

First Australian Pliocene molossid bat: *Mormopterus (Micronomus)* sp. from the Chinchilla Local Fauna, southeastern Queensland

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Abstract – An isolated upper canine from the Pliocene Chinchilla Local Fauna of southeastern Queensland is identified as representing the Australian molossid genus *Mormopterus*, subgenus *Micronomus*. It is the first Australian Pliocene representative of the cosmopolitan family Molossidae and the first Tertiary representative of the *Micronomus* lineage. Approximately six *Micronomus* species are today widely distributed across the Australian mainland, Papua New Guinea and Ambon, and are found in most habitat types from desert to rainforest. The discovery of an indeterminate species of *Micronomus* in the Chinchilla Local Fauna does not contradict the palaeoenvironmental interpretation of the area as woodland savannah.

INTRODUCTION

A variety of taxa has been recovered from the early to middle Pliocene freshwater fluviatile Chinchilla Sand northwest of Chinchilla, southeastern Queensland (Archer 1977, 1982; Archer and Dawson 1982; Bartholomai 1962, 1963, 1966, 1967, 1971, 1973, 1975, 1976; Bartholomai and Woods 1976; Dawson 1982; Flannery and Archer 1983; Gaffney 1981; Gaffney and Bartholomai 1979; Godthelp 1990; Hutchinson and Mackness submitted; Kemp and Molnar 1981; Mackness and Scanlon in press; Olson 1975, 1977; Patterson and Rich 1987; Woods 1956, 1960, 1962; Wroe and Mackness 1998). Collectively this assemblage is known as the Chinchilla Local Fauna (Archer and Bartholomai 1978; Woodburne *et al.* 1985; Rich *et al.* 1991).

This paper describes an isolated canine recovered from the Chinchilla Sand which represents the first Australian Pliocene representative of the cosmopolitan family Molossidae, and the first Tertiary representative of the modern Australian molossid lineage *Micronomus*. Two older molossids, described from Miocene deposits at Riversleigh in northwestern Queensland, are members of extinct molossid lineages (Hand 1990; Hand *et al.* 1997).

Taxonomy and dental terminology follow Legendre (1984a), Hand (1990) and Strahan (1995). The prefix QM F indicates specimens registered in the fossil collection of the Queensland Museum, Brisbane.

SYSTEMATIC PALAEOLOGY

Suborder Microchiroptera Dobson, 1875

Superfamily Vespertilionoidea Gray, 1821
(Weber, 1928)

Family Molossidae Gray, 1821

Mormopterus (Micronomus) sp.

Material Examined

QM F30575, a left upper canine (Figure 1).

Measurements: Length 1.17 mm, width 0.98 mm, height 1.93 mm.

Locality and Age

North bank of the Condamine River, Chinchilla Rifle Range (26°48'S., 150°41'E.). The Chinchilla Sand was named by Woods (1960) for a sequence of weakly consolidated grey to yellowish and light brown sands, ferruginized heterogeneous conglomerates, grits, sandy clay and clays. These outcrops range from shallow beds to sections several metres deep. Wilkinson's Quarry has been continuously worked by two of us (C.E.W., D.M.W.) for over ten years. The specimen described comes from a fossil-bearing unit within the quarry that lies unconformably on top of an indurated layer of fine sand. The sediments are primarily fluviatile in nature and represent a number of depositional events. Most fossils in these units occur as isolated pieces.

Tedford *et al.* (1992) concluded that the Chinchilla Local Fauna biocorrelates with the Kanunka Local Fauna of the Tirari Desert, South Australia. On the basis of magnetostratigraphy, they concluded that the latter is approximately 3.4 million years old, or late early Pliocene in age.

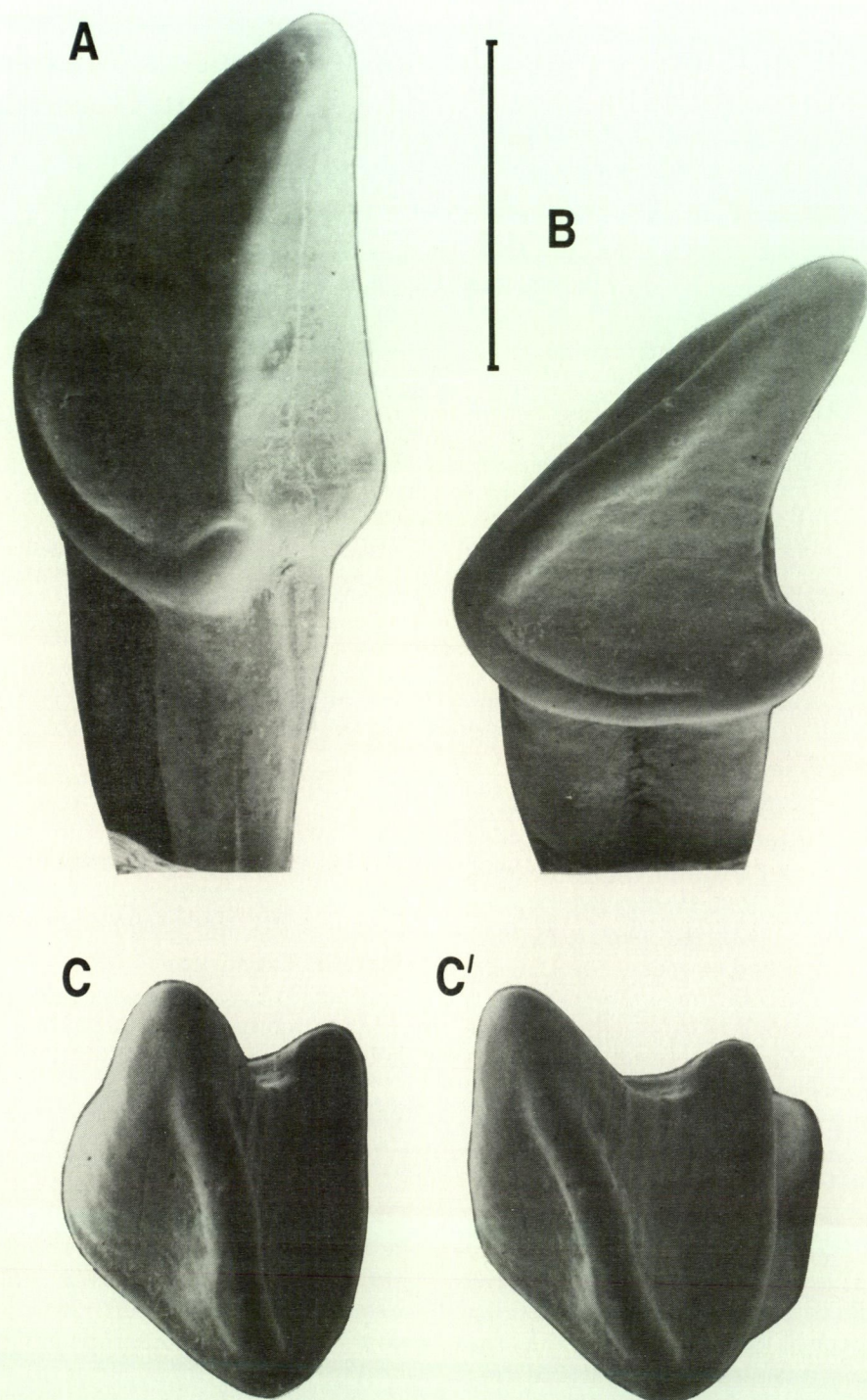


Figure 1 *Mormopterus (Micronomus)* sp., from the Pliocene Chinchilla Local Fauna, southeastern Queensland. QM F30575, left upper canine. A, posterior view; B, lingual view; C-C', stereopair, antero-occlusal view. Scale bar = 1 mm.

Description

QM F30575 is massively-rooted with a tall, slender, dominant main cusp (Figure 1). There is a narrow cingulum around the whole tooth and a small but distinct posterolingual cingular cusp. There are no other cingular cusps. The basal outline of the crown is subtriangular. The antero- and posterolingual corners of the main cusp (paracone) are defined by vertical crests; the posterobuccal surface is convex. The shaft is recurved posteriorly

such that the anterolingual blade is convex and the posterolingual crest concave. There is no development of a secondary cusp on either blade. The crown is flattened on the lingual side, and the lingual margin is very straight (i.e., in occlusal view it is neither concave nor convex). The anterobuccal face is marked by a broad groove which is attenuated towards the apex of the cusp. This groove results in a distinct concavity in the anterobuccal margin of the crown and contributes

to the tooth's triangular (rather than semi-circular) occlusal outline. In occlusal view, there is also a broad and marked indentation in the posterobuccal margin, perhaps for the following tooth (but see Remarks below). The massive root is oval in cross-section with a deep groove longitudinally bisecting its flattened lingual face.

Remarks

Comparisons Made

Its small size, complete cingulum, flattened lingual face and lack of posterior heel suggest that QM F30575 is the upper canine of a microchiropteran bat. Megachiropteran canines are generally larger, lack a complete cingulum (absent buccally, variably developed lingually and posteriorly) and are generally not subtriangular in cross-section. Many megachiropteran canines (e.g., *Pteropus* spp.) have very conspicuous ridges on the shaft; in others a secondary cusp is formed by slight elongation of the cingulum (e.g., *Nyctimene* spp.) or is developed on the posterior edge of the shaft (e.g., species of *Pteralopex* and *Harpyionycteris*; the latter may have well-developed posterior and lingual cingula and/or posterolingual basal cusps). Like the Chinchilla canine, species of *Macroglossus*, *Syconycteris*, *Notopterus* and *Eonycteris* have a deep longitudinal groove on the anterior face of the shaft (in *Melonycteris* the groove is bounded by sharp ridges), but otherwise differ strikingly from the fossil in their very weak and incomplete cingula and rounded or square basal outline.

The Chinchilla canine has been compared with representatives of all microchiropteran groups, except the monotypic Craseonycteridae and Tomopeatinae. It differs strikingly from emballonurid and rhinopomatid canines in its subtriangular occlusal outline, anterior groove and lack of well-developed anterior and posterior cusps and/or cingular cusps. In most emballonuroids (e.g., *Rhinopoma*, *Emballonura* and New World diclidurines), there is no distinct cingulum, lateral compression is marked, heel development common, and anterior and posterior cusps are developed at the base of the anterior and posterior cutting edges. The upper canines of species of *Taphozous* and *Saccolaimus* have very large heels and deep, well-developed lingual cingula, often with pronounced lingual cusps. In lateral view, emballonuroid canines are typically more recurved posteriorly than the Chinchilla canine.

The fossil differs from rhinolophoid (rhinolophid, hipposiderid, megadermatid and nycterid) upper canines in its subtriangular (rather than laterally compressed) crown and its anterior groove. Additionally, it differs from megadermatids and many hipposiderids in lacking a posterior secondary cusp at the base of the shaft and an

anterior cingular cusp. It differs from nycteridids in its flattened (rather than concave) lingual face and lack of anterior cingular cusp, and from rhinolophids in its complete and conspicuous cingulum.

The Chinchilla canine differs from those of most noctilionoids (phyllostomids, mormoopids and noctilionids) in having a distinctive anterior groove. However, some phyllostomines (e.g., *Phyllostomus* and *Trachops* species) do possess a broad groove on the anterior face of the shaft as well as a less developed one on the anterobuccal face. But these are large species with much larger canines, which usually also differ in having a rather bilobed lingual margin. Many stenodermatines differ in having a dorsal expansion of the buccal face of the canine. In *Vampyrum* the shaft is flattened in front but, like the Chinchilla tooth, it has a moderately developed cingulum and distinct posterolingual cingular cusp. In most phyllostomines (e.g., *Micronycteris*), the upper canine is simple with the anterior shaft smoothly rounded and with a well-developed cingulum but no extra cusps. In desmodontine phyllostomids, the canine is large, long and narrow, with an acute point and very sharp cutting edge.

In the other phyllostomid subfamilies (America's glossophagines, stenodermatines, phyllonycterines) there is even more variation in the basic form of the upper canine, making generalizations difficult. Miller (1907) has described the dentition of many taxa in this speciose group, and the following comparisons with the Chinchilla canine can be made. In glossophagines, the canine tends to be simple with a slightly developed cingulum and no secondary cusps, though in some species (e.g., *Leptonycteris*) the cingulum is obsolete but represented anteriorly and posteriorly by short, well-developed cusps. In other species (e.g., *Sturmira*) the inner surface is strongly concave and thus unlike the Chinchilla tooth. Stenodermatine canines appear to be quite unlike the Chinchilla tooth. In many stenodermatines, the canine is nearly as long as tall, the cingulum is well developed and there are no secondary cusps; in some species (e.g., *Ardops*, *Phyllops* and *Ariteus*) the canine is only just taller than the large premolar. In other stenodermatines (e.g., *Brachyphylla*) the lingual cingulum forms two low but very distinct cusps (rarely, a secondary cusp extends nearly to the middle of the posterior edge). Some taxa (e.g., *Pygoderma*) have a wide posterolingual heel and minute posterior cingular cusp, others (e.g., *Centurio*) are flattened antero-posteriorly (rather than laterally). In phyllonycterines, the canine is simple but has a poorly defined cingulum, without secondary cusps and with the lingual face slightly concave.

In noctilionoids the canine is short (antero-posteriorly) and very tall with a distinctly oblique

cingulum without secondary cusps, the shaft's lingual surface slightly concave with a median ridge, the outer surface uniformly convex. In mormoopids, the canine has a conspicuously concave lingual surface, distinct anterior and posterior cutting edges and a fairly well developed cingulum (though weak buccally) without secondary cusps.

The Chinchilla canine more closely resembles the upper canines of vespertilionoids s.l., mystacinids and molossids. Vespertilionoids s.l. (vespertilionids, natalids, thyropterids, furipterids, myzopodids) and mystacinids, like most bats, lack the anterior groove distinguishing the Chinchilla canine. Among vespertilionine canines, three basic types were recognized by Menu (1985), none of which matches the morphology of the Chinchilla tooth. In Type A (as in, e.g., *Myotis* and *Lasionycteris* species) and Type C canines (e.g., species of *Eptesicus*, *Ia*, *Scotophilus*, *Scoteanax*, *Otonycteris* and *Histiotis*) the base of the crown is oval rather than subtriangular. Further, Type A canines are simple with a distinct though rather small cingulum and no secondary cusps; Type C canines are more complex with a distinct lingual crest. *Histiotus* has an anterior groove, but unlike the Chinchilla fossil it is developed between a strong anterolingual crest and an anterior ridge, and there is a lingual cingular emargination. Type B canines (e.g., *Pipistrellus* species) have a subtriangular base more like the Chinchilla canine but no anterior groove nor posterobasal cusp, the posterior cutting edge often has an incipient secondary cusp, and an indentation in basal outline occurs posterolingually rather than posterobuccally. The canines of miniopterines (very round, tall and simple), nyctophilines (concave lingual face, convex lingual shelf), kerivoulines (laterally very compressed) and most murinines are simple in form with distinct but low cingula without cusps, generally with a circular or oval basal outline.

In natalids and myzopodids, like kerivoulines, the canine is simple, with a distinct but small cingulum without secondary cusps, the shaft appearing compressed due to its concave lingual face. Thyropterids are similar, although lingual cingular cusps are developed in some species but not others (Czaplewski 1997). In some natalids (e.g., species of *Nyctiellus*) and in furipterids, the canine is greatly reduced in size, being only just taller than the posterior premolar. Furipterids further differ from the Chinchilla tooth in having a well-developed secondary cusp on the posterior cutting edge and a well-developed cingulum forming a conspicuous anterior basal cusp and smaller posterior one.

The upper canine of mystacinids has no distinct (but perhaps an incipient) groove, a semicircular rather than subtriangular basal outline, and no obvious posterobasal cusp. It does, however, have a

complete cingulum and is of similar proportions to the Chinchilla canine. There is no posterobuccal indentation in basal outline.

Only molossid canines characteristically exhibit a broad and distinct groove on the anterior surface of the shaft, as in the Chinchilla canine. This groove is found in both Old and New World molossids including species of *Mormopterus*, *Micronomus*, *Sauromys*, *Platymops*, *Chaerephon*, *Molossops*, *Cheiromeles* and *Eumops*. It is present but less distinct in many species of *Nyctinomus* and *Eomops*. Most molossids also share the distinct but small cingulum and distinctly flattened lingual face seen in the Chinchilla tooth. Species of *Nyctinomus*, *Chaerephon* and *Molossops* lack noticeable cingular cusps, but a posterobasal cusp is found in species of *Cheiromeles*, *Platymops*, *Mormopterus*, *Sauromys* and *Micronomus*. Compared with the Chinchilla tooth, *Cheiromeles* canines are much more robust, while those of *Platymops* are short and weak (shaft diameter conspicuously less than crown diameter). In *Sauromys* the basal outline is lingually concave and more posterolingually extended, and the posterior cutting edge more pronounced. Species of *Mormopterus* (*Mormopterus*) (e.g., *M. minutus*, *M. acetabulosus*) have lost P² (or it is reduced to a spicule) and, possibly as a consequence, lack the deep posterobuccal indentation in occlusal outline seen in the Chinchilla canine. However, among *Mormopterus* species an indentation in posterobasal outline does not always accommodate the following premolar. For example, in *Sauromys petrophilus* there is a distinct posterobuccal indentation but P² occurs (more lingually) in the toothrow. Unlike the Chinchilla tooth, the canines of *Chaerephon* and *Mops* species typically have a marked median longitudinal crest bordered by grooves on the lingual face of the shaft.

In overall size, relative length and height, occlusal basal outline, extent and position of groove, degree of posterior curvature, development of cingulum, size and position of posterocingular cusp, and groove in the lingual face of the root, the Chinchilla canine closely resembles the canines of the six or so living species of *Mormopterus* (*Micronomus*) distributed across Meganesia. It is less similar to Australia's much larger *Nyctinomus australis* which has a semicircular occlusal outline, a distinct lingual crest and shelf, and no posterobasal cusp nor marked indentation for the following tooth. It differs from the medium-sized *Chaerephon jobensis* in its subtriangular rather than semicircular occlusal outline and in lacking a median crest and grooves on the lingual face. Canines of Riversleigh's Miocene molossids *Petramops creaseri* Hand, 1990, and *Mormopterus* (*Hydromops*) *riversleighensis* Hand *et al.*, 1997, are not yet known, but other species of *Hydromops* (Revilliod 1920; Legendre 1982; Legendre *et al.* 1988) appear to differ from the

Chinchilla tooth in characteristically exhibiting a strong medial rib on the buccal face of the crown (Engesser 1972; Legendre *et al.* 1988).

Differences in occlusal basal outline, development of lingual shelf, and size and position of posterocingular cusp and posterobasal shelf seem to distinguish the various *Micronomus* species. In such features, the Chinchilla tooth is less similar to *M. beccarii*, the species found in the Chinchilla area today (McKenzie 1995; but see Allison 1996), than to other species including *M. norfolcensis* of eastern New South Wales. However, because intraspecific variation (including sexual dimorphism) may be considerable in molossid bat canines (e.g., Engesser 1972), it has not been possible to refer the Chinchilla canine to any particular species of *Micronomus*.

DISCUSSION

Chinchilla is the seventh Australian locality to produce Tertiary-aged bats, the other six localities being: Murgon, southeastern Queensland (early Eocene Tingamarra Local Fauna); Lake Palankarina, central Australia (late Oligocene Ditjimanka Local Fauna); Riversleigh, northwestern Queensland (late Oligocene to Pliocene faunas); Bullock Creek, Northern Territory (middle Miocene Bullock Creek Local Fauna); Hamilton, Victoria (early Pliocene Hamilton Local Fauna); and Wellington Caves, central New South Wales (early-middle Pliocene Big Sink Local Fauna); (Turnbull and Lundelius 1970; Archer 1978; Archer *et al.* 1994; Hand *et al.* 1988, 1994, 1998). From the Australian Pliocene sites, the bat families Hipposideridae, Megadermatidae, Emballonuridae and Vespertilionidae have been recorded (Turnbull and Lundelius 1970; Hand *et al.* 1988; Archer *et al.* 1994; Hand 1995, 1996; Hand and Godthelp this volume).

The Chinchilla bat is the first Australian Pliocene representative of the cosmopolitan bat family Molossidae. Worldwide, some 80 living molossid species are referred to between 9 and 12 genera (Freeman 1981; Honacki *et al.* 1982; Legendre 1984b) with another 20 or so fossil (Tertiary) taxa reported from all continents except Antarctica (Legendre 1985; Hand 1990; Czaplewski 1997). In Australia today, the Molossidae is represented by one species each of the genera *Nyctinomus* and *Chaerephon* and at least six species of *Mormopterus* (*Micronomus*) whose taxonomy remains confused (Allison 1989, 1996; Parnaby 1991; Richards 1995).

Currently, Australian Tertiary molossids are known only from late Oligocene and early Miocene deposits at Riversleigh in northwestern Queensland, and now from Chinchilla. They are not yet known from Riversleigh's Pliocene Rackham's Roost Site (Archer *et al.* 1994). The Riversleigh molossids represent at least two species, *Petramops*

creaseri (Hand 1990) and *Mormopterus* (*Hydromops*) *riversleighensis* (Hand *et al.* 1997), both of which appear to lie outside the radiation of living Australian molossids. They lack several derived traits exhibited by species of *Micronomus*, *Nyctinomus* and *Chaerephon*, and seem to have been part of an older, archaic bat fauna that was widespread, had close relatives in Europe and North America, and left no living descendants in Australia (Hand 1990).

Legendre (1984a, 1984b, 1984c, 1985) speculated that the genus *Mormopterus* was probably derived at the end of the Eocene or beginning of the Oligocene from European species of *Cuvierimops*, and from there expanded worldwide to wherever climatic conditions were favourable. Species of *Mormopterus* reached South America by the late Oligocene (i.e., *M. (Neomops) faustoi*; Paula Couto 1956; Paula Couto and Mezzalana 1971), and Australia by the late Oligocene (i.e., *Mormopterus* (*Hydromops*) *riversleighensis*). The latter subgenus, *Hydromops*, is known also from the early Miocene of Thailand (Legendre *et al.* 1988) and the early to middle Miocene of Europe (Revilliod 1920), disappearing from Europe after that time. Close relatives (though not descendants) of the *M. (Hydromops)* lineage include the living African species *M. (Platymops) setiger* and Australia's *M. (Micronomus)* species (Legendre 1984a, 1984b; Legendre *et al.* 1988; Hand *et al.* 1997).

The ancestors of the Australian endemic *Micronomus* lineage are thought to have arrived in the Australian region from Asia by at least the late Oligocene, independently of *Petramops*, *Nyctinomus* and *Chaerephon* species (Legendre 1984a, 1984b, 1984c, 1985; Hand 1990). The Chinchilla molossid testifies that the *Micronomus* lineage itself had evolved by the middle Pliocene. Today, the four named living *Micronomus* species (*beccarii*, *loriae*, *norfolcensis* and *planiceps*) and at least two others (separable on fur and penis characters; Richards 1995) are distributed across the Australian mainland, with two, *loriae* and *beccarii*, found also in New Guinea, and *beccarii* occurring on Ambon island (McKenzie 1995).

Micronomus species, like other molossids, are fast, direct fliers which forage for flying insects in open areas above the canopy or over open water and typically roost in tree hollows, rock crevices and caves. In Australia, they occur in desert, semi-arid and mesic regions, foraging over rainforests, mangroves, open woodland and savanna (Strahan 1995). All Riversleigh molossid specimens have been recovered from karstic sediments which appear to have accumulated within closed forest (Hand 1990; Hand *et al.* 1997). However, molossids are rare at Riversleigh compared with other bat taxa (especially rhinolophoids) and it is not yet clear whether they lived in caves or forest, or were

brought in as prey from adjacent habitats by carnivorous megadermatids (Hand 1990). In Europe, Tertiary molossids have been recorded as whole skeletons from strictly lacustrine deposits (Sigé 1971).

While the exact nature of the Chinchilla palaeoenvironment has yet to be interpreted, the nature of the sediments suggests a fluvial rather than lacustrine depositional environment. The composition of the mammalian fauna suggests a woodland environment with a lack of any undoubted closed-forest taxa. The predominance of grazing kangaroos and diprotodontids indicates that grasslands were part of the environment. The presence of a molossid bat does not contradict that interpretation.

ACKNOWLEDGEMENTS

The study of the Chinchilla material was supported in part by an ARC Program Grant to M. Archer; a grant from the Department of Arts, Sport, the Environment, Tourism and Territories to M. Archer, S.J. Hand and H. Godthelp; a grant from the National Estate Program Grants Scheme to M. Archer and A. Bartholomai; and grants in aid to the Riversleigh Research Project from the University of New South Wales, Wang Australia Pty Ltd, ICI Australia and the Australian Geographic Society. The following people kindly provided access to comparative specimens in their institutions: B. Engesser, H. Felten, T.F. Flannery, W. Fuchs, L. Gibson, J.E. Hill, M. Hugueney, P. Jenkins, D.J. Kitchener, K. Koopman, P. Mein, R. Rachl, B. Sigé, N.B. Simmons, G. Storch, and S. Van Dyck. We thank Jenni Brammall for the photographs which were produced in the University of New South Wales Electron Microscopy Unit.

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Manuscript received 18 March 1998; accepted 26 October 1998.