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## Oligocene Marsupials of the Geilston Bay Local Fauna, Tasmania

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### ABSTRACT

Fragmentary remains of marsupials from the later Oligocene travertine deposits of Geilston Bay, River Derwent estuary, near Hobart, Tasmania, appear to represent elements of a temperate rainforest fauna then at about 50°S latitude. These deposits are capped by alkali basalt that yielded a whole-rock age of  $23.0 \pm 0.5$  Ma, a minimum age for the Geilston Travertine. Identified taxa include a dasyurid, two petauroids, and

a burramyid, all belonging to scansorial and arboreal groups having important representation in present-day forested environments. Only the petauroids are complete enough for phylogenetic analysis and both are more primitive than other known members of that superfamily. Their presence indicates a pre-Oligocene time of differentiation of the Diprotodontia in accordance with molecular and paleontological interpretations.

### INTRODUCTION

The fossiliferous limestones at Geilston Bay, on the eastern shore of the Derwent, opposite Hobart, Tasmania, were quarried as early as 1841 when Robert McCormick, surgeon on H.M.S. *Erebus* visited James Bay (now Geilston Bay) and recorded the remains of plants and shells in the excavation (Banks, 1971). The quarry came to the attention of several other naturalists in the 1840s and collections were forwarded to England, but it

was not until 1866 that fossil bones were reported. Mr. Morton Allport, who had been collecting fossils from the quarry for 12 years, exhibited the "mutilated" remains of fossil mammals before the Royal Society of Tasmania in 1865 (Allport, 1866). Subsequently, the material was sent to Richard Owen at the British Museum for identification. Allport had determined that the fossiliferous "Geilston Travertine" dipped east-

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ward from the western part of the quarry beneath a capping basalt flow. These observations were later confirmed by many geologists. Johnston (1888) gave one of the first measured sections, which indicated the presence of at least 10 m of clays, marls, ostracod limestone, and travertine beneath 1.5 m of weathered basalt. Moore (1965) published a map of the Geilston Bay area and confirmed the subbasaltic position of the "Geilston Limestone." He also mentioned a report by Nye (1924), who observed that in the active quarry "thin layers of limestone occur above the basalt" as well as below.

Allport (1868) received a reply from Owen in 1867 who identified the bones sent to him as "a small kind of *Hypsiprymnus*, with probably also *Perameles* and *Phalangista*." Nine years later Allport (1877) considered the fossil marsupials "to belong to existing species, viz., *Phalangista fuliginosa*, *Hypsiprimni*" and concluded that "the travertine must be of recent tertiary or post-tertiary age" thus placing the basalt at a still younger age.

After Von Mueller analyzed a large collection of the seeds and leaf impressions from the travertine, Allport (1877) concluded that the flora resembled those from the "tertiaries of Victoria" (primarily those from Yallourn), thus providing "fresh and unmistakable proofs of the earlier age of the travertine." Allport attempted to reconcile the paradox in age determination from vertebrate and plant remains by postulating that the bones were introduced to the travertine through fissures formed at the time of volcanic eruption and later occupied by a carnivore that accumulated the remains. By the time Johnston (1888) published his summary of the geology of Tasmania, including a further study of the Geilston Bay area, the whereabouts of the fossil marsupial material were unknown and he "feared they have not been preserved."

As we reported in 1975 (Tedford et al., 1976), the Allport collection was found in the British Museum (Natural History) by the late Jack Mahoney in 1973. That preliminary note set out the evidence for the provenance of the collection and provided a radiometric date on the overlying lavas to establish a minimum geological age. Only a few notes

were contributed on the fauna itself, and as these need correction and amplification, the present paper describes the material with comments on its systematic position and significance to the history of the Australian Marsupialia. Recent mapping of the Hobart area and new evidence on the age and relationships of the volcanics in the Derwent estuary that are relevant to the age of the fossil assemblage are also reviewed.

#### ACKNOWLEDGMENTS

We again thank the trustees of the Natural History Museum, London, for permission to study the Geilston Bay local fauna, and acknowledge the vital role played by the late Jack Mahoney of the University of Sydney in bringing the collection to light. We were aided in important ways by two geologists with intimate knowledge of the Tasmanian volcanics, Ian McDougall (Australian National University, Canberra) and F. Lin Sutherland (Australian Museum, Sydney) and by Tasmania's senior geologist and historian, Max Banks. The illustrations of fossils were prepared by Lorraine Meeker and Chester Tarka of AMNH. This research was partly-funded by NSF Grant GB 18273X to the senior author and by funds of the Department of Vertebrate Paleontology, AMNH. The manuscript was reviewed by M. O. Woodburne, W. D. Turnbull, A. Baynes, K. P. Aplin, and J. Brammall to whom we offer sincere thanks for helping to improve this work.

#### GEOLOGY

Many geological observations have been published on the Geilston Bay Tertiary deposits over the past century and a half. Most of the information available in the 19th century was summarized by Johnston in 1888 (pp. 286–288). In the 20th century, workers were concerned only with the limestone resources (production ceased around 1924) or with the volcanics and larger geological setting of the locality. The limestone quarry was eventually filled in to form part of the playing fields of the adjacent Geilston Bay High School (Banks, 1971). The text of the Hobart 1:50,000 sheet (Leaman, 1976) and data on the volcanics (Sutherland and Wellman,

1986; Sutherland, 1989) are also utilized in the summary that follows.

**TERTIARY SEDIMENTS** (Derwent beds of Gill, 1962): Tertiary alluvial, fluvial, and lacustrine sediments were deposited on an irregular surface formed on deformed Permian and Triassic sediments and volcanics in and adjacent to the Derwent estuary in a pattern that implies the presence of a river valley, or interconnected valleys, topographically similar to that of the present (fig. 1). The deposits in Geilston Bay fill the narrow end of a valley excavated along a fault displacing Permian sediments. More than 10 m of sediments, passing below sea level, are preserved in this Tertiary paleovalley. They include interstratified travertine, marl, and clays, the upper meter of which has been silicified. To the west a sediment-filled paleovalley passes southeastward from Elwick Bay to Cornelian Bay beneath Glenorchy and Moonah. These deposits, at least 40 m in thickness and best exposed in the Cornelian Bay area, consist of flat-lying laminated white claystone overlain by sands. Both lithologies contain locally abundant plant macrofossils.

To the south at Sandy Bay, plant-bearing laminated clays and sands more than 180 m thick, are contained in a half-graben bordered by Permian and Triassic sediments and Jurassic dolerite. These deposits are folded into a syncline whose major axis parallels the graben-bounding faults.

At One Tree Point (now Blinking Billy Point) at the southern end of Little Sandy Bay, a coarse bouldery alluvium of locally derived Jurassic dolerite underlies the plant-bearing laminated clays and sands, implying that the Mount Nelson dolerite mass immediately to the southwest had considerable relief—as it does today. At this site, within the overlying Tertiary basalts, Johnston (1888: 281) reported finding a “bone breccia” in the “cooling joints of an older sheet of basalt . . . subsequently overlain by another flow.” He figured the site (figure opposite p. 280) and some of the specimens obtained from the breccia (pl. L, figs. 12–13). He identified some as “undoubtedly belonging to a marsupial of the genus *Hypsiprymnus*,” and a “well-preserved incisor of a marsupial allied to the existing wombat.” Unfortunately the

illustrations are of inadequate quality for confirmation of these identifications. The material does, however, suggest marsupials of the size and general morphology of those from the Geilston Travertine. To our knowledge, these specimens have not been found in collections in Hobart.

South of Blinking Billy Point, at Tarooma, plant-bearing siltstones and interbedded sandstones crop out along the Derwent where they overlie and are faulted against Jurassic dolerite. Over 600 m of sediments are preserved at this locality. Chelid turtle remains occur in concretions in the siltstone (Warren, 1969).

**TERTIARY VOLCANICS:** Basaltic flows and associated pyroclastics (fig. 1) conformably overlie the Tertiary sediments in the Derwent paleovalley (Sutherland, 1976; Sutherland and Wellman, 1986; Sutherland, 1989). Olivine tholeiitic basalt flows can be traced fairly continuously from the north near Brighton (Brighton Basalts of McDougall, 1959) in the Jordan River valley into the Derwent valley where they overlie the plant-bearing sediments around Glenorchy. Alkali basalts overlie fossiliferous sediments at Geilston Bay, Lindisfarne Bay, and at Selfs Point north Cornelian Bay. They pass below sea level beneath the Tasman Bridge and extend along the floor of the Derwent estuary almost to Rosny Point. The 20-m-thick alkali basalt capping the Risdon volcanic center, 4 km north northwest of Geilston Bay, is interbedded with 30 m of amphibole tuff. Both units overlie small remnants of a dense olivine nephelinite. The extrusions flowed southwestward down a narrow valley toward the Derwent at Risdon Cove but did not join the flow from Geilston Bay. A volcanic center whose remnant forms Blinking Billy Point has flows and pyroclastics interbedded with and overlying the fossiliferous sediments of the Sandy Bay graben. These lavas include alkaline basanites and form a chemically distinctive group relative to the basalts just to the north northwest.

The diversity of petrology and geochemistry of the lavas suggests different sources and some are clearly related to volcanic centers that remain in outcrop. In all cases however, the lavas cap the fossiliferous sediments, the contact may be entailed or inter-

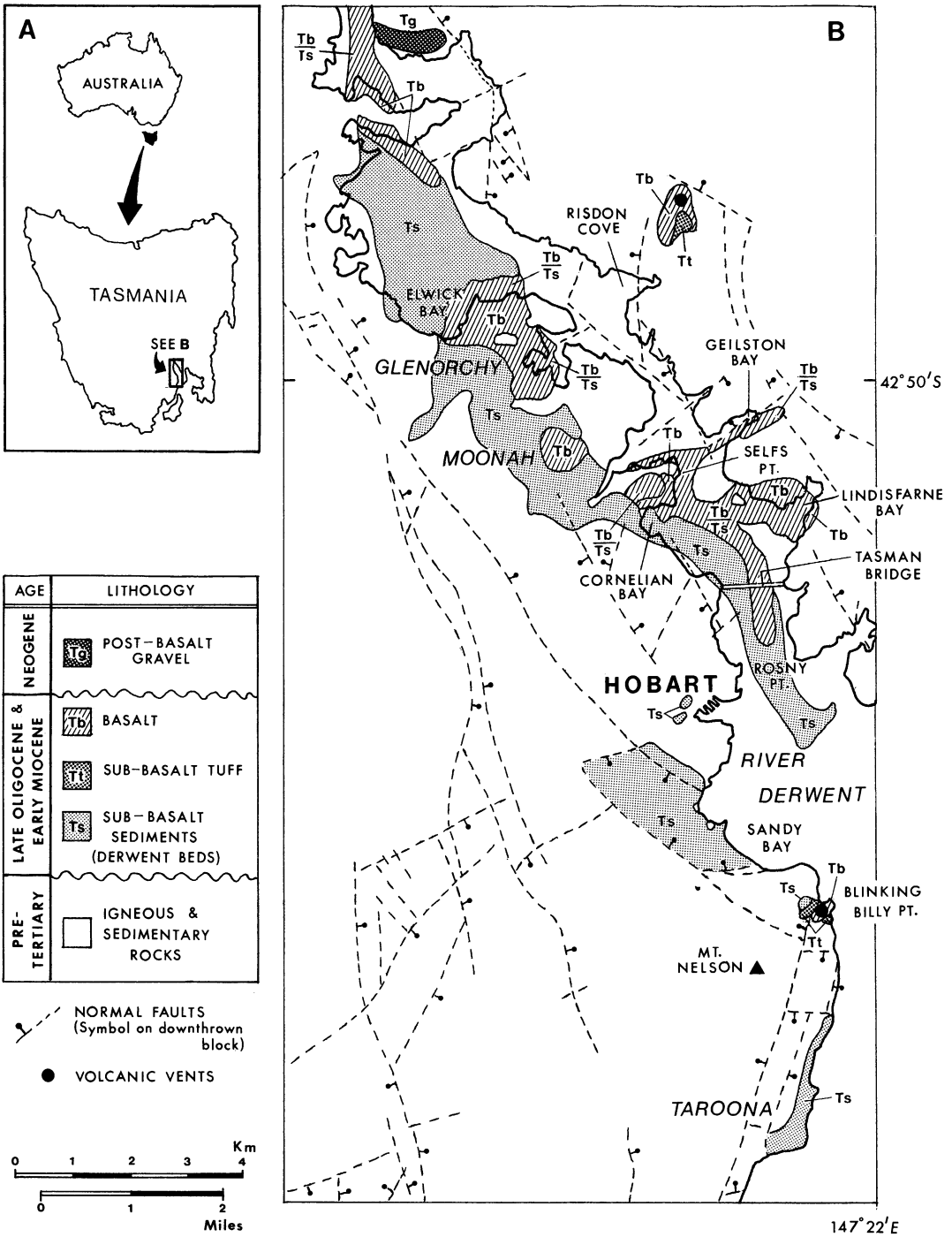


Fig. 1. Geological map of lower reaches of the Derwent at Hobart. Map combines data from outcrops above and below sea level (Leaman, 1976) shown on the Hobart sheet, 1:50,000, and supplementary map.

fingering and may show some hydrothermal silicic and calcic alternation, but in no case is there cause to believe that much time passed between deposition of the sediments and the volcanic activity. In the case of the Geilston Bay outcrops, travertine deposition continued after emplacement of the lava. The lavas are often capped by fluvial gravels of diverse provenance that may record reestablishment of drainage lines at a significantly younger date.

### AGE

Historically, the ages of the subvolcanic sediments were based on the botanical relationships of the contained floras compared with those elsewhere in Tasmania and Australia (Allport, 1877; Johnston, 1988). The evidence was summarized by Gill (1962: 237; see list of references) who concluded that they were younger than the Eocene and Oligocene floras of the Launceston Group in the Tamar graben of northern Tasmania and probably of Miocene age correlative with the floras of the Yallourn coal field of Victoria. Subsequently, Harris, in an unpublished report on Tasmanian microfloras discussed by Baillie and Leaman (1969: 365), reported a Paleocene age for the siltstones with turtles at Tarooma. Duigan (*in* Warren, 1969) regarded the microflora from the same outcrops to be possibly as young as Miocene. The floras of the Derwent beds are all of a similar facies and represent rainforest environments with podocarp and araucarian conifers, and *Nothofagus*, Proteaceae, Lauraceae, and Myrtaceae among the angiosperms.

In recent years some of the volcanics of this area have been isotopically dated. The basalt overlying the Geilston Travertine (Tedford et al., 1975, see data) yielded  $22.4 \pm 0.5$  Ma, which can be corrected following Dalrymple (1979) to  $23.0 \pm 0.5$  Ma. At the nearby Risdon volcanic center the amphibole tuff dated at  $30.2 \pm 1.0$  Ma while the upper flow at the volcanic center at Blinking Billy Point is  $26.5 \pm 0.3$  Ma in age (Sutherland and Wellman, 1986). Thus the K-Ar ages of the overlying basalts suggest minimal medial to late Oligocene ages for the underlying clastic Derwent beds and their travertine facies.

### SYSTEMATIC PALEONTOLOGY

In the comparison of postcranial remains that follows we have utilized the comparative anatomical specimens in the Department of Vertebrate Paleontology and the skeletal collections of the Department of Mammalogy, American Museum of Natural History (AMNH), representing the following species: *Dasyurus maculatus*, *Trichosurus vulpecula*, *Pseudocheirus peregrinus*, *Phalanger orientalis*, and *Phascolarctos cinereus*. Dental comparisons that underpin the phyletic analysis (summarized in table 1) ranged across the entire collection of relevant taxa available including most vombatoid genera (fossil and living) represented by specimens and casts in the collections of the AMNH.

We follow Marshall et al. (1990) for the content of higher taxa within the Diprotodontia, but use the term Phalangerida Aplin and Archer, 1987, as a replacement for Phalangeriformes Woodburne, 1984, because of preoccupation pointed out by Aplin and Archer (1987: xlv). Therefore, the concept of Phalangerioidea (Thomas, 1888) and Petauroidea (Gill, 1872) is broader than that recognized by Aplin and Archer (1987) but these two groups, together with the Macropodoidea (Gray, 1821), collectively contain all the genera placed in the Phalangerida by Aplin and Archer (1987).

Epoxy casts of the most important of the Geilston Bay marsupials, including all the figured teeth and rami contained in the Natural History Museum (NHM), London, have been deposited in the following collections in Australia: Australian Museum, Sydney; Australian Geological Survey Organization, Canberra; Flinders University, Adelaide; Monash University, Clayton, Victoria; National Museum of Victoria, Melbourne; Queensland Museum, Brisbane; Tasmanian Museum, Hobart; and the Western Australian Museum, Perth. All measurements are in millimeters.

### DESCRIPTION

SUPERORDER MARSUPIALIA ILLIGER, 1811

ORDER DASYUROMORPHIA GILL, 1872

FAMILY DASYURIDAE GOLDFUSS, 1820

A fragment of the proximal end of a right femur (NHM M82020, fig. 2), lacking the

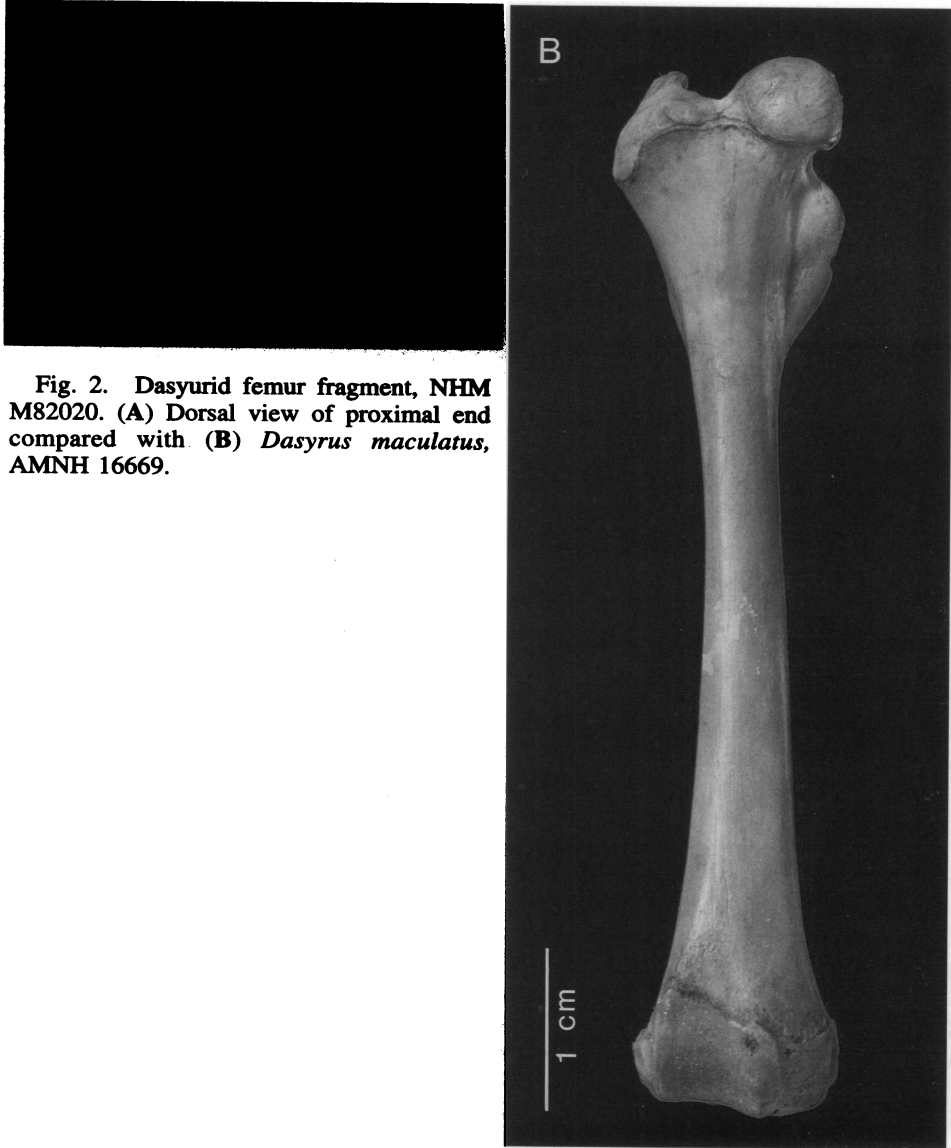


Fig. 2. Dasyurid femur fragment, NHM M82020. (A) Dorsal view of proximal end compared with (B) *Dasyurus maculatus*, AMNH 16669.

epiphysis of the greater trochanter can be identified as a dasyurid about the size of *Dasyurus maculatus*. Critical to this identification is the relatively small size of the lesser trochanter and its close proximity to the capitulum, the lack of expansion of the greater trochanter, and the smaller size of the capitulum relative to the size of the proximal end as a whole. This fragment differs very little from the corresponding element in *Dasyurus maculatus*. The trochanteric fossa may be relatively smaller and the trochanter itself

smaller than in the living form, but breakage in that area makes it difficult to assess the extent of these differences if indeed they do exist.

COMMENTS: This modern-looking dasyurid bone is an indication of the state of differentiation of the postcranial skeleton of dasyurids by mid-Tertiary time.

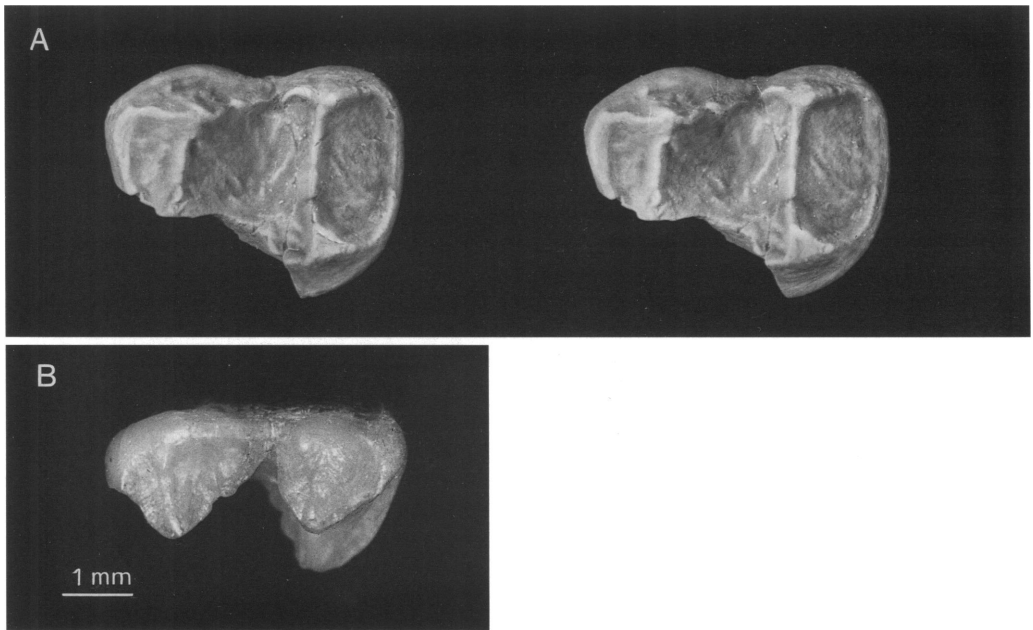


Fig. 3. Petauroid gen. and sp. indet. A. Left M1, NHM 82000, (A) stereopair of occlusal view, (B) labial view.

ARCHER, 1987

SUPERFAMILY PETAUROIDEA (GILL, 1872, SENSU  
MARSHALL ET AL., 1990)

FAMILY INCERTAE SEDIS

Genus and species indet. A

Most of the remains comprising the Geilston Bay collection represent a primitive petauroid identified as a likely phalangerid by Tedford et al. (1975). This form is similar in size to the larger taxa grouped in that superfamily. None of the remains is known to compose a single individual but all those listed seem logically associated with one taxon because of their appropriate size, morphology, and frequency of cranial to postcranial remains. The material consists of an unerupted left M1 lacking its protocone (NHM M82000, fig. 3); a left m2 or 3 (NHM M82001, fig. 4); a left P3 lacking the anterior end and root (NHM M82003, fig. 5); a left ramal fragment with lower incisor, alveoli for ?i2, p1, p3, m1 (NHM M82005, fig. 6A–C); left ramal fragment with alveoli for m1–4 (NHM M82006, fig. 6D–F); right ramal fragment with alveoli for the posterior root p3, m1–4 (NHM M82007, fig. 6G–I); two small

jaw fragments with alveoli for undetermined molars (NHM M82008, M82009); right lower incisor (NHM M82010); left lower incisor (NHM M82011); two upper canines (NHM M82012a–b); right humerus lacking entepicondyle (NHM M820123, fig. 8); proximal end left radius (NHM 32014); fragment of proximal end of left ulna (NHM M82015); proximal end of left tibia lacking medial trochlea (NHM M82016); shaft of right tibia (NHM M82017); distal epiphysis of right tibia (NHM M82018); and left calcaneum (NHM M82019, fig. 9).

The unerupted upper molar (NHM M82000, fig. 3, length 4.4; width of metaloph 3.3) appears to be an M1 judging from the oblique orientation of the bladeliike paracone and its cristae relative to the metacone, and the large anterior cingula shelf and anterolabial cingulum. It is a simple bilophodont tooth, lower crowned than in living phalangeroids, but similar to those of living forms in its lophodonty, enamel crenulation, prominent anterior and posterior cingula, and the metastyle (stylar cusp C) at the posterior end of the postparacrista. There is also a short premetacrista but these crests do not

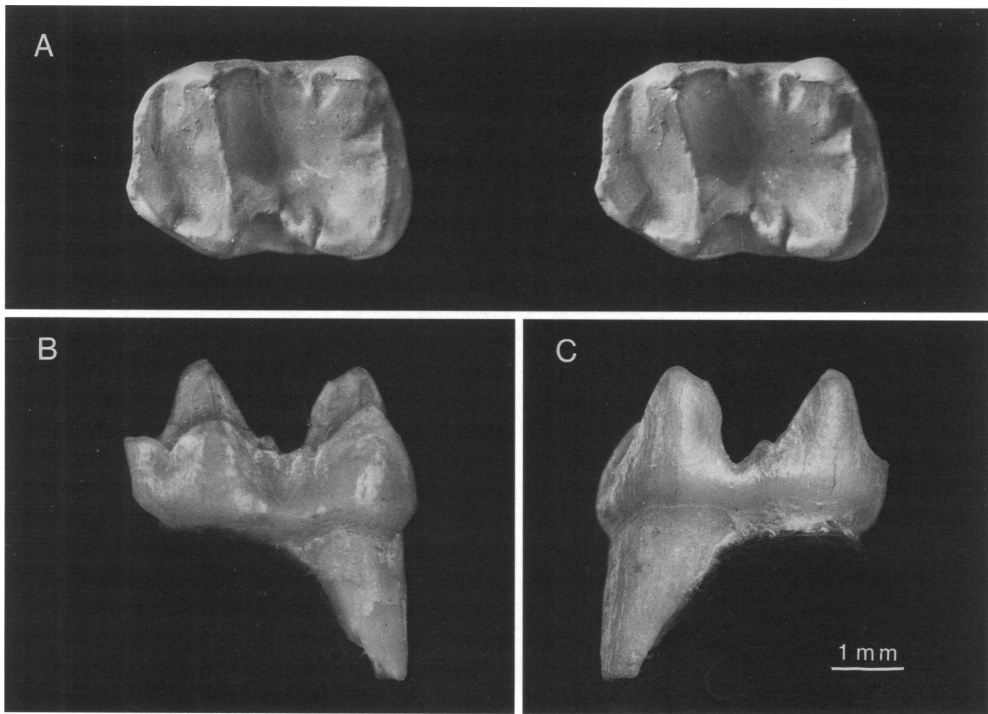


Fig. 4. *Petauroid* gen. and sp. indet. A. Left M2 or 3, NHM 82001, (A) stereopair of occlusal view, (B) labial view, (C) lingual view.

block the median valley. The remnant of the postprotocrista on the anterior face of the metaconule ("hypocone") implies a more lingual position for this crest and probable lack of a kink characteristic of living phalangeroids. There is no suggestion of a neo-metaconule, but the metaloph is created by a fissure lying in the lingual half of the loph. The pattern of crenulations emanates from the principal cusps, particularly the labial ones.

The lower molar, m2 or 3 (NHM M82001, fig. 4, length 4.2; width across the protolophid 2.8; width across talonid 3.0), is in early wear, but worn sufficiently to obscure some of the low crenulations that occurred in the talonid basin. The major cusps are peripheral, the lingual much higher than the labial ones, their apices placed slightly in front of the labial cusps. A sharp-crested protolophid is present. The trigonid retains a paraconid separated from the protoconid by a sharp cleft yet continuous with the anterior cingulum lingually. The postmetacristid has a low metastylid at its termination in the median

valley. There is no hypolophid, instead the posthypocristid terminates in a low cusp (hypoconulid) separated from the entoconid by a groove at the posterior base of the latter. There is a pre-entocristid, but this does not block the median valley. There is no posterior cingulum. The talonid basin is deeply concave and bowl-like to receive a large bunodont protocone; the shallower basin formed by the anterior cingulum predicts that the talon of the occluding upper molars will resemble that of the *petauroids*. However, there is a kinked crista oblique resembling the condition in phalangerids. The anterior part of the crista is created by a sharp groove about halfway along the prehypocristid. The crista bifurcates just in front of this crease, sending a short segment lingually into the talonid basin. A sharp crease separates the two contributions to the crista obliqua. The crista obliqua blocks the median valley and a low cingula shelf encloses a shallow pocket against the crista labially.

The left P3 (NHM M82003, fig. 5, length approx. 3; width 2.3) has the base of the an-



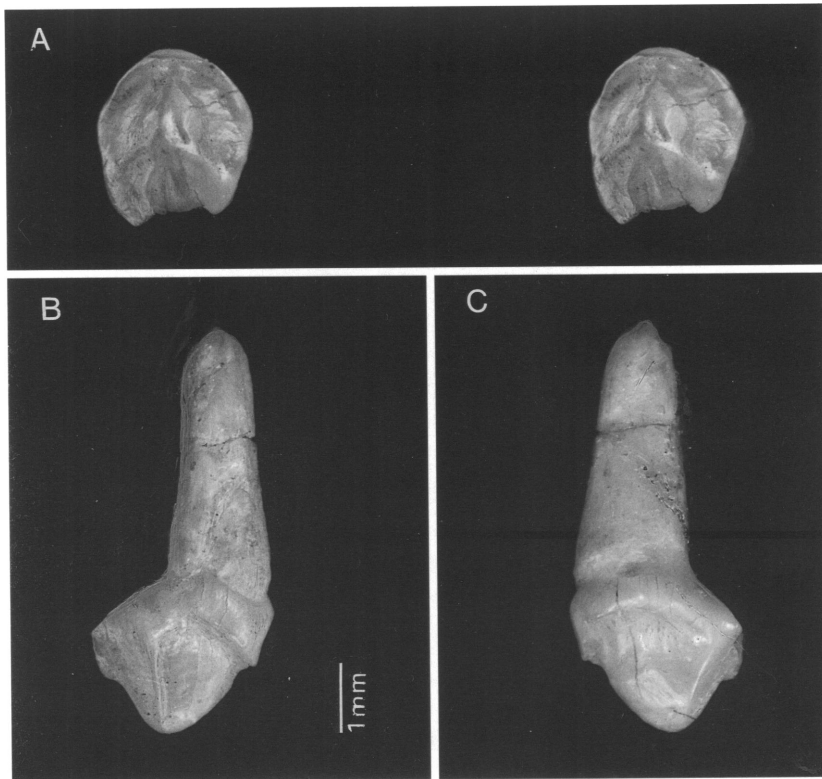


Fig. 5. Petauroid gen. and sp. indet. A. Left P3, NHM M82003, (A) stereopair of occlusal view, anterior end below, (B) labial view, (C) lingual view.

terior end of the crown broken away. The crown is a laterally flattened cone completely surrounded by a cingulum that is wider in the posterior half of the tooth and narrower anteriorly. Two low crests pass from the anterior part of the apex to the labial and lingual cingula, and the anterior surface of the crown is faceted between these crests. The labial member of this pair bears an anterior cusplet that stands well above the cingulum. The posterior crest also reaches the cingulum where a small cusplet is formed. Identification of this tooth as an upper premolar is based on the fact that the posterior root is not only larger but also much wider than the anterior root. The P3 is conical like those of petauroids rather than bladelike and rotated labially as in most phalangeroids.

The lower incisors (NHM M82005, fig. 6A–C; M82010, M82011), like the cheek teeth, resemble those of phalangeroids but are more procumbent, show slightly greater dorsoventral curvature and relatively shorter

crowns. The crowns are wide at the tip and do not taper to a point as in petauroids.

The upper canines differ from each other in that NHM M82012a has a longer and more robust root than NHM M820126, possibly representing sexual dimorphism. The crowns are compressed blades and resemble those of phalangeroids and petauroids.

Three jaw fragments (NHM M82005, M82006, M82007, fig. 6A–I) help reconstruct the form of the horizontal ramus and show some details of the masseteric fossa (fig. 7). These specimens show that the lower dental formula is similar to that of living phalangerids and pseudocheirids:  $i1-2, p1, p3, m1,2,3,4$ . The alveolus for  $i2$  lies nearly horizontally in the diastemal crest, indicating a recumbent tooth as in phalangerids and petauroids. It probably bore a beadlike crown resting on the dorsal surface of the  $i1$  although no facet can be seen on that tooth. The alveolus for  $p1$  shows a single root slanting backward at a lesser angle than  $i2$ . A

diastema separates p1 from the double-rooted p3. The anterior root of p3 is about half the diameter of the posterior and is more shallowly implanted. The whole tooth is slanted slightly forward. Alveoli show that p3 was about  $\frac{3}{4}$  the length of m1 with the anterior root about half the size of the posterior. Alveolar lengths and widths indicate the following molar gradient:  $m1 = m2 > m3 > m4$ , not unlike that of living phalangerids and petaurids. The symphysis extends backward to beneath m1, where its posterior margin is slightly flanged and is thus visible from the labial side. A large mental foramen occurs just beneath the anterior root of p3, one or two small foramina pierce the body of the mandible on the labial side beneath the m1-2 junction. A masseteric foramen occurs within the masseteric fossa and opens into the interior dental canal opposite the mandibular foramen.

The masseteric fossa is strongly rimmed dorsally by the masseteric crest and the cheek tooththrow lies mostly anterior to the base of the coronoid process. The fossa shallows into the lateral side of the horizontal ramus beneath m4. Overall the morphology of the ramus resembles that of phalangerids more closely than petauroids or other phalangeroids.

The humerus (NHM M82013, fig. 8) resembles that of *Trichosurus*, differing only in having a more robust deltoid ridge, deeper bicipital groove, narrower head, and relatively shorter shaft. In these features it more closely resembles the petauroid *Pseudocheirus* than the phalangeroid *Trichosurus* and it differs even more markedly from *Phalanger*. The fragments of the radius (NHM M82014) and ulna (NHM M82015) differ in no remarkable way except size from their counterparts in *Trichosurus*. The shape of the proximal articular surface of the radius is oval rather than nearly round as in *Pseudocheirus* and *Phalanger*. Likewise the tibia fragments (NHM M82016, M82017, M82018) produce a composite which differs very little from that of *Trichosurus* and rather markedly from *Phalanger* or *Pseudocheirus*. The shaft is strongly flattened as in *Trichosurus*, not triangular in cross section as in *Phalanger* or *Pseudocheirus*, and the proximal end is narrow as in the brush-tail

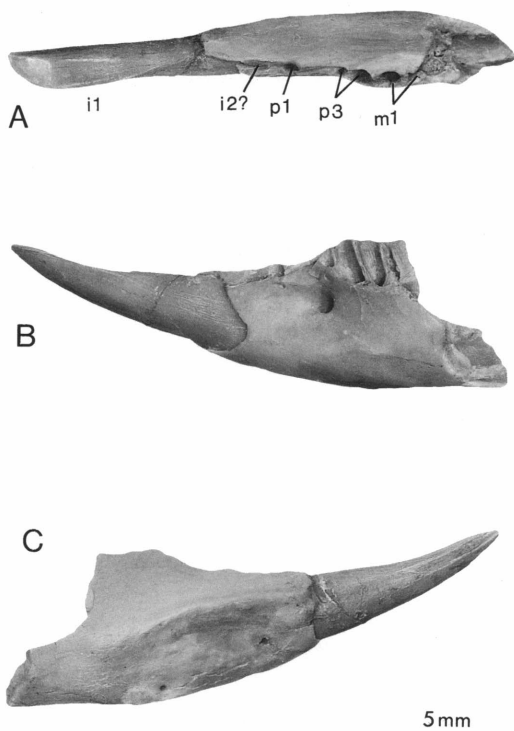


Fig. 6. Petauroid gen. and sp. indet. A. Left ramal fragment with lower incisor, NHM 82005, (A) occlusal view, (B) labial view, (C) lingual view. Left ramal fragment, NHM M82006, (D) occlusal view, (E) labial view, (F) lingual view. Right ramal fragment, NHM 82007, (G) occlusal view, (H) labial view, (I) lingual view.

possum rather than wide as in other possums. A well-marked crest on the anterior edge of the flattened shaft, about  $\frac{1}{3}$  of the probable total length from the proximal end, closely resembles that in *Trichosurus*. This process is more prominent than in *Phalanger* and *Pseudocheirus*. The distal articular surface closely resembles that of *Trichosurus*; the lateral malleolus is produced and faceted as in the brush-tail possum, rather than being flattened as in *Phalanger* or produced to a point as in *Pseudocheirus*.

In essential proportions, the calcaneum (NHM M82019, fig. 9) of the fossil form differs from those in other petauroids and resembles the form in *Trichosurus*; the tuber is large and deeper than the cuboid articulation and not so bent posteriorly on the distal part of the bone. The lateral articular surface

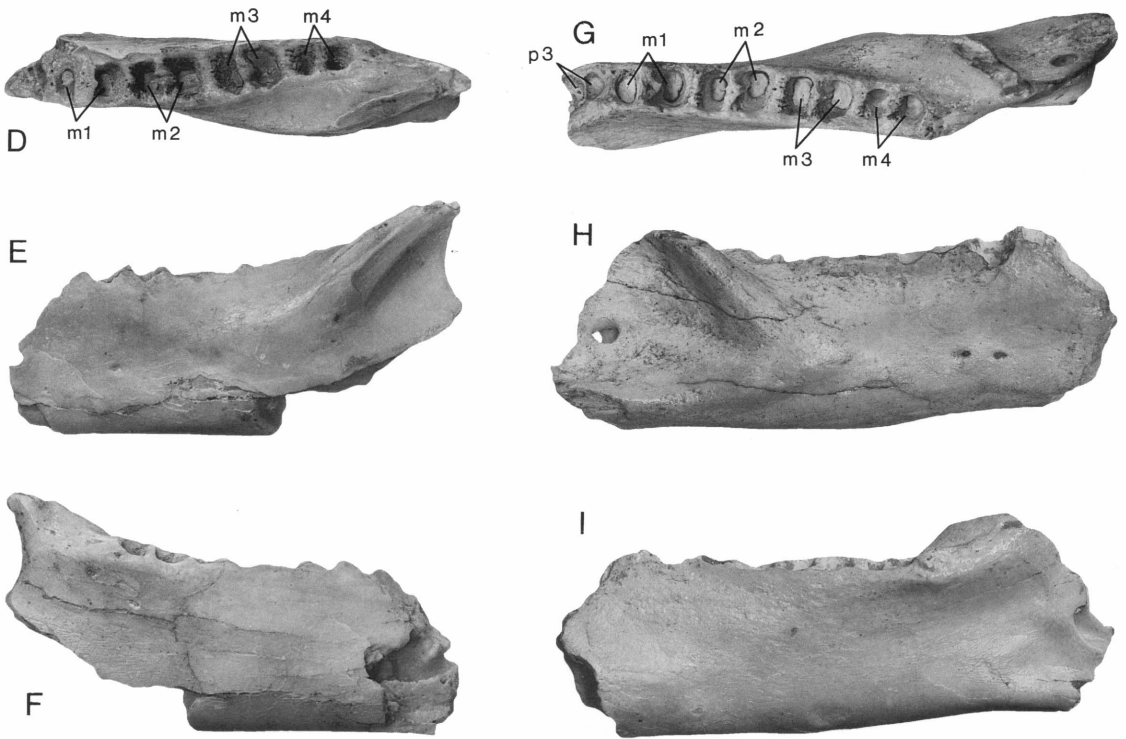


Fig. 6. Continued.

for the astragalus is a narrow, pointed projection as in petauroids and *Trichosurus* rather than the large knob seen in the cuscus and koala.

COMMENTS: Despite the number of skeletal resemblances to *Trichosurus*, the Geilston Bay possum cannot be unequivocally referred to the Phalangeridae without a more comprehensive phyletic analysis of the postcranial skeleton. However, the referred limb

bones of the fossil possum indicate a quite "modern" stage in postcranial osteology. It is tempting to refer other unallocated metapodials and vertebral fragments (NHM 40156) to the same taxon, because these suggest that syndactyly and a long caudal column were also a part of the total morphology of this animal.

If the rami are correctly referred to the same taxon as the lower molar, they dem-

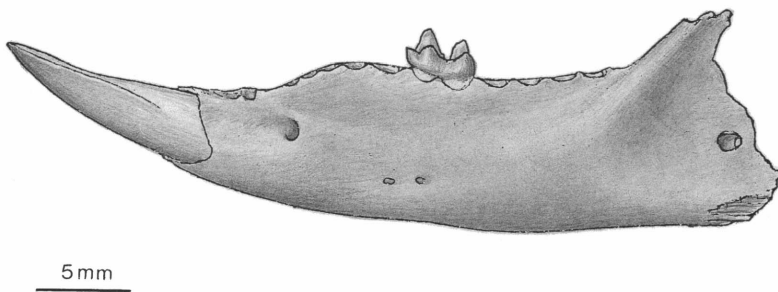


Fig. 7. Petauroid gen. and sp. indet. A. Reconstruction of the horizontal ramus and part of the dentition combining remains illustrated in figs. 4 and 6.



Fig. 8. Petauroid gen. and sp. indet. A. Fragment of right humerus, NHM 82013, compared with *Trichosurus vulpecula*, AMNH 3771, (A) ventral view, (B) dorsal view.

onstrate three synapomorphies shared with other families of the Petauroidea: loss of p2 (pseudocheirids only), reduction in size of P3 and p3 (except pseudocheirids), and lower molars in which the entoconid is the tallest talonid cusp (all families). The crista obliqua retains the kinked morphology shared with the phalangeroids, a feature modified to a more curved or linear form and a more peripheral position on the crown in more derived petauroids. These relationships are further discussed below and summarized in table 1 and figure 13.

Since the enigmatic *Wynyardia bassiana* Spencer, 1901, was the first Tasmanian Tertiary marsupial to be described, and of a geologic age (early Miocene) not too far re-

moved from the material presented herein, it may be of some interest to compare relevant parts of the Tasmanian specimens. Unfortunately, there are few comparable limb elements of *W. bassiana* and its holotype lacks dentition. Of the skeletal fragments assigned to petauroid gen. et sp. indet. A, only the tibia can be compared with that of *W. bassiana*. Although it is about half the size of the *W. bassiana* tibia, it also compares favorably with that of *Trichosurus*. Wood-Jones (1931) showed that the skeletal elements of *W. bassiana* are those of a diprotodontian close to those of the Phalangeridae s.l. The skull of *W. bassiana*, although clearly that of a diprotodontian, has a primitive-appearing auditory region. Aplin (1987),

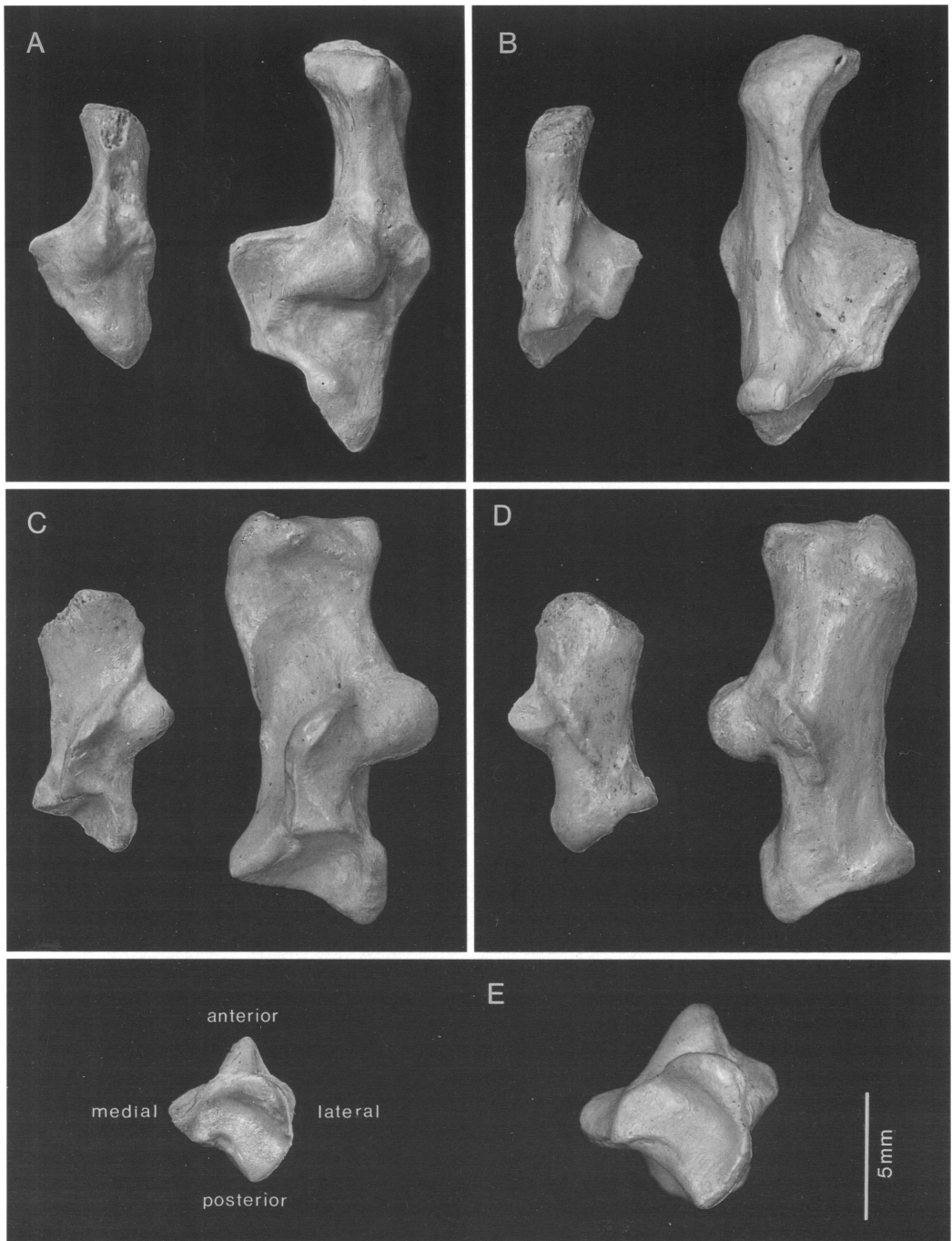


Fig. 9. Petauroid gen. and sp. indet. A. Left calcaneum, NHM M82019, compared with *Trichosurus vulpecula*, AMNH 3771, (A) anterior view, (B) posterior view, (C) medial view, (D) lateral view, (E) distal view.

searching beyond these primitive features, showed that its closest affinities are actually with vombatiform diprotodontians. The phalangerid resemblances in the limbs must represent primitive diprotodontian features, as is also the case for petauroid gen. et sp. indet. A, whose referred limbs also resemble those of a range of arboreal phalangeridans.

#### Genus and species indet. B

The associated worn molar row, NHM 40167 (fig. 10), was tentatively identified by Tedford et al. (1975) as an upper dentition of a palorchestid about 65% of the size of *Ngapakaldia tedfordi*. On closer examination, this specimen is clearly seen to be a lower tooththrow comprising the lingual half of m1 and m2-4, well worn but mostly intact. Critical to this reinterpretation is the simple proportions of the teeth, which are longer than wide as in the lower molars of most Diprotodontia, and the observation of the orientation of the individual teeth which tilt inward at the rear of the tooththrow and outward at the front rather than the opposite relationship typical of the upper dentition in diprotodontians. M2 length 8.5, anterior width 7.0, posterior width 6.8; M3 8.2, 7.0, 6.3; M4 8.0, 5.8, 5.7.

Interpretation of the crown pattern is difficult due to the advanced wear of the teeth, but the less worn m4 and the form of the wear patterns of individual teeth can be unambiguously interpreted. The teeth gradually decrease in length posteriorly and increase in height of crown anteriorly. In general, the worn pattern is lophodont: the principal cusps are peripheral on the crown and connected by cristids to form a protolophid anteriorly and possibly a hypolophid posteriorly. The lingual and labial faces of the crown appear vertical, further emphasizing the lophodonty. The lingual cusps are more prominent than the labial ones. The crista obliqua is labially situated and blocks the wide, shallow talonid valley. Coarse crenulations cross the valley on m4 and probably also on the other molars before removal by wear. The talonid valley is nearly closed lingually by converging cristids from the principal cusps and a low cingulum lies across the lingual end of the valley. The m2-4 have a wide an-

terior cingulum that apparently arises from the protoconid, passes across the entire anterior face of the tooth, and ascends the metaconid. The posterior cingulum is also wide and becomes shelflike on m4. Wear has obliterated the details of structure but that cingulum appears to have arisen from the posterior face of the hypoconid and passed to a cusplet (hypoconulid) at the posterior base of the entoconid. There does not appear to be a "hypolophid pocket" developed between that crest and the posterior cingulum. The crista obliqua originates from the anterolabial side of the hypoconid and passes directly anteriorly to meet the shorter contribution from the posterolabial side of the protoconid. There is a concavity in the labial border of the m2-4 where these segments of the crista meet and a sharp external cleft on m2-3. The anterior end of the crista bifurcates just before reaching the protoconid contribution. The metaconids of m1-4 bear a metastylid which, with the interconnecting cristid, forms a posteriorly directed crest emanating from the lingual end of the protolophid.

It is unfortunate that more of the m1 is not preserved, but the fragments of the lingual ends of the lophids have the same form as the molars that succeed them. The metaconid-metastylid crest seems to be more obliquely oriented than in m2-4, implying a narrowing of the trigonid anteriorly, which would bring the protoconid and metaconid closer together as seen in most diprotodontians. The high crown of the metaconid and its bladelike forms suggests the presence of a bladelike p3.

Such a p3 is indicated by the posterior half of a crown (width 5.6) and supporting root, NHM M82004 (fig. 11), of an appropriately sized left p3 that is tentatively referred to the same taxon as the molar row. This fragment bears a stout root; the crown lacks serrations and is a rather simple trenchant tooth bordered by a posterolingual swelling of the cingulum and no distinct cuspule. A wear facet marked by vertical striations truncates the surface of this swelling and extends to the crestal part of the tooth implying shearing occlusion with a secant upper premolar.

COMMENTS: The features displayed by these specimens agree best with those of the petauroids despite their much greater size

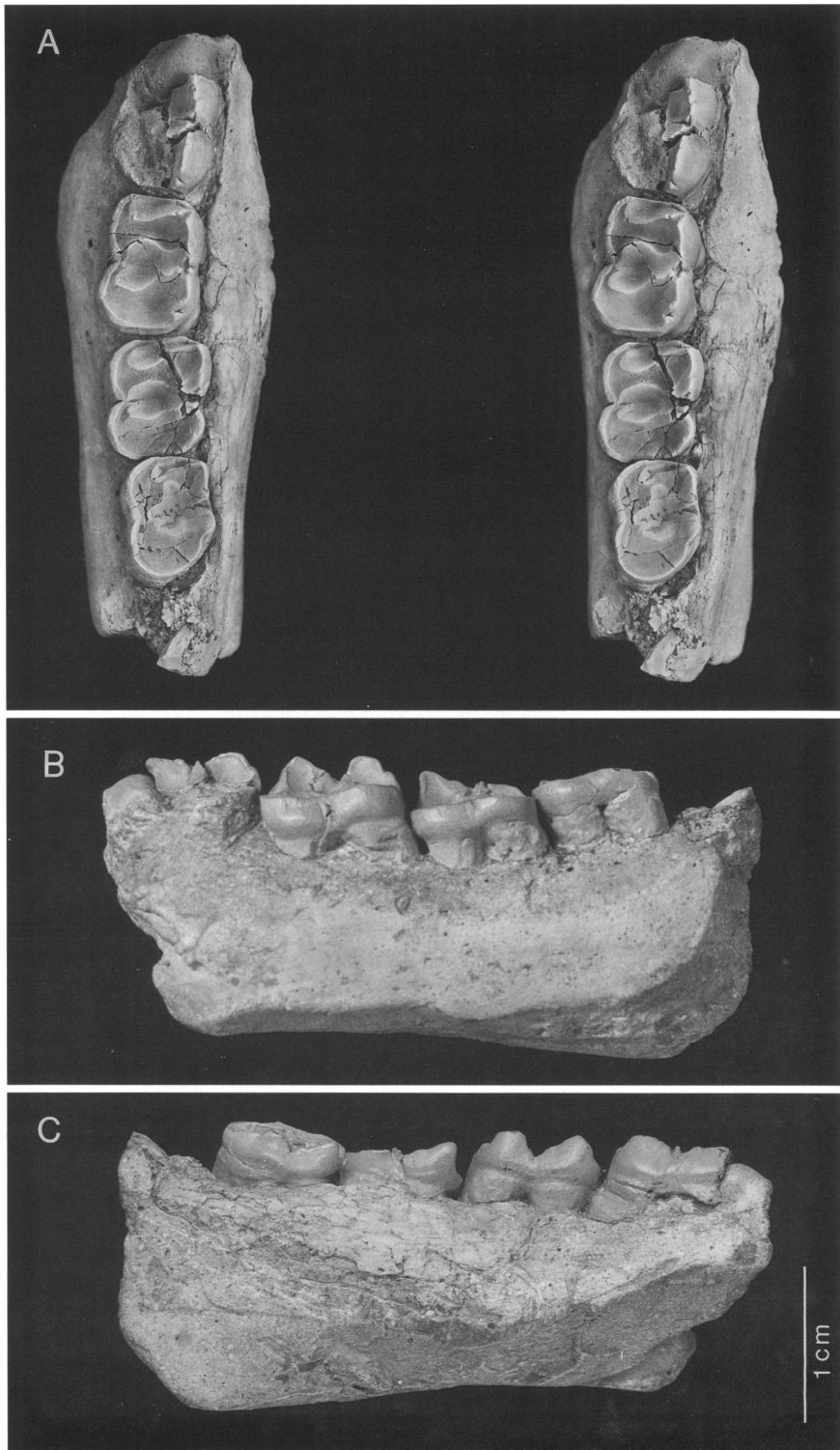


Fig. 10. *Petauroid* gen. and sp. indet. B. Fragment of left ramus, NHM 40157, (A) stereopair of occlusal view, (B) labial view, (C) lingual view.

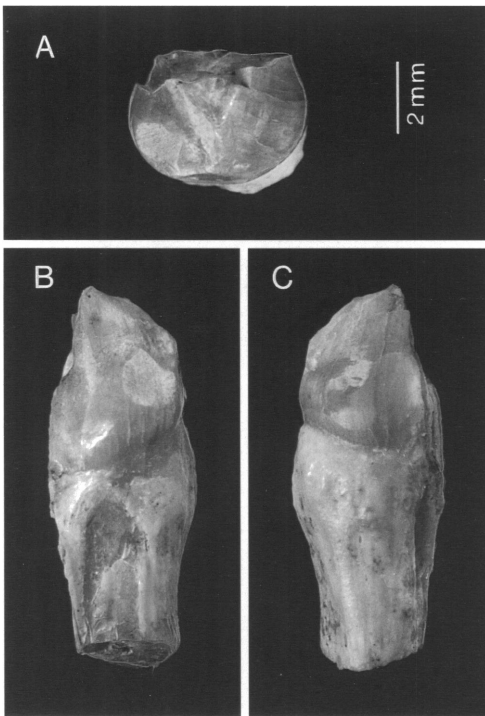


Fig. 11. Petauroid gen. and sp. indet. B. Fragment of left p3, NHM M82004, (A) occlusal view, anterior to top, (B) labial view, (C) lingual view.

than those in living or described late Tertiary fossil forms. Primitive features would include the relatively larger p3 (if correctly associated) and lower molar length gradient along the toothrow. Both features are shared with the pseudocheirids. Derived features held in common with those of petauroids would include increasing height of crown anteriorly, a linear, peripheral crista obliqua, and an entoconid as the largest talonid cusp. The peripheral major cusps, presence of a low protolophid and perhaps a hypolophid, and the lack of strong indentation of the labial and lingual borders are derived features shared with phalangeridans. The presence of metastylids throughout the molar row is probably an autapomorphy for the Geilston Bay species although metastylids are also present in pseudocheirid petauroids. Further discussion of the phylogenetic position of this form is given below and summarized in table 1 and figure 13.

Although no teeth were associated with the holotype of *Wynyardia bassiana* Spencer,

1901, some Australian late Oligocene or early Miocene taxa have been postulated as representatives of the family Wynyardiidae proposed by Osgood (1921) solely for the type species. The only published bases for this were some superficial similarities in limb morphology noted by Tedford et al. (1977) between the limbs of *Wynyardia* and those of a form of the genus *Muramura* Pledge (1987) from the Namba Formation of the Lake Frome region in South Australia. Pending a detailed analysis of these materials (Pledge, in prep.), the resemblances noted by Tedford et al. (1977) are just as likely to be primitive diprotodontian features as noted above in the comparison of the limbs of *W. bassiana* with phalangeridans including petauroid gen. et sp. indet. A. They are thus not at present indicative of phylogenetic relationships beyond that of inclusion in the order Diprotodontia. As noted by Aplin and Archer (1987: xlvi), reference of species of *Muramura* or *Namilamadeta* Rich and Archer 1979 to the Wynyardiidae is now moot.

Nevertheless, it is germane to compare the dentitions of these "wynyardiid" genera to that of petauroid gen. et sp. indet. B, if only to reject close relationship. Despite the heavy wear in the Geilston Bay form, it can be seen to differ from *Muramura williamsi* Pledge, 1987, in lower crown height, less organized lophodonty, peripheral placement of the crista obliqua, and greater molar height and length gradient (m1 apparently the highest, longest tooth, m4 significantly shorter than m1-3). These features are more compatible with phalangeridans than vombatiforms.

#### FAMILY BURRAMYIDAE (Broom, 1898)

##### Genus indet.

A single right lower incisor (NHM M82002, fig. 12) is the only identified remains of a species assignable to this family. The diagnostic features are the needlelike form and flattened, upturned tip of the crown. This tooth is most similar to those of *Cercartetus* and *Burramys*, especially the former, although it is about twice the size of any living species of that genus (crown length 7.6, crown depth at base 1.7, crown width at base 1.3). This tooth differs from those of acrobatids such as *Distoechurus*, in





Fig. 12. Burramyid gen. indet. Right lower incisor, NHM M82002, (A) stereopair of dorsal view, (B) lateral view.

being more attenuated and lacking the medial bend shown by the tip of the incisor in the pentailed possums. There is also some resemblance to the larger needlelike lower incisor of the macropodoid *Hypsiprymnodon*, but the fossil form is shorter-crowned, somewhat shallower, and shows a terminal flattening and upward flexure not seen in the muskrat kangaroo.

COMMENTS: This specimen extends the antiquity of the burramyid petauroids into the late Oligocene of Tasmania where pygmy possums with similar incisors remain part of the living marsupial fauna of this temperate region.

#### DISCUSSION

The Geilston Bay local fauna contains an array of taxa that differ in composition from those of nearly contemporary sites elsewhere

in Australia (Archer et al., 1989; Woodburne et al., 1994). The prevalence of petauroid diprotodontians is of particular interest in affording a view of a group that is not diversely represented in the Oligocene and early Miocene faunas of the mainland.

Because the association of elements composing the two petauroid genera and species indet. A and B is necessarily subjective, the phylogenetic analysis of these forms is limited primarily to the morphology of the lower dentition and secondarily to the rami. Its scope is thus highly constrained by the range of characters available in the fossils under comparison. The characters used as a basis for the analysis and resulting cladogram are summarized in table 1 and illustrated in figure 13. The analysis ranges across the Phalangerida, Aplin and Archer, 1987, and uses the Vombatiformes Woodburne, 1984, as the outgroup.

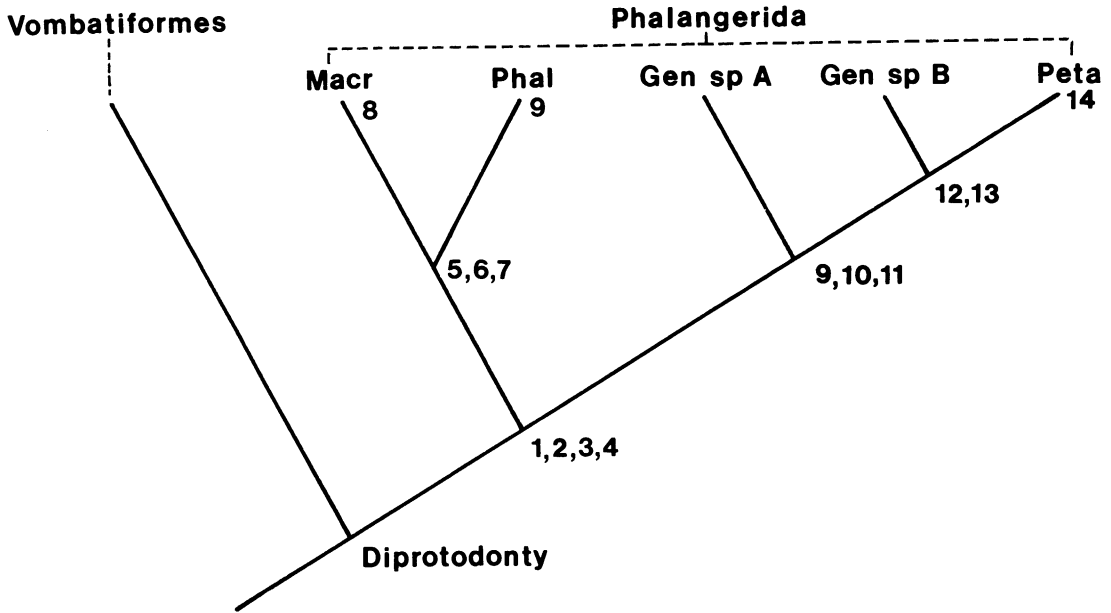


Fig. 13. Cladogram showing postulated phylogenetic relationships of the Geilston Bay petauroids to Macropodoidea (Macr), Phalangeroidea (Phal) and other Petauroidea (Peta). The Vombatiformes serve as the outgroup. Taxa sensu Marshall et al., 1990. Character numbers refer to table 1.

TABLE 1

**Distribution of Derived (1) and Primitive (0) Character States Used in Cladistic Analysis of the Geilston Bay Petauroids**

Macr, Macropodoidea; Phal, Phalangeroidea; Peta, Petauroidea (all taxa sensu Marshall et al., 1990)

	Macr	Phal	Gen A	Gen B	Peta
1. Principal lower molar cusps central (0) or peripheral (1) on crown.	1	1	1	1	1
2. Crista obliqua central (0) or labial (1) on crown.	1	1	1	1	1
3. Lower molars without (0) or with (1) protolophid.	1	1	1	1	1
4. Crista obliqua linear (0) or kinked (1).	1	1	1	0	0
5. Lower molars without (0) or with (1) hypolophid.	1	1	0	1?	0
6. P3/p3 conical, smooth (0) or bladeliike, serrated (1).	1	1	0	0	0
7. P3/p3 axis in line with molar row (0) or axis deflected (1) from molar row.	1	1	0	0	0
8. Masseteric canal absent (0) or present (1).	1	0	0	0	0
9. p2 present (0) or absent (1).	0	1	1	?	0-1
10. Lower molar entoconids smaller/equal to hypoconids (0) or larger than hypoconids (1).	0	0	1	1	1
11. P3/p3 unreduced (0) or reduced (1) in size relative to M1/m1.	0	0	1	1	1
12. Crista obliqua linear (0) or curved (1).	0	0	0	1	0-1
13. Lower molars do not (0) or do (1) increase in height anteriorly.	0	0	?	1	1
14. Lower incisor tip broad (0) or pointed (1).	0	0	0	?	1

In the course of this character analysis most relevant living and fossil phalangeridan genera were examined through specimens, casts, or the literature. Important discussion and references were found in Archer and Clayton (1984, especially the excellent drawings of living phalangeridan dentitions by M. O. Woodburne), Aplin and Archer (1987), Springer and Woodburne (1988), and Marshall, et al. (1990).

The Phalangerida are defined by four features of the lower molars (characters 1–4, table 1) in this analysis: 1) peripheral placement of the major cusps on the crown; 2) their organization into a semilophodont arrangement through establishment of at least a protolophid; 3) crista obliqua nearly continuous across the labial end of the median valley; and 4) marked inflection or “kink” where crista obliqua crosses the medial valley. The imposition of selenodonty (*Pseudocheiridae*) or lophodonty (*Macropodoidea*) has modified some of these characters, but this distribution seems to imply that these features are present among the stem groups of the phalangeridan families. Geilston Bay genus and species indet. A retains a “kinked” crista obliqua along with its more derived petauroidlike features. Modification of the crista into a more curved structure is considered a further derivation characteristic of other petauroids. Further modification to the linear crista obliqua of pseudocheirids is a development consequent to the groups strong selenodonty.

Petauroids show less reduction of the number of anterior premolars than other phalangeridans, although some groups, notably Geilston Bay genus and species indet. A, and the pseudocheirids, lose p2. The p3 is relatively reduced in the petauroids (except in the pseudocheirids where it is submolariform) compared with that of kangaroos and phalangeroids. It lacks serrations and has an anteroposterior orientation with the molar row unlike the bladelike and oblique p3 of the latter groups. Furthermore, the lower molars of petauroids have large lingual cusps, especially the entoconid, and a hypolophid fails to form in any of these taxa except possibly Geilston Bay genus and species indet. B. The latter seems a little more proximal to the living petauroids, despite its large size, in

the gently curved crista obliqua and the increase in crown height of the molars anteriorly.

The hypothesis of relationships advanced here is admittedly based on the very limited evidence imposed by the nature of the fossil material being considered. Nevertheless, it has been possible to relate the two Geilston Bay phalangeridans specifically to the clade that includes the living petauroids. They appear to constitute a stem group that gives some evidence of the sequential acquisition of the synapomorphies that unite the living members of this clade. These fossils also give further evidence of a greater diversity of petauroids than afforded by the previous records and pushes the initiation of cladogenesis of the Diprotodontia back into the Eocene.

## CONCLUSIONS

The fossiliferous travertine at Geilston Bay, southeastern Tasmania, has been investigated by earth scientists for 150 years, but only in the mid 19th century were fossils collected in situ by hand-operated quarrying. The fragmentary vertebrate fossils found in about 1865 and reported by Morton Allport (1866) remain the sole evidence of the fauna contemporaneous with a rich macroplant assemblage in the marl and travertine deposits. This collection was sent to Richard Owen at the British Museum in 1866 and was retained there unnoticed for more than 100 years until its rediscovery by the late Jack Mahoney in 1973. A preliminary account of the material and its geological age was announced in 1975 by the authors of the present work assisted by three geological colleagues (Tedford et al., 1975). At that time, these remains were the oldest terrestrial mammals known from Australia.

A complete description and analysis of the Geilston Bay local fauna was fortunately delayed while studies of other Tertiary faunas from Australia were completed. At the same time, wider-ranging phylogenetic studies of the Australian marsupials were presented (Archer and Clayton, 1984, Aplin and Archer, 1987, Marshall et al., 1990) that yielded hypotheses of relationships with which the fossils could be compared. Additional infor-

mation on the age of the deposit and its local correlatives and the volcanic history were also obtained (Leaman, 1976; Sutherland and Wellman, 1986). These data can be summarized as follows.

The Geilston travertine appears to represent a facies of a largely fine-grained, clastic infilling of a predecessor of the River Derwent that flowed southeastward through a rugged terrain, clothed by a rainforest of conifers and angiosperms representing a diverse sample of the mid-Tertiary flora of southern Australia. In the Oligocene, Tasmania was positioned on the trailing edge of the northward-moving Australian continent, at about 50°S latitude (Wilfold and Brown, 1994). Unfortunately, samples of the Geilston Bay flora have not been preserved in Tasmanian collections so that the flora cannot be reevaluated beyond the data available in the 19th century, but its composition, as far as known, is matched by other low elevation Tasmanian floras of Oligocene and early Miocene age (Carpenter et al., 1994). These indicate the presence of microthermal rainforests that imply a mean annual temperature in the range of 12°C, under a wet and humid climate.

The Geilston Bay local fauna consists of a minimum of four taxa: A dasyurid, whose femur resembles that of living scansorial *Dasyurus* spp. Two petauroid genera and species whose dentitions and postcranials are more primitive than those in living members of any of the families in that superfamily. (They were undoubtedly arboreal in lifestyle, as shown by the limbs assigned to genus and species indet. A.) There is also a single lower incisor representing a burramyid petauroid larger than any known living or fossil member of this group. The prevalence of scansorial over arboreal forms is consistent with the rainforest environment indicated by the flora.

The contrast in composition of the Geil-

ston Bay local fauna with near contemporary assemblages in the Lake Frome and Lake Eyre regions of interior South Australia is striking, and along with the evidence of further compositional contrasts with approximately coeval faunas of western Queensland at Riversleigh, implies significant latitudinal zoogeographic differentiation across Australia in the late Oligocene and earliest Miocene, paralleling the phytogeographical gradients deduced from microfloras (Martin, 1994).

Our phylogenetic analysis of the Geilston Bay local fauna also constrains aspects of the history of the Australian marsupial fauna. The occurrence of a highly derived suite of petauroids in the middle to late Oligocene of Tasmania implies a prior age for the fundamental cladogenesis within the Phalangerida and even earlier age for the differentiation of the Diprotodontia. Springer and Kirsch (1991) deduced, based on single-copy DNA hybridization experiments, that the sequence of divergence within the Diprotodontia was vombatiforms (macropodoids ((phalangeroids + petauroids))). This cladogenesis was calibrated by paleontological data interpreted by Spring and Kirsch (1991) to indicate a divergence of macropodids and potoroids between 25 and 15 Ma, averaged to 20 Ma (actually the groups were separated by 25.5 Ma according to Woodburne et al., 1994, implying an even earlier divergence date). The rate of single-copy DNA divergence per million years obtained from these data postulated a mid-Eocene, 49-45 Ma origin of the phalangeridans, a conclusion compatible with the presence of the stem petauroids nested within that group at 23 Ma at Geilston Bay. The claimed low level of differentiation of marsupials in the Tingamarra local fauna of putative early Eocene age (Godthelp et al., 1992) also supports a later Eocene origin of the Diprotodontia.

## REFERENCES

- Allport, M.  
 1866. Notice of some fossils recently discovered near Risdon, Tasmania. Pap. Proc. R. Soc. Tasmania, 1865: 73-75.  
 1868. [Untitled report]. Pap. Proc. R. Soc. Tasmania, 1867: 18.  
 1877. [Untitled report]. Pap. Proc. R. Soc. Tasmania, 1876: 60-61.

- Aplin, K. P.  
1987. Basicranial anatomy of the early Miocene diprotodontian *Wynyardia bassiana* (Marsupialia: Wynyardiidae) and its implications for wynyardiid phylogeny and classification. In M. Archer (eds.), *Possums and opossums: studies in evolution 1*: 369–391, Sydney: Surrey Beatty and the Royal Society of New South Wales.
- Aplin, K., and M. Archer  
1987. Recent advances in marsupial systematics with a new syncretic classification. In M. Archer (eds.), *Possums and opossums: studies in evolution 1*: xv–xxii. Sydney: Surrey Beatty and the Royal Society of New South Wales.
- Archer, M., and G. Clayton  
1984. Vertebrate zoogeography and evolution in Australia (animals in space and time). Carlisle, Western Australia: Hesperian Press, xxiv + 1203 pp.
- Archer, M., H. Godthelp, S. T. Hand, and D. Megirian  
1989. Fossil mammals of Riversleigh, north-western Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zool.* 25: 29–65.
- Baillie, P. W., and D. E. Leaman  
1969. Southeastern Tasmania, In C. F. Burrett and E. L. Martini (eds.), *Geology and mineral resources of Tasmania*. Geol. Soc. Australia, Spec. Pub. 15: 365.
- Banks, M. R.  
1971. A fossil spring deposit at Geilston Bay. *Tasmanian J. Educ.* April 1971: 48–49.
- Carpenter, R. J., R. S. Hill, and J. G. Jordan  
1994. Cenozoic vegetation in Tasmania: the macrofossil evidence. In R. S. Hill (ed.), *History of Australian vegetation, Cretaceous to Recent*: 276–298. Cambridge: Cambridge Univ. Press.
- Dalrymple, G. B.  
1979. Critical tables for conversion of K-Ar ages from old to new constants. *Geology* 7: 558–560.
- Gill, E. d.  
1962. Cainozoic history. In A. Spry and M. R. Banks (eds.), *The geology of Tasmania*. *J. Geol. Soc. Australia* 9: 236–253.
- Godthelp, H., M. Archer, R. Cifelli, S. J. Hand, C. F. Gilkeson  
1992. Earliest known Australian Tertiary mammal fauna. *Nature* 356:514–516.
- Johnston, R. M.  
1888. Systematic account of the geology of Tasmania. Hobart: Gov. Printer, xxii + 408 pp.
- Leaman, D. E.  
1976. Hobart, Tasmania, Department of Mines, Geological Survey, Explanatory Report, Geological Atlas, 1:50,000 series.
- Marshall, L. G., J. A. Case, and M. O. Woodburne  
1990. Phylogenetic relationships of the families of marsupials. In H. H. Genoways (ed.), *Current mammalogy 2*: 433–505. New York: Plenum Press.
- Martin, H. A.  
1994. Australian Tertiary phytogeography: evidence from palynology. In R. S. Hill (ed.), *History of Australian vegetation, Cretaceous to recent*: 104–142. Cambridge: Cambridge Univ. Press.
- McDougall, I.  
1959. The Brighton basalts, Tasmania. *Pap. Proc. R. Soc. Tasmania* 93: 17–28.
- Moore, W. R.  
1965. Geology of the Risdon Vale area. Tasmanian Department of Mines, Tech. Rept. 9 (1964): 77–88.
- Nye, P. B.  
1924. Underground water resources of the Richmond-Bridgewater-Sandford District. Tasmanian Department of Mines, Underground Water Supply, Paper No. 3.
- Osgood, W. H.  
1921. A monographic study of the American marsupial *Caenolestes*. *Field Mus. Nat. Hist., Publ. Zool. Ser.* 14: 1–162.
- Pledge, N. S.  
1987. *Muramura williamsi*, a new genus and species of ?wynyardiid (Marsupialia: Vombatoidea) from the middle Miocene Etadunna Formation of South Australia. In M. Archer (ed.), *Possums and opossums: studies in evolution 1*: 393–400. Sydney: Surrey Beatty and the Royal Zoological Society of New South Wales.
- Spencer, W. B.  
1901. A description of *Wynyardia bassiana*, a fossil marsupial from the Tertiary beds of Table Cape, Tasmania. *Proc. Zool. Soc. London*, 1900: 776–794.
- Springer, M. S., and M. O. Woodburne  
1988. The distribution of some basicranial characters within the Marsupialia and a phylogeny of the Phalangerimorphia. *J. Vertebr. Paleontol.* 9: 210–221.
- Springer, M. S., and J. A. W. Kirsch  
1991. DNA hybridization, the compression effect, and the radiation of diprotodon-

- tian marsupials. *Syst. Zool.* 40: 131–151.
- Sutherland, F. L.  
 1972. Cainozoic volcanic rocks. In D. E. Leaman, Hobart, Tasmania, Geological Atlas, 1:50,000 series, Tasmanian Department of Mines, Geological Survey, pp. 35–56, Appendix 5, p. 111.
1989. Tertiary volcanism. In C. F. Burrett and E. L. Martin (eds.), *Geology and mineral resources of Tasmania*, Geological Society of Australia, Spec. Pub. 15: 383–398.
- Sutherland, F. L., and P. Wellman  
 1986. Potassium-argon ages of Tertiary volcanic rocks, Tasmania. *Pap. Proc. R. Soc. of Tasmania*, 120: 77–86.
- Tedford, R. H., M. R. Banks, N. R. Kemp, I. McDougall, and F. L. Sutherland  
 1975. Recognition of the oldest known fossil marsupials from Australia. *Nature* 225: 141–142.
- Tedford, R. H., M. Archer, A. Bartholomai, M. Plane, N. S. Pledge, T. Rich, P. Rich, and R. T. Wells  
 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *J. Aust. Geol. Geophys.* 2: 53–57.
- Warren, J. W.  
 1969. Chelid turtles from the mid-Tertiary of Tasmania. *J. Paleontol.* 43: 179–182.
- Wilford, G. E., and P. J. Brown  
 1994. Maps of late Mesozoic-Cenozoic Gondwana break-up: some paleogeographical implications. In R. S. Hill (ed.), *History of Australian vegetation, Cretaceous to recent: 5–13*. Cambridge: Cambridge Univ. Press.
- Wood-Jones, F.  
 1931. A re-examination of the skeletal characters of *Wynyardia bassiana*, an extinct Tasmanian marsupial. *Pap. Proc. R. Soc. Tasmania* 1930: 96–115.
- Woodburne, M. O.  
 1984. Families of marsupials: relationships, evolution and biogeography. In T. W. Broodhead (ed.), *Mammals: notes for a short course*, Univ. Tennessee, Dept. Geol. Sci. Stud. Geol. 8: 48–71.
- Woodburne, M. D., B. J. MacFadden, J. A. Case, M. S. Springer, N. S. Pledge, J. D. Power, M. J. Woodburne, and K. B. Springer  
 1994. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (late Oligocene) of South Australia. *J. Vertebr. Paleontol.* 13: 483–515.



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