; and smaller size.

MATERIAL. HOLOTYPE: QMF19710 (Fig. 1E), a mid-trunk vertebra from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, south-east Queensland. PARATYPES: Anterior trunk vertebrae: QMF19023 (Figs 1C, 2A),QMF19711-16, QMF23892; middle trunk vertebrae: QMF19717 (Figs 1D, 2B), QMF19718-20, QMF24395, QMF24468, QMF24471, QMF24749; posterior trunk vertebrae: QMF19027 (Fig.

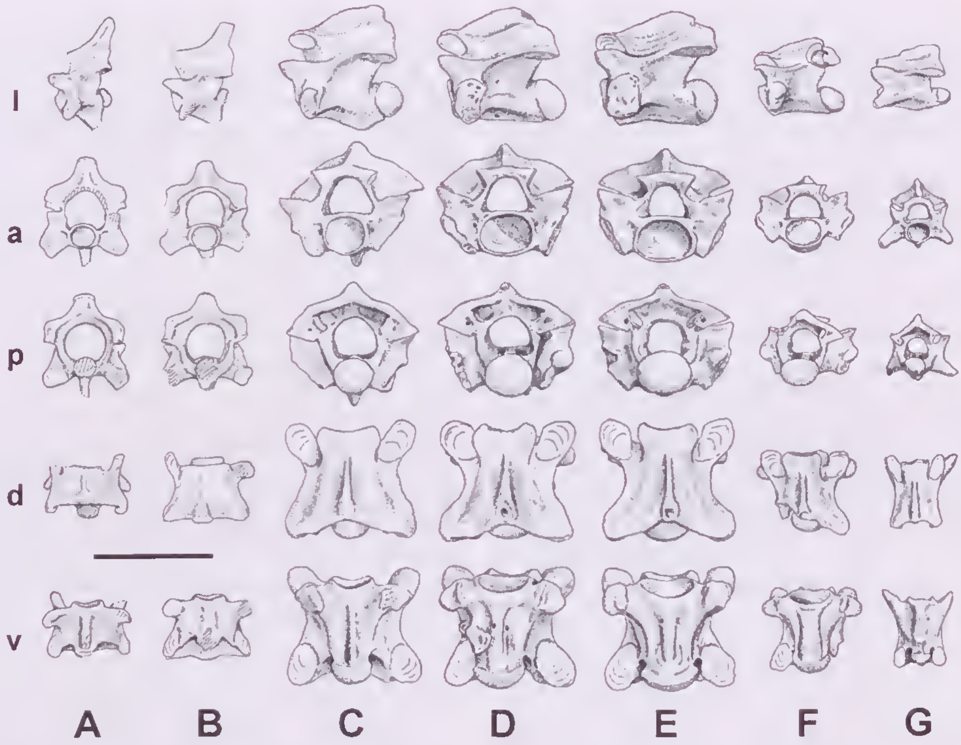

FIG. 1. Type and referred vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, Queensland. A (QMF22806), B (QMF20240), likely 3rd and 4th cervical vertebrae; C (QMF19023), anterior trunk; D (QMF19717), middle trunk; E (QMF19710), middle to posterior trunk, holotype; F (F19027), posterior trunk; G (QMF19024), mid-caudal. l, lateral; a, anterior; p, posterior; d, dorsal; v, ventral views. Scale bar = 3 mm. Photographically reduced copies of C-G were previously published in Scanlon (1993: fig. 1).

1F), QMF19030, QMF19721-26 (Fig. 3), QMF24391, QMF24393-94, QMF24576, QMF24754; caudal vertebrae: QMF19024 (Fig. 1G), QMF19727-28, QMF24252, QMF24575a. REFERRED MATERIAL: Based on relative abundance and size, the following specimens are referred provisionally to the same species: anteriormost trunk ('cervical') vertebrae F19716, F20240 (Fig. 1B), F22806 (Fig. 1A); ribs F19032 (Fig. 4A), F20824, F23285, F23894, F24464 (Fig. 4B), F24465, F24466, F24575b, F24750; dentary F29617 (Fig. 5). It is likely that the available fossils (type and referred) are derived from the remains of several adult individuals. Most of the specimens are fragmentary, and there are numerous additional pieces probably of the same form, but too incomplete to distinguish taxonomically at this stage.

AGE. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

ETYMOLOGY. Neo-Latin, 'from Australia'.

DESCRIPTION OF HOLOTYPE. A mid-trunk vertebra, intact except that the articular surfaces of the paradiapophyses are slightly worn, the lateral margin of the left postzygapophysis is chipped, and the dorsoposterior extremity of the neural spine (possibly a separate ossification) is missing. The centrum and transverse processes are relatively massive, the neural arch broad (slightly wider than long across the zygapophyses) but shallow, and the neural spine very low (contributing barely 10 percent of the total height of the vertebra).

Prezygapophyseal facets are trapezoidal (lozenge-shaped), postzygapophyseal facets obovate, both with long axes at about 30-40° from the sagittal plane; the zygapophyses are moderately steeply inclined (approximately 25° from horizontal) and elevated, defining planes that pass above the internal lateral ridges of the neural canal, and intersect above the floor of the canal. Interzygapophyseal ridges are well developed, and smoothly concave laterally. The

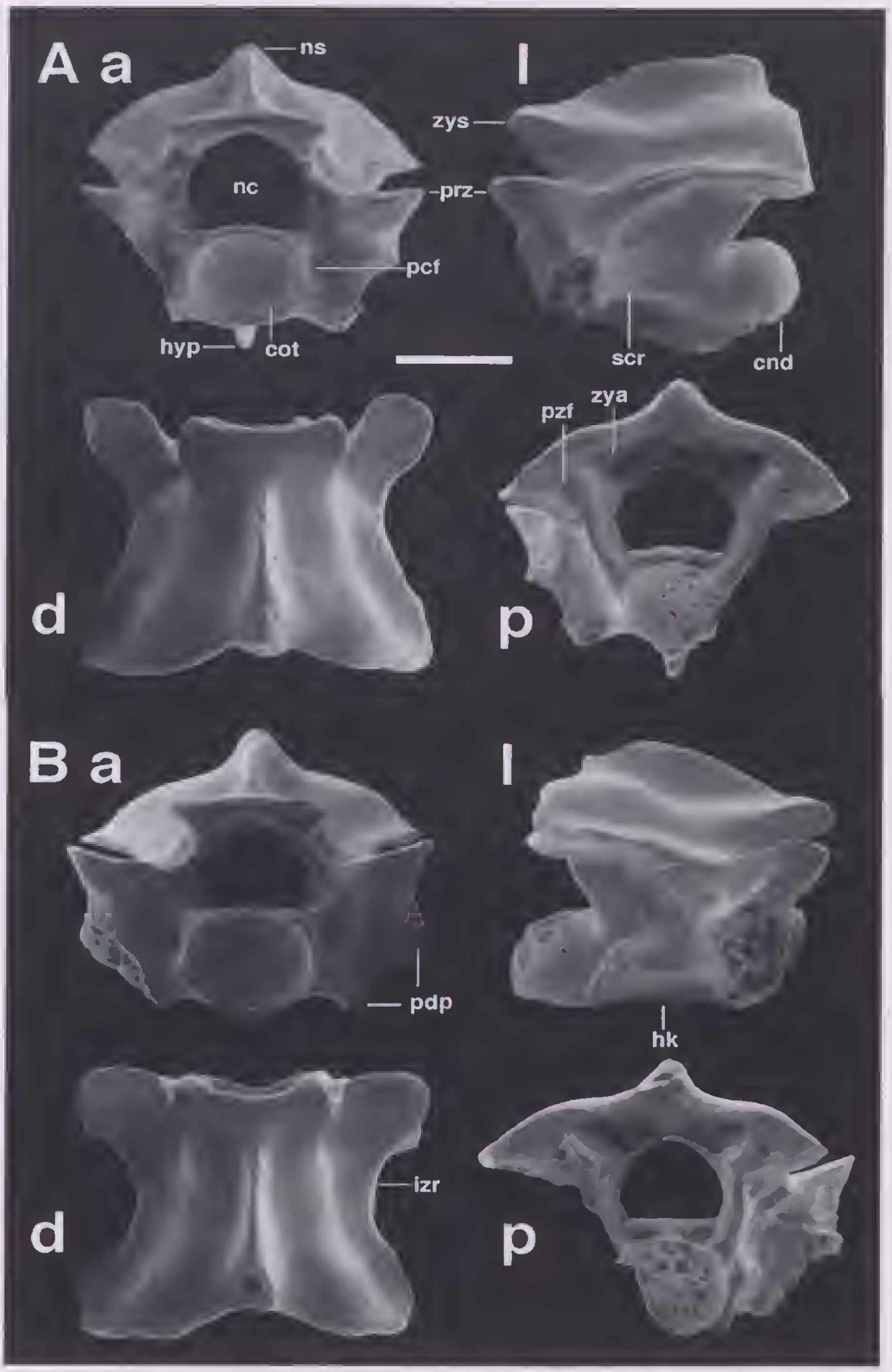

FIG. 2. Referred vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, scanning electron micrographs. A (QMF19023), anterior trunk; B (QMF19717), middle trunk vertebra; a, anterior; l, lateral; p, posterior; d, dorsal; v, ventral views. Some parts are obscured by mount; the same vertebrae are shown in Fig. 1C and D. Scale bar = 1mm.

condyle and cotyle are large, wider than high, and only weakly inclined, so that a considerable part of the condylar surface is visible from below. Neural canal arched in anterior view (appearing more square from behind), about as high as wide, and rather smaller than cotyle.

Zygosphene not overhanging preygapophyseal facets but wider than cotyle, and much wider than deep, with lateral facets more than 30° from vertical. The zygosphene is very weakly arched in anterior view, its shallow anterior face weakly demarcated from the interior of the neural canal, and concave for its full width in dorsal view. The zygantral roof is thin medially where it is interrupted (not overhung) by the posterior edge of the neural spine, and becomes slightly thicker laterally; in dorsal view the posterior margin of the neural arch forms a broad concavity, not demarcated laterally from the convex postzygapophyseal margins; the condyle is broadly exposed in dorsal view, but none of the neural canal floor. The parazygantral area on the rear of the neural arch is a narrow trapezoid bounded on its three longer sides by the postzygapophyseal and zygantral facets and neural arch roof, the ventromedial border short.

The neural spine commences anteriorly as a low, blunt ridge near the posterior limit of the zygosphene, and rises uniformly for about three-quarters of its length (just under 30° from horizontal); the posterior quarter slopes down posteriorly, and in dorsal view forms an oval expansion with a central cavity exposed by slight damage.

Subcentral ridges, distinct on the lateral side but not demarcated from the main ventral surface of the centrum, extend from the parapophyses to the base of the condylar 'neck', which is defined by a moderate constriction. The ridges are strongly concave laterally, narrowing fairly steeply just behind the transverse processes but nearly parallel on the posterior part of the centrum. The haemal keel is defined by slight depressions or (on the middle and posterior part of the centrum) shallow step-like grooves; the depressions diverge anteriorly, not reaching the rim of the cotyle but passing around it to the paracotylar depressions. Posteriorly the keel is weakly trilobed, with a faint outer pair of grooves defining a broad posterior expansion (equivalent of the 'paired hypapophyses', Simpson, 1933) onto which the low median keel extends. In lateral view the centrum is concave ventrally, and the posterior part of the keel projects very weakly below the level of the condyle.

The transverse processes are worn distally, but still extend nearly as far laterally as the zygapophyses, and are visible from above. The articular surfaces for the ribs are subrectangular and vertically aligned in lateral view, not distinctly subdivided into dia- and parapophysis, with only a weak concavity in the posterior margin; they are less than twice as wide as deep, and slightly deeper than the cotyle, extending beyond it dorsally but not ventrally. The diapophyseal surface is partly preserved on the right, extending broadly onto the posterior aspect of the process. The cranial and caudal margins of the articular surfaces are posterior to those of the zygosphenal facet, and much of the cotylar rim is visible laterally.

Paired subcentral, paracotylar, and parazygantral foramina present, all about the same size; lateral foramina smaller.

*Measurements* (mm). length from prezygapophysis to postzygapophysis (ppl) 2.94, width across prezygapophyses (pzw) 3.21, width across paradiapophyses (pdw; slightly worn) 3.09, width across postzygapophyses (ptw) 3.13, minimum width of neural arch (naw) 2.04, width of zygosphene (zsw) 1.45, width of zygantrum (zaw) 1.61, width of condyle (cnw) 1.34, height of condyle (cnh; maximum oblique measurement) 1.03, width of cotyle (ctw) 1.36, height of cotyle (cth) 1.12, centrum midline length (cml; cotyle to condyle rim on ventral surface) 2.07, height of neural canal (nch) 0.76, width of neural canal (ncw) 0.81, maximum distance across neural spine and condyle (nse) 2.79, maximum distance across neural spine and haemal keel (nsh) 2.82, thickness of zygosphene (zyh) 0.30, depth from zygosphene to cotyle (zct) 2.19, length of paradiapophyseal articular facet (pdpl; worn) 1.22, anteroposterior width of paradiapophyseal articular facet (pdpw) 0.75, width between ventral (inner) margins of paradiapophyseal articular facets (piw) 1.82.

*Other vertebrae and serial variation*. Several vertebrae are known from the region immediately posterior to the axis (Fig. 1A, B), here considered cervicals. The figured specimens may be the third and fourth vertebra of a single individual, as they have regional features comparable to the third cervical vertebra of *Yurlunggur camfieldensis* Scanlon, 1992 ('No. 1', fig. 1A in that work), and an anterior cervical referred to *Yurlunggur* sp. from Riversleigh

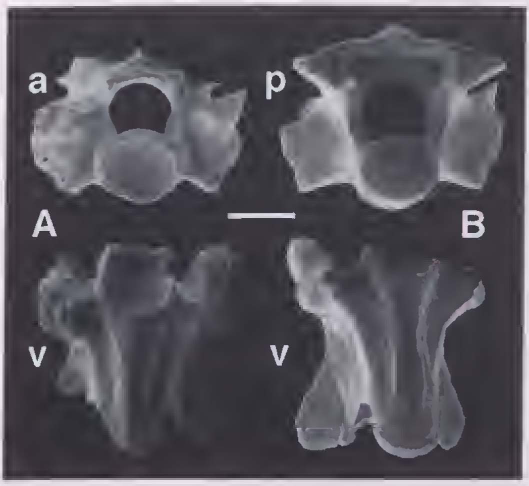

FIG. 3. Referred posterior trunk vertebrae of *Patagoniophis australiensis* sp. nov. from the Tingamarra Local Fauna, Murgon, scanning electron micrographs. Specimens shown in A and B come from the series QMF19721-19726 with the same data, but individual registrations are uncertain. a, anterior; p, posterior; v, ventral views. Scale bar = 1mm.

(QMF23036; Scanlon, 1996). QMF19716 (not figured, consisting of the centrum with both paradiapophyses, but lacking the condyle, hypapophysis and most of the neural arch) has relatively larger cotyle and larger but less ventrally prominent paradiapophyses, so comes from a slightly more posterior position than the other two.

The zygapophyseal articular surfaces are almost horizontal in QMF22806 and QMF20240, well above the floor of the neural canal; in QMF19716 the remaining prezygapophyseal facet is steeper, but would still intersect the midline above the neural canal floor. The facets are narrowly subtriangular, with long axes almost parallel to the midline; the interzygapophyseal ridges are laterally concave but weakly defined. The transverse processes project posteriorly in QMF22806 but laterally in QMF20240; the articular facets, weakly subdivided into diapophysis and parapophysis, are inclined at about 45° in lateral view, face ventrally as much as laterally, and are broadly exposed posteriorly. The cotyle is slightly wider than high. The neural canal is approximately the same absolute size in all three vertebrae, much larger than the cotyle and approximately circular except that distinct internal lateral ridges define small ventrolateral lobes. The centrum in ventral view is wider than long; subcentral ridges are barely defined. The haemal keel begins just behind the cotylar rim, immediately forming a steep but ventrally concave anterior edge of the hypapopysis. The depth of the hypapophysis is considerably more than that of the condyle, but incomplete in all these specimens; the remaining section of the posterior edge is almost vertical in both more complete specimens, and the broken distal surface shows dense bone pierced by small channels (anteroposteriorly double in QMF19716). The zygosphene (preserved only in QMF20240) is formed by a slight thickening of the anterior edge of the neural canal roof, with facets barely defined; it is strongly arched, with the anterior margin straight in dorsal view. The neural arch and spine are similar in both more complete specimens, with concavities above and below the level of the zygosphene, the lateral ones being rather small. The posterior edge lacks a distinct median emargination in dorsal view, and its lateral portions are vertical or slightly overhung, forming dorsolateral processes which are rounded in QMF22806 but more angular in the larger QMF20240. The neural spine begins just posterior to the zygosphene as a narrow ridge, concave above; it is thin anteriorly, becoming broad posteriorly, with an anteroposteriorly short, triangular dorsal expansion that faces slightly posteriorly. The zygantral facets are hardly defined. Small subcentral, lateral, paracotylar, parazygantral and zygantral foramina are present at least unilaterally (some obscured by matrix remaining in hollows).

Until both intracolumnar and ontogenetic variation are more fully known, the taxonomic identification of these cervical vertebrae is uncertain, but several factors make it more probable that they belong to *Patagoniophis* rather than *Alamitophis*. One is the relative frequency of trunk vertebrae of the two taxa; vertebrae of *Patagoniophis* are several times more abundant than those of the other form. As both of the more complete cervicals are similar enough to belong to the same taxon, it is thus more likely to be the more abundant of the two (the slightly larger fragment seems likely to be of the same taxon as the others, but is too incomplete to identify). Moreover, the characters used to distinguish trunk vertebrae can also be applied here: the zygantral roof become thicker (not thinner) laterally; the postzygapophyses are not distinguished by an angular concavity from the interzygapophyseal ridge; the diapophyses do not extend anteriorly beyond the cotylar rim; the zygosphene lacks a median anterior prominence; the neural spine widens sharply posteriorly; the subcentral depressions do not extend forward to the cotylar rim. These morphological features are consistent with those of *Patagoniophis*, being the lack of (mostly autapomorphic) characters of *Alamitophis*. However, some or all of these could be expected to be reduced in the extreme anterior region of *Alamitophis*, so that a definite identification cannot be made until vertebrae from this region are known from both taxa.

The neural spine is both relatively and absolutely higher in these specimens than in more posterior vertebrae of *Patagoniophis*. However, it is common in snakes for vertebrae in the most anterior trunk to have a relatively high neural spine (e.g. pythonines, erycines, many colubroids; Hoffstetter & Rage, 1972; Rage, 1972; LaDuke, 1991; *Wonambi naracoortensis*, Barrie, 1990), although in some madtsoiids the opposite is the case (*Yurlunggur camfieldensis* Scanlon, 1992).

Some other aspects of intracolumnar variation were reported previously (Scanlon, 1993). The virtues of basing taxonomic comparisons on 'posterior trunk' vertebrae are that they are the most numerous in the skeleton, hence the most likely to be represented in a small sample of isolated bones (Simpson, 1933), and also that the form of the haemal keel in this region (e.g. presence of hypapophyses) provides useful taxonomic information in extant groups, as has long been recognised. The vertebra selected as the holotype is from the region transitional between anterior trunk sensu lato (with single narrow haemal keels and/or hypapophyses) and posterior trunk (in this taxon, with broader, flatter keels defined laterally by distinct grooves). Such a transitional region with more or less trilobed haemal keels is now represented in a number of madtsoiid taxa (including *Wonambi* spp., *Yurlunggur* spp., and *Nanowana godthelpi*; Scanlon, 1992, 1996, 1997; Scanlon & Lee, 2000); this should be useful for comparisons between these taxa, as the transition occurs close to the position of maximum vertebral size and identifies a relatively precise region (cf. LaDuke, 1991: 6), in contrast to 'posterior trunk' which encompasses wide variation in size and shape within a single skeleton.

*Ribs*. As described previously (Scanlon, 1993), two distinct kinds of rib heads are represented by multiple specimens (Fig. 4A-D). No ribs have been identified from any small South American madtsoiids (A. Albino, pers. comm.), so the best we can do is state that the more abundant rib type (e.g. QMF19032, Fig. 4A) is likely to represent the same taxon as the more abundant vertebrae, i.e. *Patagoniophis australiensis* sp. nov.

The proximal articulating surface in this form is roughly similar in shape to those of *Wonambi naracoortensis* and *Yurlunggur* spp., but it differs in several details. The rib head is elongate dorsoventrally in proximal view, about three times as high as wide, including the dorsomedial process here called the 'tuber costae' (without implying homology with structures in taxa other than snakes). The medial edge is slightly sinuous (concave dorsally and convex ventrally), formed by a ridge bounding the articulating surface and prolonged dorsally onto the tuber costae. The lateral edge forms two subequal rounded lobes corresponding to the concave diapophyseal and saddle-shaped parapophyseal surfaces. The tuber costae forms about one third of the total height and is trapezoidal in shape, slightly more than half the width of the rib head at its base, with straight lateral and medial margins tapering to a squarish tip, still more than a third of the total width. The overall outline thus resembles an inverted Greek letter β with a thick stem.

The rib shaft is oval in cross-section distally, joining the head smoothly so that ridges and hollows in the proximal part of the shaft correspond to convexities and concavities in the margin of the articulating surface. A foramen is present on the lateral face of the shaft, on the ridge corresponding to the broadest part of the diapophyseal facet.

The rounded, subequal lateral lobes recall the 'waisted' 8-shape typical of alethinophidian taxa examined, which is approached more closely in *Madtsoia camposi* Rage, 1998 and in one Murgon specimen described below. The length of the tuber costae (as measured from either the concavity of the lateral edge, or the slightly more dorsal boundary of the concave articular surface) seems to be unique among known madtsoiids. However, its orientation (only slightly deflected medially from the long axis of the articulating surface) is similar to that in *Wonambi* and *Yurlunggur* (Scanlon, 1996), differing from *Madtsoia bai* Simpson, 1933 and *M. camposi*, as well as most alethinophidians, where it is distinctly angled. As in other madtsoiids (Simpson, 1933; Scanlon, 1996; Rage, 1998), the tuber costae is relatively broader and less sharply defined from the articular surface than in any

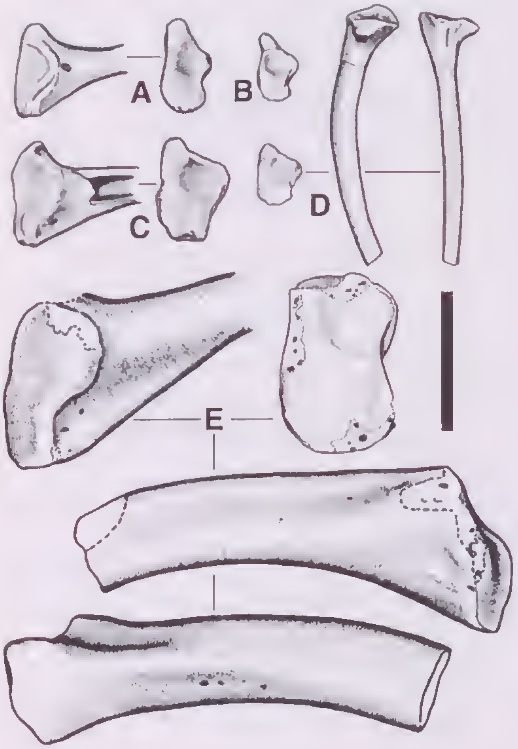

FIG. 4. Rib-heads of snakes from the Tingamarra Local Fauna (ribs from left side of body except A and E, which are reversed for ease of comparison). A (QMF19032) and B (QMF24464) referred to *Patagoniophis australiensis* sp. nov.; C (QMF19033) and D (QMF23898) referred to *Alamitophis tingamarra* sp. nov.; E (QM F52167), ?Madtsoiidae indet., cf. *Madtsoia* sp. Shown in anterolateral (A,C,E), proximal (A-E), dorsal (D, centre), lateral (D, far right), dorsoposterior and ventral (E, lower two figures) views. Scale bar = 3 mm. Specimens in A and C previously figured in Scanlon (1993: fig. 3), redrawn.

modern snakes compared (Alethinophidia and Scolecophidia).

*Dentary.* The two dentaries known from the deposit (Figs 5, 8) are similar to each other in most comparable respects, but have several differences that suggest they represent distinct taxa. Both resemble *Nanowana godthelpi* Scanlon, 1997 in the absence of ankylosed teeth from most alveoli, enlargement pattern of alveoli, relative size and shape of mental foramina, and presence of a distinct smooth 'bulb' on the anteromedial tip. Absence of teeth in these specimens is attributable to post-mortem wear, in contrast to *N. godthelpi* where they are also absent in unworn specimens, implying the presence of fibrous attachment (probably 'hinges', i.e. arthrodont dentition) rather than ankylosis (Scanlon, 1997). Differences between the Murgon specimens include size, position of first alveolus relative to anterior tip, degree of disparity in alveolar diameter, and detailed form of the crests defining the meckelian groove. As available vertebral material indicates that *Patagoniophis* is generally somewhat smaller than *Alamitophis*, the jaw fragments are provisionally referred to the two taxa on the basis of relative size (see Discussion).

QMF29617 (Fig. 5) is the anterior portion of a left dentary, broken posteriorly through the 11th alveolus; total length 5.71 mm, length from anterior tip to rear of 6th alveolus 3.13, maximum depth (at 6th) 1.52, max. alveolar width 0.51, lateral edge to dorsal margin of meckelian groove 1.03. There do not appear to be traces of ankylosed teeth in any except the 11th alveolus, which retains the stump of a tooth. Alveolar diameter varies little along the preserved part of the jaw (but the 6th is apparently the largest), and the row is only slightly (but sinuously) curved; the anteromedial extremity is prominent (similar to the 'bulb' in some Riversleigh taxa, but more dorsoventrally flattened), with nearly enough space for an additional alveolus anterior to the first. In lateral view, the dorsal edge can be viewed as horizontal (i.e. the alveolar margins lie approximately within a plane). There are three mental foramina, level with alveoli 3-4, 5-6, and 8; the third is smaller than the other two. The meckelian groove is open ventromedially, constricted anteriorly by incurved crests, but widens posterior to the fifth alveolus. Its dorsal edge is continuous anteriorly with the ventral edge of the bulb, and strongly overhung (hence sharply defined in medial view) for its full length, but somewhat concave and 'bevelled' at the level of the 8th alveolus (ventral view). The ventromedial edge (forming a lower 'lip' for the groove, thinnest from the third to fifth alveolus) is damaged posterior to the 7th alveolus, but intact more anteriorly; it differs from other madtsoiids in being steeply inclined, projecting ventrally rather than medially, so that the meckelian groove is open in ventral view. This resembles the common and apparently primitive condition in lizards (cf. Lee, 1998, character 115), so could be considered a reversal.

QMF29617 probably had at least 15 alveoli (and possibly 17 or more), because the anterior edge of the lateral fossa is not visible, and is followed by 4 to 6 or more teeth in other madtsoiids where the dentary is known. It differs from species of *Nanowana* and *Yurlunggur* (but resembles *Wonambi* and *Madtsoia*) in the meckelian groove being sharply defined dorsally for its full length, without a smooth or 'soft' middle portion apparent in medial view.

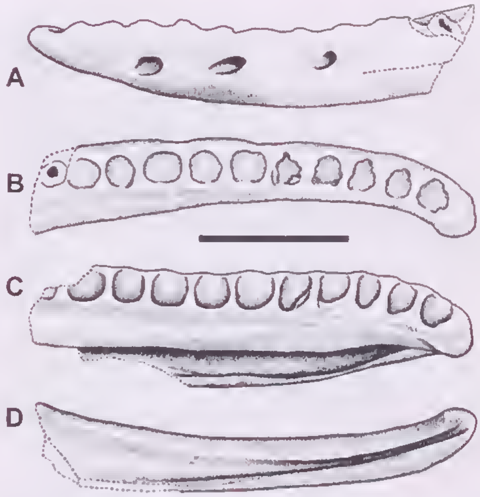

FIG. 5. Anterior portion of left dentary (QMF29617) from the Tingamarra Local Fauna, referred to *Patagoniophis australiensis* sp. nov. A, lateral, B, dorsal, C, dorsomedial, and D, ventral views. Scale bar = 2mm.

## **Alamitophis** Albino, 1986

TYPE SPECIES. *Alamitophis argentinus* Albino, 1986

REFERRED SPECIES. *Alamitophis elongatus* Albino, 1994

DIAGNOSIS (modified from Albino, 1986, 1987, 1994; Scanlon, 1993): small madtsoiids (vertebrae up to about 8mm wide), centrum relatively narrow. Haemal keel extends to cotylar rim anteriorly; in posterior trunk vertebrae, keel thick and delimited laterally by deep depressions. Zygapophyses weakly to strongly inclined from horizontal. Neural arch moderately elevated; neural spine moderately high, back-sloping, transversely thin (but not sharp-edged) anteriorly and thicker posteriorly. Zygosphene dorsoventrally thin, and not or only slightly wider than cotyle; zygantral roof thinning laterally in mid- and posterior trunk. Paradiapophyses of trunk vertebrae project anteriorly beyond rim of cotyle.

The relatively high neural arch and spine, narrow zygosphene, and form of the haemal keel distinguish *Alamitophis* from the other small madtsoiids (*Patagoniophis*, *Herensugea*, *Nanowana*); among larger forms, most have similar or higher neural arches or spines, but only *Wonambi* has such relatively narrow zygosphenes, and its haemal keels are also different (weakly defined laterally by shallow depressions). The distinct lateral thinning of the zygantral roof and relatively anterior position of the paradiapophyses appear to be unique to this genus.

### **Alamitophis tingamarra** sp. nov.
(Figs 4C-D, 6-8)

*Alamitophis* sp. cf. *A. argentinus* Albino, 1986 (Scanlon, 1993: p. 5-6, figs 2, 3B)

DIAGNOSIS. Distinguished from *A. argentinus* (and species of most other madtsoiid genera) by smooth median prominence on the anterior border of the zygosphene (synapomorphy with *A. elongatus*); from *A. elongatus* by the less elongate centrum (lack of a probable autapomorphy of the latter species); and from both species by smaller size, and more weakly defined subcentral ridges (probable autapomorphies). The zygapophyses are only slightly angled above the horizontal (less than 10° in material examined), similar to most described *Alamitophis* material but differing from the holotype of *A. elongatus*, which has strongly inclined zygapophyses (Albino, 1994).

MATERIAL. HOLOTYPE: QMF19729 (Figs 6C, 7), a mid- to posterior trunk vertebra from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, south-east Queensland. PARATYPES: Anterior trunk vertebrae: QMF19735 (Fig. 6A); middle trunk vertebrae: QMF19029, QMF19730, QMF19731, QMF19734 (Fig. 6B); posterior trunk vertebra QMF20233; caudal vertebrae: QMF19732 (Fig. 6D), QMF19733. REFERRED MATERIAL: Ribs: QMF19026, QMF19033 (Fig. 4C, D), QMF20920, QMF23898; dentary: QMF23893 (Fig. 8).

AGE. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

ETYMOLOGY. Referring to the Local Fauna and the property from which it was collected.

DESCRIPTION OF HOLOTYPE. A vertebra from the anterior part of the posterior trunk region, well preserved except that the articular surfaces of the paradiapophyses are worn, and the margin of the left postzygapophysis and right prezygapophysis are chipped. The centrum is massive, the transverse processes relatively small and in a low position, the neural arch broad (wider than long across the zygapophyses), vaulted, with a moderately high neural spine (contributing nearly 20 percent of the total height of the vertebra).

Prezygapophyseal facet (complete on left side) trapezoidal, postzygapophyseal facets obovate, both with long axes at about 30-40 from the sagittal plane; the zygapophyses are weakly inclined (less than 10 from horizontal) but moderately elevated, defining planes that pass through the weak internal lateral ridges of the neural canal, and intersect above the floor of the canal. Interzygapophyseal ridges are well developed, with slight angularities where they meet the zygapophyses. The condyle and cotyle are large, wider than high, and moderately inclined, so that a considerable part of the condylar surface is visible from below. Neural canal subtriangular in anterior view (appearing more square from behind), slightly wider than high, and rather smaller than cotyle.

Zygosphene not overhanging prezygapophyseal facets, slightly narrower than cotyle, width about twice depth of facets,which slope at about 30 from vertical. The roof of the zygosphene is horizontal in anterior view, the anterior face about half as deep in the midline as at the lateral facets, weakly demarcated from the interior of the neural canal; in dorsal view the anterior margin is trilobate, the rounded median projection slightly more prominent than the lateral lobes, and somewhat asymmetric. The zygantral roof is thickest medially where it is interrupted and overhung by the posterior edge of the neural spine, and becomes noticeably thinner laterally; in dorsal view the posterior margin of the neural arch forms a broad, rounded concavity for the width of the zygantrum, somewhat distinct from the (posteriorly sinuous) postzygapophyseal margins; the condyle is broadly exposed in dorsal view, about as far as its anterodorsal margin. The ventromedial margins of the parazygantral surfaces are about as long as the zygantral facets, and form fairly distinct, ventrally concave ridges.

The neural spine commences anteriorly as a blunt ridge near the anterior edge of the zygosphene, and rises for about three-quarters of its length (sigmoid with two angular inflections, and steepest in the middle part at aboout 45); the posterior quarter slopes down posteriorly, and in dorsal view forms a teardrop- or bottle-shaped expansion with a smooth, transversely convex surface.

Subcentral ridges, only indistinctly defined from the lateral and ventral surfaces of the centrum, extend from the parapophyses to the base of the condylar 'neck', which is defined by a moderate constriction. The ridges are weakly sinuous or arcuate, tapering almost uniformly but slightly convex laterally in the central part. The haemal keel is defined by deep depressions that diverge anteriorly, not reaching the rim of the cotyle but passing around it to the paracotylar depressions. Posteriorly the keel is very faintly trilobed, with a faint inner pair of grooves defining short, posteriorly divergent lateral branches from the median ridge. In lateral view the centrum is concave ventrally, and the posterior part of the keel projects slightly below the level of the condyle.

The small transverse processes are worn distally, and hidden in dorsal view by the prezygapophyses. The articular surfaces for the ribs face more ventrally than laterally, are subrectangular in lateral view, less than twice as wide as deep, and considerably less deep than the cotyle, level with it ventrally but extending barely above the level of its centre. The diapophyses extend posteriorly beyond the zygosphenal facets, while the parapophyses (weakly delimited by concavities in anterior and posterior margins) project anteriorly beyond the zygosphene. The diapophyseal articular surface is partly preserved on the left, extending broadly onto the posterior aspect of the process.

Paired subcentral, lateral, paracotylar, and parazygantral foramina present, the parazygantrals largest.

*Measurements* (mm; abbreviations defined above). ppl 2.86, pzw 3.38, pdw (worn) 2.98, ptw 3.31, naw 2.82, zsw 1.43, zaw 1.67, cnw 1.30, cnh 1.17, ctw 1.48, cth 1.26,cml 2.19, nch 0.78, ncw 0.97, nsc 3.42, nsh 3.32, zyh 0.27, zct 2.40, pdpl (worn) 1.00, pdpw 0.78, piw 1.64.

*Other vertebrae and serial variation.* The number of well-preserved vertebrae available is small, but anterior, middle and posterior trunk, and anterior caudal regions are represented.

The most anterior vertebra complete enough to identify as *Alamitophis* (QM F19735, Fig. 6A) has similar regional features to F19023 (*Patagoniophis*, Fig. 1C). The neural canal is wider than the cotyle, the zygosphene is arched, and the hypapophysis is prominent and narrow. The paradiapophyses do not project anteriorly to the extent seen in other vertebrae of this species.

Middle trunk features are seen in F19734 (Fig. 6B), the largest well-preserved vertebra known from the site. The zygosphene roof is slightly concave dorsally, the facets distinctly concave laterally. The haemal keel is narrow and extends slightly below the centrum for most of its length, but does not form a vertical anterior edge below the cotyle as in the *A. argentinus* holotype (Albino, 1986).

Holotype QMF19729 described above, previously reported as a middle trunk vertebra (Scanlon, 1993: fig. 2), is now considered 'posterior trunk' (or transitional) based on the anterior expansion of the haemal keel to almost the full width of the cotyle, in contrast to the anteriorly narrow keel seen in the largest mid-trunk vertebra. It also has the posterior part of the keel very weakly trifid, with faint lateral ridges not indicated in the drawings but shown in scanning electron micrographs (Fig. 7). As noted above for the holotype of *Patagoniophis australiensis* sp. nov., the development of lateral ridges on the median keel represents the transition between the single keel of the anterior trunk, and the posteriorly expanded, bifid keel characteristic of the posterior trunk in most madtsoiids (called 'paired hypapophyses' by Simpson, 1933, based on their prominent development in *Madtsoia bai*). No vertebrae of this taxon with broad or obviously bifid keel are known, but the sample of posterior trunk vertebrae remains small, and absence of more distinct paired hypapophyses can not be stated conclusively at this time.

*Ribs*. The less common type of rib (Fig. 4C, D) is provisonally referred to *Alamitophis* on the basis of relative abundance. The rib head is less than twice as high as wide in proximal view, the medial edge is convex rather than sinuous, the diapophyseal surface is much broader and more angular laterally than that for the parapophysis, and the tuber costae relatively small (less than a quarter of the total height, and about a third of the width). A foramen is present on the lateral face of the shaft, but more ventral in position, in the concavity below the diapophyseal ridge.

*Dentary*. QMF23893 (Fig. 8) is the anterior portion of a right dentary, broken posteriorly through the 8th alveolus and along parts of the ventral edge; total length 7.12mm. There is no sign of ankylosed teeth, but alveolar diameter varies considerably with an alternating pattern (1<2<7<3<5<4<6), due to variation of diameter with stage of tooth development and replacement as well as tooth size. The ventral edge is slightly concave anteriorly, and although worn from below the 4th to 6th alveoli it appears to have extended medially as a widened shelf in this region, as the portion preserved below the 6th-7th is concave; possibly this concavity marks the anterior limit of the lower process of the splenial. Two mental foramina below the 4th and 6th-7th alveoli have sharply defined oval margins except anteriorly. The anterior foramen is distinctly higher and deeper than the other; a third may or may not have been present beyond the broken posterior edge. The lateral face is smooth, with a rounded dorsolateral ridge just below the alveolar margin, and a shallow longitudinal concavity below the foramina. The medial ridge defining the upper edge of the meckelian groove is strongly overhung for most of its length, but gently so in the area of the 5th alveolus. This ridge swells ventrally and medially at its anterior end, forming a distinct median bulb medial to the groove level with the first and second alveoli. The groove is open anteriorly, forming an anterior notch in the first alveolus, not an enclosed foramen. No definite evidence of the splenial facet or lateral posterior fossa is preserved.

QM F23893 differs from known material of *N. godthelpi* in the second mental foramen being posterior to the 6th alveolus, and third (if present) posterior to the 7th; the absence of a groove on the dorsomedial face diverging from the meckelian groove, extending parallel to the tooth row from below the bulb; and the meckelian groove opening anteriorly into the first alveolus by a notch. The 'break' in the upper edge of the groove occurs below the 5th (cf. 8th) alveolus; assuming this feature is related to the extent of the upper splenial process (i.e. that the 'bevelled' section of the ridge corresponds to the foramen between dentary and splenial for the lingual branch of the inferior alveolar nerve), this may imply the dentary was considerably shorter and thus relatively more robust than in *Nanowana* or other known Australian madtsoiids, or that the splenial was relatively larger.

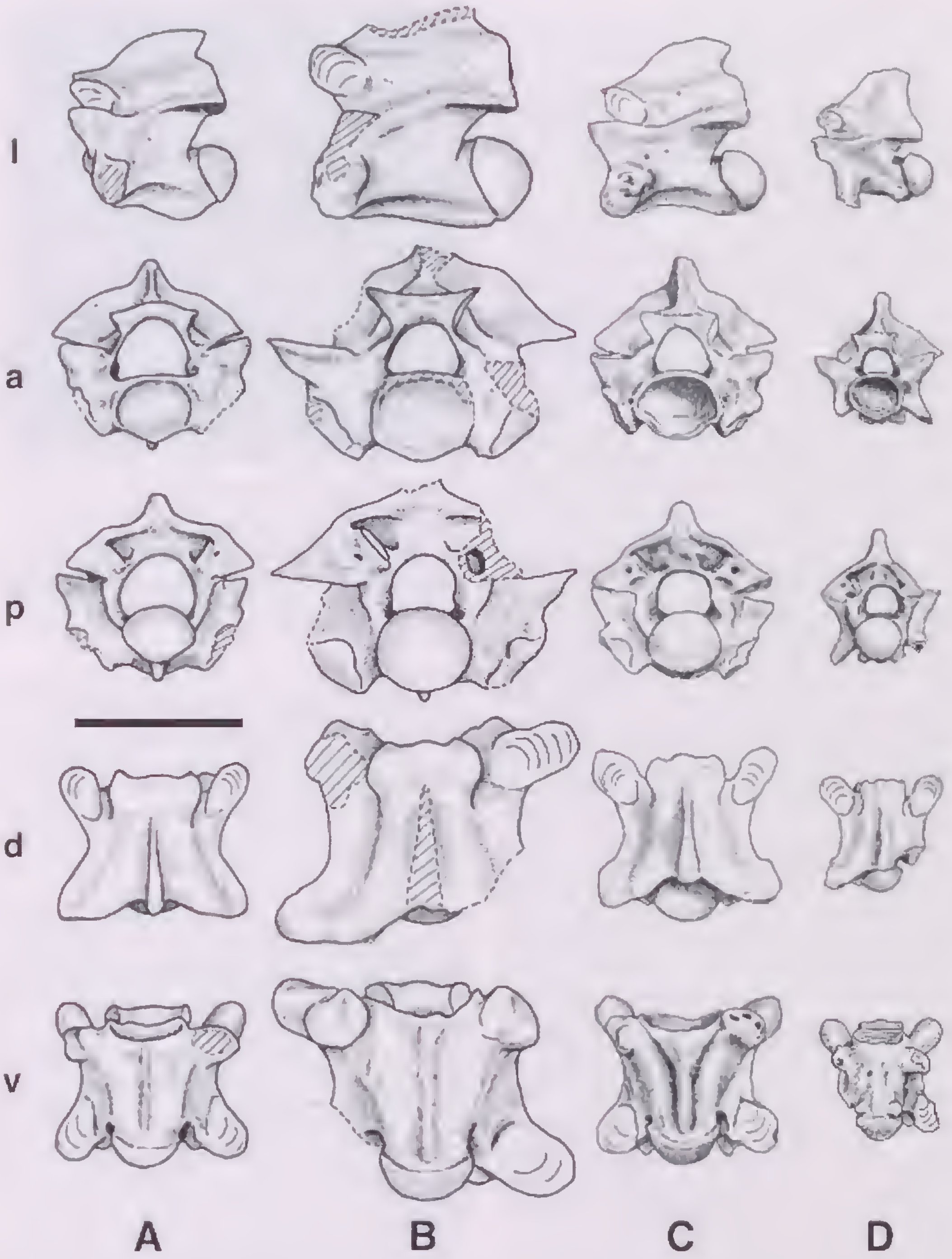

FIG. 6. Vertebrae of *Alamitophis tingamarra* sp. nov. from the Tingamarra Local Fauna, Murgon, Queensland. A, QMF19735 (anterior trunk); B, QM F19734 (mid-trunk); C, QM F19729 (posterior trunk, holotype); D, QMF19732 (anterior caudal). l, lateral; a, anterior; p, posterior; d, dorsal; v, ventral views. Scale bar = 3mm. Photographically reduced copies of C-D previously published in Scanlon (1993: fig. 2).

### Family ?MADTSOIIDAE indet.

### cf. **Madtsoia** sp.
Fig. 4E

MATERIAL. QMF52167, a single rib fragment from the right side of the trunk from MP1 horizon, Main Quarry, Tingamarra, Boat Mountain, near Murgon, southeast Qld. Tingamarra Local Fauna, Early Eocene, 54.6 +/- 0.05 MYBP (Godthelp et al., 1992).

DESCRIPTION. The specimen comprises the rib head and proximal portion of the shaft, but lacks the tuber costae. The proximal articulating surface has a sinuous medial edge and subequal, rounded lateral lobes as in the rib form referred to *Patagoniophis*, but is much larger (approximately 3.9 x 2.6 mm as preserved) than the paradiapophyses of any vertebrae yet known from the site. In addition to a pair of foramina in the ventrolateral hollow adjacent to the parapophyseal facet, there is a small foramen in the dorsal 'groove' (elongate hollow corresponding to the concavity of the proximal margin between the diapophyseal facet and tuber costae), and several more in a slight hollow on the ventrolateral surface. Foramina in a dorsal groove have not been seen in ribs of other Australian madtsoiids, but occur in *Madtsoia bai* (Simpson, 1933). In shape of the articular head it is much more similar to *M. camposi* (Rage, 1998), where no such foramina have been described; however, the '8'-shaped articular surface is also typical of alethinophidians.

The tuber costae is broken off too short to determine whether it was robust (typical of madtsoiids, also seen in *Dinilysia*) or slender in proximal view (characterising most if not all alethinophidian and scolecophidian ribs; Rage, 1998; pers. obs.), or its orientation relative to the axis of the articular surface (variable within Madtsoiidae).

In view of its relatively large size (discussed below), distinctive shape, and extra foramina on the shaft, this specimen is inconsistent with the two other rib forms and cannot be referred to either of the taxa named above. It cannot conclusively be excluded from Alethinophidia, but as far as preserved it is most similar to ribs of *Madtsoia* spp., although still considerably smaller than any reported form of that genus.

## DISCUSSION

*Vertebral morphology and systematics*. Because the additional material allows variation along the vertebral column to be reconstructed more fully than when initially reported, the Murgon madtsoiid taxa can now be adequately compared to isolated vertebrae from other localities (cf. Rage, 1974: 274). Consequently, both forms are now diagnosable as distinct from the South American members of their genera, and also from other taxa of small madtsoiids described in recent years (*Herensugea* Rage, 1996; *Nanowana* Scanlon, 1997).

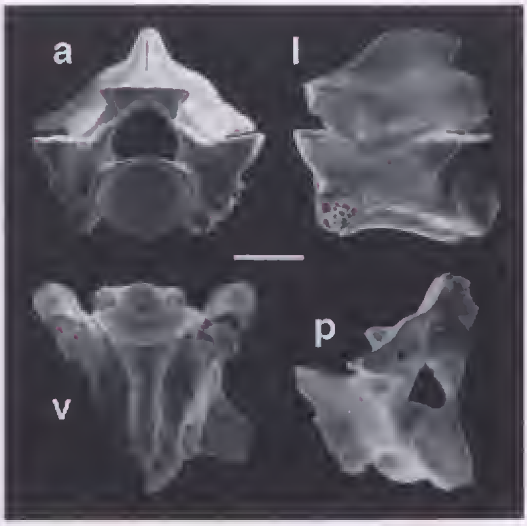

FIG. 7. Holotype posterior trunk vertebra (QM F19729) of *Alamitophis tingamarra* sp. nov., scanning electron micrographs; a, anterior; l, lateral; v, ventral; p, posterior views. Some parts are obscured by mount (outline partly restored in a); the same vertebra is shown in Fig. 6C. Scale bar = 1mm.

The specimens of *P. parvus* figured in ventral view (Albino, 1987) have the haemal keel extending with near-parallel and sharply defined lateral borders to near the cotylar rim; in the Murgon material representing all regions of the column in *P. australiensis* sp. nov., the keel becomes less sharply defined anteriorly and fails to reach the cotyle (polarity unclear, both states occur in other madtsoiids). Also, the subcentral ridges are more strongly concave in the material described here than in *P. parvus* (possible autapomorphy of *P. australiensis*, though also similar to *Herensugea caristiorum* Rage, 1996, and *Coniophis* sp., e.g. Gardner & Cifelli, 1999); size of the adult vertebrae is somewhat smaller (making *P. australiensis* the smallest known madtsoiid, an apomorphic extreme); and the zygosphene is relatively broader (possibly attributable to size difference) but less arched. These differences indicate at least a specific level

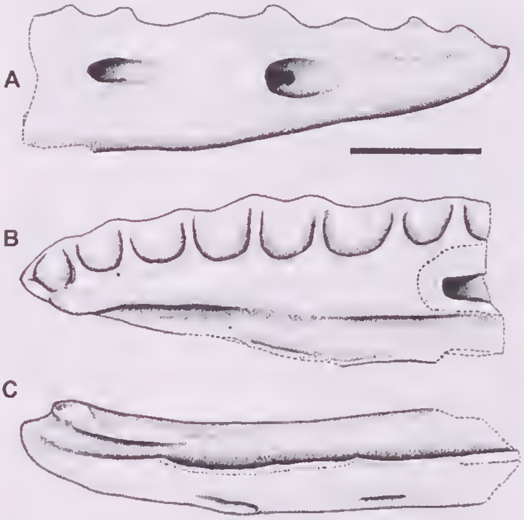

FIG. 8. Anterior portion of a right dentary (QMF23893) from the Tingamarra Local Fauna, referred to *Alamitophis tingamarra* sp. nov. A lateral, B dorsomedial, and C ventral views. Scale bar = 2mm.

of divergence. The small European form *Herensugea* (Rage, 1996) is also comparable with *P. australiensis* (in small size, depressed neural arch and very low neural spine, shallow posterior emargination of the neural arch, and the shape of the centrum, particularly the subcentral ridges in ventral view), but differs in having weakly inclined zygapophyses and (apparently) weakly trilobate zygosphenes (cf. *Alamitophis*), distinct subcentral grooves in mid-trunk vertebrae (holotype; Rage, 1996: fig. 2), and a pair of dorsal longitudinal ridges flanking the neural spine in most vertebrae (cf. some *Coniophis*, 'Aniliidae'; Gardner & Cifelli, 1999).

*Alamitophis* vertebrae from Murgon can now be compared with two species from the Late Cretaceous of Patagonia: *A. argentinus*, from the Los Alamitos (Cerro Cuadrado, Bajo Trapaleó and El Palomar localities, central Río Negro province; Campanian) and La Colonia Formations (La Colonia locality, north-central Chubut province; Campanian-Maastrictian), and a second form *A. elongatus* also from the Los Alamitos (Cerro Cuadrado and Bajo Trapaleó; Albino, 1994, 2000). The three forms are similar in many details, several of the features used in the generic diagnosis being quite distinctive. While the *A. argentinus* holotype is rather damaged, that species apparently lacks the median prominence on the zygosphene that is well-developed in both *A. elongatus* and the Murgon specimens, and separates these taxa from all other Madtsoiidae. This character (considered distinct from the broader, straight or weakly convex median lobe in some *Nanowana*) is a synapomorphy if Madtsoiidae is monophyletic, but polarity would be rendered uncertain if *Alamitophis* were more closely related to Scolecophidia and Alethinophidia, in which the zygosphene usually has a similar median lobe (this position was found in some unpublished analyses; Scanlon, 1996). Differences of *A. tingamarra* sp. nov. from both of the others are more weakly defined and anteriorly divergent subcentral ridges, and (if samples are representative) smaller size. The haemal keel widens anteriorly to the full width of the cotyle in posterior trunk vertebrae of *A. tingamarra*; this feature is not known in the other species, but this region may not yet be represented in the Patagonian samples.

*Alamitophis* represents a highly distinctive group within Madtsoiidae, and can be regarded as a clade based on the probable apomorphies mentioned above. The status of *Patagoniophis* is more problematic, as in overall morphology the vertebrae of these species resemble, or are intermediate between, both non-madtsoiid taxa (*Dinilysia*, *Coniophis* and other anilioids; e.g. Hecht, 1982; Gardner & Cifelli, 1999) and some later Australian madtsoiids (species of *Nanowana* and *Yurlunggur*; Scanlon, 1992, 1997). This probably reflects generally plesiomorphic morphology rather than synapomorphy; thus, rather than *Patagoniophis parvus* and *P. australiensis* being sister taxa, it may be seen as more likely that the latter represents the sister taxon or possible ancestor of younger Australian madtsoiids. However, as the two forms resemble each other more closely than any other madtsoiid and neither has clear synapomorphies linking it with a third taxon or clade, they are retained in a single genus until more evidence for relationships is available.

*Dentary.* The total length of the mandible (and thus skull) corresponding to the larger dentary specimen can be estimated roughly as three times the length of the fragment, or around 21 mm (based on proportions of the most similar known taxon, *Nanowana godthelpi* Scanlon, 1997). This is consistent with either of the two taxa known from vertebrae, whose total lengths are estimated to reach about 50cm and 80cm in *Patagoniophis* and *Alamitophis* respectively (Scanlon, 1993).

The assignment of the jaw elements to taxa on the basis of relative size is therefore uncertain and provisional.

To interpret the significance of those features in which the two dentaries differ from each other, and potentially test their assignment to the respective taxa, comparisons with other madtsoiids are required. South American species of *Madtsoia* may be useful in estimating the plesiomorphic character states of the dentary in Australian madtsoiids; further outgroup comparisons are desirable, but the analysis of Lee and Scanlon (2002) implies that the next relevant outgroups would be *Dinilysia* (where the dentary remains poorly known; Estes et al., 1970; Caldwell & Albino, 2002) and Serpentes (all modern snakes) in which morphology varies greatly among basal lineages (e.g. Lee & Scanlon, 2001). Two *Madtsoia* specimens are known; one referred by Hoffstetter (1960) to *Madtsoia* cf. *M. bai* (Riochican, Upper Paleocene of Argentina), and one of *M. camposi* (Itaboraian, Upper Paleocene of Brazil; Rage, 1998). These are relatively robust as well as large elements (particularly the Patagonian specimen) and share the following features: a well-developed but smooth 'symphyseal bulb' medial to 1-2; alveoli of relatively uniform size (apparently not reducing by the 8th); three mental foramina (below 3, 5-6, 7-8 and 2, 4, 6 respectively); the lateral fossa extending anteriorly to below the 8th alveolus; and a well-developed ventromedial shelf below the meckelian groove (widest below the 7th alveolus in both specimens). There is no visible 'smooth gap' in the dorsal margin of the meckelian groove, so the position of the inferior alveolar nerve foramen is unknown. The close similarity of the two specimens confirms Hoffstetter's (1960) referral of the isolated element to *Madtsoia*, which was questioned by Albino (1996) after discovery of large boid (sensu stricto) vertebrae in similar-aged deposits in the same area (Albino, 1993).

The position of the lateral fossa is unknown in both Murgon specimens, but was posterior to the middle of the 8th alveolus in F23893, and beyond the middle of the 11th in F29617; alveolar size is reducing by the 7th; the (putative) inferior alveolar nerve foramen, and widest point of the medioventral shelf, are below the 5th. As noted above, they differ in several respects, but these are either likely to be size-related or even ontogenetic (absolute size, and degree of disparity in alveolar diameter) or one of the alternate states cannot be equated to that in another taxon (position of first alveolus relative to anterior tip, and detailed form of the crests defining the meckelian groove) and thus cladistically informative.

Extending comparisons for the remaining features to other Australian madtsoiids (Scanlon, 1996, 1997; Lee & Scanlon 2001; and unpublished data), the following binary or multistate characters can be evaluated (see Table 1, which also includes *Cylindrophis ruffus* (Laurenti, 1768) as an exemplar of the outgroup Alethinophidia):

1. Symphyseal region with smooth 'bulb' medial to 1st alveolus (0); no bulb but longitudinal ridges and grooves present in this region (1).

2. Alveoli relatively uniform, not reducing in size by 8th (0); region of moderately enlarged alveoli and/or teeth, size reducing by 8th alveolus (1); region of greatly enlarged alveoli and/or teeth from 2nd to 4th (2). Ordered 0-1-2.

3. Dorsal margin of meckelian groove sharply defined up to at least 8th alveolus, 'smooth gap' in crest (inferior alveolar nerve foramen?) posterior to this position or possibly absent (0); 'smooth gap' present below 8th-9th alveoli (1); present below 5th alveolus (2). Unordered, because possible absence of the feature cannot be distinguished from a far posterior position in incomplete specimens.

4. Lateral fossa for surangular extends to level of the 8th alveolus (0); apex of lateral notch below 9th-12th (1); below or posterior to 13th (2). Ordered 0-1-2.

5. Ventromedial shelf of dentary well developed anteriorly, flooring meckelian groove at level of first two alveoli (0); reduced or directed more ventrally than medially, so that anterior part of meckelian groove is open ventrally (1).

6. Ventromedial shelf broadens gradually toward rear of dentary, maximum width posterior to 8th alveolus (0); maximum width around level of 7th alveolus (1); maximum at 5th alveolus (2). Ordered 0-1-2, but plesiomorphic state is hypothesised to be the intermediate state 1.

7. Single mental foramen on each dentary (0); two or three mental foramina (1). Polarity based on outgroup comparison with *Pachyrhachis*, *Haasiophis*, Scolecophidia, and Alethinophidia, assuming phylogeny of Lee and Scanlon (2002: fig. 11). A reconstruction of *Wonambi naracoortensis* with two mental foramina

Table 1. Taxon x character-state matrix (characters 1-7 defined in text; state 0 inferred to be plesiomorphic unless stated otherwise; '1/2' = either state 1 or 2). Madtsoiids *Madtsoia*, *Nanowana*, and *Wonambi* indicated by initials. Extant alethinophidian *Cylindrophis ruffus* (based on SAM R36779) included for comparison with eight madtsoiid taxa.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| *M. bai* | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *M. camposi* | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| F29617 *(?P. australis)* | 0 | 1 | 2 | 2 | 1 | 2 | 1 |
| F23893 *(?A. tingamarra)* | 0 | 1 | 2 | 1/2 | 1 | 2 | 1 |
| *N. godthelpi* | 0 | 1 | 1 | 1 | 1 | 0 | 1 |
| *N. schrenki* | 1 | 2 | 1 | 2 | 1 | 0 | 1 |
| *W. naracoortensis* | 1 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Yurlunggur* | 1 | 0 | 0 | 2 | 0 | 0 | 1 |
| *Cylindrophis ruffus* | 0 | 0 | 1 | 1 | 0 | 1 | 0 |

(Scanlon & Lee, 2000: fig. 1) was not based on direct examination of the dentary in that taxon; further preparation by the author confirms that the foramen is actually single in the only known specimen (as originally reported by Barrie, 1990; see also Rieppel et al., 2002).

The data in Table 1 are too limited to allow a meaningful phylogenetic analysis at this stage, but provide some measures of similarity among taxa. The two *Madtsoia* species are indistinguishable in these features, *Wonambi* and *Yurlunggur* resemble each other nearly as closely, and the two *Nanowana* species are also quite similar despite their divergent dentitional specialisations (Scanlon, 1997). The two Murgon specimens resemble each other more closely than either does any other madtsoiid taxon, and although they have other differences that make it unlikely they could come from the same species, they are indistinguishable in terms of characters 1-7. The dentary morphology thus appears to provide no evidence for either of the Murgon species to be more closely related to younger Australian madtsoiids, but also cannot show they are most closely related to each other, because their shared characters could all be symplesiomorphic for Australian Madtsoiidae.

RIBS. In snakes the dimensions of the rib head correspond approximately to those of the paradiapophysis to which it articulates, and the long dimension of the paradiapophysis is approximately one third of vertebral width across the prezygapophyses (mean = 0.335, n=25 vertebrae of *Patagoniophis* and *Alamitophis* from Tingamarra; unpublished data). Using the ratio of maximum vertebral width to total vertebral column length adopted as a 'standard' (1:136.9 in a skeleton of *Aspidites melanocephalus*; Scanlon, 1993), the rib QMF52167 came from a snake approximately 1.6m long (3.9mm x 3 x 137 = 1603mm), or somewhat longer if it was not among the largest in the skeleton. It can be concluded from this specimen that at least one additional snake taxon (approximately twice the size of *Alamitophis tingamarra* sp. nov.) was present in Australia during the early Eocene; this was also most likely a member of Madtsoiidae, both because of morphological similarities to *Madtsoia* spp., and because no non-madtsoiid snakes are known in Australia until much later (Scanlon, 2001; Scanlon et al., 2003).

The three rib-head morphotypes from Murgon represent greater diversity in this region of the skeleton than has been documented in any recent family of snakes (Hoffstetter & Gasc, 1969), although this may be due partly to neglect of rib morphology in favour of other features. The form referred to *Alamitophis tingamarra* sp. nov. differs conspicuously in proportions from all other madtsoiids known from Australia, and is more comparable to those of *Madtsoia bai* (Simpson, 1933: fig. 5) and perhaps also *Dinilysia patagonica* Woodward, 1901 (Rage & Albino, 1989: fig. 1E). The more abundant form, referred to *Patagoniophis*, is more similar to those of *Wonambi naracoortensis*, *Yurlunggur camfieldensis*, and material from Riversleigh representing several additional taxa (Scanlon, 1996); as noted previously (Scanlon, 1993) this is consistent with *Patagoniophis australiensis* forming the sister taxon or ancestor of all post-Eocene madtsoiids. It would be equally consistent with either *Alamitophis tingamarra* or a (*Patagoniophis*, *Alamitophis*) clade forming the sister taxon (but not ancestor) of later madtsoiids, if the rib morphology attributed to *A. tingamarra* were autapomorphic for the species; however, this is considered less likely due to its greater resemblance to *Madtsoia* and *Dinilysia*.

## BIOGEOGRAPHY AND ECOLOGY

The known distribution of *Patagoniophis* and *Alamitophis* implies that their geographic ranges were connected across Antarctica at some stage between the Late Cretaceous and early Eocene (Scanlon, 1993). While long-term geographic continuity is not distinguishable from 'dispersal' on the currently sparse fossil evidence, it may be simplest to assume that only one-way dispersal was allowed by what may have been a transient habitat corridor, cut off from the west before connecting to the Australian landmass. Woodburne and Case (1996) reviewed geophysical and some of the palaeontological evidence bearing on the dispersal route between South America and Australia at this time, concluding that South America and the Antarctic Peninsula remained in contact until the opening of the Drake Passage about 36 Ma (late Eocene), but Australia was separated from East Antarctica by about 64 Ma (early Paleocene). Evidence for environmental conditions in Antarctica at the time mainly relates to the Antarctic Peninsula, indicating it possessed a warm- to cool-temperate climate and a plant community dominated by conifer rainforest of podocarps and araucarians, with angiosperms (including Proteaceae and *Nothofagus*) becoming more diverse through this interval (reviewed by Woodburne and Case, 1996; see also Case et al., 2000 for evidence of dinosaurian dispersal from South America to Antarctica). Climatic conditions in the rest of Antarctica, closer to the pole, were presumably less benign, and are likely to have constituted a filter barrier that limited the extent of faunal interchange (see Godthelp et al., 1999: 292). In particular, there is currently no palaeontological evidence for any other lineage of squamates either occupying Antarctica or using it as a 'bridge' between South America and Australia (Hutchinson & Donnellan, 1993; Scanlon, 2001; Scanlon et al., 2003).

Thus, it is possible that *Patagoniophis* and *Alamitophis* lived closer to the South Pole than any other contemporaneous squamates. Recent snakes of the highest latitudes are small, heliothermic, and viviparous (Shine, 1985) and extend beyond the climatic limits of lizards, so these conditions are also likely in the most southerly snakes of other times. The Australian species of both *Patagoniophis* and *Alamitophis* have smaller body sizes than their earlier Patagonian congeners, consistent with a process of 'dwarfing' affecting both lineages; if the larger rib actually belongs to an adult of a *Madtsoia* sp., it is even more dramatically dwarfed relative to South American congeners (estimated as up to 9 m long; Simpson, 1933). This inferred process of reduction in body size (along with the known temporal distribution in each area, which might be discounted due to the sparseness of the records) is more consistent with dispersal from South America to Australia, rather than the reverse. The morphological losses associated with live-bearing in amniotes are possibly irreversible (Lee & Shine, 1998), and it can therefore be suggested that descendants of any of these lineages (presumably including all later madtsoiids in Australia, such as *Wonambi* and *Yurlunggur*) were also likely to have been viviparous.

## ACKNOWLEDGEMENTS

I thank Henk Godthelp and Mike Archer (UNSW) for providing access to the fossil material described here as well as support and encouragement during and after my PhD studies, and for critical readings of the manuscript; Jean-Claude Rage, Adriana Albino, and Zbigniew Szyndlar for discussions of fossil snakes and comments on drafts of this work. Coral Gilkeson (Westmead Hospital Dental Clinic) and Jeanette Muirhead (UNSW School of Biological Sciences) assisted with SEM photography. The University of Adelaide (Department of Environmental Biology) and South Australian Museum (especially Mike Lee and Mark Hutchinson) provided laboratory facilities and access to comparative material. For financial support I also thank the Australian Research Council, Australian Commonwealth Postgraduate Awards scheme, and University of New South Wales Faculty of Biological and Behavioural Sciences.

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# HEBER ALBERT LONGMAN (1880-1954), QUEENSLAND MUSEUM SCIENTIST: A NEW BIBLIOGRAPHY

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Turner, S. 2005 05 31: Heber Albert Longman (1880-1954), Queensland Museum scientist: a new bibliography. *Memoirs of the Queensland Museum* **51**(1): 237-257. Brisbane. ISSN 0079-8835.

This paper presents for the first time a bibliography of nearly 90 formal scientific publications and the numerous, over 350 articles of Heber Albert Longman. During his 34-year tenure at the Queensland Museum first as Assistant Director and then Director, despite lack of formal training and in many ways isolated from the scientific community at large he engaged in many fields of natural history and described 22 new taxa. His selection of vertebrate palaeontology as his discipline of choice put Queensland and the museum onto the world stage in this field. Local societies to which he significantly contributed include The Royal Society of Queensland where Longman was editor of the journal and twice President, and he presented some 80 exhibits and talks on all aspects of natural history and anthropology. Longman wrote for and was the subject of articles in many newspapers and magazines; he was and would have been regarded today as a leader in scientific journalism, science communication and popularisation. Most prolific were his weekly columns, "Nature's Ways" published in *The Courier Mail* from late 1947 until the week before he died.

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Heber Longman came to Australia from England in 1902 for health reasons, settling at and turning his hand to a career in newspapers in Toowoomba (Gill, 1986). He quickly became a leading light in local natural history ventures and with zoologist Ronald Hamlyn-Harris. became a co-founder of the local Field Naturalists' Club (Herbert, 1954). When appointed Director of the Queensland Museum, Hamlyn-Harris recognised Longman's worth and potential as a scientist and persuaded him in 1911 to leave Toowoomba to come to Brisbane to join his staff. Longman's scientific life blossomed, as his publication record indicates. Longman succeeded Hamlyn-Harris as Director in 1917 (Fig. 1) and proceeded to build a reputation as an innovative and perceptive scientist especially in his chosen field of vertebrate palaeontology. However, he was always bedogged by lack of funds and beset by a measure of isolation (Mather, 1986). Meetings with peers and colleagues were rare in early to mid 20th century Australia, the most notable being those of the British and Australasian Associations for the Advancement of Science. Even these Longman only rarely was able to attend, one such being the A.N.Z.A.A.S. meeting in Brisbane in 1930 when he was a vice-president for the Geology Section. He made up for this lack by what today we would call 'networking', maintaining a massive correspondence with international, national and Queensland people from all walks of life and by making contact with the international scientific community and institutions (viz. Queensland Museum Archives).

From his earliest days, however, Longman tried personally to address the whole range of organisms represented in the State's fauna and flora. He identified all that came his way as best he could, going on to work on every vertebrate group and several invertebrates. As well he maintained his first love of plants and his garden. Much of his time was devoted to his work in local societies, presenting numerous exhibits at the Queensland Field Naturalists' Club and especially at the Royal Society of Queensland. He also promoted the museum through the media or directly by contact in public lectures and by assisting local groups as diverse as the Lyceum Club and a fishermen's supplies company (e.g., The Distributors of the Emperor Fishing Equipment c. 1935). Mirroring his wife's concerns he was involved in Women's clubs and fostered museum education, teaching local schoolchildren (e.g., Mather, 1986; Fallon, 2002). One talk "Wonders of the Past" presented to the Brisbane Women's Club in 1929 featured donations and scientific research done by women

FIG. 1. Heber A. Longman when Director of the Queensland Museum c. 1920s.

in the State (Fallon, 2002). From his ability to tackle all and sundry which came his way at the Museum (e.g., Fig. 2), he became a doyen of Queensland natural history for nearly half a century. This fact is reflected in his numerous contributions to local societies, newspapers and magazines (Herbert, 1955; Turner & Mather, 1986; Gill, 1986; and see below). Longman was also the media star of his day in Brisbane (e.g., Brown, 1926; Lack, 1936). Even after his retirement his achievements were acclaimed in the press (Lack 1949). Nevertheless during the centenary year in the era of his successor, George Mack, his achievements were hardly noted (Covell, 1955).

Longman was supported in his dedication by his wife Irene (Fig. 3); in 1929 she became the first woman parliamentarian in Queensland (Fallon, 2002). Being a true 'scientific' wife, she shared his collecting trips such as to Masthead Island for plants (Longman, 1914a) and western Queensland, which were their joint form of relaxation (Herbert, 1955). Irene supported his directorial work at the museum by welcoming and looking after visiting scientists including Sir Julian Huxley at their home in Chelmer and hosting social occasions such as the visit of The Queensland Field Naturalists' Club in July 1920 (Anon., 1920). At home they worked side by side in a book-lined study containing volumes reflecting their shared interests from philosophy and history to drama and poetry (Fallon, 2002). Irene also helped Heber with preparation work and at least one major ecological study. In their study of the Magnificent Spider they made full use of a fine collection of the classic volumes in German on Australian spiders he acquired for the Museum library in 1913 (V. Davies, pers. comm., 2003). With his reliance and interest in books, the Queensland Museum Library was one of his main priorities.

He did have an interest in the lifestyles of invertebrates and especially with identification of specimens brought to the museum but mostly Longman concerned himself with vertebrates. Despite his successor George Mack suggesting that Longman did not take up fossils until he became director in 1917 (Mack, 1956), there is every sign that he had been 'bitten' by the fossil 'bug' before that (Longman, 1913b, 1915c, 1916c and in Royal Society of Queensland exhibits 1916d, e). In fact he 'confesses' to his love of ammonites as a small boy where they were found in his Wiltshire garden (Longman 15th Sept. 1951). He early on began considering some of the mammalian megafauna, especially the kangaroos and diprotodons that his predecessor Charles Walter De Vis had studied (Archer & Clayton, 1984; Mather, 1986; Turner et al., 1990). He tackled taxonomic problems raised by De Vis' earlier splitting (1916c). Most important was his erection of a new genus *Euryzygoma* for one of De Vis' taxa (Longman, 1921e, Howchin, 1925-30). He returned to the diprotodons throughout his life, understanding their journalistic 'pulling power' (Longman, 1923c, Feb. 21st 1948, 6th Oct. 1951). He also made use of the lessons of the sudden megafaunal extinctions, keeping abreast of the research even late in his retirement when he noted the work of the visiting Californian marsupial expert Ruben Stirton at Lake Callabonna (Longman, 11th July 1953).

For his scientific research Longman did much of his own preparation and photography, sometimes spending long hours in the museum even on Christmas Day (Turner & Wade, 1986). In his papers he tended to illustrate with his own photographs and restorations rather than line drawings (only five of his papers have text-figures) so that perhaps he did not regard himself as good at scientific drawing. He sometimes made use of graphics gaining help even from the best artists of the day, such as Douglas J. Annand, a well-known Brisbane painter, to help reconstruct the past scenes of Queensland. O.W. Tiegs and Cecily Sandercock provided a wonderful set of skull and restoration drawings for the *Euryzygoma* work (Longman, 1921e, 1934a; Mather, 1986, fig. on p. 80). James Edgar Young, a fellow Queensland 'Nat.' who had collected vertebrate fossils since the 1920s when he joined the Hubert Wilkins-BMNH expedition (Wilkins, 1929; Turner, 1986), illustrated the final scientific paper (Longman, 1943). Gaining funds for fieldwork was not easy but with the help of local managers and landowners he did visit several important sites especially in the search for the giant reptiles that he made world-famous (e.g., Turner & Wade, 1986; Rich & Vickers-Rich, 2003). Generally, he was assiduous in following up information on interesting deposits but he did miss the chance with a few important possibilities, notably an unknown reptilian mandible from Rewan in central Queensland found by geologist Harold Jensen (Longman, 1923e), a "crocodilian" which turned out to be a labyrinthodont amphibian, part of a fascinating Early Triassic fauna (e.g., Thulborn, 1986). Alan Bartholomai, Longman's successor as Director in 1969 investigated this site thoroughly when he was Curator of Geology to reveal that the bones at Rewan included both new fossil amphibians and lizard-like forms (e.g., Turner & Wade, 1986).

Longman had clearly struggled with his Christian upbringing. In his first major publication and his only book, published by the Rationalist Press Association in 1914 (Fig. 4), he nailed his agnostic colours to the wall, a brave thing to do in the Brisbane of the Great War era (World War I). In the book he notes how he was brought up as a Nonconformist but has through "many years of study and thought and a period of practical work as a naturalist," ..."gladly come to the emancipated position of an Agnostic". Essentially Longman was a humanist, a disciple of Thomas Henry Huxley (Longman, 1926i) who introduced the term. He also believed in scientific truth and did much to educate people about animals and plants in their environment. He wrote at length about unusual specimens, pathologies and unique Queensland species such as the lungfish, *Neoceratodus* and did much to dispel the popular myths of the day about them walking on land and so on. Like others in the early 20th century he upheld the tenets of evolution and was interested in eugenics; Longman promoted understanding of evolutionary theory, heredity and the contemporary ideas on eugenics both in scientific and popular circles such as in his lectures to societies and university students. One debate on Darwinism was set up between Longman as "the scientist" and an "Archbishop Downey" (denomination unknown) representing religious views (Connolly, 1935). Longman (e.g., 1914, 1914b, 1921a) returned several times to these themes.

FIG. 2. Longman and older man (possibly the collector, G. Hissted, or more likely the donor, W. Hiddens, Qld Govt Inspector of Fisheries) holding a prize fish, a Dolphinfish or Mahi Mahi, *Coryphaena hippurus*. T.C. (Tom) Marshall then the QM modeller & artificer made a cast of the 38 inch specimen for display around 14th January 1929 (Jeff Johnson pers. comm. 2003).

Longman's voluminous correspondence will be considered in detail elsewhere. He fostered the landowners and managers in the State to encourage donations; notable being Frederic(k)

L. Berney of Barearolle and A. Browne of Durham Downs. Both these men were immortalised with the naming of a fossil species. Longman may have met Berney around 1910 through the Royal Australasian Ornithological Union, which conducted field camps at Masthead Island. After Berney's death (Bryant, 1949), Longman (*Nature's Ways* 26th March 1949) proffered a brief memorial, celebrating nearly four decades of friendship. Major correspondence spanning 25 years was between Longman and his mentor in matters dinosaurian, Professor Dr Baron Friedrich von Huene (1875-1969, Fig. 5) of the Institut und Museum für Geologie und Paläontologie der Universität Tübingen in south Germany (Turner & Maisch, 2003). Their letters between 1923 and 1950 continue sporadically through the war years but document the delight both have in the new finds and show von Huene easing Longman towards greater understanding of the significance of his specimens. Von Huene planned an expedition to Australia, to work together with Longman and to dig for more Lower Jurassic sauropods. Sadly for science, and despite their mutual longing for the event, neither the expedition nor their meeting took place because of the severe economic and then political difficulties of the thirties and forties. Other important influences on Longman include British palaeontologists, Professor D.M.S. Watson (1886-1973) at University College, London (e.g., Parrington & Westoll, 1974; Watson, 1951) and Dr W.E. Swinton, Curator of Reptiles, British Museum Natural History. Australian zoologist Jock Marshall, later Foundation Professor of Zoology at Monash University, corresponded from the 1930s to the 50s (QM Archives, NAA coll. Drysdale, 1966). Heber also eulogised on field time spent with his friend, entomologist Robin Tillyard (1881-1937) (Longman, 17th January 1953).

FIG. 3. A, Irene Maud Longman (nee Bayley) 1877-1964, Heber's staunch supporter; B, shared field trips: the young couple Irene and Heber Longman on hilltop in Glasshouse Mountains or Toowomba with their niece, Marian Milful and her father Percy Fritz Rowland, headmaster of Rockhampton then Townsville schools, c. 1912.

Heber Longman's scientific contributions were wide-ranging, introducing 22 new taxa to the Australian fauna, in addition to his earlier herbaria (Herbert, 1954, 1955). He was a modest man and did not seek praise or recognition. He gained no honorary degree, which would have been fitting. Nevertheless, he was honoured during his lifetime. One newspaper, *The Queenslander*, cited him as "F.R.S.", which is not strictly untrue. In August 1931 he was invited to be a Foundation member of the Royal Society of Australia, which gave way to the Australian Academy of Sciences in 1954 by becoming the Royal Society of Canberra (Martyn, 1967). He did become a Fellow of the Linnean Society of London early on in 1922. For his interests and education in human origins, he was also made a Fellow of the Royal Anthropological Institute (F.R.A.I.) and was a Communicating Member of the Zoological Society of London. In 1946 he received the Australian Natural History Medallion and later, the prestigious Mueller Medal (Anon., 1953). If he had lived a little longer this might have been the basis for his acceptance into the fledgling Australian Academy of Sciences, which began in the year of his death, 1954 (Fenner, 1995). Perhaps the most fitting legacy is the taxa named for him (see

THE RELIGION
OF A
NATURALIST

BY
HEBER A. LONGMAN

LONDON:
WATTS & CO.,
17 JOHNSON'S COURT, FLEET STREET, E.C.
1914

CONTENTS

FIG. 4. Title page and contents of Longman's book, *The Religion of a Naturalist* (Watts & Co., issued for the Rationalist Press Assoc. Ltd, London, 1914).

below), which will surely increase as his worth is recognised by posterity.

The scientific publications of Longman, which number well over 100, cover mainly the subjects he dealt with in the museum (comparative anatomy, zoology, vertebrate palaeontology). His articles and papers also cover aspects of museology, natural history and anthropology. Other contributions include assistance to contemporary researchers and writers (e.g. Johnstone & Bancroft, 1921; Longman, 1925g, 1929 c, d). Most of his published work was in the 'flagship' *Memoirs of the Queensland Museum* initiated by his predecessor, Hamlyn-Harris (Mather ed., 1986). Interestingly, Longman was almost exclusively a sole author of his papers, which probably reflects the isolation in which he worked rather than any lack of desire to cooperate with colleagues. He certainly kept pace with the purported modern ideal of two papers a year, usually exceeding four or five with articles and short notices in the *Proceedings of the Royal Society of Queensland* (RSQ). Often he did more, especially in the early years at the museum when he was establishing himself.

The early years when he was Deputy Director were busy not least gaining publicity for the museum (e.g., Cazna, 1923). He was actively involved in the Royal Society of Queensland and the Queensland Field Naturalists' Club. 1915 was especially prolific and was the year of his first major but tentative and formally unpublished fossil identification of an Australian dicynodont from the Cretaceous of Hughenden (Longman 1916d), which may prove to be one of his most perceptive identifications. In the early 1920s through to the 1930s he was perhaps in his prime when his work on dinosaurs and other large fossil reptiles took off. In his book (Longman, 1914), he talks of dinosaurs and the like as "Brobdingnagian monsters", which "came across the stage of this great panorama of extinct life serving no useful purpose". However, later, by his own work in describing Jurassic and Cretaceous dinosaurs and other giant marine reptiles Longman went on to show their significance and in so doing transformed the museum and made its scientific reputation abroad. He published around 30 papers on fossil fish, amphibians, reptiles and marsupials, erecting six new endemic taxa (see below). He described the Mesozoic and Tertiary specimens including the first complete and definite dinosaurs from Australia (Rich & Vickers-Rich, 2003). Not least Longman did pioneer work on Cainozoic cave faunas in Queensland from the Marmor and Gore quarries first identified by L.C. Ball (Longman, 1925d, e, 1945b; Hocknull, 2003).

Heber Longman was not a trained geologist or palaeontologist but he was a good anatomist and morphologist and perceptive naturalist. His powers of identification have become legendary from the recognition of one of the world's largest marine vertebrates (*Kronosaurus*) from only a piece of jawbone and one battered tooth. Recent work (Thulborn & Turner, 2003a-c) has shown, 90 years after the event, how Longman

FIG. 5. Longman's mentor for reptilian palaeontology, Friedrich Baron Hoyningen (better known as Friedrich Freiherr von Huene, (1875-1969) of the Institut und Museum für Geologie und Paläontologie, Karl-Eberhardt Universität Tübingen (photo received from Dr M. Maisch).

tentatively recognised the first Cretaceous dicynodont, which he did not feel confident in publishing formally in 1915. Longman (1924a, 1926c) maintained a fairly fixist stance regarding the biogeography of Australia's unique fauna, which is probably why he did not risk publishing on the mammal-like reptile. Howchin (1925-30, p. 699), a pro-Gondwana geologist, pointed out that Longman was probably right about the concentration of the marsupial fauna to the north based on suitable climate and environments but for the wrong reasons.

Longman was not able to go as much into the field as he would have liked because through the depression years museum finances were lacking, inadequate or tightly controlled by the relevant government department (Mather ed., 1986). He did manage, however, with the help of locals to visit some of the important sites such as 'Durham Downs', the site for *Rhoetosaurus* (*in litt.* with A.J. Browne, QM archives), and the Ipswich coalmines to see dinosaur footprints (Longman, 1935b, 23rd July 1949). Occasionally he reminisced in later life about the visits he made sometimes on his vacation such as the meeting with Mrs E. Lumley Hill who researched fossil plants on her property, Bellevue (DT 31st May 1929; Longman, 19th Sept. 1953). He maintained close links with the University of Queensland where Professor H.C. Richards was an early 'Honorary' of the museum, and the Queensland Geological Survey for whom he identified specimens (e.g., Longman, 1932c). Longman also began to ask other people to work on material from the museum collections. He encouraged Edwin Sherbon Hills of Melbourne University published a series of papers on Tertiary fishes in Australia such as the Eocene Redbank Plains fauna (e.g., Turner & Long, 1989; Sherratt & McCarthy, 1992).

The main research tools at his disposal were the QM (Fig. 7) and his own libraries and the comparative QM collection (Mather, 1986). Through his contacts, Longman may also have had access to the budding UQ library. From his earliest days in the museum he encouraged the purchase of taxonomic volumes. In his day he initiated exchange with most of the major museums especially of interest to him, for instance, the Museum of Palcontology, University of California at Berkeley; the Royal National Museum of Natural History of Belgium in Brussels; and the Logan Museum, Wisconsin (as recorded in the 1929 QM scrapbook).

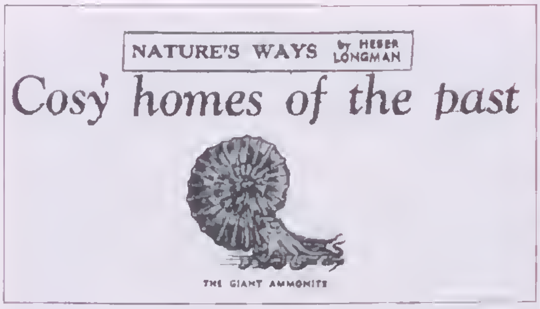
FIG. 6. Longman in his major research tool, the QM library, which he helped to augment during the difficult Depression years; Longman in the library with Nora Holdsworth, 1933 (after Mather, 1986).

Longman himself gathered articles and reprints of interest by exchange. Some items in his archival box relate to his interest in fossil man and where we come from and include one the 'Globe Trotter' (1918) on the controversial Talgai skull from the Darling Downs and a copy of the Philosophical Transactions of the Royal Society of London paper on the same specimen. He probably attended the British Association for the Advancement of Science meeting in Brisbane in 1914 for there is an article in his archival box relating to the mummified bodies from the Torres Strait, which were examined by the scientists including D.M.S. Watson. Other significant items are his copy of 'The Proofs of Evolution' by Henshaw Ward (1928) and an anti-evolution pamphlet (Nicholson undated). Several of Longman's Royal Society and public lectures and presentations deal with human remains and prehistoric relationships (e.g., Longman 1925f, 1939c). The papers and talks on prehistory and evolution were part of his popular repertoire leading to his portrayal as Hamlet contemplating the human skull and brain within (Lack, 1936, Turner & Wade, 1986: fig. on p. 138). His and his wife's interest in aboriginal history, culture and welfare inspired an invitation to visit Thursday Island (Fallon 2002). One of his abiding interests in human evolution and the remains and artifacts left by both prehistoric men and native Australians was a passion shared with another person of influence, noted geologist, Professor Sydney J.B. Skertchly (1850-1926) (Longman, 1926d). When Skertchly died in 1927 Longman delivered a eulogy on his life's work at the graveside at Nerang Cemetery (Fig. 7).

He became ill during the thirties (*in litt.* 1933 to von Huene) and his output slowed considerably and he began to withdraw from society business. Was this stress-related? During The Depression there was considerable stagnation in conditions and consequent cuts in salary at the museum. Funds dried up and there were missed opportunities such as the loss of the first complete *Kronosaurus* because the Government would not provide field expenses to Longman to join the prestigious Harvard expedition led by W. 'Bill' Schevill (Turner & Wade, 1986). Looking at pictures of him at this time in his life the tiredness and strain show (Fig. 6). His thoughts are perhaps epitomised in his presidential address to the Royal Society of Queensland in 1941 entitled "*Homo sapiens*: turbulentus" where he decries the wasteful force of human beings. Not just the war but also the preceding years of depression and the struggle to keep the museum afloat must have sapped him and added to his agnosticism.

FIG. 7. Longman giving the eulogy at Professor S.B.J. Skertchly's graveside at Nerang Cemetry, 30th October 1927. Photo N. Nixon (from QM Archives).

Following his retirement in 1945, however, he again took on the role of journalist (to eke out the State pension?) and became a regular columnist with *The Courier Mail*. In these final years his accumulated wisdom as a journalist and a natural historian came to the fore. He acknowledged the pivotal experiences in his life and featured notable Queenslanders, many of whom were his friends. Longman tells us in these pieces what were some of the most enjoyable moments of his life as for instance his visit down the Lanefield Colliery in the Ipswich Coalfield to view underground dinosaur footprints with Government Chief Geologist, Lionel Clive Ball (1877-1955) (Longman, 1935c). Herbert (1955) commented that his weekly column reached a wider audience than his scientific writings having a great following throughout Queensland. Herbert noted with regret that the newspaper articles were of "such an ephemeral nature". Longman must also have had input into deciding the artwork provided with the text (Fig. 8). His last years in the 1950s were again affected by illness. Longman had retired from the museum suffering from overwork and stress and Irene gave up her public life to tend for him during his last debilitating illness (Fallon, 2002). Nevertheless, they both drew strength from their surroundings (Fig. 8) as he recounted in many of his columns. Longman's weekly output continued until just before the week of his death on February 16th, 1954. The next week, in place of his usual article, came an obituary by



NATURE'S WAYS by HEBER LONGMAN

Cosy homes of the past

THE GIANT AMMONITE

FIG. 8. An example of the 'Nature's Ways' byline and sketches, from 18th September 1948, artist unknown.

FIG. 9. Heber and Irene Longman in the garden at 'Cotley', Chelmer, where he wrote many of his articles and entertained visitors to Brisbane.

Associate Professor M.F. Hickey of the University of Queensland. Hickey praised Longman's wisdom and achievement and mourned the loss of an old friend who has "lived life to the full in the pursuit of truth and the welfare of his fellowmen".

*Abbreviations.* C.A.V.E.P.S., Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics; CM, *Courier Mail*; DT, *Daily Telegraph*; NAA, National Archives of Australia; QM, Queensland Museum; RSQ, The Royal Society of Queensland.

## SOURCES

The main sources for this study have been the archives and library of the Queensland Museum (Longman - QM Library Box 284; Folder with reprints and newspaper articles; Colliver archive, Box 22, QM C120 - some cuttings from 'Nature's Ways'). There is also a Longman collection in the archive at the Adolph Basser Library, Australian Academy of Sciences, Canberra. The State Library of Queensland houses several items under Longman's name as well as being the source for *The Courier Mail* articles. Correspondence with von Huene was found at QM and in the Institut für Geologie und Paläontologie der Universität Tübingen in Germany. Fallon (2002) led me to the Irene Longman scrapbook housed at Miegunyah by Queensland Women's Historical Association and links with Longman family and relatives archives.

## ACKNOWLEDGEMENTS

Very many thanks to Alison Fogerty, Marion and John Milful, Fay Sanders and Betty Bayley, relations of Heber and Irene Longman who kindly offered family memories and sent previously unpublished photographs and Helen Piispanen, a relative of Heber, who donated original documents. Dr Patricia Mather (Queensland Museum) has supported my work on Heber Longman throughout especially during the time of her editing of the Queensland Museum history; I thank her for critically reading an earlier draft of this paper. Dr Alan Bartholomai kindly read the manuscript and gave critical comments. Early in 2003, Dr Judith Mackay (Queensland Museum) enabled me to meet Pat Fallon (Bethania) whose own work on Irene Longman has been pivotal to the understanding of the man; I thank Pat for generously sharing her knowledge and for allowing me to read a copy of her MPhil. thesis. Dr Geoff Monteith located the copy of Longman's book, which had been donated to the Queensland 'Nats'. Members of the Queensland Museum, Patrick Couper, Val Davies, Jeff Johnston, Pat Mather and Steve Van Dyck gave advice on reptile, spider, fish, worm and mammalian nomenclature, respectively. Dr Michael Maisch (IGP, Tübingen) helped find letters from Longman to von Huene and Dr Tom Rich (Museum of Victoria, Melbourne) shared information he had obtained in his recent study of the history of Australian dinosaurs. I particularly wish to thank the Queensland Museum librarians for all their help through several years since 1981 when I began work on the archives: Ted Wixted, Kathy Buckley, Victoria Harrison and Meg Lloyd. Judy Bracefield (Queensland Museum) gave staunch research assistance locating articles at the State Library of Queensland and we thank librarians at that institution. Rosanne Walker

(librarian) helped at the Basser Library in Canberra. The *Courier Mail* kindly allowed reproduction of some of the artwork from Longman's articles and Cathrin Matthieson (CM) assisted with archival material. Part of this paper was offered as a Keynote address to the 9th C.A.V.E.P.S. Heber Longman Memorial Symposium in July 2003.

## TAXA DESCRIBED BY HEBER A. LONGMAN

*Aspidites collaris* Longman, 1913 is a junior synonym of *Aspidites ramsayi* (Macleay, 1882) - Woma or Ramsay's Python.

*Pseuochirus (Hemibelideus) cervinus* Longman, 1915 - marsupial phalanger petaurid, now a junior synonym of *Hemibelideus lemuroides*.

*Cratochelone berneyi* Longman, 1915 - fossil turtle.

*Diemenia carinata* Longman, 1915 - *to Desmansia* Waite & Longman 1920 is now considered to be a junior synonym of *Pseudonaja nuchalis* Günther, 1858 - Western Brown Snake. The Western Brown Snakes are regarded as a species complex so there is a chance that this may be resurrected from synonymy at a later date (P. Couper pers. comm.).

*Furina multifasciata* Longman, 1915 valid = *Vermicella multifasciata* (Longman, 1915) Northern Bandy-bandy (venomous burrowing snake).

*Diplodactylus hillii* Longman, 1915 - called a "Mungana Chillagoe lizard" is a junior synonym of *Diplodactylus conspicillatus* Lucas and Frost, 1897 Burrow-plug Gecko.

*Lygosoma bancrofti* Longman, 1916 is a junior synonym of *Anomalopus leukartii* (Weinland, 1862) Two-clawed Worm-skink.

*Lygosoma (Hinulia) tryoni* Longman, 1918 valid = *Eulamprus tryoni* (Longman, 1918) Tryon's Skink. Recently resurrected from synonymy with *Eulamprus murrayi* by Ross Sadlier from Australian Museum (P. Couper pers. comm.).

*Denisonia maculata* var *devisi* nom. nov. Waite & Longman 1920 = *Denisonia devisi* Waite & Longman 1920 - De Vis's Banded Snake.

*Euryzygoma* Longman, 1921 - fossil marsupial diprotodontid genus for *E. dunense*.

*Nyctimene tryoni* Longman, 1921 - tube nose bat now a junior synonym of *Nyctomine robinsoni*.

*Macropus welsbyi* Longman, 1922 - marsupial macropodid now a junior synonym of *Wallabia bicolor*.

*Kronosaurus qneenslandicus* Longman, 1924 - giant fossil reptile, pliosaur

*Petaurus breviceps longicaudatus* Longman, 1924 - marsupial petaurid

*Rattus youngi* Longman, 1926 - rodent, now a junior synonym of *Rattus sordidus*.

*Mesoplodon pacificus* Longman, 1926 - Cetacean ziphiid Longman's Beaked Whale (now placed in *Indopacetus*, see Dalebout 2002).

*Rhoetosaurus brownei* Longman, 1926 - giant fossil reptile, sauropod, first Queensland dinosaur

*Flindersichthys denmeadi* Longman, 1932 - fossil fish

*Austrosaurus mckillopi* Longman, 1933 - giant fossil reptile, sauropod dinosaur

*Rhodona allanae* Longman, 1937 = *Lerista allanae* (Longman, 1937) Retro Slider (a burrowing skink). Possibly Australia's first extinct reptile species since European colonisation.

*Lasiorhinus latifrons barnardi* Longman, 1939 - marsupial vombatid, now a junior synonym of *Lasiorhinus krefftii*

*Austropelor wadeleyi* Longman, 1941 - fossil temnospondyl amphibian

## TAXA NAMED FOR LONGMAN

*Scoliodon longmani* Ogilby, 1912 - fish, considered to be a junior synonym of *Rhizoprionodon acutus* (Ruppell, 1837).

*Hydromys longmani* Thomas, 1923 - rodent, now a junior synonym of *Hydromys chrysogaster*.

*Petrogale longmani* Thomas, 1926 - marsupial, macropodid, synonymised with *Petrogale brachyotis*.

*Digaster longmani* Boardman, 1932 - giant earthworm, now in *Megaloscolis*.

*Asquamiceps longmani* Fowler, 1934 - fish ["following a pleasant visit in Brisbane"].

*Lutjanus longmani* Whitley, 1937 - fish, now a junior synonym.

*Platypterygius longmani* Wade, 1990 - fossil reptile, ichthyosaur.

## BIBLIOGRAPHY

The following bibliography of Longman's work updates a publication list given by Herbert (1955) and includes the full list of scientific journal and other less formal articles, such as those in newspapers. References to Longman in newspapers, articles and books are also listed. Longman seemed anxious to publish in the budding journals and newsletters of the day, and later when more established he was invited to contribute further work. In addition, the more general articles and numerous weekly contributions on natural history and other scientific matters, which Longman maintained throughout his life, are categorised for the first time. Nevertheless, he was so productive and inventive in finding new ways to publish his work and to publicise the Queensland Museum that the list may yet be found to be incomplete.

## PUBLICATIONS AND ARTICLES BY YEAR

*Items relevant to his work in palaeontology are annotated with the stratigraphic age and/or taxonomic significance. Where possible, date of publication is given to keep chronological track of papers. Plates and figures are noted as appropriate. Use has been made of a typed list in the QM archives possibly updated after Longman's death by his friend and obituarist Desmond A. Herbert, Professor of Botany at UQ, or some member of the museum (see numbers following reference). This list was based on a typed and handwritten one made by Longman (kindly donated to the QM by Helen Piispanen via Pat Fallon, 2003) shortly before he died.

### BOOK

LONGMAN, H. A. 1914. The Religion of a Naturalist. (Watts & Co., issued for the Rationalist Press Assoc. Ltd, London) i-viii +123pp.

### PUBLICATIONS

LONGMAN, H.A. 1912. Herpetological notes. Memoirs of the Queensland Museum 1: 23-25. [27th Nov.] - 1

1913a. Herpetological notes. Part I: systematic, including the description of one new species. Part II: Ethological. Memoirs of the Queensland Museum 2: 39-45. [10th Dec. 1913] - 3.

*1913b. Note on *Portheus australis* A.S. Woodward. Memoirs of the Queensland Museum 2: 94 -95. Cretaceous fish put in Ichthyodectidae [10th Dec. 1913] - 4.

1914a. The plants of Mast-Head Island. Proceedings of the Royal Society of Queensland 25: 17-23, [read June 27th 1913; published 1914] - 2

*1914b. Radiogenesis in evolution. Proceedings of the Royal Society of Queensland 26: 23-39. [read May 25th 1914; published 1914] - 6. [Gives indication of Longman's reading on evolution and palaeontology].

1915a. New 'room' show-cases in Queensland Museum. Memoirs of the Queensland Museum 3: 1-2 + 4 plates. [28th Jan. 1915] - 9.

1915b. A new phalanger from North Queensland. Memoirs of the Queensland Museum 3: 22-23. [28th Jan. 1915] - 10.

*1915c. On a giant turtle from the Queensland Lower Cretaceous. Memoirs of the Queensland Museum 3: 24-29 + Pls XII-XIII [28th Jan. 1915] - *Cratochelone berneyi* named for collector Frederick L. Berney - 7.

1915d. Reptiles from Queensland and the Northern Territory. Memoirs of the Queensland Museum 3: 30-34 + Pls XIV-XV [28th Jan. 1915] - 8.

*1915e. Modern Evolutionary Thought. Presidential address, January 1914. The Queensland Naturalist 2, 1, July: 8-15. - 5.

1916a. List of Australasian and Austro-Pacific Muridae. Memoirs of the Queensland Museum 5: 23-45 [10th July 1916] - 12.

1916b. Snakes and lizards from Queensland and the Northern Territory. Memoirs of the Queensland Museum 5: 46-51 + Pl. VI [10th July 1916] - 11.

*1916c. The supposed artiodactyle Queensland fossils. Proceedings of the Royal Society of Queensland 28, no. 4: 83-87 - correcting De Vis's ideas and identification of Darling Downs material regarding "Prochoerus celer" De Vis - *Thylacoleo carnifex*, *Nototherium*. [read 1st May 1916; published 25th Sept. 1916] - 14.

1916d. Notes on the classification of common rodents, etc. Quarantine Service Publication No. 8: 23 pp. + 8 pls & 7 text-figs. - 13.

1917a. Note on climbing habits of a snake. The Queensland Naturalist 2, 2, April: p. 68.

1917b. Mouse Plagues. Queensland Agricultural Journal, N.S. 7: 295-300, June. - 16.

LONGMAN, H.A. & WHITE, C. T. 1917. The flora of a single tree. Proceedings of the Royal Society of Queensland, XXIX, No. 6, 64-69, - 18.[read Aug. 27th 1917; published Sept.]

1918a. A rare marsupial. Queensland Agricultural Journal, N.S. 8, March: 117-119. *Sminthopsis virginiae* - 19.

1918b. Notes on certain human crania in the Queensland Museum. Memoirs of the Queensland Museum 6: 1-4, Pls I-V [19th Dec. 1918] - 22.

1918c. Notes on some Queensland and Papuan reptiles. Memoirs of the Queensland Museum 6: 37-44, Pls XI to XV. [19th Dec. 1918] - 21.

LONGMAN, H.A. & WHITE, C. T. 1918. Mutation in a proteaceous tree. Proceedings of the Royal Society of Queensland 30, No. 10: 162-165, - 20. [read 30th Sept 1918: published 11th Oct. 1918].

1919. A simple method of preparing crania. The Australian Zoologist 1, pt 7: p. 208. Nov. - 25.

1920a. *Ziphius cavirostris* on the Queensland Coast. Proceedings of the Royal Society of Queensland 31, No. 8: 90-93, Pls III-IV. [read Aug. 8th 1919; published Jan. 20th 1920] - 24.

1920b. Little Penguin in Queensland. Memoirs of the Queensland Museum 7, pt 1: p. 64 [June] - 29.

1920c. General Zoology (H.A. Longman). The Queensland Naturalist, 2, 4, p. 92 [Oct.].

WAITE, E. R. & LONGMAN, H. A. 1920. Description of little known Australian snakes. Records of the South Australian Museum 1, No. 3: 173-180, pl. XXVII, [June] - 30.

1921a. Factors in variation. Proceedings of the Royal Society of Queensland 32, No. 1: 1-18 [Presidential address given 31st March 1920, issued 24th April 1920; published Jan. 20th 1921] - 27

1921b. A Death Adder's meal. The Queensland Naturalist 2, 5: p.120. [Jan. 1921] - 31.

*1921c. A new genus of fossil marsupials. Memoirs of the Queensland Museum 7, Pt 2: 65-60, Pls IV-VII [Feb.] - 32.

1921d. A new nyctimene from south Queensland. Memoirs of the Queensland Museum 7, 3: 179-181. Pl. XII [4 Nov 1921] - 35.

1921e. Cannibalism among snakes. The Queensland Naturalist 3, 1, p. 22-23 [July]. - 33.

1922a. The Magnificent Spider: *Dicrostichius magnificus* Rainbow. Proceedings of the Royal Society of Queensland 33, No. 5: 91-98, Pls vii-viii, 25a, Condensed account [issued 17th Aug. 1921 published 16th Jan 1922] - work done jointly with Irene (Herbert 1955) - 34.

1922b. A Queensland Rabbit-Bandicoot. The Queensland Naturalist 3, No. 3: p. 52-53 [Feb.] - 37.

1922c. Our marsupials. The Queensland Naturalist 3, No. 5: 90-91, lecture June 19th 1922 [Aug.] - 36.

1922d. The Queen of Spinners. The Magnificent Spider: *Dicrostichius magnificus* Rainbow. Australian Museum Magazine 1, No. 6: 186-189 [October] - 34 dup.

*1922e. An ichthyosaurian skull from Queensland. Memoirs of the Queensland Museum 7, 4: 246-256, Pls XV-XVI [19th Dec. 1922] - 39

1922f. John Gould's notes on John Gilbert. Memoirs of the Queensland Museum 7, 4: 291-294 [19th Dec. 1922] - 41.

1922g. South Queensland marsupials. Memoirs of the Queensland Museum 7, 4: 297-300. [19th Dec. 1922] - 40.

1923a. The Rat Menace. Health, Melbourne, 1, no. 2: 35-36 [Feb.] - 42.

1923b. Is the Kangaroo doomed? Australian Zoologist 3, iii: 103-107 [7th June 1923] - 45.

1923c. Prehistoric Nature. The Queensland Naturalist 4, no. 2: 29-30, lecture 21st May 1923 [Sept.]

1924a. The Zoogeography of marsupials, with notes on the origin of the Australian fauna. Memoirs of the Queensland Museum 7, 1: 1-15. [30th Jan. 1924] - marked copy - 46.

*1924b. Some Queensland fossil vertebrates. Memoirs of the Queensland Museum 7, 1: 16-25, Pls I-IV [30th Jan. 1924] - 47.

*1924c. A new gigantic marine reptile from the Queensland Cretaceous. Memoirs of the Queensland Museum 7, 1: 26-28. Pls [30th Jan. 1924] *Kronosaurus queenslandicus*

1924d. Notes on land vertebrates (Moreton Island). The Queensland Naturalist 4, no. 2: 93-95. [Sept.] - 48.

1925a. Protection of fauna in Queensland. pp. 191-199. In: Sir James Barrett ed. Save Australia: a plea for the right use of our flora and fauna. Macmillan & Co.: Melbourne - 50.

1925b. *Crocodilus johnsoni* Krefft. Memoirs of the Queensland Museum 8, 2: 95-102, Pls XXIII-XXIV [7th July 1925] - 52.

*1925c. A crocodilian fossil from Lansdowne Station. Memoirs of the Queensland Museum 8, 2: 103-105, Pls XXV-XXVI [7th July 1925] - 54a. *Pallimnarchus pollens*.

*1925d. Ophidian vertebrae from cave deposits at Marmor Quarry. Memoirs of the Queensland Museum 8, 2: 111-112 [7th July 1925] - 54.

*1925e. Fossil marsupials from Marmor. Memoirs of the Queensland Museum 8, 2: 129-130, Pl. XXVI [7th July 1925] - 53. *Bettongia* sp., birds and skink.

*1925f. Fossil remains of Man. The Queensland Naturalist 5, no. 3: 35-36. [resumé of lecture given, 20th July 1925].

1925g. Notes on mammals and reptiles that may be found in the Canungra district. 25-28. In: Queensland Corroboree. Australian Boy Scouts Association, Brisbane, Govt Printer, 76 pp.

*1926a. A new giant dinosaur from Durham Downs. Memoirs of the Queensland Museum 8, Pt 3: 183-194, Pls XXIX-XXXIII. *Rhoetosaurus brownei*, new genus and species. [31st Mar. 1926] - 56.

1926b. 1926. New records of Cetacea with a list of Queensland species. Memoirs of the Queensland Museum 8, 3, 266-278. Pl. XLIII [31st Mar. 1926] - 57.

*1926c. The uniqueness of Australian fossil marsupials. Report, Sectn D, Australasian Association for the Advancement of Science (1924), Adelaide, 17: 362-365 [August 1924] - 58.

1926d. The late Professor S.B.J. Skertchly. The Queensland Naturalist 5, No. 5: 70-72 + photo by A.H. Chisholm, address given 22nd Feb. 1926 [April] - 63. See Fig. 7.

*1927a. The giant dinosaur *Rhoetosaurus brownei*. Memoirs of the Queensland Museum 9, 1: 1-18, Pls I-V [28th April 1927] - 59.

*1927b. Australia's largest fossil - the *Rhoetosaurus* dinosaur. Australian Museum Magazine 3, No. 3: 97-102 [July-Sept.] - 60.

1927e. Open season for the Koala or Native Bear. The Queensland Naturalist 6, pt 3: 42-45 + Pl. 1 [October] - 62. Report of paper given.

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*1928c. Discovery of juvenile lung-fishes, with notes on *Epiceratodus*. Memoirs of the Queensland Museum 9, 2: 160-173 [16th June 1928] marked copy - 65.

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1929d. Introduction. 1p. In: Stevens, J.M. & Hart, J.H. With Pen and Pencil in Southern Queensland. Barker's Book Stores, Brisbane, 54 pp.

1930a. The Queensland Aborigines. In: Handbook for Queensland. A.A.A.S. Meeting, May-June, 9-15 - 68.

1930b. The vertebrate fauna of Queensland. In: Handbook for Queensland. A.A.A.S. Meeting, May-June, 63-70 - 67.

*1930c. *Kronosaurus queenslandicus*, a gigantic Cretaceous pliosaur. Memoirs of the Queensland Museum 10, Pt 1: 1-7, Text-figs 1-5 [28th Aug.] - 69.

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*1932a. A new Cretaceous fish. Memoirs of the Queensland Museum 10, Pt 2: 89-97, Pls X-XI, Text-figs 1-3 [30th Mar. 1932] *Flindersichthys denmeadi*. - 71.

*1932b. Restoration of *Kronosaurus queenslandicus*. Memoirs of the Queensland Museum 10, 2: p. 98, Pl. XII. [30th Mar. 1932] painting by Wilfred Morden.- 72.

*1932c. Remarkable Sapphire Discovery. Interesting fossil bone from Anakie. Queensland Govt Mining Journal, 33, p. 253 [Sept.].

*1932d. Interesting fossil bone from Anakie. Queensland Govt Mining Journal, 33, p. 261-262 [Sept.] - 73.

*1933a. A new dinosaur from the Queensland Cretaceous. Memoirs of the Queensland Museum 10, Pt 3: 133-144, Pls XV-XVII, Text-figs 1-3 [March] - *Austrosaurus mckillopi* - 75.

*1934a. Restoration of *Euryzygoma dunense*. Memoirs of the Queensland Museum 10, Pt 4: 210-202, Pls XXX-XXXI [June] - 82.

*1935a. Palaeontological notes. Memoirs of the Queensland Museum 10, Pt 5: 236-239 [Oct.] - 83.

1937a. Herpetological notes. Memoirs of the Queensland Museum 11, Pt 2: 165-168, Pl. XIV [24th June] - 84.

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1939b. A bicephalous snake. Memoirs of the Queensland Museum XI, Pt 3, 213-233 + Pl. XXVII [17th March 1939] - 86.

1940a. Our prehistoric animals. Discoveries on the Downs. Darling Downs Centenary Souvenir, pp. 29, 31. Toowoomba. - 88.

1941a. Presidential address. *Homo sapiens*: turbulentus. Proceedings of the Royal Society of Queensland, LII, No. 1, 1-9. [Published March] - 87.

*1941b. A Queensland fossil amphibian. With notes by F.W. Whitehouse, Ph.D., D.Sc., on the age of the beds. Memoirs of the Queensland Museum 12, 1: 29-32 + Pl. V [13th June 1941] - 89.

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1942b. New Guinea fauna. In: General Blamey ed? Guinea Gold 1, no. 2, Nov. 25th 1942, war publication, War Office newspaper, Port Moresby, - 90.

*1943. Further notes on Australian ichthyosaurs. Memoirs of the Queensland Museum 12, Pt 2: 101-104, Pl. X [date] - 92.

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*1945b. Fossil vertebrates from Gore Quarries. Memoirs of the Queensland Museum 12, Pt 3: p. 164 [6th Aug.] - 94.

## EXHIBITS TO THE ROYAL SOCIETY OF QUEENSLAND

Longman held all levels of office in the Royal Society of Queensland including Honorary editor in 1926. The publication list preserved in the QM box has a note at the end indicating "LONGMAN, H. A. 1912. Proceedings of the Royal Society of Queensland, Abstracts, new records." However, there is no mention of Longman in the 1912 volume other than of his joining RSQ, presumably when he first came to live in Brisbane.

There are numerous offerings from Longman from 1914 onward, mostly in the form of an exhibition of topical items from the museum collections. Those of palaeontological interest, especially those recording a new record or taxon have been asterisked in the publication list. Most notable was his tentative recognition of the first dicynodont in Australia (Longman 1916a), which has been confirmed as a Cretaceous record (Thulborn & Turner 2003).

1914. Longman, H. A. Member RSQ 1912 - listed in Appendix D. Proceedings of the Royal Society of Queensland 25, p. v [May 25th 1914]

1914. Proceedings of the Royal Society of Queensland 26: 30 fossil marsupials, 35 Qld Cret ammonites.

1915f. A live snake, *Dipsadomorphus fuscus*, Gray, brown tree snake, captured at Toowong. Abstracts of Proceedings of the Royal Society of Queensland, 26, Nov. 30th 1914, p. xiv.

*1916d. A tentative Dicynodontia from north western Queensland. Abstracts of Proceedings of the Royal Society of Queensland, 27, pt II, p. ix, July 26th 1915.

* 1916e. 1) a fragment of left maxilla with 3 abraded molars of *Diprotodon* from Flinders R. nr Hughenden, donated by Mr R. Pool, the locality record being of considerable interest, 2) dermal ossifications and parietal region of *Trachysaurus rugosus;* 3) live *Typhlops wiedii,* 'blind snake' to show transparency. Abstracts of Proceedings of the Royal Society of Queensland, 27, pt II, p. viii, August 30th 1915.

1916f. HAL exhibits live *Physignathus lesueurii* from Montville and a giant cricket Abstracts of Proceedings of the Royal Society of Queensland, 27, pt II, p. iv. April 26th 1915.

1916g. HAL exhibits live *Phyllurus platurus*. Abstracts of Proceedings of the Royal Society of Queensland, 27, pt II, p. vi. May 31st 1915

1916h. HAL exhibits *Acrochordus javanicus* Hornst. from Leichhardt R. 7' in length, snake. Abstracts of Proceedings of the Royal Society of Queensland, 27, pt II, p. viii. June 28th 1915.

1916i. HAL exhibits live *Neprurus asper* Gthr., 'Ball-tailed gecko' from central Queensland. Abstracts of Proceedings of the Royal Society of Queensland, 28, p. x. May 1st 1916.

1916j. HAL exhibits skin of *Hydrus platurus*, sea snake. Abstracts of Proceedings of the Royal Society of Queensland, 28, p. xi-xii. May 1st 1916.

1916k. Skin of *Python amethystinus* Schneid., 21' long, from Cairns and a crab *Podophthalmus vigil* (Fabr.). Abstracts of Proceedings of the Royal Society of Queensland, 28, 26th June 1916, p. xiii.

1916l. Crania of Dingo, marsupial wolf; collection of plants from Currumbin Creek made by HAL exhibited by C.T. White. Abstracts of Proceedings of the Royal Society of Queensland, 28, 25th Sept. 1916, p. xv-xvi.

1916m. Fasciated growth of *Lepidium fasciculatum* Phellung from the Darling Downs.; live *Lialis buroni* Gray, which had swallowed two skinks in captivity; large Bandy-bandy snake *Furinia occipitalis* D & B. Abstracts of Proceedings of the Royal Society of Queensland 28, 27th Nov. 1916, p. xviii.

*1917c. Cranium of fossil wombat *Phascolomys latifrons-gillespiei* type from Clermont. Abstracts of Proceedings of the Royal Society of Queensland, 29, p. xii, 28th May 1917, - 15.

1917d. Orchid *Cryptostylis erecta* R. Brown, a terrestrial orchid new to Queensland, which he had collected from Noosa Heads. Proceedings of the Royal Society of Queensland, Abstracts, 29, p. xiv, 25th June 1917. - 17.

1917e. A white-crowned snale *Pseudelaps harriettae* (Krefft) from Brisbane. Proceedings of the Royal Society of Queensland, Abstract, 29, p. xv. 29th Oct 1917.

1917f. An aboriginal ax. Proceedings of the Royal Society of Queensland, Abstract, 29, 26th Nov 1917, p. xvi.

1918d. Centipede *Cormocephalus aurantiipes*, New., devouring its young. Proceedings of the Royal Society of Queensland, 30, abstract, 27th May 1918, p. ix.

1918e. *Neoceratodus forsteri* of 495 mm from Coomera River. Proceedings of the Royal Society of Queensland, 30, 30th Sept 1918, p. xi.

1919 - Longman President

1920d. Cranium of *Delphinus delphis*? Luggage Point, Moreton Bay. Abstracts of Proceedings of the Royal Society of Queensland 31, 26th May 1919, p. x. - 23.

1920c. *Nardoa boa*, constricting snake. Abstracts of Proceedings of the Royal Society of Queensland 31, p. xi, 30th June 1919.

1920f. *Diplodactylus hillii*, Longman, Mungana Chillagoe lizard. Abstracts of Proceedings of the Royal Society of Queensland 31, p. xiii, 25th Aug. 1919.

1920g. p. xv - photos of venomous snake teeth/fangs/number. Abstracts of Proceedings of the Royal Society of Queensland 31, 29th Oct. 1919.

1920h. Live *Gymnodactylous miliusii*, gecko Wallumbilla, and whip-like alcyonarian *Juncella gemmacea* from State trawler. Abstracts of Proceedings of the Royal Society of Queensland 31, 29th Nov 1919 p. xvi -

1921f. Report of Council for 1919. Proceedings of the Royal Society of Queensland, 32, v-vi. - 26. [4th March 1920]

1921g. *Pteropus poliocephalus* Temminck, flying fox, from Dulbydilla, beyond Mitchell - extension of range. Abstracts, Proc. Roy. Soc. Qld., 32, p. x. April 28th 1920. - 38.

1921h. Skins common opossum *Trichosurus vulpecula* and varieties. Proceedings of the Royal Society of Queensland, Abstracts, Proc. Roy. Soc. Qld., 32, p. xi. may 31, 1920.

1921i. Marsupial crania showing variations in the perforations of the cribriform plate. Proceedings of the Royal Society of Queensland, Abstract, Proc. Roy. Soc. Qld., 30th June 1920, 32, p. xii. - 28.

1921j. Phyllopod *Lepidurus viridis* Baird, from Tara, Darling Downs, *Aspus australiiensis* Sp. & Hall from F.L. Berney of Barcarolle. Proceedings of the Royal Society of Queensland, Abstracts, 27th Sept 1920, 32, p. xvi.

1922h. *Trachysaurus rugosus*, the shingle-back lizard born in Museum. Proceedings of the Royal Society of Queensland, Abstract, 33, p. x, 27th June 1921, - 43.

1922i. A malformed hoof of a horse from Beerburrum. Proceedings of the Royal Society of Queensland, Abstract, 33, 25th July 1921, p. xi.

*1922j. Mandibles of *Phascolonus gigas* and *Eurygygoma dunense*. Proceedings of the Royal Society of Queensland, Abstract, 33, 26th Sept 1921, p. xiii.

*1922k. Mandible of *Sarcophilus laniarius* from Mt Etna Guano Fertiliser Co. of Rockhampton. don. P.H. Ebbott. Proceedings of the Royal Society of Queensland, Abstract, 33, 31st Oct 1921, p. xiv.

1922l. Type of *Nyctimene tryoni*, tubular new nosed bat. Proceedings of the Royal Society of Queensland, Abstract, 33, 28th Nov 1921, p. xv.

1923d. *Diplodactylus taenicauda* De Vis, ribbon-tailed gecko. Proceedings of the Royal Society of Queensland, Abstract, 34, p. viii, 11th April 1922.

*1923e. Extremely large bandicoot and unknown reptilian mandible from Rewan. Proceedings of the Royal Society of Queensland, Abstract, 34, p. viii, 31st May 1922.

1923f. Obscure markings on sandstone from Adavale. Proceedings of the Royal Society of Queensland, Abstract, 34, p. xi, 26th June 1922.

1923g. Albino wallaby *Macropus dorsalis*, and large cuttle bone. Proceedings of the Royal Society of Queensland, Abstract, 34, p. xiv, 26th Sept 1922.

*1924e. Australian marsupials lecture with discussion of derivation of fossil fauna from the north. Proceedings of the Royal Society of Queensland, Abstract, 35, 27th June, 1923. p. xii. - 43.

1924f. Skins of pouch embryos of the grey kangaroo. Proceedings of the Royal Society of Queensland, Abstract, 35, 24th July 1923, July. - 44.

1924g. Sub-fossil aboriginal mandible from Indooroopilly. Young flying fox. Proceedings of the Royal Society of Queensland, Abstract, 35, 24th Nov, 1923, p. xvii.

*1925g. A marsupial of the *Petaurus breviceps* type and maxilla of *Euryzygoma dunense*. Proceedings of the Royal Society of Queensland, Abstract, Abstract Proc. Roy. Soc. Qld., 36, 28th April 1924, p. ix - 49.2.

*1925h. A chiton, a periscope-eyed crab, & the type species *Kronosaurus queenslandicus*. Proceedings of the Royal Society of Queensland, Abstract, 36, 26th May, p. xi.

1925i. An aged male aboriginal cranium unearthed at Lonsdale Farm nr Warwick. A specimen of *Acrobates pygmaeus*, a phalanger from Rollingstone, tame wallaby photo. Proceedings of the Royal Society of Queensland, Abstract, 36, 25th Aug. 1924, p. xiv - 49.3.

*1925j. A spirit specimen of a starling, *Sturnus vulgaris* from Adavale; and a cast of a fossil egg of a Horned Dinosaur. Proceedings of the Royal Society of Queensland, Abstract, 36, 29th Sept. 1924, p. xv - 49.1.

1925k. Proximal end of tibio-tarsus of an emu, closely comparable with that of *Dromaius novae-hollandiae*. Portion of left maxilla of *Sarcophilus laniarius*; and four vertebrae of a snake. Proceedings of the Royal Society of Queensland, Abstract, 36, 27th Oct. 1924., p. xvii - 49.4.

1926e. Proceedings of the Royal Society of Queensland, Abstract, A specimen of *Liasis childreni*; and a specimen of *Crocodilus johnsoni* from the Wickham River, N.T. Abstract Proc. Roy. Soc. Qld., 37, 27th April 1925, p. ix - 51.

1926f. 23 eggs in a brownsnake, a cast of *Hesperopithecus haroldcooki*. Proceedings of the Royal Society of Queensland, Abstract, 37, p. xi, 29th June 1925 1925

1926g. Fragments of Fossil Molars of *Palorchestes*?; and a 'Liangle' of aboriginal wooden battle axe. Proceedings of the Royal Society of Queensland, Abstract, , XXXVII, 27th July, 1925, p. xii - 55.1.

1926h. Exhibit of specimens of the 'Magnificent Spider' Proceedings of the Royal Society of Queensland, Abstract, 37, 31st Aug. 1925, p. xiii - 55.2.

1926i. Huxley: personal characteristics. Proceedings of the Royal Society of Queensland, Abstract, 37, p. xv, 26th Oct. 1925, a talk, title only published.

*1926j. New geological specimens from Galaly Gorge, near Hughenden, *Diprotodon* from the Flinders R. near Maxwellton. Proceedings of the Royal Society of Queensland, Abstracts, 37, 30th Nov 1925, p. xv.

1927d. An exceptionally large human mandible from Rockhampton, Donor, H.A. Craig. Proceedings of the Royal Society of Queensland, Abstracts, 38, 28th April, 1926, p. viii.

*1927e. Mandible of *Diprotodon minor* Huxley, from near Murgon. Proceedings of the Royal Society of Queensland, 38, 26th July 1926, p. xi.

1927f. Leathery turtle juvenile from the Solomon Islands. Proceedings of the Royal Society of Queensland, 38, 30th Aug. 1926, p. xiii.

1927g. Photographs of aboriginal rock carvings near Hugenden sent by Mr J.R. Trundle. Proceedings of the Royal Society of Queensland, 38, 25th Oct. 1926, p. xv.

1927h. Paratype of a new rodent *Rattus youngi*, from March Island from the collection of Mr James Edgar Young; embryo & pelvic girdles of *Pteropus poliocephalus*; small venomous snake *Furina annulata* partly swallowed by *Denisonia*. Proceedings of the Royal Society of Queensland, 38, 29th Nov. 1926, p. xvi.

1928d. Aboriginal remains. Proceedings of the Royal Society of Queensland, 39, 2nd May 1927, p. vii.

1928e. Talk on The Life of Newton. Proceedings of the Royal Society of Queensland, 39, 27th June 1927, p. ix.

*1928f. Giants of the past. Proceedings of the Royal Society of Queensland, 39, 29th August 1927, p. xi.

*1928g. Fat-tailed pouched mouse, *Sminthopsis crassicaudata*; *Macropus giganteus* skull, N. Queensland; maxilla of *Diprotodon australis* from N. Queensland. Proceedings of the Royal Society of Queensland, 39, 28th Nov. 1927, p. xiv.

*1929c. Neanderthal skull from Galilee. Proceedings of the Royal Society of Queensland, Abstract, 40, 30th April 1928, p. viii.

*1929d. Fossil dicotyledonous leaves from Coolabumi; *Macropus anak* from Beaudesert. Proceedings of the Royal Society of Queensland, Abstract, 40, 25th June 1928, p. vx.

1929c. Juvenile *Epiceratodus forsteri* from Enogerra. Proceedings of the Royal Society of Queensland, 39, 26th Nov. 1928, p. xv.

*1930e. Fossil from limestone from Magnetic island with barnacles; lower jaws of *Macropus anak* and *M. raechis* - contra De Vis. Proceedings of the Royal Society of Queensland, 41, 24th June 1929, p. x.

1932e. *Astrotia stokesi* and *Voluta bednalli* (Exhibits). Proceedings of the Royal Society of Queensland, 43, Abstract, 26th Sept. 1931, p. - 74.

1933b. Results of collection in the Glass House Mountains area. Proceedings of the Royal Society of Queensland, Abstract, 44, 24th April 1932, p. - 75 or 6.

1933c. Microcephalicranium of an aboriginal (Exhibit). Proceedings of the Royal Society of Queensland, Abstract, 44, 29th May 1932, p. - 76.

*1934b. Photographs of a restored model of an extinct giant marsupial quadruped, *Euryzygoma*, from Queensland. Proceedings of the Zoological Society of London, Abstract, 31st Oct., p.? - 81. NOT FOUND.

*1935b. A specimen of *Diprotodon* collected at Ranges Bridge, Condamine River, near Dalby, coll. Mr T. Jack; (b) A fossil claw, or ungula phalanx of an unknown animal from Boat Mountain, Murgon (Pleistocene), coll. Mr R.A. Cooper; gorilla jaw. Proceedings of the Royal Society of Queensland, 46, Abstract, 28th May 1934, p. x [May] - 79.

*1935c. Photographs of fossil footprints taken in the Lancfield Colliery by L. C. Ball. Proceedings of the Royal Society of Queensland, 46, Abstract, 25th June 1934, p. xi - 80.

1935d. Moreton Bay vertebrates from Queensland Museum collections. Proceedings of the Royal Society of Queensland, 46, Abstract, 24th Sept. 1934, p. xviii .

1935c. Skin and skull of a polecat (*Mustela putorius*) and need for prohibition. Proceedings of the Royal Society of Queensland, 46, Abstract, 29th Oct. 1934, p. xix-xx.

*1936. Fossilized vertebrae large teleost fish from tunnel under Davies Park, S. Brisbane, cf. a groper, coll. Mr John Struby; fossil femur of rodent from King's Creek, Darling Downs, coll. Mr R. Frost. Proceedings of the Royal Society of Queensland, 47, Abstract, 23rd April 1935, p. vii.

*1937b. Fossilized *Trionyx australiensis*, freshwater turtle, fragment crocodile jaw, Pleistocene, Boat Mountain, Murgon, coll. Mr R.A. Cooper; nest arboreal trapdoor spider from Thursday Island; large living *Phyllurus platurus* from Glenapp. Proceedings of the Royal Society of Queensland, 48, Abstract, 31st Aug. 1936, p. xiv-xv.

1939 - Longman President

1939c. Contribution to discussion on homotaxy and the Australian Flora and Fauna and relationship of Australian aboriginals to Neanderthals. Proceedings of the Royal Society of Queensland, 50, Abstract, 31st October 1938, p. xviii-xix.

1939d. Two long-tailed opossums from Mt Spurgeon, via Mt Carbide, Cape York Peninsula. Proceedings of the Royal Society of Queensland, 50, Abstract, 6th June 1938, p. xi.

*1940b. An abraded bone from the Walloon Sandstone, near Lowood, coll. Mr John Wadley - a "tentative upper jaw with alveoli of a very large amphibian; long-tailed dormouse *Eudromica macrura* from near Innisfail. Proceedings of the Royal Society of Queensland, Abstract, 51, 26th June 1939, p. x.

1941c. An unusually large mottled stargazer *Ichthyscopus lebeck* and remarks on the Uranoscopidae. Proceedings of the Royal Society of Queensland, 52, 24th June 1940, p. xi.

## AUSTRALIAN ENCYCLOPAEDIA

1925-1927. Articles on Amphibia, Chelonians, Lizards, Snakes. [NOT SEEN]

## MEDIA

### POPULAR LECTURES

*LONGMAN, H. A. 1916. A Story of Fossil Bones. Exhibition Hall, 26th April 1916 - many lantern slides. See Brisbane Mail 27/4/1916, 29/4/1916 and Courier Mail 27/4/1916.

*LONGMAN, H. A. 1916. The Origin of "Man". Notable Lecture - June 1xth 1916 - lecture given at the Queensland Museum the preceding Sunday.

Lyceum Club (Fallon 2002).

Brisbane Women's Club - "Wonders of the Past" (Fallon 2002).

National Council of Women - "Some modern day problems" (Fallon 2002).

### RADIO

LONGMAN, H. A. 1933. The Natural History of Queensland. Series broadcast through 4QG. Introduction in The School Paper, July. - 77.

LONGMAN, H. A. 1934. Our Aborigines 1-4. Lecture series broadcast through 4QG. April. Published in The Queenslander - see below. - 78.

## ARTICLES IN THE QUEENSLANDER (WEEKLY)

LONGMAN, H. A. 1912. The Queensland Museum. An historical sketch. The Queenslander, 25 May 1912, p. 17.

LONGMAN, H. A. 1934. Whole World is interested in Australia's Stone Age. National Obligation to Aid Aborigines. Museum Director Explains. The Queenslander, 19-4-1934, 1p. - 78.1.

LONGMAN, H. A. 1934. The Aboriginal was an artist in Wood and Stone. Mr Longman talks about Native weapons and Implements. The Queenslander, 26-4-1934, 1p. - 78.2.

LONGMAN, H. A. 1934. Grubs that resembled scrambled eggs. Roasted, They were Native Delicacy, says Mr Longman. The Queenslander, 3-5-1934, 1p. - 78.3.

LONGMAN, H. A. 1934. Is Australian Aboriginal Doomed? Civilisation Destroying primitive Social Life. The Queenslander, 10-5-1934, 1p. - 78.1.

## NEWSPAPERS (DAILY)

### 'The Daily Standard'

LONGMAN, H. A. 1916. The Origin of 'Man'. The Daily Standard, June 17th, p. x.

The Origin of 'Man'. Notable Lecture - June 17th 1916 The full text of a lecture given at the Queensland Museum the preceding Sunday 'under the auspices of the Australian Socialist Party'. Motif - 'Truth is a thing to be shouted from the housetops' - W.K. Clifford, in essay Right or Wrong.

### 'The Daily Telegraph'

"Wonders of the Past" - 31st May 1929 - Mr H. A. Longman talk to Brisbane Women's Club including female collectors, Mrs Lumley Hill and Mrs T. Pattison (Fallon 2002).

### 'The Brisbane Daily Mail'

Chance for 'Australian Millionaires' 27th April 1916 - Mr H. A. Longman on 'Fossil Bones'.

Romance of Fossils. Instructive Lecture. 29th April 1916 - Mr H. A. Longman on the Story of Fossil Bones on Friday night at museum.

"Diversified Meeting". Royal Society of Queensland 30th April 1916 - on 29th April Mr H. A. Longman exhibited a very large snake's skin.

"Diversified exhibits" Royal Society 27th June 1916 - Mr H. A. Longman exhibited a curious crab and skin of python.

"Museum and education" 27th June 1916 - Mr H. A. Longman lectured on physiology to pupils of South Brisbane school with specimens from the museum [now State High, Maryvale St] on 26th June.

Women's rightful place - H. A. Longman, 11th May 1918 (Fallon 2002).

### 'The Sunday Mail'

Sunday Mail Magazine, Brisbane 20th Jan. 1935. "Come I to speak at Darwin's Funeral". - by Roy Connolly. Debate between Longman 'the scientist' and Archbishop Downey on Darwinism.

### 'Patriot'

Pre-Adamite conditions - 1929 (Fallon 2002).

### 'The Courier Mail'

A Story of Fossil Bones - 27/4/1916. - Mr H. A. Longman on the Story of Fossil Bones on Friday 26/4/1916 at museum.

### *'The Courier Mail'~ "Nature's Ways" columns.*

Heber A Longman's articles were always on a Saturday and on p. 2; only rarely did he miss a week. In mid 1948 there was temporary one-off change of title to "Back To Nature". The range of subjects covered in over 300 articles present a snapshot of Brisbane over 50 years ago as Longman often uses his own garden as the backdrop; bird lists and frog sightings are particularly poignant in retrospect. He recycles his greatest days from the Queensland Museum as in his article on *Kronosaurus* (When our State was beneath the waves: 20th March 1948) when he gives new details of the discoveries.

Harmless – And Also Handsome (For a Snake). 6th Dec. 1947.

Squatted for Four Years – No Eviction. 13th Dec. 1947.

Big Money Once in Gold Beetles. 20th Dec. 1947.

Treasure Trove on the Beaches. 27th Dec. 1947.

Imported Birds That Should Not be There. 3rd Jan. 1948.

"Forty Hour Week is No Use to Our Wasps". 10th Jan. 1948.

The 'Oom-Oom' Bird is a Friendly Creature. 17th Jan. 1948.

Collin's Big Claw Was Dredged From Mud Is. 24th Jan. 1948.

*Our Lungfish Don't Walk On The Land. 31st Jan. 1948.

Dionne doctor wanted to study baby whales. 7th Feb. 1948.

Blame the bandicoot for holes in the lawn. 14th Feb. 1948.

*Bizarre marsupial with colossal cheek. 21st Feb. 1948 - Pleistocene *Euryzygoma*.

A Rabelaisian touch about Kookaburra. 28th February 1948.

Butterflies aren't born that way. 6th March, 1948

Eels is Queer Fish. March 13th 1948

*When our State was beneath the Waves. March 20th 1948

Size doesn't count. March 27th 1948

Sea Snake Saga. 3rd April 1948

Plenty of Brain. April 10th 1948

Pincer movement. April 24th 1948

Queen of Spinners. 1st May 1948

Bedtime stories. May 8th 1948

Dolphins Please! May 15th 1948

More "Noes" than Yes. May 22nd 1948

Sea garden of the Pacific. May 29th 1948

Dividends for bird watches. 5th June 1948 – [Temporary change to new name "Back To Nature"]

No doubt who is the Boss in the Web.12th June 1948

Who's Who in the Zoo. 19th June 1948

Some people really have thick skulls. 26th June 1948

Birds of Paradise. 3rd July 1948
Good shooting. 10th July 1948
Lady of the lagoon. 17th July 1948
The barking lizard. 24th July 1948
No place like home. 31st July 1948
It's a "Shocker". 7th August 1948
Toilet tactics. 14th August 1948
Moonlight snakes. 21st August 1948
Catch him by the toe. 28th August 1948
Red-backed Spiders. 4th September 1948
Spring Songs in the Air. 11th September 1948
*Cosy homes of the past. 18th September 1948
Feather-tailed gliders. 25th September 1948
The death adder. 2nd October 1948
True – False? Crow or Raven. 9th October 1948
This Maiden was not Coy. 16th October 1948
No Eight Hour Day Here. 23rd October 1948
Fat Boy of the Ocean. 30th October 1948
Some Fishermen can, some can't catch their bait. 6th November 1948
Native birds prefer native trees for nesting. 20th November 1948 [two book reviews, NOT Nature's Ways]
Birds don't raise large families during droughts. 27th November 1948
A snake is not rude when it sticks out its tongue. 4th December 1948
Sandfly's bite is better known than it's life history. 11th December 1948
Eggs by the Million. 18th December 1948
About eagles, waterfalls and frilled lizards. 1st January 1949
What are the wild swamp pheasants saying? 8th January 1949
Electric light bowls can hold a lot of surprises. 15th January 1949
Consider the birds who build where they please. 22nd January 1949
Snakes an interesting way to kill them. 29th January 1949
A kingfisher's first flight. 12th February 1949
Cook's kangaroo caused argument. 19th February 1949
Dragon flylikened to miniature plane. 26th February 1949
Australian bird names had welcome change. 5th March 1949
Stick Insects. 12th March 1949
Turkey dinner- and extinct bustard. 19th March 1949- F.L. Berney
*Pre-historic turtle bears a Queenslander's name. 26th March 1949- F.L. Berney, Cretaceous turtle
Chameleons really know how to stick out their tongues. 2nd April 1949
Where do the bats go in the winter time? 9th April 1949
Net-throwing spiders. 16th April 1949
A Roman nose need not mean Roman ancestry. 23rd April 1949
… the bulge was Freddie (the frog). 30th April 1949
*Opinions differ on "fossil" horses. 7th May 1949
Dingoes probably came to Australia with aborigines. 14th May 1949
Bee-eaters should not be black-listed. 21st May 1949
The wandering butterfly. 28th May 1949
Rabbit bandicoots have keen sense of smell. 4th June 1949
Even a quiz-kid might be stumped by this question. 11th June 1949
It's just a matter of getting used to it. 18th June 1949
Baby kangaroos are not born in their "cuddle seats". 2nd July 1949
That low gurgling noise in the jungle is not a bunyip. 9th July 1949
It's still a mystery why cuckoos, don't raise their own young. 16th July 1949
*Footprints in the coal date back 140,000,000 years. 23rd July 1949
This "Bird Madness" is not a pathological condition. 30th July 1949
We've learnt a lot from frogs. 6th August 1949
*Even the Giant Dinosaurs had to put up with Floods. 13th August 1949 - Cretaceous
Bird's nests maybe pecked at – but not robbed. 20th August 1949
Fish stories are not the only ones to be treated with caution. 27th August 1949
Spring songs are in the air. 3rd September 1949
Boring beetles are playing havoc with our trees. 10th September 1949
Possums are becoming quite suburbanite these days. 17th September 1949
Our coo-ee birds are back again. 24th September 1949
There's no objection to a snake being a cannibal. 1st October 1949
Our common dove was imported. 8th October 1949
Wombats have "honest faces" and make good house pets. 15th October 1949
No end to snake yarns! 22nd October 1949
Thrasher sharks or killer whales. 29th October 1949
Why shoot our eagles? 5th November 1949
Nursemaid to a kingfisher trio. 12th November 1949
Giraffes were just born that way. 19th November 1949
Only enterprising hens need apply. 26th November 1949
Flying snakes quite harmless. 3rd December 1949
Plainly not a tooth-ache victim! 10th December 1949
You don't have to be an expert. 17th December 1949
We have Mermaids in Moreton Bay. 24th December 1949
Cleaning the Slate for New Year. 31st December 1949
Even dictionary spells it wrongly! 7th January 1950
Don't be terrified of " tarantulas". 14th January 1950
Wasps have their own kindergartens. 21st January 1950
*How much can be blamed on our ancestors? 28th January 1950
Some deep-sea monsters carry searchlights. 4th February 1950
There's a silk factory in every garden. 11th February 1950
In a garden nursery. 18th February 1950
You can tell a snake by its scales. 25th February 1950
Russian wrangles on heredity. 4th March 1950
Don't look for beauty in the Bufo. 11th March 1950
Surprises lurk in suburban gardens. 18th March 1950

*Fascinating study in human fossils. 25th March 1950
Queensland has her own Izaak Walton. 1st April 1950
Nature hides most of her casualties. 8th April 1950
We've a lot to learn about New Guinea. 15th April 1950
Eels (and elvers) are very funny fish. 22nd April 1950
Case of the disappearing butterfly. 29th April 1950
The early riser sees the birds. 6th May 1950
Man can't beat the "loopers". 13th May 1950
A rat with a blood-thirsty reputation. 20th May 1950
Carries his own trowel and fork . 27th May 1950
*Many, many millions of years ago. 3rd June 1950
Think twice before you kill a spider. 10th June 1950
The spider with a fishing rod. 17th June 1950
It would be a dull world without birds. 24th June 1950
Fisherman didn't call them "stargazers". 1st July 1950
Was it a Morganatic marriage? 8th July 1950 (Bower birds).
A butterfly in July is compensation. 15th July 1950
*Washaways may expose fossils. 22nd July 1950
Goanna's are not very lovable. 29th July 1950
Back to nature for the show. 5th August 1950
Deaf – but snakes can't stand bird chatter. 12th August 1950
Fishing spiders. 19th August 1950
Mistletoe birds worth watching. 26th August 1950
The "Greeks" had a word for "Stone the Crows". 2nd September 1950
Baby spiders cross oceans on threads of Gossamar. 9th September 1950
Rats and mice by the million. 16th September 1950
Some tricks in handling killer snakes. 23rd September 1950
"Ants in the pants" is not unknown to birds. 30th September 1950
Birds, obviously, have a sense of humour. 7th October 1950
Beware the Ant-Lion when it's magnified. 14th October 1950
Just what are these pygmy people? 21st October 1950
Cicadas may be rowdy because their wives are voiceless. 28th October 1950
The males usually "live out". 4th November 1950
The big toe gave us our advantage. 11th November 1950
Nature's victims of nature's wrath. 18th November 1950
Birds get tangled up in seasons, too! 25th November 1950
A bird's eye view of birds eyes. 2nd December 1950
Snake bounty might rid State of the killers. 9'th December 1950
The ideal time to watch the gulls. 16th December 1950
Mother – love in the Barnyard. 23rd December 1950
… of bats, snakes and caterpillars. 30th December 1950
We need more bird lovers. 6th January 1951
Butterflies are not teetotalers. 13th January 1951
Meet a handsome suburban visitor. 20th January 1951
Gum trees have community life of their own. 27th January 1951
Bower-birds make their own paint brushes for decorating. 3rd February 1951
They couldn't "swallow" story of the Bombay duck. 10th February 1951
Lizard which masquerades as a snake. 17th February 1951
"Snowstorms" of butterflies are a riddle of nature. 24th February 1951
Bluff is main weapon of the Frilled Lizard. 3rd March 1951
Should Sea Shells stay on the Sea Shore? 10th March 1951
Sometimes the hunter becomes the hunted. 17th March 1951
Birds will soon be off to the Arctic (with photo). 24th March 1951
Foes among the Fauna are Getting Busy Now. 31st March 1951
Ladybirds have most unladylike appetites. 7th April 1951
Birds Live at High Temperatures. 14th April 1951
Even spider appreciate a silver lining. 21st April 1951
*A lot can be learned from a single tooth. 28th April 1951
Sparrows are not taking kindly to the Machine Age. 5th May 1951
*Backyard find was a surprise. 12th May 1951
Science too, marches on. 19th May 1951
[NB. The following article ONLY called "Modern Science"]
The Greeks had a word for it. 26th May 1951
Barnacles travelled overseas – underseas. 2nd June 1951
On a minor twig of the tree of life. 9th June 1951
*A remarkable bird is the Archaeopteryx. 16th June 1951 - Jurassic
The queer mouse with a fluffy tail. 23rd June 1951
House animals have bigger brains. 30th June 1951
Science owes much to bird watchers. 7th July 1951
The platypus is shy but eats well. 14th July 1951
What has happened to our young bird lovers. 21st July 1951
Short peeps behind a famous "green curtain". 28th July 1951
We should take pigs more seriously. 4th Aug. 1951
A bold, bad bird but we love him! 11th Aug. 1951
If only whales could talk! 18th Aug. 1951
Some male butterflies use scent. 25th Aug. 1951
The lay-spider with a red-headed husband. 1st Sept. 1951
Gardens are a boon to honeyeaters. 8th Sept. 1951
*Just a mere 100 million years old! 15th Sept. 1951
How frogs survive droughts. 22nd Sept. 1951
Queensland's "mystery" bird. 29th Sept. 1951
*Mighty droughts wiped out our Diprotodonts. 6th Oct. 1951
Trust cuckoos to know where the nests are. 13th Oct. 1951
The marvels of jungle life. 20th Oct. 1951
Honey-eaters are tough on flowers. 27th Oct. 1951
Mosquitoes that "sit on trees and bark". 3rd Nov. 1951
Hawk Moths have 'noses' 10 inches long. 10th Nov. 1951
Word hybrid has changed in meaning. 17th Nov. 1951
Those odd-looking things on gum-tree leaves. 24th Nov. 1951
No antidote for a death adders bite. 1st Dec. 1951

Why do flowering trees look so bright now? 8th Dec. 1951
Our busiest waterside workers! 15th Dec. 1951
Our budgerigars are a marvel of breeding. 22nd Dec. 1951
Bush lore not always reliable. 29th Dec. 1951
Helicopters could learn a lot from hover flies. 5th Jan. 1952
It is not only the good who die young. 12th Jan. 1952
A "Treasure Island" on the Barrier Reef. 19th Jan. 1952
Sea monsters are often harmless. 26th Jan. 1952
How natives learn out of tracking. 2nd Feb. 1952
Our alligators are crocodiles. 9th Feb. 1952
Birds have to work much harder during droughts. 16th Feb. 1952
Our "pixie-cap" spiders build well. 23rd Feb. 1952
The rainbows that gleam in the moonlight. 1st March 1952
"Bird-watching" is rapidly growing hobby these days. 8th March 1952
Kangaroos didn't need baby sitters. 15th March 1952
Just think what golfers are missing. 22nd March 1952
Rare beauty and colour among snakes. 29th March 1952
This diving beetle is stream-lined. 5th April 1952
*The "Peking Man" is lost again. 12th April 1952
Sawfish are of no use to carpenters, but -. 19th April 1952
Look what science did for dogs. 26th April 1952
Which is your favourite bird? 3rd May 1952
Public keen to protect our fauna. 10th May 1952
Beware when tame cats go "bush". 17th May 1952
Ibis flocks on visit to Brisbane. 24th May 1952
This mouse can be troubadour. 31st May 1952
Authentic story of the Taipan. 7th June 1952
*Fossils tell history of mankind. 14th June 1952
Beauty is not judged by size in a garden. 21st June 1952
Visitors smile at our winter. 28th June 1952
A special patience is needed by bird lovers. 5th July 1952
One bubble that can't be pricked. 12th July 1952
Big carpet snakes can really hug. 19th July 1952
Sleepyheads don't welcome the kookaburra's chorus. 26th July 1952
Does our platypus hibernate? 2nd Aug. 1952
How Birdsville was named. 9th Aug. 1952
Birds have an eye to beauty. 16th Aug. 1952
The tales of sails. 23rd Aug. 1952
Birds are lucky – They can peek at a mirror. 30th Aug. 1952
Collecting eggs in not always bad. 6th Sept. 1952
The Painted Lady is found in most parts of the world. 13th Sept. 1952
Which runs faster – snake or man? 20th Sept. 1952
They pay no rates but they have their rights -
Brisbane has more birdlife than any other city. 27th Sept. 1952
"We can't leave everything to nature". 4th Oct. 1952
Birds have never flown faster. 11th Oct. 1952
The snakes' backbone was too much! 18th Oct. 1952
Some people want their fish right in the pan. 25th Oct. 1952
Indian doves sent here to produce Music. 1st Nov. 1952
*The Australian lion was a fierce feeder. 8th Nov. 1952, *Thylacoleo carnifex*.
When is a Pest a Pest? 15th Nov. 1952
Identifying the warblers in the garden. 22nd Nov. 1952
Father chose the site, but left the work to Mother. 29th Nov. 1952
A wasp had a good reason to swear. 6th Dec. 1952
"Where did butterflies come from?" 13th Dec. 1952
The snakes you could run into round Brisbane. 20th Dec. 1952
Kookaburras make early rising easy - Sometimes. 27th Dec. 1952
Our quaint burrowing marsupials. 3rd Jan. 1953
U.S accepts our koala's challenge. 10th Jan. 1953
Mysteries of our fresh-water streams. 17th Jan. 1953
You could get to like our prettiest snake. 24th Jan. 1953
Peewees do build an extra nest. 31st Jan. 1953
"There are some people who see a great deal". 7th Feb. 1953
*Queensland, too, has a living fossil!. 14th Feb. 1953
The spider keeps on spinning. 21st Feb. 1953
Sometimes nature seems to delight in destroying. 28th Feb. 1953
The Falstaff of bees is a carpenter. 7th March 1953
Even the elephant beetle must be itchy at times. 14th March 1953
The Sole wasn't born like that. 21st March 1953
Frilled lizard as a star performer. 28th March 1953
Even pests can awe with their beauty. 4th April 1953
Not all birds keep to strict timetable. 11th April 1953
*We shouldn't laugh loudly at stories of sea monsters. 18th April 1953 (the second coelacanth discovery)
The butcher birds have an unfortunate name. 25th April 1953
Kangaroo's fur-comb. 2nd May 1953
Net-throwing spiders. 9th May 1953
Mystery migration of birds. 16th May 1953
Who discovered the earth revolved? 23rd May 1953
The keen sight of a dragonfly. 30th May 1953
"Mystery" birds are intriguing. 6th June 1953
Does a bird sing by instinct? 13th June 1953
He hides by looking like a leaf. 20th June 1953
The bird's head is snakey. 27th June 1953
They never have indigestion. 4th July 1953
*The real "Jack the giant-killer". 11th July 1953 (diprotodonts)
Flying seems so easy-for birds. 18th July 1953
Jabiru is a stork-but it doesn't bring babies. 25th July 1953
Insects need a surname, too. 1st Aug. 1953
It's taken centuries to breed a racehorse. 8th Aug. 1953
Great power in the beaks of local birds. 15th Aug. 1953
Some birds fly at 240mph. 22nd Aug. 1953
Mystery of buried eggs at Sherwood. 29th Aug. 1953
Our sea birds have slum problems, too. 5th Sept. 1953
The "walk to work" bird follows out his orders. 12th Sept. 1953
*Governor's lucky accident. 19th Sept. 1953
Many weapons used in war against snakes. 26th Sept. 1953

The five fingers of Man hold "Nature's Riddles". 3rd Oct. 1953

Many local birds are dying out. 10th Oct. 1953

Birds lovers will miss the duke. 17th Oct. 1953

It is nectar - not honey, in the trees. 24th Oct. 1953

Exquisite beauty of our coral. 31st Oct. 1953

Beetles by the thousands. 7th Nov. 1953

Our birds of prey are ruthless. 14th Nov. 1953

Parasites are not all obnoxious. 21st Nov. 1953

Most of our snakes are "practically harmless". 28th Nov. 1953

Willie-wagtails raise a fierce fighting call. 5th Dec. 1953

Even centipedes are useful. 12th Dec. 1953

Wasp's KO Power. 19th Dec. 1953

Making pets of magpies. 26th Dec. 1953

Don't let long names scare you. 2nd Jan. 1954

"Quin" bird got twice its share. 9th Jan. 1954

A snake in the garden is no cause for panic. 16th Jan. 1954

How frogs survive a drought. 23rd Jan. 1954

Bird's that are always in a hurry. 30th Jan. 1954

A scientist really needs three lives. 6th Feb. 1954

Our pests wax fatter as we grow more food. 13th Feb. 1954

VALE-Heber Longman by M.F. Hickey. 20th February 1954

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# A NEW SPECIES OF *OXYURA* (AVES: ANATIDAE) FROM THE NEW ZEALAND HOLOCENE

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Worthy, T. H. 2005 05 31. A new species of Oxyura (Aves: Anatidae) from the New Zealand Holocene. *Memoirs of the Queensland Museum* **51**(1): 259-275. ISSN 0079-8835.

A new species of *Oxyura* is described from Holocene age lacustrine deposits at Lake Poukawa, Hawke's Bay, North Island, New Zealand. It is similar to the blue-billed duck *Oxyura australis* Gould from Australia, but is smaller and differs in qualitative features of the major skeletal elements. The previous report of the blue-billed duck *Oxyura australis* from Lake Poukawa is not substantiated by re-examination of all anatid material from the sites. The addition of this new species reveals that 10 species and 7 genera of an original late Holocene fauna of 20 species and 12 genera of waterfowl are now extinct. ❒ Anatidae, *Oxyura vantetsi* sp. nov., blue-billed duck, Lake Poukawa, Holocene, New Zealand

*T.H. Worthy, Palaeofaunal Surveys, 2A Willow Park Drive, Masterton, New Zealand; 30 July 2003.*

The Holocene avifauna of New Zealand is well known with hundreds of fossil sites distributed throughout the country (Worthy & Holdaway, 2002). Of the 245 species formerly breeding in the New Zealand biogeographic region, 66 are now globally extinct and others exist only as translocated intensively managed populations (Appendix 1, Worthy & Holdaway, 2002). The Anatidae are the most diverse family of land and freshwater birds in the New Zealand region with 18 species in 11 genera breeding in the New Zealand biogeographic region in the Holocene prior to human influence (Worthy & Holdaway, 2002). To this total can be added *Anas rhynchotis* (Gould, 1856), previously excluded as being a recent immigrant, but now known from the Holocene fauna of Lake Poukawa (Worthy, 2004).

A major limitation of the fossil faunas of New Zealand is that relatively few faunas are known from lacustrine deposits – most are from cave, dune, or swamp deposits. In the South Island, the only two lacustrine deposits are Pyramid Valley, which was a small shallow lake (Holdaway & Worthy, 1997; Worthy & Holdaway, 1996), and one on the edge of the large coastal lagoon of Lake Grassmere, in the dune deposits of Marfells Beach (Worthy, 1998). In the North Island, the only lacustrine fauna described is from the Holocene site of N141/XII on the shores of Lake Poukawa (Fig. 1) where some 3500m$^2$ was excavated by T.R. Price et al., over the period 1966-1975 (Horn, 1983).

The Poukawa deposits have revealed a huge and largely undescribed fauna. Price (1963, 1965) briefly described excavations in Sites I and II in and on the edges of the natural outflow channel from Lake Poukawa. At Site I, about 75m$^2$ of stream bed and 164m$^2$ of stream bank and about 115m$^2$ on the headland were excavated. At Site II, c. 200m$^2$ of stream bed and adjacent bank were excavated. Price interpreted the faunal deposits on the stream bank and in the stream bed to be primarily associated with the middens on the headland and that people had occupied the area prior to the Waimihia eruption.

This contentious claim was examined by McFadgen (1979) who studied the stratigraphy of site N141/XII which Price considered displayed a similar history of deposition to that seen in sites N141/I&II. McFadgen concluded that the Maori middens indicated occupation on parts of the site 150-300 years ago and that most of the fauna was of natural origin occurring mainly either between the Taupo Ignimbrite (1850 yrs BP) and the Waimihia Tephra (3300 yrs BP), or below the latter (tephra nomenclature and dates follow Froggatt & Lowe 1990). The tephras at Poukawa have been studied by Puller (1965) and Howorth et al., (1980). Environmental studies of the Lake Poukawa palaeovegetation by McGlone (1978) and Pocknall & Millener (1984) also found no evidence of humans in the Poukawa catchment below the Taupo Ignimbrite. Anderson (1989, Appendix B) published a list of nine radiocarbon dates on moa bones from Price's excavations that indicated the deposits extended to at least 7246 years old, supporting the chronology given in Horn (1983).

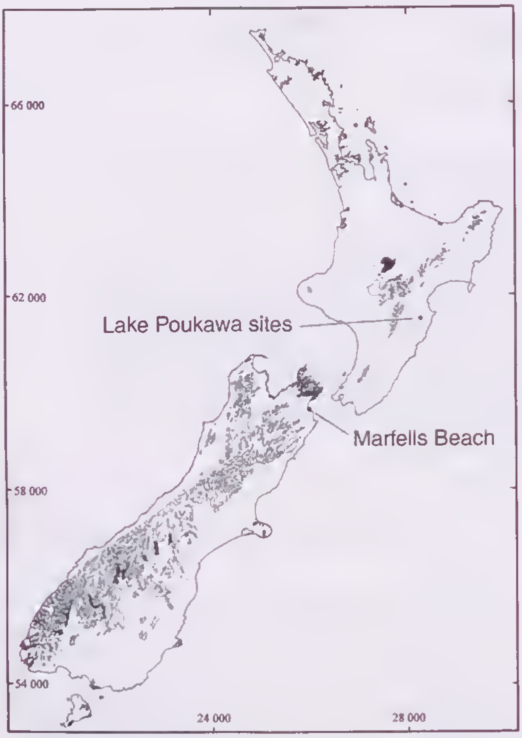

FIG. 1. Location of the sites Lake Poukawa and Wairau Bar, from which *Oxyura vantetsi* are known in New Zealand. The NZMS 260 map grid is indicated on the border (1 square is 400km). The 1000m contour lines are shown.

Despite Price's (1963, 1965) record of substantial faunas from Sites I and II, no analysis of these has yet been published and Horn's (1983) analysis is the only one available for Site N141/XII. However, notable records for some species are known; for example parts of two individual pelicans (*Pelecanus conspicillatus* Temminck, 1824) were found (Scarlett, 1966; Rich & van Tets, 1981; Gill & Tennyson, 2002), and the largest series of the New Zealand musk duck (*Biziura delautouri* Forbes, 1892) was found (Scarlett, 1969; Worthy, 2002).

Horn's (1983) analyses of 12,403 bones of birds other than moas from N141/XII indicated 23 waterbirds, 26 terrestrial species, and four seabirds, making it one of the most diverse faunas ever recorded in New Zealand. Among the taxa listed, the records of *Biziura* and *Mergus australis* Hombron & Jacquinot, 1841 were notable records of rare species. Horn also reported *Oxyura australis* Gould, 1836 (blue-billed duck) and *Dupetor flavicollis* (Latham, 1790) [now *Ixobrychus*] (black bittern) from New Zealand for the first time, though for the latter it was noted that Millener suggested it might belong to *Ixobrychus novaezelandiae* (Potts, 1871) (New Zealand little bittern), and it is to this latter taxon that they are now accepted as belonging (Turbott, 1990; Holdaway et al., 2001).

The possible presence of *Oxyura* in New Zealand was remarkable and little commented on by Horn (1983). While he reported the presence of *Oxyura australis* in both Layer 2 (16 bones) and Layer 3 (4 bones) of Site N141/XII, he unfortunately did not state what bones he referred to *Oxyura*, nor how or for what reason they were so identified. However, Horn acknowledged Dr G. F. van Tets for help in bone identification and it was he who made the identification (Peter Horn, pers. comm. e-mail to THW, 14 May 2002).

The Poukawa collection was subsequently gifted to the National Museum of New Zealand (now Museum of New Zealand Te Papa Tongarewa) by the Hastings Cultural Centre (per Mr Ray Dixon, Director), Mr David Buddo, and Mr Peter Horn in July 1982, and the bones identified and catalogued by Dr Philip R. Millener in 1982-3. He catalogued none as *Oxyura*, though bag labels suggest numbers 22168-178 were first labelled "*Oxyura/Aythya*" before being catalogued as *Aythya*, and so these may have been part of Horn's original *Oxyura* series. Subsequently, Millener (1991: 1329) stated "my examination suggests that the material is more correctly referable to *Aythya*", but he did not indicate which specimens he had considered. Thereafter, *Oxyura* has been dropped from the New Zealand fauna, e.g. Holdaway et al., (2001).

However, Millener had left unidentified several thousand anatid bones. In the course of their reassessment and that of all previously identified anatid bones of all taxa other than *Cygnus* from the entire Poukawa collection, I discovered several bones that did not belong to any known New Zealand species that I subsequently identified as *Oxyura*. In all, 33 humeri, 18 ulnae, 15 femora, 16 tibiotarsi, six tarsometatarsi, 15 coracoids, and two crania were identified as *Oxyura*, and a sternal fragment and a synsacrum as probably *Oxyura*, in the Poukawa collection derived from sites N141/I, N141/II and N141/XII catalogued in the Museum of New Zealand Te Papa Tongarewa. In addition, a single left humerus was located in the Canterbury

TABLE 1. Measurements (mm) of humeri of *Oxyura* species. Modern *Oxyura australis* CM Av31408 and AM O65518 specimens, and summary statistics for fossil *Oxyura vantetsi* sp. nov. from Poukawa (MNZ S 1081, 1115, 2107, 3277, 3370, 3527, 3777, 3778, 4104, 4553, 5915, 8942, 9745, 9746, 10077, 10731, 11218, 11316, 12165, 12425, 12638, 13685, 13686, 13687, 13730, 15650, 15952, 20191, 20228, 20605, 41025, 41259) and CM Av10777.

| | Length | PW, tub. dorsale to ventral edge crista bicipitalis | SW, minimum in cranial view | DW, cranial view | Diameter tub. dorsale to jn crista bicipitalis & shaft |
|---|---|---|---|---|---|
| Mean | 65.50 | 14.38 | 4.01 | 8.72 | 13.14 |
| Std Error | 0.482 | 0.133 | 0.035 | 0.058 | 0.150 |
| Std Deviation | 1.805 | 0.516 | 0.183 | 0.288 | 0.654 |
| Minimum | 61.6 | 13.5 | 3.6 | 7.8 | 12.0 |
| Maximum | 68.4 | 15.5 | 4.4 | 9.3 | 14.4 |
| Count | 14 | 15 | 27 | 25 | 19 |
| CMAv10777 | 64.5 | 14.4 | 3.9 | 8.9 | 13.7 |
| CM Av31408 | 73.8 | 15.8 | 4.1 | 10.2 | 14.6 |
| AM O65518 | 72.6 | 15.6 | 3.8 | 10.0 | 15.0 |

Museum Christchurch (CM Av10777) that has no locality data preserved with it. However, the presence of mica flakes in the dirt covering parts of the bone indicates a South Island origin for the specimen, and its preservation (colour of staining and presence of shallow rootlet grooves) is similar to material from middens preserved in the alluvial sediments of the Wairau Bar river mouth near Blenheim (pers. obs.).

Study of these *Oxyura* bones indicated consistent differences for all specimens of each element between them and recent specimens of *O. australis*. Here I describe this material as a new species and present extensive comparisons with the most similar sympatric species in New Zealand, *Aythya novaeseelandiae* (Gmelin, 1789), to facilitate its future identification.

## METHODS

The following abbreviations are used throughout the text.

INSTITUTIONS. AM, Australian Museum, Sydney, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand, Dominion Museum, and Colonial Museum), NZ.

SKELETAL ELEMENTS AND DESCRIPTIVE TERMS. The following abbreviations apply to single and plural usage of the elements. Cor, coracoids; Fem, femora; Hum, humeri; subad, subadult; Tmt, tarsometatarsi; Tib, tibiotarsi. When listing material, bilateral elements are identified as left (L) or right (R) sides. L or R prefixed by 'p', 's', or 'd' indicates 'proximal', 'shaft', or 'distal' part of the element respectively, e.g., pR fem means the proximal part of a right femur.

Anatomical nomenclature for specific bone landmarks follows Baumel & Witmer (1993). Some common terms are abbreviated as follows: artic. for articularis; cond. for condylus; proc. for processus; tub. for tuberculum.

MEASUREMENTS. Values were obtained with Tesa® dial callipers and rounded to 0.1mm. TL: greatest length, except for the coracoid, which was measured down the medial side, and femora, which were measured from the proximal end of the crista trochanteris to the cond. lateralis. PD: the proximal depth of femora was measured through the crista trochanteris. PW: proximal width in the lateromedial plane; femora were measured from the caput femoris through the mid-depth point of the neck to the lateral side. SW: shaft width at mid-length (unless otherwise stated, when it may be a minimum value e.g. SW min) in a lateromedial plane. SD: shaft width in a dorsoventral plane (depth) at the point SW was taken. DW: distal width. Tibiotarsi AL: length measured from the proximal articular surfaces to the cond. lateralis. Tibiotarsi PW: measured across the articular surface. Tarsometatarsus DW was measured with one side of the calliper along the lateral side.

COMPARATIVE MATERIAL. All material is from modern skeletons.

*Oxyura australis* Gould, 1836 Blue-billed duck: CM Av31408, Lake Cowal, New South Wales, Australia; AM O65518, Taronga Zoo, Australia. *Aythya novaeseelandiae* (Gmelin, 1789) New Zealand

TABLE 2. Measurements (mm) of ulnae of *Oxyura* species. *O. australis* CM and AM specimens, and summary statistics for *O. vantetsi* nsp (specimens MNZ S2398, 4512, 5316, 8653, 9727, 10917, 11118, 11634, 12107, 15697, 16618, 16732, 18178, 19128, 20617, 20180, 22179). Abbreviations as in Methods.

| | Length | PW, cranial view | Mid SW cranial view | Min DW cran view | Caudal diam cond. dorsalis ulnaris | Max DW |
|---|---|---|---|---|---|---|
| Mean | 55.55 | 6.15 | 3.45 | 3.89 | 5.67 | 6.52 |
| Std Error | 0.468 | 0.111 | 0.054 | 0.076 | 0.090 | 0.119 |
| Std Deviation | 1.750 | 0.384 | 0.207 | 0.304 | 0.347 | 0.476 |
| Minimum | 51.2 | 5.4 | 3.0 | 3.3 | 4.9 | 5.6 |
| Maximum | 58.3 | 6.6 | 3.9 | 4.4 | 6.1 | 7.0 |
| Count | 14 | 12 | 15 | 16 | 15 | 16 |
| CM Av31408 | 60.97 | 6.64 | 3.35 | 4.54 | 6.00 | 6.50 |
| AM O65518 | 60.92 | 6.42 | 3.25 | 4.70 | 6.04 | 6.72 |

scaup: CMAv22382; CMAv22413; MNZ 8726; MNZ 13685; MNZ 16588; MNZ 16589; MNZ 17001; MNZ 17002; MNZ 17003; MNZ 23144; MNZ 24245. *Aythya australis* (Eyton, 1838) Australian white-eyed duck: AM O65772, New South Wales, Australia. *Aythya affinis* (Eyton, 1838) lesser scaup: MNZ 24041, Michigan, USA.

Examples of all other anatids mentioned were examined in the collections of the MNZ.

SITE LOCALITIES. In the specimen lists, Sites N141/I, N141/II, and N141/XII are given as I, II, and XII, respectively. All were collected by T. R. Price *et al.*, at various dates in the 1960s and 1970s as catalogued. I use the nomenclature on the labels with respect excavation depth, e.g. '< Taupo', to avoid interpretation error. But I believe that '<' means 'below' and '>' means 'above' the respective tephra in the excavated section. Depth is indicated in inches or as Layer as recorded by the excavators. I note that a sample is unlikely to come from a specific depth, but rather a depth range in the excavation, and so it is probable each bag lot, from which all bones have been catalogued in a series, actually comes from a depth range that is to the stated value from the depth where the preceding spit ended in the same square. Establishment of the correctness or otherwise of this interpretation has not been attempted. This is significant for samples that have data such as '2" <Taupo', most likely could actually mean from '1" >Taupo to 2" < Taupo'.

Sites N141/I and N141/II are located near Lake Poukawa, Hawke's Bay, New Zealand at NZMS 260 series map reference V22/296525 or 39°46'24"S, 176°43'54"E. Site N141/XII is at the map reference V22/283523, or 39°46'34"S, 176°43'0"E.

## AGE OF HOLOTYPE

The holotype was found below the Taupo Ignimbrite and is therefore older than 1850 yrs BP. It is likely to be younger than the Waimihia tephra (3300 yrs BP, Froggatt & Lowe, 1990) as that tephra was not mentioned and all material was related to either Taupo or Waimihia tephras, the latter when samples were from below it. All Poukawa specimens are from the peat deposits or overlying sediments, and as peat deposition began about 6500 yrs BP (McGlone, 2002), all the material can be considered mid- to late-Holocene in age.

## SYSTEMATIC PALAEONTOLOGY

Class AVES
Order ANSERIFORMES (Wagler, 1831)
Family ANATIDAE Leach, 1820
Subfamily OXYURINAE (Phillips, 1926)

**Oxyura** Bonaparte, 1928

The holotypic humerus described below is referred to *Oxyura* as it shares with members of the genus the following combination of characters: 1, closed fossa pneumotricipitalis; 2, tub. dorsale is much elevated above the shaft; 3, the caudal surface of the caput humeri is deeply excavated between the tub. dorsale and the incisura capitis; 4, the incisura capitis is blocked by a low ridge at its dorsal end; 5, the crus dorsale fossae (proximal margin of the pneumotricipitalis) in caudal aspect is directed distally relative to the alignment of the shaft; 6, the shaft narrows markedly distally with minimum width near the distal end; 7, the tub. supracondylare ventrale is large, and extends proximad of the cond. dorsalis and its flat face is parallel to the shaft; 8, the attachment point of the M. pronator superficialis is not distinct, having merged with

TABLE 3. Measurements (mm) of coracoids of *Oxyura* species. *O. australis* CM and AM specimens, and summary statistics for *O. vantetsi* (specimens MNZ S3363, 3781, 8933, 9444, 11212, 11404, 12163, 13722, 13773, 16176, 16972, 18056, 22439). Abbreviations: fac. artic. hum., facies articularis humeralis; cotyla scap., cotyla scapularis; proc. acro., processus acrocoracoideus

| | Length (internal) | Length fac. artic. hum. | Width fac. artic. hum. | Length cotyla scap. to proc. acro. | Shaft width | Width fac. artic. sternalis |
|---|---|---|---|---|---|---|
| Mean | 36.72 | 7.15 | 4.56 | 10.70 | 3.82 | 16.31 |
| Std Error | 0.492 | 0.072 | 0.060 | 0.112 | 0.059 | 0.306 |
| Std Deviation | 1.476 | 0.269 | 0.223 | 0.355 | 0.219 | 0.809 |
| Minimum | 34.6 | 6.8 | 4.2 | 10.1 | 3.5 | 15.1 |
| Maximum | 38.3 | 7.9 | 4.9 | 11.2 | 4.1 | 17.2 |
| Count | 9 | 14 | 14 | 10 | 14 | 7 |
| CM Av31408 | 41.5 | 8.0 | 5.2 | 12.2 | 4.1 | 18.1 |
| AM O65518 | | 7.5 | 4.8 | 11.7 | 3.9 | 17.7 |

the margin of the tub. supracondylare ventrale; 9, the fossa m. brachialis is deep with a narrow ridge defining its ventral margin.

All species examined in *Anas*, *Hymenolaimus*, *Chenonetta*, *Mergus*, *Nettapus*, *Tadorna*, and *Dendrocygna* differ in many ways, not least of which is that all have an open fossa pneumotricipitalis. Both *Malacorhynchus membranaceus* (Latham, 1801) and *M. scarletti* Olson, 1977 have a closed fossa pneumotricipitalis but greatly differ in having a marked capital shaft ridge and the shaft has equal diameter along its whole length. *Biziura*, uniquely among the taxa examined here, shares with *Oxyura* the absence of a distinct attachment point of the M. pronator superficialis. However, both *Biziura lobata* (Shaw, 1796) and *B. delautouri* are larger and the humerus is much more elongate with a marked capital shaft ridge and the caput humeri is not deeply excavated between the tub. dorsale and the incisura capitis caudally. *Aythya* differs from *Oxyura* in several ways, notably that the tub. dorsale is not raised above the shaft, the attachment point of the M. pronator superficialis is distinct, and the caput humeri is not deeply excavated between the tub. dorsale and the incisura capitis caudally. Other differences are detailed below.

### **Oxyura vantetsi** sp. nov.
(Figs 2-9; Tables 1-7)

MATERIAL. HOLOTYPE MNZ S108; Site N141/XII, Square 4K, < [below] Taupo Ignimbrite, Lake Poukawa, Hawke's Bay, New Zealand. Map reference: NZMS 260 series, V22/283523, and 39°46'34"S, 176°43'0"E. Collected by T. R. Price et al., 20 November, 1967. A complete and unworn left adult humerus that is unmineralised, although it is stained brown, and has some adhering sediment in grooves. PARATYPES. Poukawa, Sites N141/I, N141/II, and N141/XII: MNZ S3370, R Hum; Site XII, Sq. 3J, Layer 2, 13 April, 1968; MNZ S3527, R Hum; Site XII, Sq. 21 (SE), Layer 5, 3 June, 1967; MNZ S5915, L Hum, Site XII, Sq. 10 (NE), 18" < Taupo, 6 Sept., 1969; MNZ S9745, L Hum; Site XII, Sq. 4B (NW-NE), base *Hyridella* midden, 4 June, 1966; MNZ S12165, L Hum; Site XII, Sq. 5G (NW), 7" < Taupo, 28 Oct., 1972; MNZ S13730, R Hum; Site XII, Sq. 10F (NE), on Taupo, 14 Oct., 1972; MNZ S20605, R Hum; Site II, Sq. 12C, Totara Point, 15 June, 1963;. REFERRED MATERIAL. *Humeri* MNZ S1115, L Hum, XII, Sq. 11 (SW), 8" <Taupo; S2107, dL Hum, XII, Sq. 5H (NE), 2-3" <Taupo; S3277, pR Hum, XII, Sq. 6J, Layer 3; S3777, L Hum, XII, Sq. 5I (NW), <Taupo; S3778, d+sR Hum, XII, Sq. 5 (NW), <Taupo; S4104, dR Hum, XII, Sq. 11 (NE), >Waimihia; S4553, dL Hum, XII, Sq. 4C, Layer 5; S8942, pR Hum, XII, Sq. 17 (NW-SW), 4" <Waimihia; S9746, pL Hum, XII, Sq. 4B (NW-NE), base *Hyridella* midden; S10077, L Hum, XII, Sq. 86, sub 3-4, 14" <Waimihia; S10731, R Hum, XII, Sq. 4H(NE), 3-4" <Taupo; S11218, R Hum, XII, Sq. 19C (SE), 1" >Taupo; S11316, dL Hum, XII, Sq. 20B (NW), 2" <Taupo; S12425, R Hum, XII, Sq. 25A (NW), in Waimihia; S12638, L Hum, XII, Sq. 25C (SW-SE), with Taupo; S13685, L Hum, XII, Sq. 10F (SW), 1" >Taupo; S13686, dL Hum, XII, Sq. 10F (SW), 1" >Taupo; S13687, dR Hum, XII, Sq. 10F (SW), 1" >Taupo; S15650, R Hum, XII, Sq. 21H (NE), 9" <Taupo; S15952, R Hum, XII, Sq. 22G (SE), 9" <Taupo; S20191, dL Hum, II, Sq. 24B, long grid base, Totara Point; S20228, pL Hum, II, Sq. 9A, long grid base, Totara Point; S41025, L Hum, Poukawa, site unknown; S41259, L Hum, II, #89, square and layer details lost; S41288, pR Hum, XII, Sq. 1H (NE); CMAv10777, L Hum, mica

FIG. 2. Humeri of *Oxyura* species compared with *Aythya novaeseelandiae*. A, left humerus MNZ S1081, Holotype *Oxyura vantetsi*; B, right humerus S13730 *O. vantetsi*; C, right humerus *O. australis* CM Av31408; D, right humerus *Aythya novaeseelandiae* MNZ 24245. Upper row – proximal end, caudal view; middle row – cranial view; lower row – ventral view of epicondylus ventralis on distal end.

FIG. 3. Ulnae of *Oxyura* species compared with *Aythya novaeseelandiae*. A, *O. vantetsi* left ulna S8653; B, *O. vantetsi* right ulna S5316; C, *O. australis* CM Av31408; D, *Aythya novaeseelandiae* MNZ 24245. Upper row, proximal end in cranial aspect, lower row in ventral aspect.

TABLE 4. Measurements (mm) of femora of *Oxyura* species. *O. australis* CM and AM specimens, and summary statistics for *O. vantetsi* (specimens MNZ S1082, 1091, 4515, 5976, 10436, 10437, 11739, 11741, 12855, 13635, 13809, 16696, 17025, 18288). Abbreviations as in Methods.

| | Length | PW | PD | SW min | SD | DW | Distal depth (of cond. lateralis) |
|---|---|---|---|---|---|---|---|
| Mean | 41.28 | 10.07 | 7.12 | 3.77 | 4.76 | 10.20 | 7.90 |
| Std Error | 0.214 | 0.049 | 0.085 | 0.029 | 0.031 | 0.076 | 0.127 |
| Std Deviation | 0.741 | 0.183 | 0.280 | 0.107 | 0.114 | 0.229 | 0.381 |
| Minimum | 40.1 | 9.7 | 6.6 | 3.6 | 4.5 | 9.7 | 7.4 |
| Maximum | 42.7 | 10.3 | 7.4 | 4.0 | 4.9 | 10.6 | 8.5 |
| Count | 12 | 14 | 11 | 14 | 14 | 9 | 9 |
| CM Av31408 | 45.8 | 11.5 | 7.7 | 3.9 | 4.7 | 10.9 | 9.0 |
| AM O65518 | 45.5 | 10.7 | 7.0 | 3.6 | 5.0 | 10.6 | 8.7 |

indicates South Island origin. It is similar to some Wairau Bar material.

*Ulnae*. MNZ S2284, dL ulna, XII, Sq. 9K (SW), <Taupo; S2398, R Ulna, XII, Sq. 3H, Layer 1B; S4512, R Ulna, XII, Sq. 8C (NE), Layer 5; S5316, R Ulna, XII, Sq. 7H (SW), 6-10" <Taupo; S8653, L Ulna, XII, Sq. 15A (NW); S9727, L Ulna, XII, Sq. 4A (NW-NE), 4" <Taupo; S10917, L Ulna, XII, Sq. 4H (SW), Layer 3, just >Taupo; S11118, L Ulna, XII, Sq. 19 (SE), 18" <surface; S11634, L Ulna, subad, XII, Sq. 2J (NE), 4" <Taupo; S12107, dR Ulna, XII, Sq. 5B (SE), <Taupo; S15697, L Ulna, XII, Sq. 21H (NW), 2" <Taupo; S16618, dR Ulna, XII, Sq. 24F (SE), 2" <Taupo; S16732, L Ulna, XII, Sq. 24G (SW), 3" <Taupo; S18178, R Ulna, II, Sq. 11B, long grid base; S19128, R Ulna, II, Sq. 4A, Totara Point; subad; S20180, L Ulna, II, Sq. 21C, long grid base; S20617, R Ulna, II, Sq. 12G, Totara Point; S22179, R Ulna, XII, Sq. 1H, >Taupo.

*Femora*. MNZ S1082, R Fem, XII, Sq. 4K, <Taupo; S1091, R Fem, XII, Sq. 5K (SE); S4515, L Fem, XII, Sq. 8C (NE), Layer 5; S5976, L Fem, XII, Sq. 10 (NW), 4" <Waimihia; S10436, L Fem, XII, Sq. 811 sub 3, 3" <Waimihia; S10437, R Fem, XII, Sq. 811 sub 3, 3" <Waimihia; S11739, L Fem, XII, Sq. 2J (SE), 4" <Taupo; S11741, R Fem, XII, Sq. 2J (SE), 4" <Taupo; S12855, L Fem, XII, Sq. 26C (NE), in Taupo; S13635, L Fem, XII, Sq. 10E (NW), 7" <Taupo; S13809, R Fem, XII, Sq. 11 (NE), > Waimihia; S16696, R Fem, XII, Sq. 24G (NE), 2" <Taupo; S17025, R Fem, I, Sq. 5 short grid; S18288, L Fem, II, Sq. 7C, long grid base; S41296, pL Fem, XII, Sq. 1H baulk.

*Tibiotarsi*. MNZ S1083, R Tib, XII, Sq. 4K, <Taupo; S2247, sL Tib, XII, Sq. 8K (NE), 4" <Taupo; S4298, L Tib, XII, Sq. 3K (SE), > third ash; S5776, pL Tib, XII, Sq. 3H (NE), Layer 3; S8348, R Tib, XII, Sq. 6G (NE), 2" <Taupo; S9632, L Tib, XII, Sq. 4H (NW), 1" >Taupo; S9976, pL Tib, XII, Sq. 83, <Taupo; S12596, dR Tib, XII, Sq. 25C (NW-NE), 2" <Taupo; S13688, pL Tib, XII, Sq. 10F (SW), 1" >Taupo; S16540, pR Tib, XII, Sq. 23F (SW), 4" <Taupo; S22170, pR Tib, Poukawa site, data lost; S22172, R Tib, Poukawa site, data lost; S22173, R Tib, Poukawa site, data lost; S22174, pL Tib, Poukawa site, data

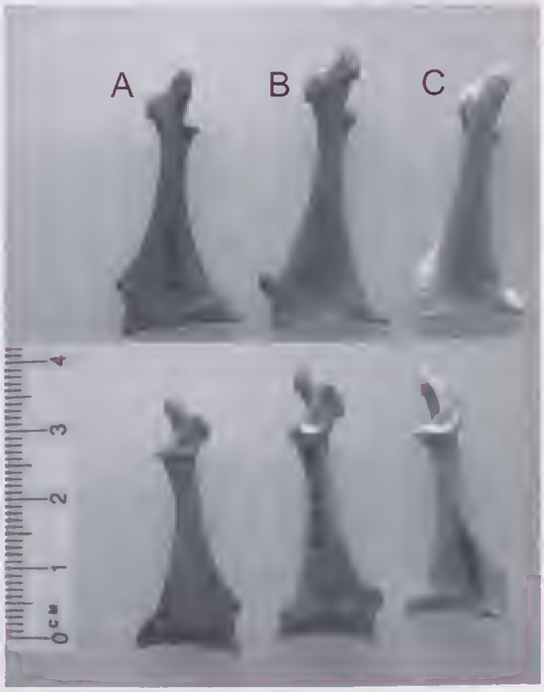

FIG. 4. Right coracoids of *Oxyura* species compared with *Aythya novaeseelandiae*. A, *O. vantetsi*, MNZ S18056; B, *O. australis* CM Av31408; C, *Aythya novaeseelandiae* MNZ 24245. Upper row, ventral aspect; lower row, dorsal aspect.

lost; S22175, L Tib, Poukawa site, data lost; S41453, sL Tib, XII, Sq. 25C (NW-NE), 2" <Taupo.

*Tarsometatarsi*. MNZ S8684, sL Tmt, XII, Sq. 15A (SW), 5-8" <Taupo; S13358, sR Tmt, XII, Sq. 2G (SE), >subsoil; S14692, R Tmt, XII, Sq. 3B (SW), <Taupo; S22176, R Tmt, Poukawa site, data lost; S22177, R Tmt, Poukawa site, data lost; S22178, L Tmt, Poukawa site, data lost.

*Coracoids*. MNZ S3363, R Cor, XII, Sq. 3J, Layer 2; S3781, L Cor, XII, Sq. 51 (NW), <Taupo; S8933, R Cor, XII, Sq. 17 (NW-SW), 4" <Waimihia; S9444, R Cor, XII, Sq. 4D (SE), Layer 1; S11212, R Cor, XII, Sq. 19C (SE), 1" >Taupo; S11404, R Cor, XII, Sq. 20I (NE), on Taupo; S12603, R Cor, XII, Sq. 25C (NW/NE), 2" <Taupo; S12163, L Cor, XII, Sq. 5G (NW), 2" <Taupo; S13722, L Cor, slightly immature, XII, Sq. 10F (NE), on Taupo; S13773, R Cor, XII, Sq. 10F, 9" <Taupo; S16176, R Cor, XII, Sq. 6B (NE), 2" <Taupo; S16972, L Cor, I, Sq. 4A, short grid; S18056, R Cor, II, Sq. 6A, long grid base; S22439, L Cor, XII, Sq. 87 east baulk, <Waimihia, in peat; S41408, R Cor, II, Sq. 1A-12A.

*Cranial material*. MNZ S41197, complete cranium, Poukawa site, data lost; S20222, posterior half of cranium, II, Sq. 9A, long grid base.

*Sternum*. MNZ S41330, anterior part, XII, Sq. 1H (NE).

ETYMOLOGY. The species is named after Dr Gerard (Jerry) Frederick van Tets (1929 - 1995).

MEASUREMENTS OF THE HOLOTYPE. Total length 66.24 mm, proximal width tub. dorsale to ventral edge crista bicipitalis 14.40 mm, shaft width minimum in cranial view 3.86 mm, distal width in cranial view 9.00 mm, Diameter tub. dorsale to junction of crista bicipitalis and shaft 13.74 mm.

DIAGNOSIS. *Oxyura* that is smaller than *Oxyura australis* (Table 1), and from which it differs by the following characters of the humerus: the epicondylus ventralis is shorter distally of the tub. supracondylare ventrale resulting in a wider angle between the caudal and distal margins of the epicondylus ventralis; there is a ridge running from the tub. dorsale down the caudal surface of the shaft at the base of the crista deltopectoralis creating a concave surface between the distal end of the ridge and the crista deltopectoralis (ridge absent in *O. australis* and comparable surface concave); the fossae pneumotricipitalis viewed from the distal end appears circular (not wider than deep).

DESCRIPTION AND COMPARISON. *Humerus* (Fig. 2) Humeri of *Oxyura vantetsi* differ from those of *O. australis* as described in the diagnosis. Among waterfowl in New Zealand they are most similar to those of *Aythya novaeseelandiae* which are slightly larger (Appendix 1) and also have a closed fossa pneumotricipitalis. However, in *Aythya novaeseelandiae*, the tub. dorsale is much less elevated; the caput humeri is less excavated under it caudally; the shaft lacks the marked narrowing distally seen in *Oxyura*; there is no ridge across the incisura capitus; the crista

FIG. 5. Left femora of *Oxyura* species compared with *Aythya novaeseelandiae*. A, *O. vantetsi* MNZ S18288; B, *O. australis* CM Av31408; C, *Aythya novaeseelandiae* MNZ 24205. Upper row in caudal aspect; lower row in lateral aspect.

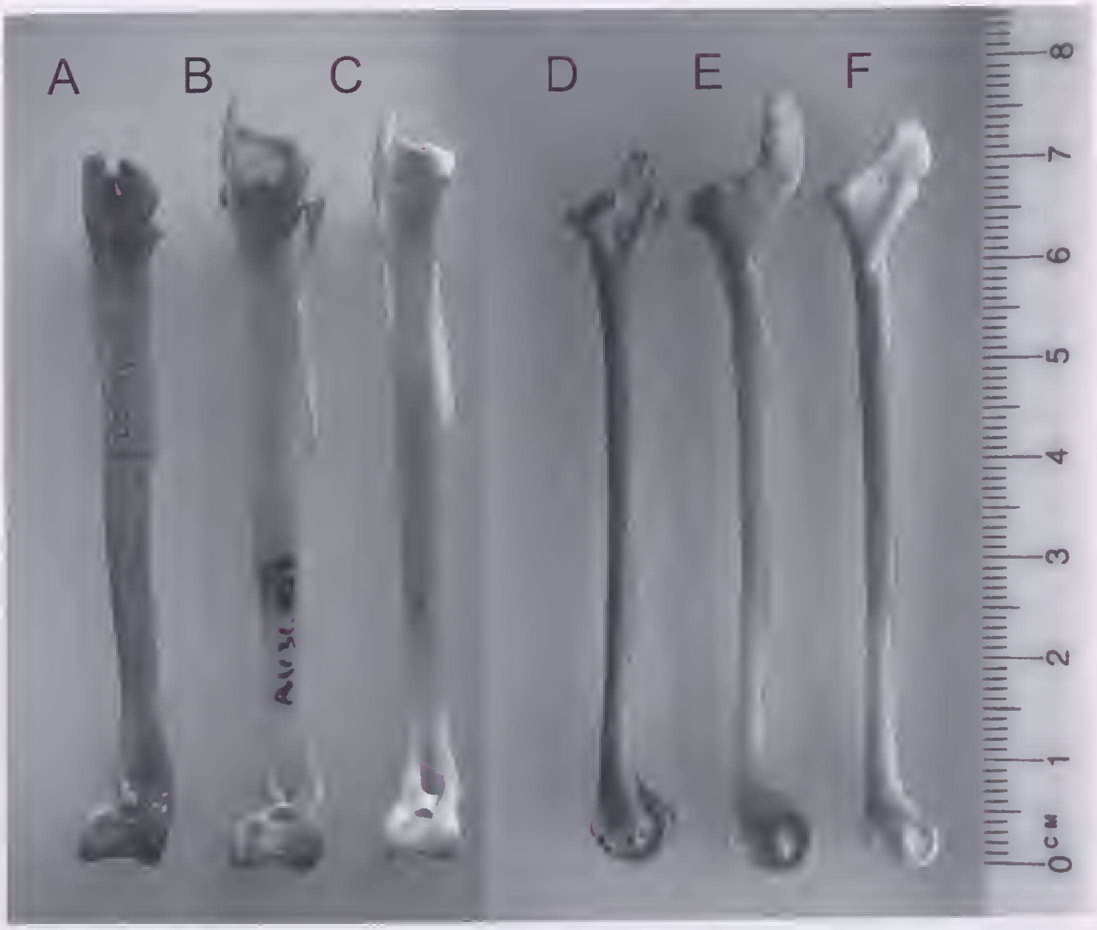

FIG. 6. Tibiotarsi of *Oxyura* species compared with *Aythya novaeseelandiae*. A,D - *O. vantetsi* MNZ S22175; B,E - *O. australis* CM Av31408; C,F – *A. novaeseelandiae* MNZ 24205. A-C in cranial aspect; D-F in medial aspect.

bicipitalis deviates from the shaft at a much shallower angle; the crus dorsale fossae is aligned at right angles to the shaft; the tub. supracondylare ventrale is smaller, not extending proximad of the cond. dorsale and its face is directed distally, and there is a distinct attachment point centrally placed in the ventral facies for the M. pronator superficialis.

*Ulna* (Fig. 3). To detect the ulnae of *Oxyura vantetsi* in the Poukawa collections I predicted their likely length range from the lengths of the humeri assuming that the humerus-ulna ratio of bone lengths for *Oxyura vantetsi* was similar to that of *O. australis* (i.e. 0.826, 0.839), which is slightly smaller than in *A. novaeseelandiae* (mean = 0.849, sd =0.0108 , n= 10). As humeri of *Oxyura vantetsi* ranged from smaller than to about the same length as small to average-sized *A. novaeseelandiae*, e.g. MNZ 24245, it was expected that their ulnae would be shorter than those of *A. novaeseelandiae*. Examination of all ulnae with the general straight slender form of either *Oxyura* or *Aythya* revealed two size groupings. There were those typical of *A. novaeseelandiae* ranging from 58-63mm long compared to 59.3-63.2mm in a modern sample (Appendix 1), but there was a distinct grouping of fossil ulnae less than 58mm long (Table 2).

These smaller ulnae had a markedly shorter cond. dorsalis ulnaris approaching the condition seen in *O. australis*, rather than it being markedly longer than wide as in *Aythya novaeseelandiae*, and so were referred to *O. vantetsi*. In general, ulnae referred to *O. vantetsi* are relatively slender

FIG. 7. Right tarsometatarsi of *Oxyura* species compared with *Aythya novaeseelandiae*. A, *Aythya novaeseelandiae* MNZ 24205; B, *O. vantetsi* MNZ S22177; C, *O. australis* CM Av31408. Upper row in dorsal aspect; lower row in plantar aspect.

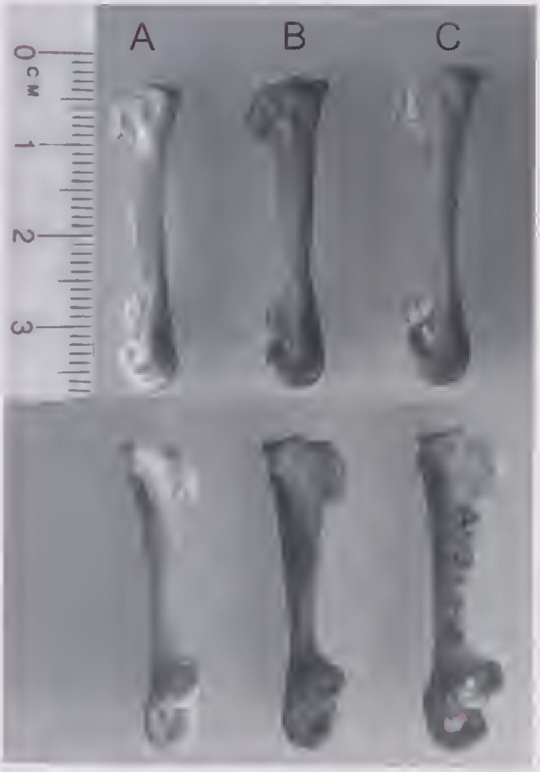

FIG. 8. Right tarsometatarsi of *Oxyura* species compared with *Aythya novaeseelandiae*. A, *Aythya novaeseelandiae* MNZ 24205; B, *O. vantetsi* MNZ S22177; C, *O. australis* CM Av31408. Upper row in lateral aspect; lower row in medial aspect.

with a shaft that tapers to a least width near the distal end in ventral or cranial view, and that have small proximal and distal ends, and so are similar to those of *A. novaeseelandiae*. They are distinguished by the following combination of characters. Length 51-58mm (Table 2). In ventral view, the caudal margin of the shaft forms a straight line extending over half the bone length from the distal end. The olecranon is small, pointed and not raised much above the cotyla ventralis. The ventral margin of the ventral cotyla is straight and forms a near right angle with the cranial margin. The impressio brachialis is deeply excavated, and in ventral aspect extends beyond half of the bone depth towards the caudal facies. The cond. dorsalis ulnaris, in caudal aspect, is rounded, with the cranial-caudal width only slightly less than its length (length longer than width in *A. novaeseelandiae*). The tub. carpale is narrow ventrodorsally and so is less robust than it is in *A. novaeseelandiae*. The depressio radialis is deeper than it is in *Aythya novaeseelandiae*.

Ulnae of *Oxyura australis* are bigger, but otherwise similar in shape to those of *O. vantetsi*. However, the cond. dorsalis ulnaris is wider craniocaudally than it is long and is markedly stepped up from the shaft on its proximal margin.

*Coracoid* (Fig. 4). Fourteen coracoids (Table 3) were referred to *Oxyura vantetsi* because of their similarity to those of *O. australis*. Coracoids of *O. vantetsi* share the following characters with *O. australis* and differ from the most similar species of New Zealand waterfowl *Aythya novaeseelandiae* by the following characters. They have a small humeral end and a disproportionately wide sternal end. The proc. acrocoracoideus is small and does not overhand the shaft medially. The dorsal part of the facies artic. clavicularis forms a small protuberance that does not extend sternally as a sharp spike into the sulcus m. supracoracoideus (unlike *A. novaeseelandiae* in which it forms a sharp spike interrupting the sulcus). The facies artic. humeralis is short and broad, with an abrupt step to the shaft adjacent to the cotyla scapularis (unlike *Aythya* in which it is relatively narrower and slopes to the shaft). The sulcus m. supracoracoidei is not excavated under the facies artic. humeralis (unlike *Aythya* in which it is deeply excavated). There is a short proc. lateralis (unlike *Aythya* which has none). The angulus medialis has a broad flange leading to it so that the angle in dorsal aspect is about 60° (unlike *A. novaeseelandiae* in which the medial angle tapers to a point at about 30°). The facies artic. sternalis is broad with a prominent centrally located ridge bounding it dorsally across the width (unlike *Aythya* in which it is narrower and the bounding ridge is offset medially). With a length range of 34.6-38.3mm, coracoids of *O. vantetsi* are smaller than in *O. australis* (Table 3), but have an overlapping length range with those of *Aythya novaeseelandiae* (Appendix 1).

*Femur* (Fig. 5.) Fifteen femora were referred to *Oxyura vantetsi*. These femora are superficially similar to those of *Aythya* as follows. They have a similar length (Table 4, Appendix 1) and the shaft is narrower than deep and bent caudally over its distal third as in *O. australis* and *A. novaeseelandiae*, but unlike all species of *Anas* in which it is straight and tends to be round in section. The depth through the crista trochanter is only slightly more than the depth of the ball, as in *Aythya*, but unlike all *Anas* species, in which the depth of the trochanter is markedly greater. The fossa poplitea is deep and bound by a compressed ridge medially as in both *Oxyura* and *Aythya*.

However, the referred femora are similar to *O. australis* and differ from the superficially similar femora of *Aythya* as follows. Both the proximal and distal ends are much more robust than in *Aythya*. There is a distinct prominence on the facies lateralis level with the end of the crista trochanteris, which is absent in *Aythya*. The proximocaudal part of the cond. medialis in medial aspect connects to the shaft at right angles rather than as a slope as in *Aythya*. The crista tibiofibularis is large and in lateral view forms a large step from the shaft (smaller in *Aythya*). The proximal margin of the trochlea fibularis in lateral aspect forms a distinct flat ledge aligned at right angles to the shaft and which extends to half of the shaft depth before merging with it. In *Aythya*, the trochlea fibularis is smaller and slopes proximally before merging at about one third of shaft depth from the caudal surface.

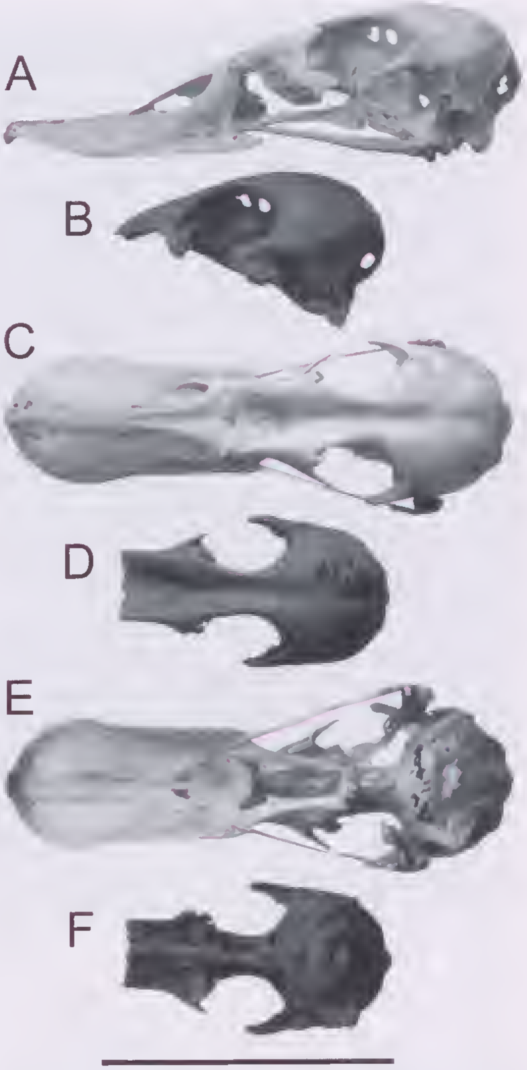

FIG. 9. Cranium of *Oxyura australis* CM Av31408 (A,C,E) compared to that of *O. vantetsi* MNZ S41197 (B,D,F).

The femora referred to *O. vantetsi* differ from *O. australis* as follows. They are smaller at 40.1-42. mm long (Table 4). The caput femoris is directed proximally and extends proximad of the crista trochanteris, it does not in *O. australis*. The ridge bounding the fossa popilitea medially is convex medially rather than straight.

TABLE 5. Measurements (mm) of tibiotarsi of *Oxyura* species. *O. australis* CM and AM specimens, and summary statistics for *O. vantetsi* nsp (specimens MNZ S1083, 2247, 4298, 5776, 8348, 9632, 9976, 13688, 16540, 22170, 22172, 22173, 22174, 22175). Abbreviations as in Methods. DW is measured from the face of the lateral condyle, rather than from the prominence in the central proximal region of the condyle which would markedly increase distal width and which homologous protuberance is located more anteriorly in *Aythya*.

| | TL | AL | PW | SW (mid) | SD (mid) | SW (min) | DW |
|---|---|---|---|---|---|---|---|
| Mean | 69.08 | 66.12 | 8.39 | 4.52 | 3.14 | 3.84 | 8.96 |
| Std Error | 0.580 | 0.796 | 0.121 | 0.049 | 0.050 | 0.034 | 0.095 |
| Std Deviation | 0.820 | 1.593 | 0.342 | 0.163 | 0.167 | 0.101 | 0.232 |
| Minimum | 68.5 | 64.6 | 7.8 | 4.3 | 2.9 | 3.7 | 8.7 |
| Maximum | 69.7 | 68.3 | 8.8 | 4.7 | 3.4 | 4.0 | 9.4 |
| Count | 2 | 4 | 8 | 11 | 11 | 9 | 6 |
| CM Av31408 | 77.3 | 69.1 | 8.7 | 4.5 | 3.0 | 4.1 | 10.0 |
| AM O65518 | 76.0 | 68.7 | 8.6 | 4.4 | 3.1 | 4.0 | 9.7 |

*Tibiotarsus* (Fig. 6). Sixteen tibiotarsi (Table 5) were referred to *Oxyura vantetsi* because of their similarity to those of *O. australis*. They have a broad flat shaft characteristic of diving ducks, but differ from those of *Aythya novaeseelandiae*, which is the most similar taxon in New Zealand, and are similar to *Oxyura* as follows. The bone is broader, especially at the proximal and distal ends than in *Aythya*, the distal end is more inflected medially, and the shaft is more flattened. The crista cnemialis is much more elevated above the articular surfaces and the ridge leading from the crista cnemialis cranialis down the medial facies is markedly inflected medially centred opposite the top of the crista fibularis (such an inflected ridge is absent in *Aythya*). The sulcus extensorius is broad and flat in its base (narrow in *Aythya*). The cond. medialis has a large robust prominence in the centre of its medial face (small prominence in *Aythya*) and its proximocranial region is expanded proximally so that in medial view there is a marked hollow in the profile between the shaft and the condyle (forms a wider angle in *Aythya*).

Tibiotarsi of *O. vantetsi* are smaller than those of *O. australis* (Table 5) and differ further by the following. The crista cnemialis lateralis continues as a prominent ridge down the facies cranialis adjacent to the upper 30% of the crista fibularis, whereas it does not in *Aythya* or in *Oxyura australis*. But in the latter, the facies cranialis is swollen adjacent to the *crista fibularis*, which with the marked ridge leading to the crista fibularis, creates a marked elongate sulcus in the upper part of the shaft region similar to that seen in *O. vantetsi*. The cond. medialis in *O. vantetsi* is more rotated proximocranially than in *O. australis*.

*Tarsometatarsus* (Figs 7, 8) The tarsometatarsi listed in Table 6 were referred to *Oxyura vantetsi* because of their similarity to those of *O. australis*. They are very short and have a flattened shaft and a compressed and caudally rotated trochlea metatarsi II characteristic of diving ducks. They differ from those of *Aythya novaeseelandiae*, which is the most similar taxon in New Zealand, and are similar to *Oxyura* as follows. While of similar length to *Aythya* tarsometatarsi (Appendix 1), they are much broader across both ends and the shaft. In dorsal aspect, the sulcus extensorius is larger, and is bound laterally by a higher and sharper ridge than in *Aythya*. The junction of the caudal and medial facies has a distinct sharp ridge extending from the crista medialis hypotarsi to about mid-length that is very much less distinct in *Aythya*. The cotyla medialis is markedly offset medially from the line of the shaft. Medially, there is a deep sulcus formed between the cotyla medialis and the crista hypotarsi medialis, compared to this region being convex in *Aythya*. The crista hypotarsi medialis draws to a point distally that is rolled over the adjacent crista intermediate hypotarsi (it is not rolled over the adjacent crista and is distally hooked in *Aythya*). The foramen vasculare distale is larger than in *Aythya*.

Tarsometatarsi of *O. vantetsi* differ from those of *O. australis* by their smaller size. They differ also in having a shallower sulcus on the lateral half of the plantar surface of the distal third of the shaft. This sulcus is in part created by a low ridge that defines a 'lens-shaped' flat surface on the lateral face. Distally this low ridge approaches

TABLE 6. Measurements (mm) of tarsometatarsi of *Oxyura* species. *O. australis* CM and AM specimens, and summary statistics for *O. vantetsi* (specimens MNZ S8684, 13358, 14692, 22176, 22178, 22177). Abbreviations as in Methods.

| | TL | PW | SW (midpoint) | SD (midpoint) | DW (parallel to lat side) | depth trochlea 3 |
|---|---|---|---|---|---|---|
| Mean | 34.18 | 9.30 | 5.09 | 3.18 | 8.36 | 5.80 |
| Std Error | 0.474 | 0.150 | 0.145 | 0.110 | 0.129 | 0.041 |
| Std Dev | 0.948 | 0.260 | 0.354 | 0.269 | 0.223 | 0.082 |
| Minimum | 33.0 | 9.1 | 4.5 | 2.8 | 8.1 | 5.7 |
| Maximum | 35.0 | 9.6 | 5.4 | 3.6 | 8.5 | 5.9 |
| Count | 4 | 3 | 6 | 6 | 3 | 4 |
| CM Av31408 | 35.3 | 9.7 | 5.3 | 3.3 | 8.9 | 6.5 |
| AM O65518 | 35.9 | 9.6 | 5.0 | 3.1 | 9.1 | 6.3 |

the dorsal face of the bone forming a sulcus greater than half the shaft depth in *O. australis*, whereas in *O. vantetsi*, this sulcus is shallower being less than half shaft depth. *O. australis* has relatively deeper trochlea compared to their width, especially for trochlea metatarsi III, than has *O. vantetsi*.

*Skull elements* (Fig. 9) One complete cranium (MNZ S41197) and one partial cranium (MNZ S20222) were identified from among the Lake Poukawa anatid bones. The skull of *Oxyura* differs markedly from those of all *Anas* species and *Aythya* in several features: notably there is an ossified septum between the nares (none in *Anas*, *Aythya*); the palate lacks a large oval foramen in the cranial end of the premaxilla; but most notably it has an ossified os ectethmoidale, that is fused in its lower half to the os lacrimale, and which has an ossified chamber attached to it anteriorly (the os ectethmoidale is not ossified in *Anas* and *Aythya*). Other than these features, skulls of *Oxyura* are characterised by the following. The os frontales, in the area between the os lacrimales, are deeply depressed forming a deep groove that extends posteriorly to behind the orbits (shallow sulcus in *Aythya*). The interorbital width is markedly less than frontal width. The preorbital processes are large with parallel dorsal and ventral margins (small points in *Aythya*). The ventral process of the os lacrimale is broad and aligned horizontally (narrow and directed ventrally in *Aythya*). The postorbital process is large. In posterior aspect, the crista nuchalis transversus is prominent and extends from the proc. paroccipitalis up over the occipital area in a continuous curve that approaches half of a circle (in *Aythya* this ridge forms a straight line along the rear margin of the fossa temporalis, then at the top of the fossa it abruptly angles towards the midline to meet in the middle, creating a quadrangular appearance). The proc. paroccipitalis, in posterior view, is larger and more robust than in *Aythya*, and in ventral view, each connects to straight, convergent, anterolateral ridges that form the ventral margin of the tympanic cavity. In *Aythya* these ridges have a very different shape: from the tip of each proc. paroccipitalis they extend anteriorly parallel to each other then form a curved and upturned flange that extends into the floor of the tympanic cavity. Thus, in lateral view, the tympanic cavity is dorsoventrally narrower with a distal ventrocaudally directed pocket. In *Oxyura*, the flat floor to the tympanic cavity results in it being nearly as high as long with no pocket. In *Oxyura*, the lamina parasphenoidalis is essentially flattened across its whole width whereas in *Aythya* there is a distinct medial rounded ridge protruding ventrally. Also, in *Oxyura* the horizontal lamina parasphenoidalis terminates caudally in a slightly transversely curved, abrupt angle, where it joins to the steeply rising posterior face of the os basioccipitale below the cond. occipitalis. *Aythya* differs markedly, as each side of the lamina parasphenoidalis joins to the foramen magnum above it in a continuous curve, and there is a circular sulcus below the cond. occipitalis and caudad of the medial ridge on the lamina parasphenoidalis, which results in an indented caudal margin to the basicranium.

The cranium S41197 has all the above characteristics of *Oxyura* crania and differs in relatively minor ways from that of *O. australis*. It is smaller (Table 7), and the central groove on top of the cranium is not as deep caudad of the point of minimum interorbital width, and the os ectethmoidale is more at right angles to the rostrum parasphenoidales. The posterior cranium

TABLE 7. Measurements (mm) of crania of *Oxyura* species. *O. australis*, CM and AM specimens, and *O. vantetsi*, MNZ specimens.

| Measurement | MNZ S41197 | MNZ S20222 | AMO 65518 | CMAv 31408 |
|---|---|---|---|---|
| Length from prominentia cerebellaris to frontal-nasal hinge | 44.9 | | 47.5 | 48.2 |
| Width across frontals at frontal-nasal hinge | 11.5 | | 13.4 | 12.8 |
| Minimum width across frontal lacrimal complex | 11.4 | | 13.2 | 12.1 |
| Preorbital width | 14.3 | | 15.5 | 15.5 |
| Minimum interorbital width | 6.9 | | 7.3 | 7.7 |
| Width across proc. postorbitalis | 25.2 | | 27.4 | 27.7 |
| Width between os squamosi at top of cavitas tympanic | 21.9 | | 24.0 | 24.4 |
| Width between proc. paroccipitales | 20.6 | | 22.3 | 22.4 |
| Height from lamina parasphenoidalis to the top of the crista nuchalis transverses | 19.6 | 19.6 | 20.7 | 21.0 |

(S20222) has the characteristic rounded alignment to the crista nuchalis transverses.

*Sternum* The single anterior fragment of a sternum is referred to *Oxyura vantetsi* as the sulci artic. coracoideus are arranged more or less at right angles to the carina sterna as in *Oxyura* and *Aythya* (whereas they form a concave anterior profile in *Anas*), and it lacks a centrally placed foramen pneumaticum dorsally caudad of the anterior margin (*Aythya* has a large foramen). The fragment lacks a prominent flattened spina externa (ventral manubrial spine) as seen in *O. australis*. The depth of the carina sterna (keel) measured from the dorsal surface between the sulci artic. coracoideus to the ventral side of the pila carinae so that one calliper is flat on the ventral surface of the carina is 14.5mm (18.2mm in CM Av31408). This small size is as expected from the relatively smaller size of other known elements.

## DISCUSSION

At present, only larger or more robust elements of the skeleton are known for *Oxyura vantetsi*. There are many carpometacarpi, scapulae and radii of small anatids in the Poukawa collection. Examination of carpometatcarpi and scapulae failed to reveal any bones referable to *O. vantetsi* based on features seen in *O. australis*, although it is possible distinguishing features between *Aythya novaeseelandiae* and *Oxyura vantetsi* are lacking in these elements. However, relatively few of these elements were referred to *Aythya novaeseelandiae*, which may relate to their relatively small size and recovery techniques used in the excavation: small bones and bones of small taxa are rare in the collection. Therefore, as these elements in *Oxyura* would be even smaller than those of *Aythya novaeseelandiae*, their absence may be due to their relative rarity and sampling bias. It is possible that *Oxyura* radii lie unidentified among the Poukawa radii that are labelled as 'anatid', but distinguishing smaller anatids and particularly *Aythya* from *Oxyura* in this element was not considered feasible.

Addition of a new species and genus to the Holocene avifauna of New Zealand is unexpected given the extent of the resource and number of prior studies on such material; (Worthy & Holdaway, 2002). However, the wealth of material from cave, dune and swamp deposits masks a general lack of lacustrine faunas known from New Zealand, and it is indeed obligate lacustrine species such as *Biziura delautouri* and *Malacorhynchus scarletti* that are among our rarest species (Worthy, 2002; Worthy & Gill, 2002). Thus the present description of *Oxyura vantetsi* adding a new genus and species to the lacustrine fauna of the Holocene avifauna is not so remarkable. A total of 20 species in 12 genera are now known for Recent waterfowl in the New Zealand region, of which 10 species and 7 genera are now extinct from the region (Table 8). A further species, *Cygnus atratus*, was extirpated from New Zealand prehistorically, but was reintroduced historically, so preserving this taxon in New Zealand waterways. The extinctions have been biased towards the primitive taxa which are mainly monotypic or low-diversity genera, and which were probably the remnants of the original anatid radiation in the Australasian region.

The descriptions and comparisons made here suggest *Oxyura vantetsi* differed in relatively minor ways from the Australian *O. australis*, mainly in smaller size and a few skeletal features. There is no indication that *O. vantetsi* had reduced powers of flight, as so many New Zealand endemic taxa including waterfowl do. However, neither would such be expected, as *Oxyura* species typically are wholly aquatic and specialised diving ducks (Marchant & Higgins, 1990), and as such would require flight to travel between widespread suitable habitats. Until further lacustrine faunas are investigated in New

TABLE 8. List of the waterfowl known to have inhabited the New Zealand region during the Holocene. * indicates extant species.

| Species | Common name |
|---|---|
| *Biziura delautouri* Forbes, 1892 | New Zealand musk duck |
| *Oxyura vantetsi* sp. nov. | New Zealand blue-billed duck |
| *Cnemiornis calcitrans* Owen, 1865 | South Island goose |
| *Cnemiornis gracilis* Forbes, 1892 | North Island goose |
| *Cygnus atratus* (Latham, 1790) reintroduced | Black swan |
| *Tadorna variegata* (Gmelin, 1789)* | Paradise shelduck |
| *Tadorna* undescribed species | Chatham Island shelduck |
| *Malacorhynchus scarletti* Olson, 1977 | Scarlett's duck |
| *Pachyanas chathamica* Oliver, 1955 | Chatham Island duck |
| *Mergus australis* Hombron & Jacquinot, 1841 | New Zealand merganser |
| *Chenonetta finschi* (Van Beneden, 1875) | Finsch's duck |
| *Anas gracilis* Buller, 1869 * | Grey teal |
| *Anas chlorotis* G.R. Gray, 1845 * | Brown teal |
| *Anas aucklandica* (G.R. Gray, 1844)* | Auckland Island teal |
| *Anas nesiotis* (J.H. Fleming, 1935)* | Campbell Island teal |
| *Anas* sp. undescribed sp. | Macquarie Island teal |
| Anas rhynchotis Latham, 1801 | Australasian shoveler |
| *Anas superciliosa* Gmelin, 1789 | Grey duck |
| *Hymenolaimus malacorhynchos* (Gmelin, 1789) | Blue duck |
| *Aythya novaeseelandiae* (Gmelin, 1789) | New Zealand scaup |

Zealand it is unlikely that the range of *O. vantetsi* will be well known. The bones known from Lake Poukawa suggest it was far less abundant than waterfowl such as *Anas superciliosa*, *A. chlorotis*, *A. rhynchotis* and *Aythya novaeseelandiae*, but more common than *Biziura delautouri* and the dabchick *Poliocephalus rufopectus* or crested grebe *Podiceps cristatus*. As *Oxyura* species are typically gregarious (Marchant & Higgins, 1990), *O. vantetsi* was unlikely to have been a rare species. The presence of a single bone of apparent South Island origin (CM Av10777) indicates this species was distributed in South Island waterways and so should be looked for in any wetland assemblage. In view of its ability to disperse, and that *O. australis* readily uses shallow inshore marine waters, saline lagoons, and estuaries (Marchant & Higgins, 1990), the former presence of *O. vantetsi* on Chatham Island cannot be discounted either, as in now known to be the case for *Malacorhynchus scarletti* (Worthy & Gill, 2000).

## ACKNOWLEDGEMENTS

This study was much advanced by the assistance of the curators and collections managers in the following institutions: AM – Walter Boles; CM – Paul Scofield; AIM - Brian Gill; MNZ – Alan Tennyson, Sandy Bartle. I thank Walter Boles for constructive advice on an earlier draft. I thank Raymond Coory, MNZ, for help in compiling the figures. The study was funded by the Public Good Science Fund of the New Zealand Foundation for Research, Science and Technology, under contracts TWO601.

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APPENDIX 1. Summary statistics for measurements of *Aythya novaeseelandiae* from specimens listed above. Abbreviations as in Methods.

| | Hum L | Hum PW | Hum SW | Hum DW | Ulna L | Ulna PW | Ulna SW | Ulna DW | Radius L | Radius Dist | Cmc L | Cmc PW | Cor L |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 72.1 | 15.4 | 5.2 | 10.4 | 61.1 | 7.1 | 4.0 | 6.9 | 57.3 | 4.6 | 38.2 | 9.1 | 38.3 |
| Std Error | 0.779 | 0.144 | 0.068 | 0.074 | 0.441 | 0.055 | 0.101 | 0.121 | 0.499 | 0.049 | 0.220 | 0.052 | 0.397 |
| Std Dev | 2.463 | 0.456 | 0.214 | 0.234 | 1.463 | 0.181 | 0.335 | 0.401 | 1.577 | 0.156 | 0.730 | 0.172 | 1.257 |
| Minimum | 69.0 | 14.8 | 4.9 | 10.0 | 59.3 | 6.9 | 3.8 | 6.5 | 55.1 | 4.4 | 37.4 | 8.8 | 36.2 |
| Maximum | 76.7 | 16.1 | 5.5 | 10.7 | 63.2 | 7.4 | 4.9 | 8.0 | 59.3 | 4.9 | 39.2 | 9.4 | 40.2 |
| Count | 10 | 10 | 10 | 10 | 11 | 11 | 11 | 11 | 10 | 10 | 11 | 11 | 10 |

| | Femur L | Femur PW | Femur SW | Femur DW | Tibia TL | Tibia PW | Tibia SW | Tibia DW | Tmt L | Tmt PW | Tmt SW | Tmt DW |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 43.1 | 9.9 | 4.0 | 9.6 | 74.2 | 7.4 | 3.6 | 8.0 | 34.6 | 8.1 | 4.1 | 8.4 |
| Std Error | 0.581 | 0.093 | 0.053 | 0.153 | 0.680 | 0.069 | 0.044 | 0.112 | 0.355 | 0.129 | 0.052 | 0.126 |
| Std Dev | 1.839 | 0.293 | 0.168 | 0.484 | 2.255 | 0.228 | 0.147 | 0.373 | 1.122 | 0.407 | 0.163 | 0.398 |
| Minimum | 40.3 | 9.5 | 3.8 | 8.6 | 71.8 | 7.0 | 3.3 | 7.5 | 33.0 | 7.0 | 3.8 | 7.8 |
| Maximum | 46.0 | 10.4 | 4.3 | 10.0 | 79.7 | 7.7 | 3.8 | 8.9 | 37.1 | 8.4 | 4.3 | 9.1 |
| Count | 10 | 10 | 10 | 10 | 11 | 11 | 11 | 11 | 10 | 10 | 10 | 10 |

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**NOTES**