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The Macropodoidea (Marsupialia) of the Early Pliocene Hamilton Local Fauna, Victoria, Australia

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The Macropodoidea (Marsupialia) of the Early Pliocene Hamilton Local Fauna, Victoria, Australia

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Abstract

The early Pliocene Hamilton local fauna from southwestern Victoria, Australia, has at least fifteen kinds of macropodoids including propleopines, potoroines, hypsiprymnodontines, sthenurines, and macropodines. New taxa described here include a potoroine, *Milliyowi bunganditj* n. gen. and sp. and the macropodines *Dorcopsis wintercookorum* n. sp., *Thylogale ignis* n. sp., and *Kurrabi pelchenorum* n. sp. The other ten genera present are represented by specimens for which no species assignment has been made. These are *Propleopus, Hypsiprymnodon, Troposodon, Simosthenurus, Dendrolagus, Protemnodon, Macropus* (*Notomacropus*), *Wallabia,* and two Macropodidae gen. indet. (1 and 2).

Several extant genera whose living species are almost exclusively rain forest or rain forest fringe dwellers occur in the fauna, suggesting that the fossil assemblage predominantly represents a rain forest environment.

Introduction

The Hamilton fossil locality was first discovered in 1952 by Edmund Gill, who found a single molar tooth. It was first identified as that of a cuscus (Gill, 1952, 1957) or phalangerid (Stirton, 1957), but it was later recognized as that of a large potoroid (Ride, 1964). The site was subsequently worked extensively and its fauna described by Turnbull and Lundelius (1970). The fossils occur in an unnamed lithic unit that rests on the marine Grange Burn Formation and is overlain by a basalt flow. The unnamed unit is about 1.3 m thick and has been interpreted as a fossil soil (Gill, 1957). Turnbull et al. (1965) published a date of 4.35 ± .1 Ma on the overlying basalt. McDougall (pers. comm., 1980) has recalculated the date as 4.46 ± .1 Ma using the constants recommended for the potassium–argon method in Steiger and Jager (1977).

The geology and stratigraphy of the site were described in Turnbull and Lundelius (1970). The site is located at 37°43′58 ± 03″S, 141°57′14 ± 04″E, based on Sheet 7222, Coleraine 1:100,000 (Edition 1) Series R652. It is on the south side of the Grange Burn about 100 m downstream from a waterfall and approximately 7 km west of Hamilton, Victoria. It is indicated as site 10 on a detailed map (text fig. 3 in Gill, 1957). Turnbull and Lundelius (1970) also show the site in their figure 1 and identify it as the "Pliocene Fossil Locality."

This paper deals with the macropodoids of the Hamilton local fauna that were collected in 1966–1967 by Turnbull and Lundelius and in 1977–1981 by Rich and Flannery. It also includes, with some revisions, those specimens collected previously and discussed in the earlier report by Turnbull and Lundelius (1970) in which nine taxa of macropodoids were recognized. At the time only two of the nine taxa, *Thylogale* and *Dorcopsis,* could be identified with certainty to the generic level owing to the fragmentary nature of the material (mainly isolated teeth). The current collection of more complete cheektooth rows in some taxa and other additional specimens has allowed the recognition of at least fourteen kinds of macropodoids, ten of which were only identified at the generic level. While many isolated macropodoid teeth are present in the collections, recognition of their proper taxonomic assignments is generally uncertain because the teeth of the taxa are very similar. Hence, only distinctive or associated teeth are discussed extensively in this paper. The many isolated teeth of unsure affinity are listed in the Appendix.

Only five Pliocene faunas with a moderately diverse macropodoid assemblage have been reported from Australia–New Guinea. These are the Hamilton local fauna from Victoria, the Bow local fauna from New South Wales (Skilbeck, 1980; Flannery & Archer, 1984), the Chinchilla and Bluff downs local faunas from Queensland (Bartholomai, 1963, 1967, 1973, 1975, 1976, 1978b), and the Awe local fauna from New Guinea (Plane, 1967). Hamilton is the most firmly dated locality and contains the second greatest diversity of macropodoids (after Bow), thus making it one of the most informative of the sites from the viewpoint of macropodoid evolution. The Hamilton site has produced almost exclusively mammalian and plant remains, the exceptions being several frog bones (which may possibly be modern). Bone was poorly preserved at the site, the most common remains being tooth caps. Mammalian groups represented are also diverse: Included are the Dasyuridae, Peramelidae, Petauridae, Burramyidae, Phalangeridae, Ektopodontidae, Vombatidae, Potoroidae, Macropodidae, Palorchestidae, Diprotodontidae, and Microchiroptera.

Materials and Methods

All specimens of macropodoids from the Hamilton local fauna not cited in the text are listed in the Appendix. Abbreviations are PM—fossil mammal collection, Field Museum of Natural History, Chicago, and NMV P—paleontological collection, Museum of Victoria, Melbourne. The diagnoses given below are not meant to be exhaustive, but cover only the fossil elements being diagnosed. Enumeration of cheek teeth differs from that in Turnbull and Lundelius (1970) and follows Archer (1978). The posterolingual cusp of the upper molars is here designated the hypocone, pending further work concerning the suggestion of Tedford and Woodburne (1987) that it is the metaconule. Paracone and metacone are retained for the buccal cusps of the protoloph and metaloph, although they may ultimately prove to be stylar cusps (Tedford & Woodburne, 1987). Measurements were taken with dial calipers.

Superfamily Macropodoidea (Gray, 1821)
Family Potoroidae Gray, 1821
Subfamily Propleopinae Archer and Flannery, 1985
Propleopus Longman, 1924
Propleopus sp.

Discussion—A species of *Propleopus* represented by isolated molars and premolars from the Hamilton local fauna has been under study by W. D. L. Ride and the late J. A. Mahoney. The first tooth (NMV P15777) discovered at Hamilton, which was recognized by Ride (1964) as the molar of a large potoroid, probably belongs within this taxon. Eight other specimens (PM 16817, PM 16819, PM 16820, PM 16832, NMV P150212, NMV P150213, NMV P150274, and NMV P150296) have been sent to Ride for incorporation into that study, which will appear elsewhere.

Subfamily Hypsiprymnodontinae (Collett, 1877)
Hypsiprymnodon Ramsay, 1876
Hypsiprymnodon sp.

Material—PM 4575, protoloph of right M^2; NMV P169186, right M_4 (fig. 1A); NMV P160153, protolophid of right M_2 or protoloph of M^3; PM 50762, nearly complete left upper molar (fig. 1B).

Description—A large, distinct trigonid basin is present on NMV P169186, the M_4, and the anterior cingulum is rounded in occlusal view. There is no fossette labial to the paracristid. The posterior cingulum is small and encloses a small posterior fossette. The protolophid is longer than the hypolophid, which is barely discernable at its midpoint. The four major cusps are located more to the outside of the tooth than is the case in other potoroines. The relative sizes of the four principal cusps are protoconid > metaconid > hypoconid > entoconid. Ride (1961) implies that the protoconid and metaconid are of equal size in the living *Hypsiprymnodon moschatus.* The cristids from the protoconid and hypoconid join to form a low wall on the buccal side of the talonid basin. The cristids from the metaconid and the entoconid do not meet on the lingual side of the talonid basin.

The upper molar (PM 50762) has a protoloph that is longer than the metaloph, which is barely discernable at its midpoint in the median valley. Part of the metacone is missing, but the tooth is

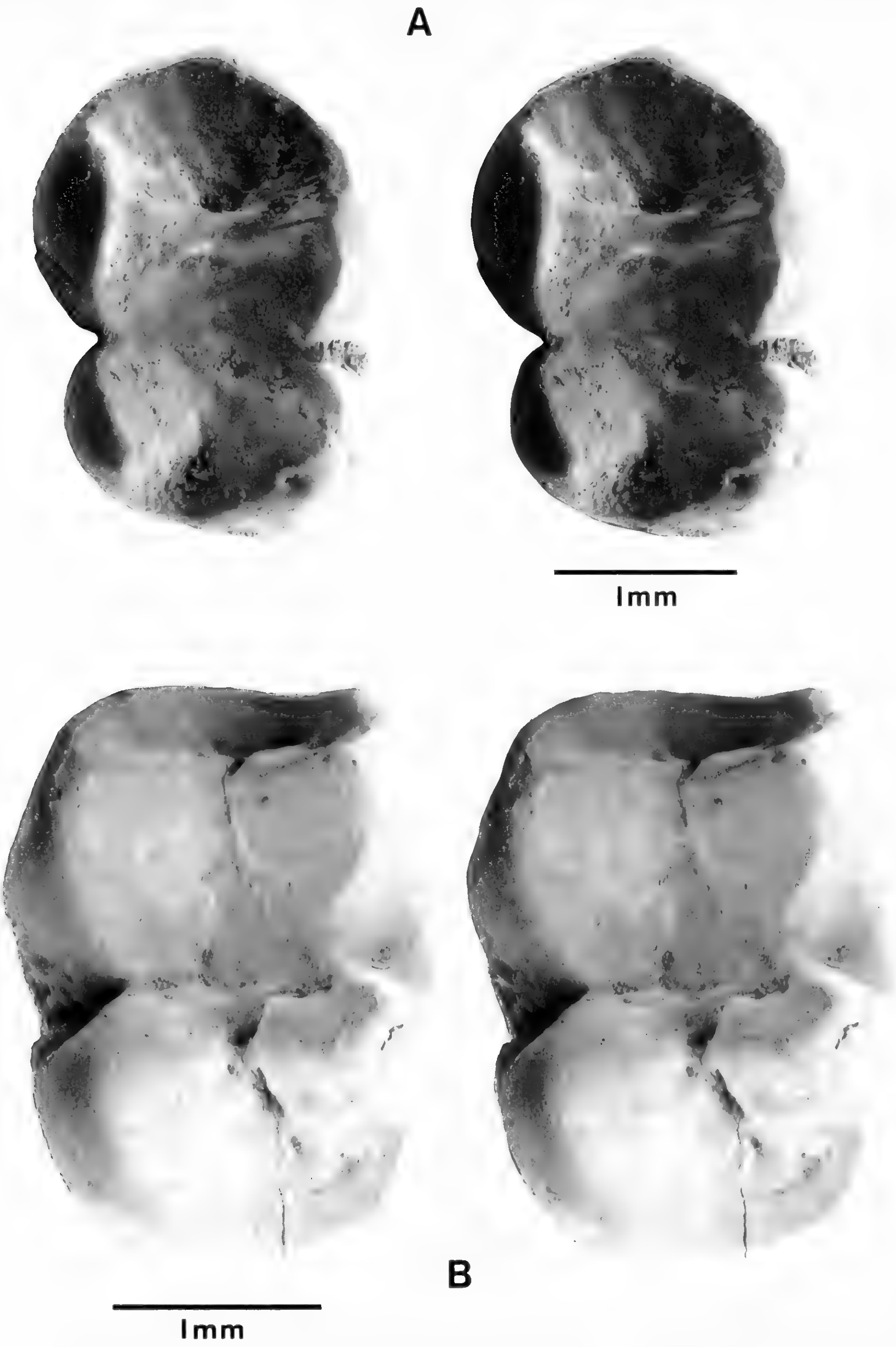

FIG. 1. *Hypsiprymnodon* sp. Scanning electron microscope stereopairs. **A,** NMV P160186, right M^4 shown in crown view at ×25. **B,** PM 50762, left upper molar shown in crown view at ×29.

nearly complete. There is a broad precingular basin, a large central basin between the lophs, and a distinct basin posterior to the metaloph. Each loph is interrupted by a fissure that crosses the loph at its lowest point. There is a small labial basin between the paracone and metacone. Labiad, the weak crests that run from the apices of these cusps meet in the transverse valley. This labial basin lies just labiad to the junction of the crests and linguad to the labial cingulum. A groove on the lingual side of the tooth, between protocone and hypocone (= metaconule of Tedford & Woodburne, 1987), serves to extend the transverse valley onto the lingual side of the crown, but the crests from those cusps interrupt the valley and groove where they join. Cusps and lophs are low, and the enamel in the valleys shows some crenulation.

Discussion—These molar fragments and molars have been referred to *Hypsiprymnodon* sp. because they are distinctly bunodont in form and are smaller than those of any potoroine or species of *Propleopus* and the lophs/ids are less well formed. This combination of characteristics is unique to *Hypsiprymnodon moschatus* in the extant Macropodoidea. Furthermore, the M^4 is more elongate than in species of *Bettongia, Aepyprymnus, Caloprymnus, Milliyowi* n. gen., or *Propleopus*. Although the upper and lower molars and molar fragments are bunodont in form, the cristae originating from the hypocone/id and protocone/id are poorly developed, especially when compared to those in species of *Caloprymnus, Propleopus, Aepyprymnus, Wakiewakie, Palaeopotorous, Bulungamaya,* and *Milliyowi.* The almost quadritubercular molar pattern resulting is only matched among macropodoids in *H. moschatus.*

A taxon similar to *H. moschatus* was recognized by Turnbull and Lundelius (1970) on the basis of PM 4575, the protoloph of an M^2. The additional material described here has allowed a more certain identification as *Hypsiprymnodon* sp. While this material is easily distinguishable from most potoroines on the basis of morphology, it is primarily the smaller size and weaker loph/id development that distinguishes it from species of *Potorous* (see table 1).

Subfamily Potoroinae Trouessart, 1898

Milliyowi n. gen.

Type Species—*Milliyowi bunganditj* n. sp.

Generic Diagnosis—*Milliyowi bunganditj* can be distinguished from all other potoroines in possessing anterior upper molars with extended sloping lingual edges and anterior lower molars with sloping labial edges. It differs from the species of *Potorous* and *Caloprymnus* (which have four to five poorly defined ridges) in having at least seven well-defined ridges on P^3. It differs from species of *Bettongia* except (variably) *B. gaimardi* in lacking a posterolingual cuspule on P^3. The teeth of *M. bunganditj* are closest in size to those of *Aepyprymnus rufescens* among Potoroinae but are slightly larger (table 2). While most similar in overall morphology to *A. rufescens,* the molars of *M. bunganditj* differ, in addition to the above characters, in having a more gently sloping posthypocristid and posthypocrista. The posterior cingulum, the metaconule, and the hypocone/id are less massive and the teeth have more open and more centrally located cingular basins than in *A. rufescens* and, to a lesser extent, *C. campestris.*

It differs from *Gumardee pascuali* in having a P^3 that lacks buccal and lingual cingulae and a large bulge on the posterolingual corner (Flannery et al., 1982). The P^3 differs from that of *Wakiewakie lawsoni* in the lack of a labial turn at the posterior end, in having an incipient posterolabial cusp, and in that the ribbing is coarser. *Milliyowi* differs from *Palaeopotorous priscus* in the larger size of the molars, in the absence of a postlink, a midlink, and a protoconule on the upper molars, and in that M_2 lacks any sign of a protostylid.

Etymology—From the aboriginal *millia* (rat-kangaroo) and *yowi* (spirit surviving the death of the body) (Parker, 1953).

Milliyowi bunganditj n. sp.

(figs. 2, 3, 4A, 5A; table 2)

Holotype—NMV P158635, associated in a single lump of matrix are enamel caps of the posterior two-thirds of right P^3, and right M^{2-3} (figs. 2A,C,E).

Referred Specimens—PM 50763, right M^1 (figs. 2B,D); NMV P158068, right M^5 (fig. 3A); PM 16821, crown of a left I_1 (fig. 5A); NMV P53223, anterior three-quarters of right P_3 (figs. 3B–D); NMV P158069, right M_1 lacking anterior portion of protoconid (fig. 3E); NMV P54137, left M_3 or M_4 (fig. 4A).

Type Locality and Age—See the Introduction for details.

Diagnosis—The diagnosis of the genus will serve as that of the species until further species are recognized.

TABLE 1. Dental measurements (mm) of some Hamilton macropodids.

		L	AW	PW
Hypsiprymnodon sp.				
NMV P160186	M_4	2.8	1.9	2.2
cf. *Dendrolagus*				
NMV P157483	P^3			4.9
NMV P157481	P^3			4.2
Dorcopsis wintercookorum				
PM 16822	P^3	9.8	3.4	3.6
NMV P158453	P^3	9.8	3.3	4.0
	M^2	4.4	4.2	4.0
	M^3	4.7	4.3	3.9
	M^4	4.8	4.6	4.0
	M^5	4.9	4.1	3.3
PM 50771	M^x	5.2	4.5	3.8
NMV P157477	P_3	9.5	2.4	3.2
NMV P158462	P_3	8.5	2.2	2.5
NMV P160221	M^1	4.8	3.6	3.8
PM 16816	M^1	5.0	3.6	3.9
PM 50767	M^2	4.8	4.0	4.3
Troposodon sp.				
NMV P158465	M^5			9.8
Simosthenurus sp.				
NMV P158633	Hypolophid			8.6
NMV P158594	Protolophid		9.6	
Protemnodon sp.				
NMV P160372	M^1	9.9	10.1	8.5
Macropus (*Notamacropus*) sp.				
NMV P54112	Hypolophid			7.3
cf. *Wallabia*				
NMV P54208	P^3	8.6	3.3	4.2
Gen. indet.				
NMV P158431	$P_{2?}$	4.4	1.8	1.7

L = length, AW = anterior width, PW = posterior width.

ETYMOLOGY—Bunganditj, the name of the aboriginal tribe that used to inhabit the Hamilton area (West, 1974).

DESCRIPTION—**P^3**—The posterior portion of the P^3 (fig. 2A) present in the holotype is ornamented with seven well-developed ridges labially and there is a suggestion of an eighth lingually at the broken surface in front. By comparison with *A. rufescens*, it appears that the fragment represents the posterior two-thirds of the tooth. The P^3 of *A. rufescens* has seven or eight ridges. It is certain that the complete P^3 of *M. bunganditj* had at least one more ridge than is preserved, and it perhaps had as many as ten if we are correct in our interpretation of the portion represented. The P^3 is weakly concave buccally and lingually and is much narrower buccolingually than that of species of *Propleopus*. The ridges form cuspules where they meet on the straight occlusal crest, except posterolingually. No posterolingual cusp is present, but the tooth thickens toward its posterior edge. The presence of a posterolingual cusp on the P^3 is variable in *A. rufescens* and *B. gaimardi,* and this character also may have been variable in *M. bunganditj.* Table 2 gives comparative measurements for the dentitions of species of *Milliyowi* and *Aepyprymnus.*

Upper Molars—The M^1 (figs. 2B,D) is an unworn, fully formed crown, clearly from a very young individual. The parastyle of M^1 is very elongate and massive. There is no suggestion of an anterior cingulum, and the anterior face of the protoloph slopes steeply to the crown base. The protoloph is low and poorly developed, has a small, posteriorly directed kink, and is shorter than the well-developed metaloph. A very prominent postparacrista is prevented from linking with a more weakly developed premetacrista by a deep fissure. The midlink is well developed, as is the metaloph. The lophs are noticeably narrow at their apices. The ectoloph is interrupted by a narrow valley that connects the interloph valley to the labial side of the crown. Anteriorly, the ectoloph divides near its end. The metaloph is noticeably kinked and the protocone is small, being much the smallest of the primary cusps. The rectangular central valley is longer than wide. A broad stout postcingulum defines a broad arcuate posterior basin. A slightly developed postlink is present on the rear face of the metaloph.

The M^2 (fig. 2C) is barely worn. The primary lophs are subequal in length and the protoloph is well formed but its connection to the base of the protocone is weakly developed. The pre- and postprotocristae are well developed. The preprotocrista forms a well-developed anterior cingulum that unites with a weakly developed preparacrista on the labial margin of the tooth. The postparacrista and premetacrista are weakly developed. They do not join at the base of the tooth, leaving the central basin open buccally. In contrast, the pre- and posthypocristae are well developed, the posthypocrista forming a posterior cingulum by uniting with the postmetacrista. The prehypocrista and postprotocrista join close to the lingual side of the central basin. The metaloph is well developed. The lingual margin of the tooth slopes gently to the crown base.

The M^3 (fig. 2E) is less worn than the M^2 and differs from it in having a more steeply sloping lingual margin. A fissure can be seen in the protoloph and another in the metaloph, both near their lingual edges. To judge by the associated valleys, this feature was probably present on M^2 before becoming obscured by wear.

The M^5 (fig. 3A), if properly assigned to this taxon, differs from M^3 in having a steeper lingual margin and in being lower-crowned. The metaloph is shorter than the protoloph, and the ridges and lophs are sharper and less bulbous than in the other specimens.

I_1—The extremely elongate and narrow enamel cap of an I_1 (fig. 5A) appears to belong to a potoroid approximately the size of *Milliyowi bunganditj* and is here tentatively referred to that species. The enamel cap is most like that of I_1 of a species of *Potorous*. It differs from I_1 of the species of *Wakiewakie, Bettongia, Caloprymnus,* and *Aepyprymnus* in possessing a slight dorsal enamel crest extending the length of the crown as in some macropodids. It differs from I_1 of all macropodids by being narrower and more elongate. The I_1 of *Gumardee pascuali* is unknown, while a poorly preserved I_1 has been reported for *Bulungamaya delicota* (Flannery et al., 1982). It is clear, however, that the I_1 of *B. delicota* is less elongate than that of *M. bunganditj.*

P_3—The P_3 (figs. 3B–D) is represented by a fragment that consists of the anterior three-fourths of a tooth. It has a nearly flat straight blade with six sharply defined cusplets and nearly vertically oriented associated ridges. The remnant of a seventh ridge can be seen on the labial side. Small subsidiary branches come off of most of the main ridges as they approach the crest. These disappear in the intervening valleys. This branching feature is not seen in any of the comparative specimens of *A. rufescens, Wakiewakie, Potorous, Bettongia, Bulungamaya,* or *Caloprymnus* available to us. A sharp ridge defines the anterior edge of the tooth. The blade is buccolingually narrow.

Lower Molars—The anterior cingulum and buccal portion of the protolophid of the M_1 (NMV P158069) are broken away (fig. 3A). The labial face of the hypolophid slopes at a gentle angle to the base of the crown. The protolophid appears to

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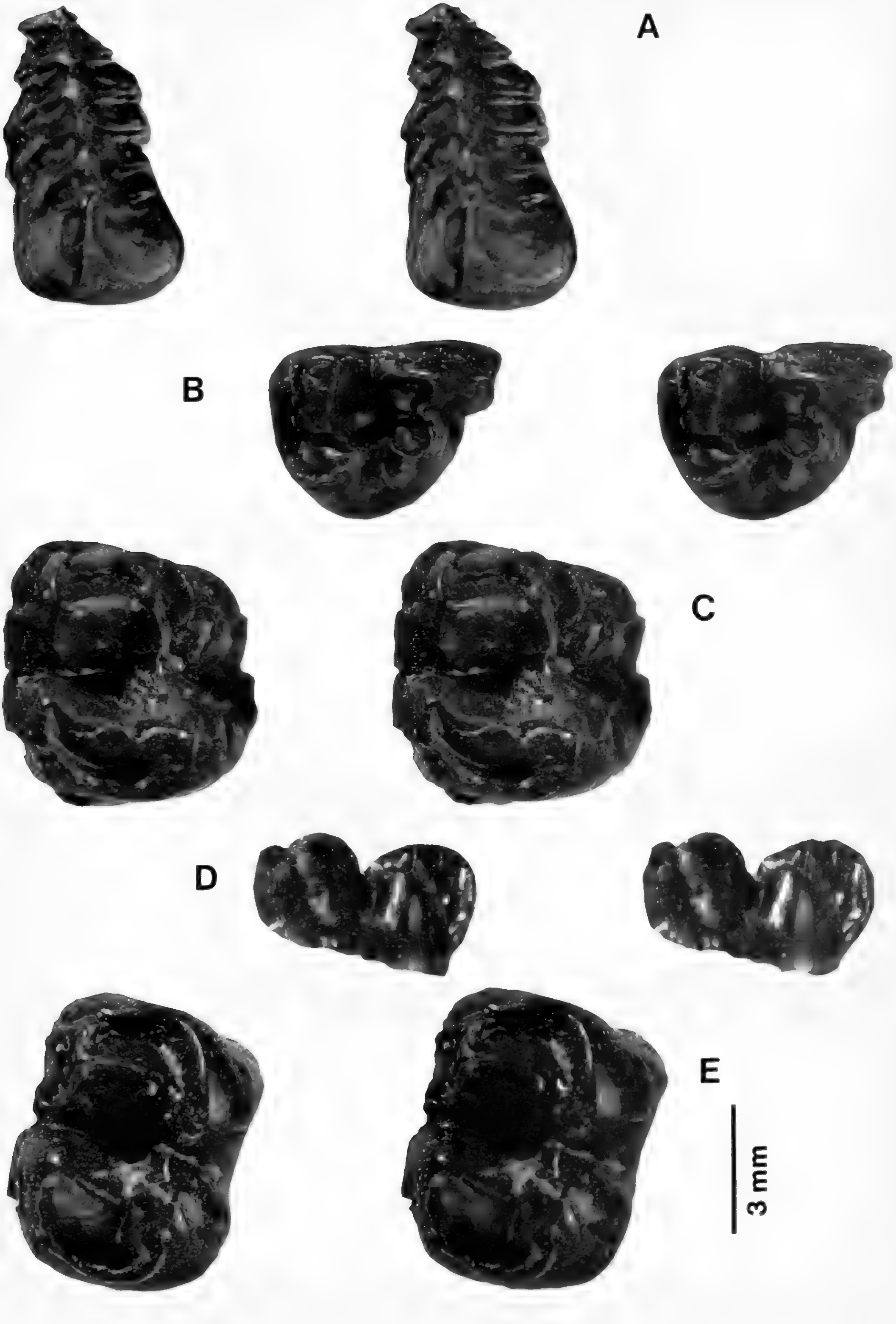
FIG. 2. *Milliyowi bunganditj.* Stereographic photopairs. All approx. ×6.8. **A, C, E,** Holotype specimen, NMV P158635, associated right P^3, M^2, and M^3 shown in crown view. **B, D,** Referred specimen, PM 50763, a right M^1 shown in crown and buccal views.

FIG. 3. *Milliyowi bunganditj.* Stereographic photopairs of three teeth. C is shown at approx. ×6.7, the rest at ×8.3. **A,** NMV P158068, a tentatively referred right M^5 shown in crown view. **B-D,** NMV P53223, right P_3 shown in buccal, lingual, and crown views. **E,** NMV P158069, a posterior two-thirds of a right M_1, lacking anterior part of protoconid, shown in crown view. (*overleaf*)

FIG. 4. Stereographic photopairs of teeth of *Milliyowi bunganditj* (A), *Troposodon* sp. (B, C), and *Simosthenurus* sp. (D, E), all shown in crown view at approx. ×6.7. **A,** NMV P54137, left M_4. **B,** NMV P158465, right M_4. **C,** NMV P26422, hypolophid of a left lower molar. **D,** NMV P158449, a protolophid of a left lower molar. **E,** NMV P158633, hypolophid of a right lower molar. (*page 9*)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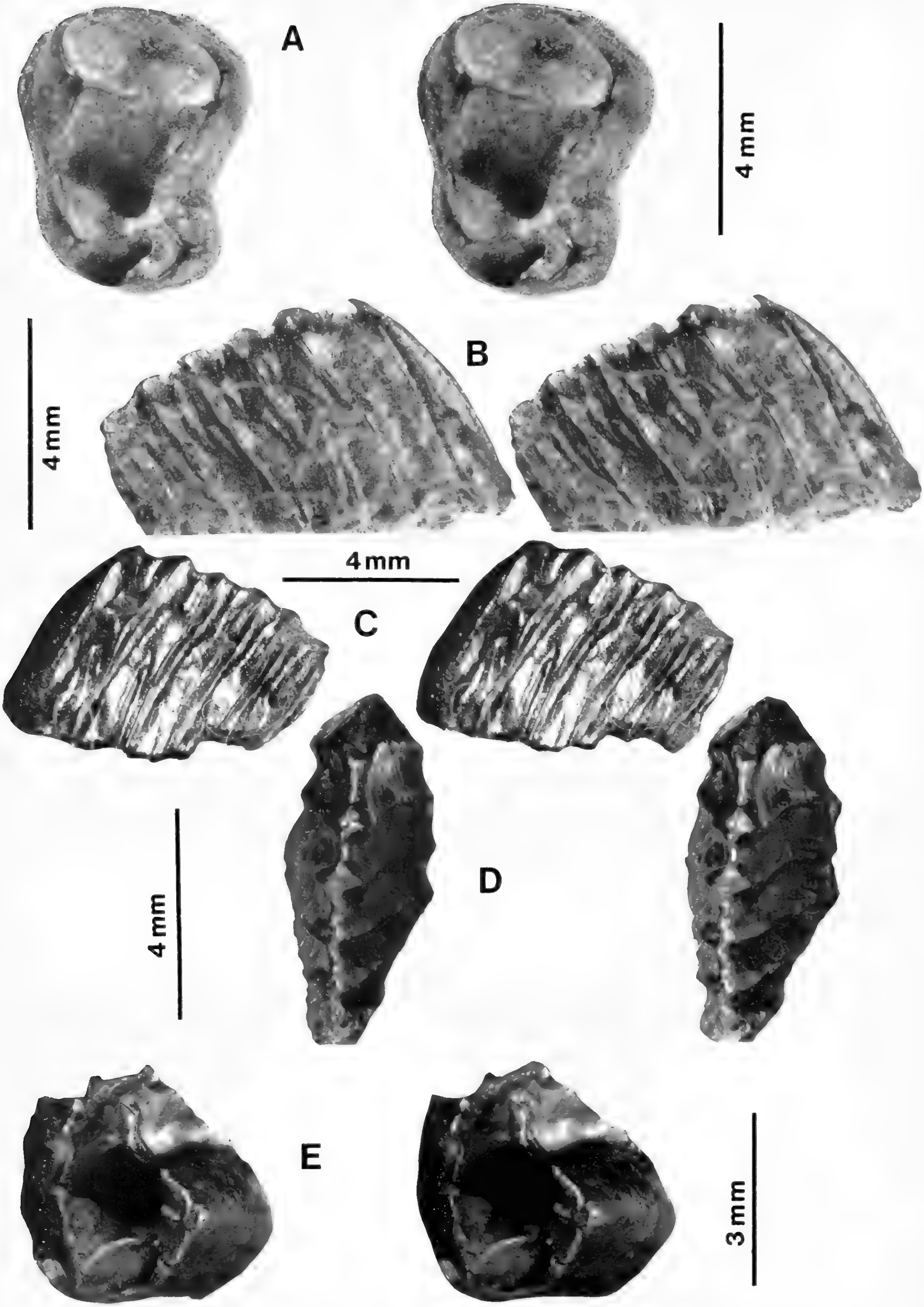
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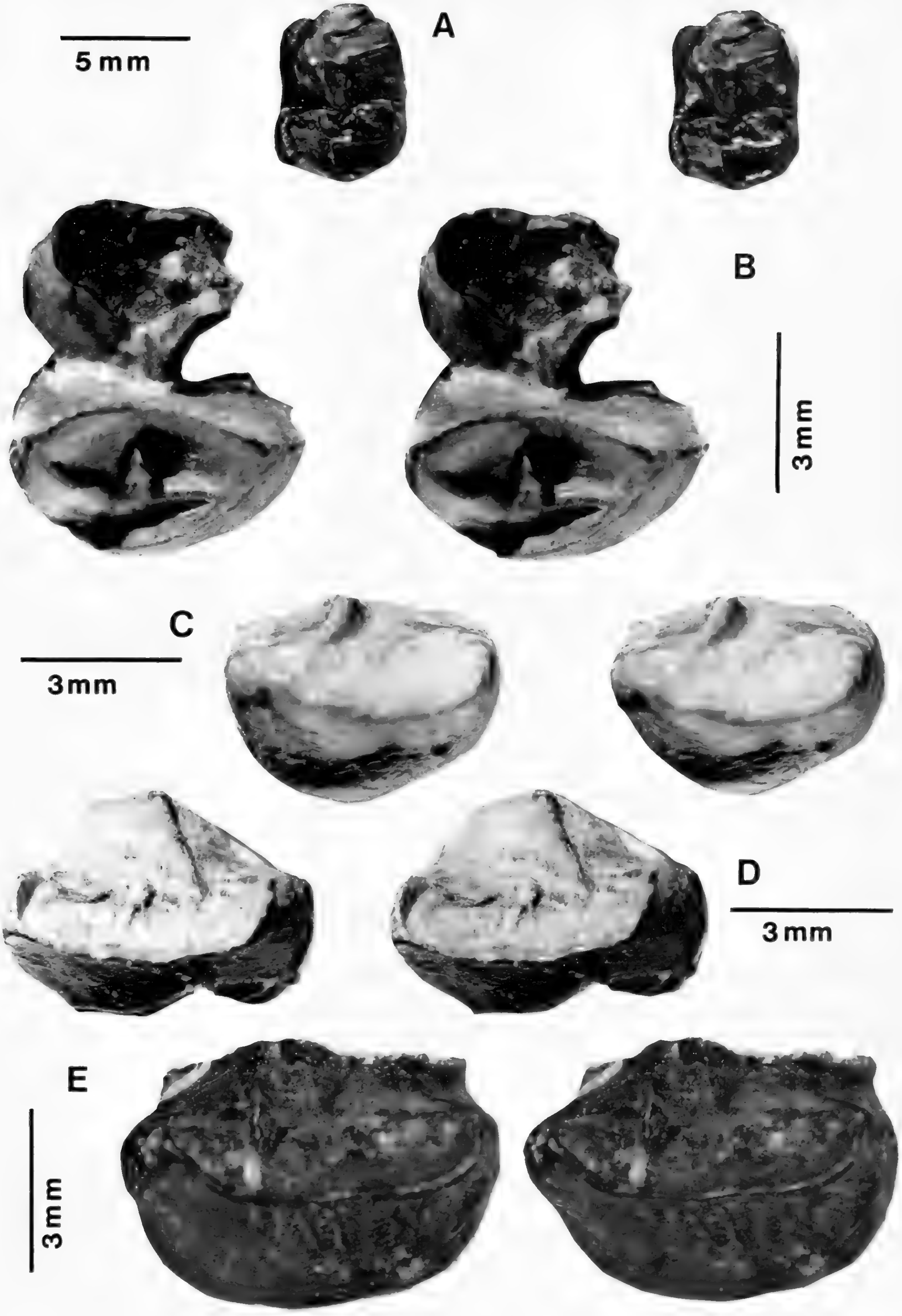
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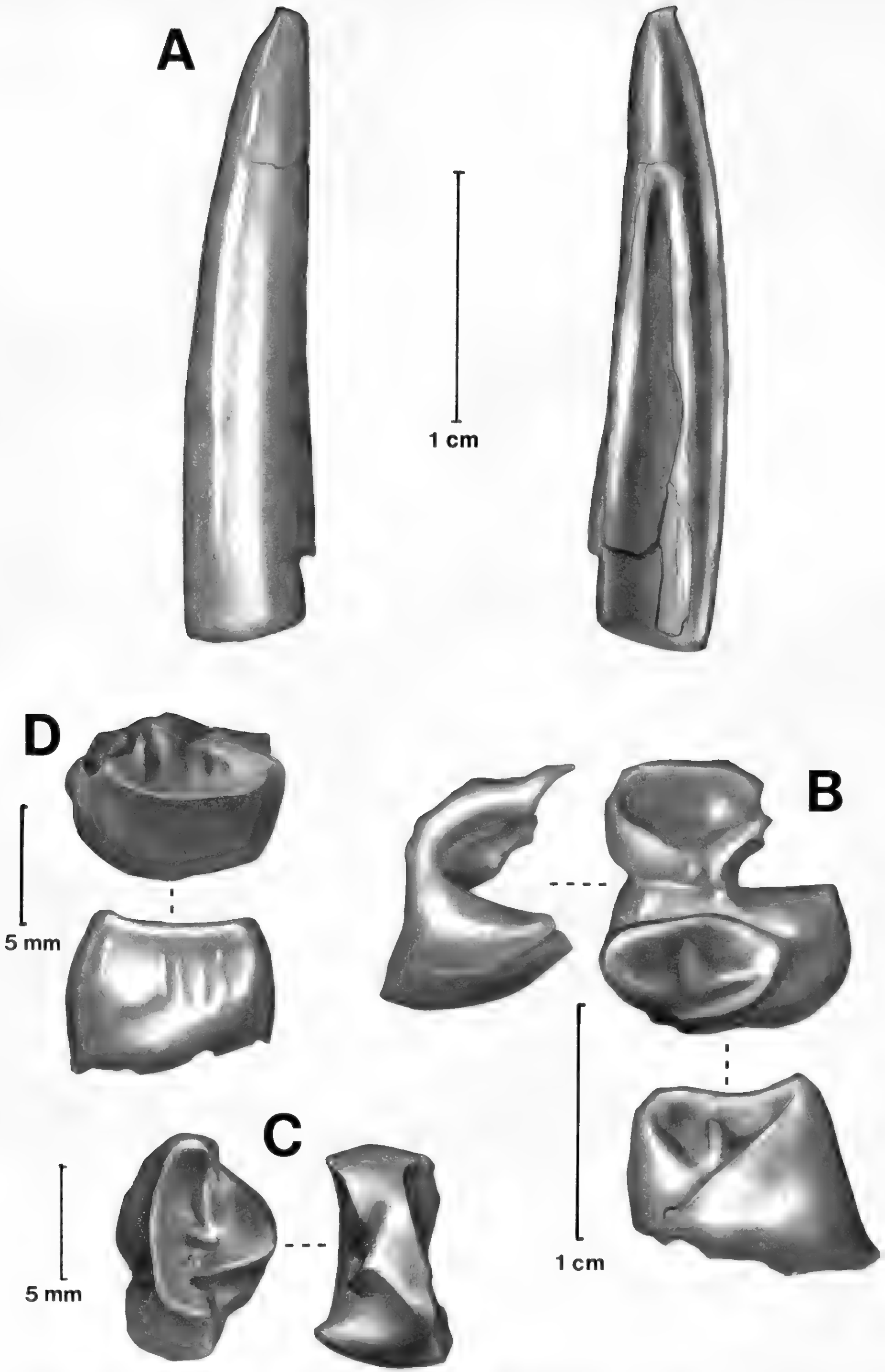

FIG. 5. Drawings of various teeth representing the same three genera as in Figure 4. All approx. ×6.7. **A,** PM 16821, a left I_1 of *Milliyowi bunganditj* shown in ventrolateral and dorsomedial views. **B,** NMV P158465, the same specimen as Figure 4B, right M^4 of *Troposodon* sp. shown in lingual, crown, and posterior views. **C,** NMV P158449, the same specimen as in Figure 4D, protolophid of a left lower molar of *Simosthenurus* sp. shown in crown and anterior views. **D,** NMV P158633, the same tooth as in Figure 4E, hypolophid of a right lower molar of *Simosthenurus* sp. shown in crown and posterior views.

TABLE 2. Dental measurements (mm) of *Milliyowi bunganditj* compared to those of *Aepyprymnus rufescens*.

				Aepyprymnus rufescens			
		Milliyowi bunganditj		**X̄**	**R**	**SD**	**N**
NMV P158635	P^3	PW	4.0	3.2	2.9–3.6	.23	7
	M^2	L	6.0	5.5	5.1–6.0	.31	12
		AW	6.4	4.3	4.0–4.5	.14	12
		PW	6.7	4.1	3.9–4.5	.18	12
	M^3	L	6.8	6.3	5.9–6.6	.22	12
		AW	5.5	4.7	4.4–5.0	.21	12
		PW	5.6	4.3	4.0–4.3	.22	12
NMV P158068	M^5	L	6.5	6.2	5.7–6.6	—	2
		AW	5.3	4.2	4.1–4.3	—	2
		PW	4.2	3.3	3.1–3.5	—	2
PM 50763	M^1	L	5.4	—	—	—	—
		AW	4.0	—	—	—	—
		PW	4.5	3.3	3.1–3.5	.21	3
NMV P158069	M^1	L	b > 5.6				
		AW	b > 4.1				
		PW	5.1				
NMV P54137	M_4	L	6.7	6.3	6.0–6.9	.32	8
		AW	4.9	4.8	4.4–5.2	.26	7
		PW	5.0	4.5	4.2–5.0	.26	8

L = length, AW = anterior width, PW = posterior width, X̄ = mean, R = range, SD = standard deviation, N = number, b = broken.

form a single cusp as in other potoroines. The cristid obliqua terminates before reaching the protoconid apex. The hypolophid is poorly developed. A slight postprotocristid and a preentocristid are present.

The presumed M_3 or M_4 (fig. 4A) has a buccal edge that slopes at a steeper angle to the crown base than in M_1. The paracristid forms the labial and anterior boundary of the extensive anterior cingulum. There is no fossette buccal to this structure as found in macropodids and some other potoroids (e.g., *C. campestris*, bulungamayines). The postprotocristid is well developed and joins a well-developed prehypocristid to form the cristid obliqua. The posthypocristid forms a well-developed posterior cingulum. A slight low point can be seen on both protolophid and hypolophid near their labial margins. The central valley has ornamentation on the lingual side.

Discussion—The relationships of *M. bunganditj* are at present unclear. Flannery (1989) included *Milliyowi bunganditj* within his analysis of the phylogeny of the Macropodoidea, giving it the informal name the "Hamilton potoroid." He found it difficult to place because of the large number of features that could not be examined due to the fragmentary nature of the fossils. He did note, however, that it lacks a significant synapomorphy that unites *Aepyprymnus* and *Caloprymnus*. This is hypertrophy of the posthypocristid on the lower molars, which in these genera slopes diagonally across almost the entire width of the hypolophid. Thus *Milliyowi* appears to lie outside the *Aepyprymnus*/*Caloprymnus* clade. We tentatively place it within the tribe Bettongini, but leave it *incertae sedis* within that group. A single upper molar fragment (PM 4492), referred to as cf. *Aepyprymnus* by Turnbull and Lundelius (1970), may be referable to *M. bunganditj*; however, it is too fragmentary for any assignment to be certain.

Family Macropodidae Gray, 1821
Subfamily Sthenurinae (Glauert, 1926)
***Troposodon* Bartholomai, 1967**
***Troposodon* sp.**

Material—NMV P158465, right M^4 missing the anterior side of the protoloph and much of the protocone (figs. 4B, 5B); NMV P26422, posterior half of a right lower molar (fig. 4C; ref. Turnbull & Lundelius, 1970, p. 63).

Description—The more complete molar (figs. 4B, 5B) lacks the anterior face of the protoloph and the protocone and the surrounding area. Enough is preserved to show that the lophs are attenuated, the midlink is well developed, and a well-developed postprotocrista is present. The posthypocrista and postmetacrista overlap and a prominent postlink is present in the center of the rear face of the hypoloph. The postparacrista extends from the crest of the paracone posterolingually on the posterior face of the protoloph and disappears before reaching the midlink. The tooth is much larger than molars of *Lagostrophus fasciatus,* and it differs from upper molars of species of *Simosthenurus, Procoptodon,* and to some extent *Sthenurus* in lacking the fine ornamentation and/or grooving of the enamel seen in these forms. There is barely discernable ornamentation on the posterior face of the protoloph.

Discussion—Turnbull and Lundelius (1970) suggested the presence of a species of *Troposodon* in the Hamilton local fauna on the basis of a hypolophid (NMV P26422). While the two molar fragments discussed here are close in morphology to *Troposodon minor,* they are too incomplete to permit assignment to a species. The combination of features seen in the upper molar fragment, including its large size, overlapping of a distinct posthypocrista and postmetacrista, very prominent postlink, and lack of any enamel crenulation, is unique to the species of *Troposodon* among Macropodoidea.

***Simosthenurus* Tedford, 1966**
***Simosthenurus* sp.**
(figs. 4D,E, 5C,D; table 1)

Material—NMV P158449, left protolophid (figs. 4D, 5C); NMV P158633, right hypolophid (figs. 4E, 5D).

Description—The two molar fragments are low-crowned; the protolophid extremely so. Their features most clearly resemble those of *Simosthenurus antiquus* but they are smaller. Other similarities are the posterior position of the premetacristid and the distinct paracristid of NMV P158449, and the sharp cristid obliqua of NMV P158633. The trigonid basin is broad, and both protolophid and hypolophid are ornamented with fine crenulations. The paracristid originates well below and lingual to the protoconid apex. The premetacristid crosses the face of the protolophid, a primitive characteristic. The hypolophid is bulbous at its base.

Discussion—This material has been assigned to a species of *Simosthenurus* because the enamel of the lower molar fragments is finely crenulate (a feature seen among macropodids only in the species of *Procoptodon* and *Simosthenurus*) and because the posterior face of the hypolophid lacks the deep grooving seen in the species of *Procoptodon* (Flannery, 1983). Also, the molar fragments are lower-crowned than those of species of either *Sthenurus* or *Procoptodon.* However, it differs from all other species of *Simosthenurus* (as well as *Procoptodon* and *Sthenurus*) in having the premetacristid located on the anterior face of, and oriented at about 45° to, the protolophid.

Simosthenurus antiquus is the only named Pliocene species of the genus. However, isolated molar and premolar fragments of an unnamed species of *Simosthenurus* are known from the Bow local fauna (Flannery & Archer, 1984) as well as from Hamilton. The Hamilton material is more primitive in its low-crowned condition than other forms and represents a new species, but more complete material is needed before it can be named. The Hamilton molar fragments represent the earliest known occurrence of a species of *Simosthenurus.*

Subfamily Macropodinae Gray, 1821
***Dorcopsis* Schlegel and Müller, 1845**
***Dorcopsis wintercookorum* n. sp.**
(figs. 6–8; table 1)

Holotype—NMV P158453, right maxilla with P^3, M^{2-5} (figs. 6A–C, 7B,C). The maxilla is badly corroded, but the enamel caps of the teeth are in good condition.

Referred Specimens—PM 16822, left P^3 (figs. 6D–F, 7A); NMV P160221, left M^1 (fig. 7E); PM 16816, right M^1 (fig. 7D); PM 4570, protoloph of right M^2; PM 50767, right M^2 (fig. 7F); PM 16807, protoloph of right upper molar, probably M^2 or M^3; PM 50771, right upper molar (fig. 7G); NMV P158462, right P_3 (figs. 8B–D); NMV P157465, anterior portion of right P_3; NMV P157477, right P_3 (fig. 8A).

Type Locality and Age—See the Introduction for details.

Diagnosis—*Dorcopsis wintercookorum* can be distinguished from other species of *Dorcopsis* in possessing the following characteristics. It is much smaller than any other species and possesses a cuspule labial to the paracone on M^2 that is not seen in any other form. The anterior edges of the $P^3/_3$ of *D. wintercookorum* slope from the base of the crown to the occlusal margin more gently than in other species. *D. wintercookorum* possesses a much less distinct lingual cingulum on the P^3 than does *D. mulleri. D. hageni* is closest in morphology to *D. wintercookorum* but is much larger (see table 1 for dental measurements of *D. wintercookorum*).

Features that distinguish *Dorcopsis wintercookorum* from *Dorcopsulus* are few. It has slightly larger upper molars, which are otherwise nearly identical in form to those of *Dorcopsulus*. The cuspule labial to the paracone of the M^2 of *Dorcopsis wintercookorum*, which is distinctive for that taxon alone among the species of *Dorcopsis*, is even better developed in the M^2's of *Dorcopsulus*. In that genus the cuspule is well developed on M^3's and is present to well developed on the M^4's, and in one specimen in the American Museum of Natural History sample of seven, it is present on the M^5's (table 1). In the P3's of *Dorcopsis wintercookorum*, the main crest has a variable number of cuspules (five or six). In *Dorcopsulus* there appear to be six.

ETYMOLOGY—Named for Mr. and Mrs. Sam Wintercook, whose hospitality made our fieldwork much more enjoyable in the years from 1977 to 1981.

DESCRIPTION—**Maxilla**—Although the maxilla of the type specimen is badly corroded, some features can be recognized. The zygomatic process appears to be short and rounded as in the living species of *Dorcopsis*, not reaching the base of the molar crowns. Sutures, the position of the infraorbital canal, and details of the palatal area are all obscured.

P^3—The P^3 of *D. wintercookorum* consists of a blade with a distinct, sharp anterior cusp and a more elongate posterior cusp, each with labial and lingual ridges (figs. 6A–F, 7A–C). Three distinct but weak ridges are present on the sides of the blade, and the associated cuspules cap the crest of the blade. Several low tubercles of enamel are present on the labial side of the base of the crown. A posterolingual cusp, which is lower than the main crest, is also present. It is connected to the main crest by a single ridge, which intersects the main crest at a 90° angle. The lingual cingulum is very weakly developed. It terminates anteriorly just posterolingual to the main cusp. The isolated P^3 is similar to that of the holotype but its lateral ridges are somewhat sharper.

Upper Molars—The relative positions of the molars of the holotype are slightly distorted. However, the cheektooth rows appear to have been straight and were probably parallel. Except for the M^1 the descriptions are based largely on the holotype.

The two M^1 specimens (figs. 7D,E) are low-crowned. A distinct and large parastyle is present. The protoloph is weakly developed, the paracone and protocone forming distinct prominences. Well-developed postparacrista and premetacrista block the lingual end of the interloph valley. The midlink is extremely poorly developed, but the metaloph is well developed. The postmetacrista and posthypocrista form a "U"-shaped posterior cingulum. A postlink is present on the rear face of the metaloph midway between the metacone and metaconule. The two halves of the tooth are nearly equal in NMV P160221, but in PM 16816 the anterior is slightly narrower than the posterior.

The M^2 differs from M^1 in the following ways. The M^2 of the holotype, which is considerably worn, is slightly larger than the M^1 described above. The protoloph is well developed, the parastyle is greatly reduced in size, and the midlink is slightly better developed. A small forelink is present, and posterobuccal to the paracone there is a small cuspule that is approximately one-half the height of the paracone. The postparacrista and premetacrista are smaller in size. Both M^2 specimens possess a stout cingular cuspule labial to the paracone.

The M^3 differs from M^2 in the following ways. It is very slightly larger. The anterior cingulum in that of the holotype is broken away. There is no cuspule buccal to the paracone. The postparacrista and premetacrista are slightly smaller than in M^2.

The M^4 is similar in morphology to M^3, differing only in that the postparacrista and premetacrista are further reduced in size.

The M^5 differs from M^4 in that the metaloph is markedly narrower than the protoloph, and in that the postparacrista and premetacrista are still further reduced.

P_3—Two complete and one partial P_3 of *Dorcopsis wintercookorum* are known. Both complete specimens have a sharp and distinct anterior cuspid and a longer posterior cuspid at the end of the main blade (figs. 8A–D). The anterior and posterior cuspids have distinct lingual and labial ridges from tip to cingulum. Three indistinct ridgelets are present between these cuspids (and there is a suggestion of one more in one specimen). Anteriorly the blade slopes at a low angle to the base of the crown. The posterior portion of the tooth is slightly broader than the anterior portion. A small, low posterolabial cuspid is present on NMV P154477. The blades of both teeth are slightly convex buccally.

DISCUSSION—The material assigned here to *D. wintercookorum* is significant in several ways. Bartholomai (1978a) suggested that *Dorcopsoides*

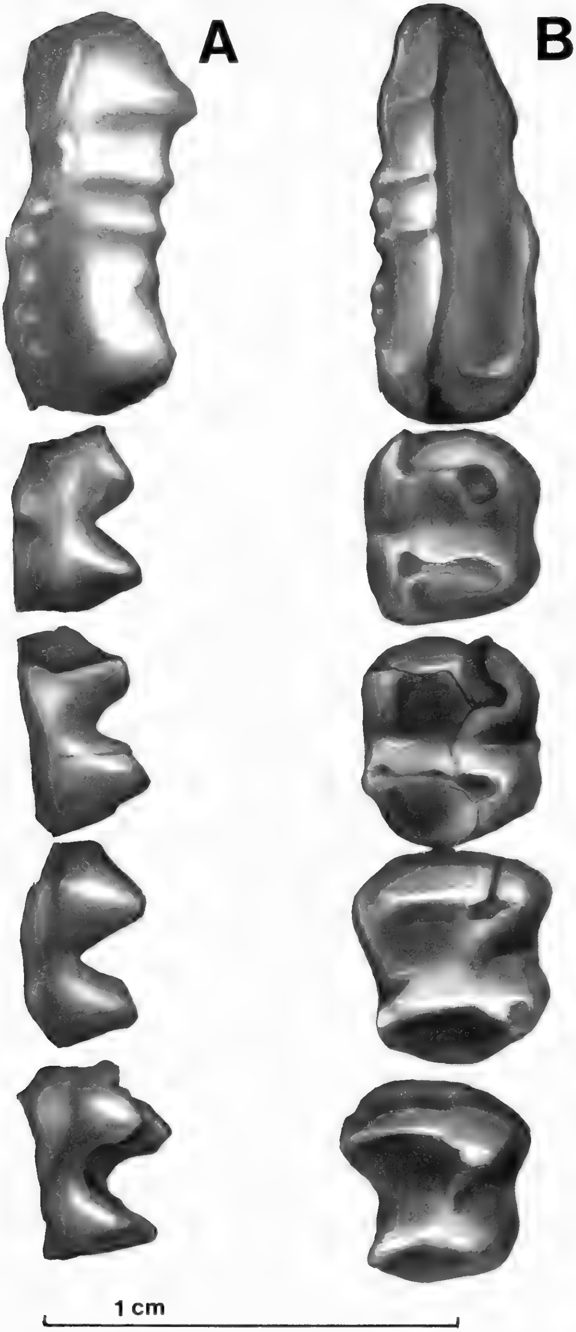

FIG. 6. **A-C,** Drawings of the holotype specimen of *Dorcopsis wintercookorum,* NMV P158453, a right maxillary fragment with P^3, M^{2-5} shown in buccal (A), crown (B), and lingual (C) views at approx. ×6.3. **D-F,** Drawings of a referred specimen of *D. wintercookorum,* PM 16822, shown in lingual (D), crown (E), and buccal (F) views at approx. ×8.6.

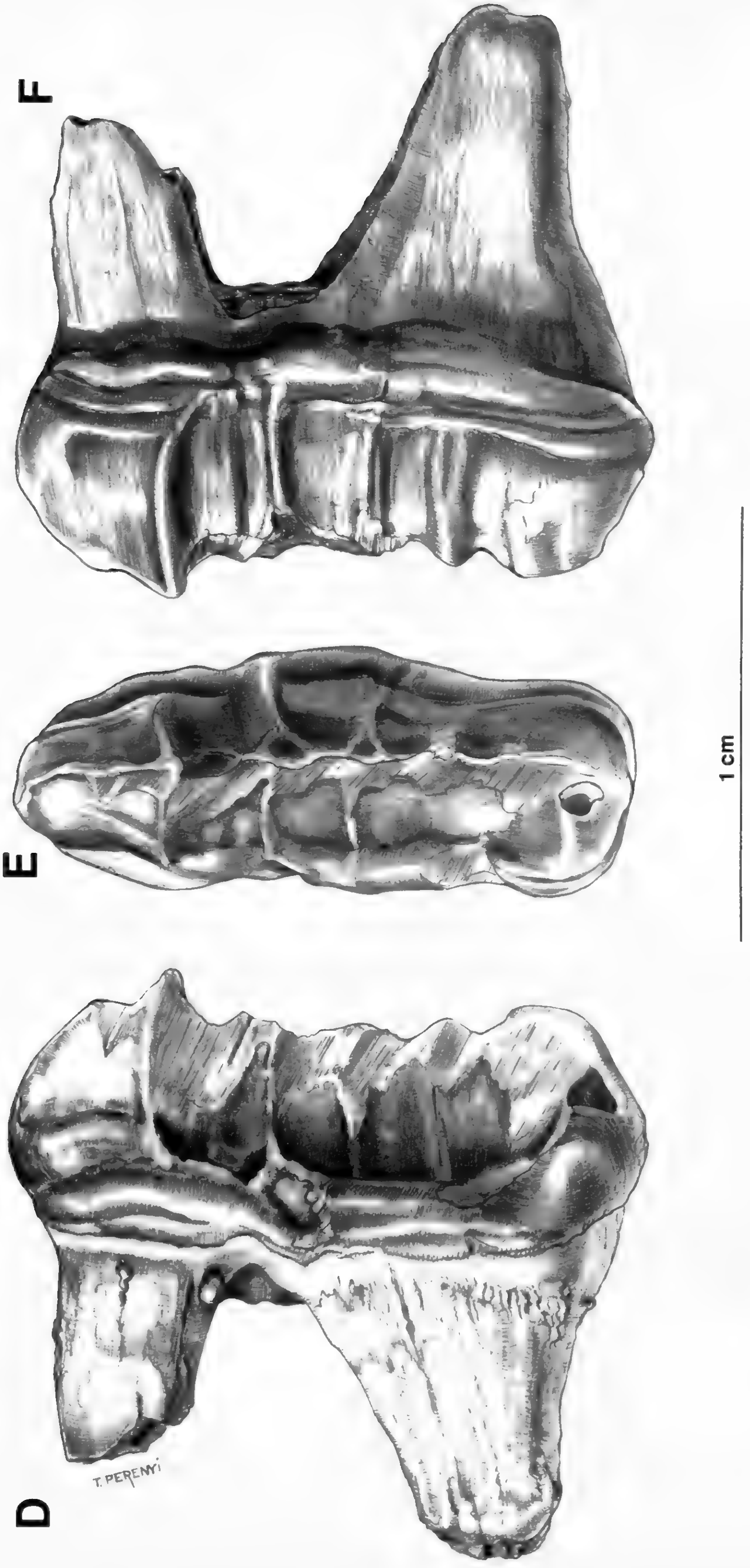

FIG. 6. Continued.

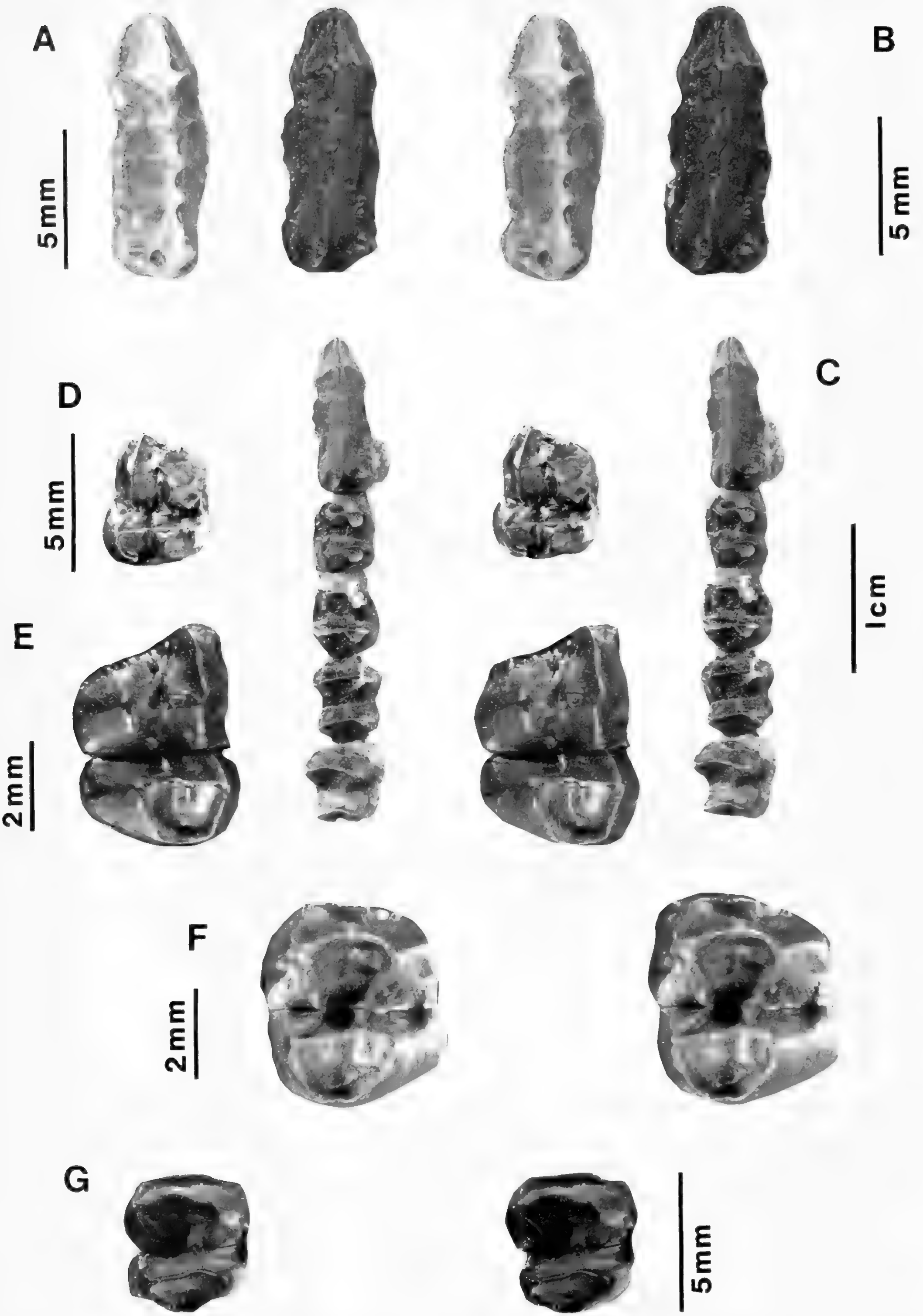

FIG. 7. Stereophoto pairs of various specimens of *D. wintercookorum*, all in crown view. **A,** PM 16822, left P^3 shown at approx. ×4.1. **B, C,** NMV P158453, the holotype specimen. In B, the P^3 is shown at the same scale as A to

should be placed in synonymy with *Wallabia,* thus challenging the only previous evidence that members of the *Dorcopsis* lineage have inhabited Australia. He suggested that study of the Hamilton material assigned to *Dorcopsis* might provide clarification as to whether or not the *Dorcopsis* lineage has ever been present in Australia. The Hamilton material does indeed provide insights into this question. It is also significant in providing insights into the taxonomy of the living genera *Dorcopsis* and *Dorcopsulus.*

We have no doubt that *Dorcopsis wintercookorum* is a member of the *Dorcopsis* lineage and bears no close resemblance to species of *Wallabia.* In his synonomy of *Dorcopsoides* with *Wallabia,* Bartholomai noted the following features in *Dorcopsoides,* which he considered indicated an affinity with *Wallabia*: the permanent cheek teeth of the two genera are very similar, the length of the premolar relative to the molars is more like that in *Wallabia,* not *Dorcopsis,* the molars are more like those of *Wallabia,* not *Dorcopsis,* the molars of *Dorcopsoides* are larger than those of *Dorcopsis, Dorcopsoides* differs from *Dorcopsulus* in that the molars vary greatly in size along the molar now, the mandible is deep and the diastema short as in *Wallabia,* the molar row is bowed labially, and what is known of the cranium is similar to *Wallabia.* In all of these features where they can be observed, *Dorcopsis wintercookorum* is similar to the *Dorcopsis* lineage and differs from the condition seen in *Wallabia.* The permanent cheek teeth are very similar to those of *Dorcopsis* and *Dorcopsulus*; the molars vary little in size, are very low-crowned, and lack the extreme development of linking along the labial edge of the crown seen in *Wallabia.* The premolars are similar in size to *Dorcopsis* relative to the molars and longer than in *Wallabia.* The upper premolar is relatively longer and narrower than in *Wallabia* and has a very weakly developed lingual cingulum, again similar to the condition seen in *Dorcopsis,* but differing from the prominent and raised lingual cingulum of the species of *Wallabia.* The teeth are very small, being similar in size to those of *Dorcopsulus vanheurni* and much smaller than those of *Wallabia,* and the cheektooth rows are parallel, not bowed as in *Wallabia.* Unfortunately the dentary and cranium of *D. wintercookorum* are not known. However, the evidence from cheektooth morphology seems conclusive: *D. wintercookorum* is a member of the *Dorcopsis* lineage and, regardless of the affinities of *Dorcopsoides,* it provides clear evidence that this lineage once existed in Australia.

Questions regarding the taxonomy of members of the *Dorcopsis* lineage are not so easily resolved. In his revision of the Macropodidae, Tate (1948) indicated that *Dorcopsulus* and *Dorcopsis* are very close in morphology, differing primarily in that the P^3 of *Dorcopsulus* is less compressed and attenuated than in *Dorcopsis,* and the skull is less elongate. Examination of a large series of *Dorcopsis* and *Dorcopsulus* held at the Australian Museum, Sydney, shows that premolar shape varies considerably within both genera and that few features except size reliably serve to distinguish living members of these genera. In general, however, the labial ridging of P^3 is more prominent in *Dorcopsulus,* and M^{2-4} (and occasionally M^5) have a cuspule positioned posterobuccal to the paracone, a feature generally lacking in *Dorcopsis.* Indeed, the features that serve to distinguish these genera are small, and it may be that future taxonomic revision will see the genera synonymized, in which case *Dorcopsis* Schlegel and Müller, 1845, would take priority over *Dorcopsulus* Matschie, 1916.

The morphology of *Dorcopsis wintercookorum* further muddies the distinction between these two genera. It is the size of *Dorcopsulus,* yet the permanent premolars have relatively poorly defined buccal ridging, typical of *Dorcopsis,* and differing from *Dorcopsulus,* which has more prominent ridges. Of the upper molars, only M^2 has a cuspule positioned posterobuccal to the paracone, and even that cuspule is small relative to that seen in *Dorcopsulus.* In view of the uncertainty surrounding the distinctness of the two genera, and the fact that *Dorcopsis* is the prior name, we have assigned *D. wintercookorum* to *Dorcopsis* pending a full revision of the two genera.

Dorcopsis sp.

REFERRED SPECIMENS—PM 4436, right P^3 (figured by Turnbull & Lundelius, 1970, pl. XIX); NMV P26417, right upper molar (Turnbull & Lundelius, 1970, pl. XXI). Both are larger than *D.*

←

facilitate direct comparison. In C, the series P^3, M^{2-5} are shown at approx. ×2.3. **D,** PM 16816, right M^1 shown at approx. ×4.1. **E,** NMV P160221, left M^1 shown at approx. ×6.8. **F,** PM 50767, right M^2 shown at approx. ×6.8. **G,** PM 50771, right upper molar (position uncertain) shown at approx. ×4.1.

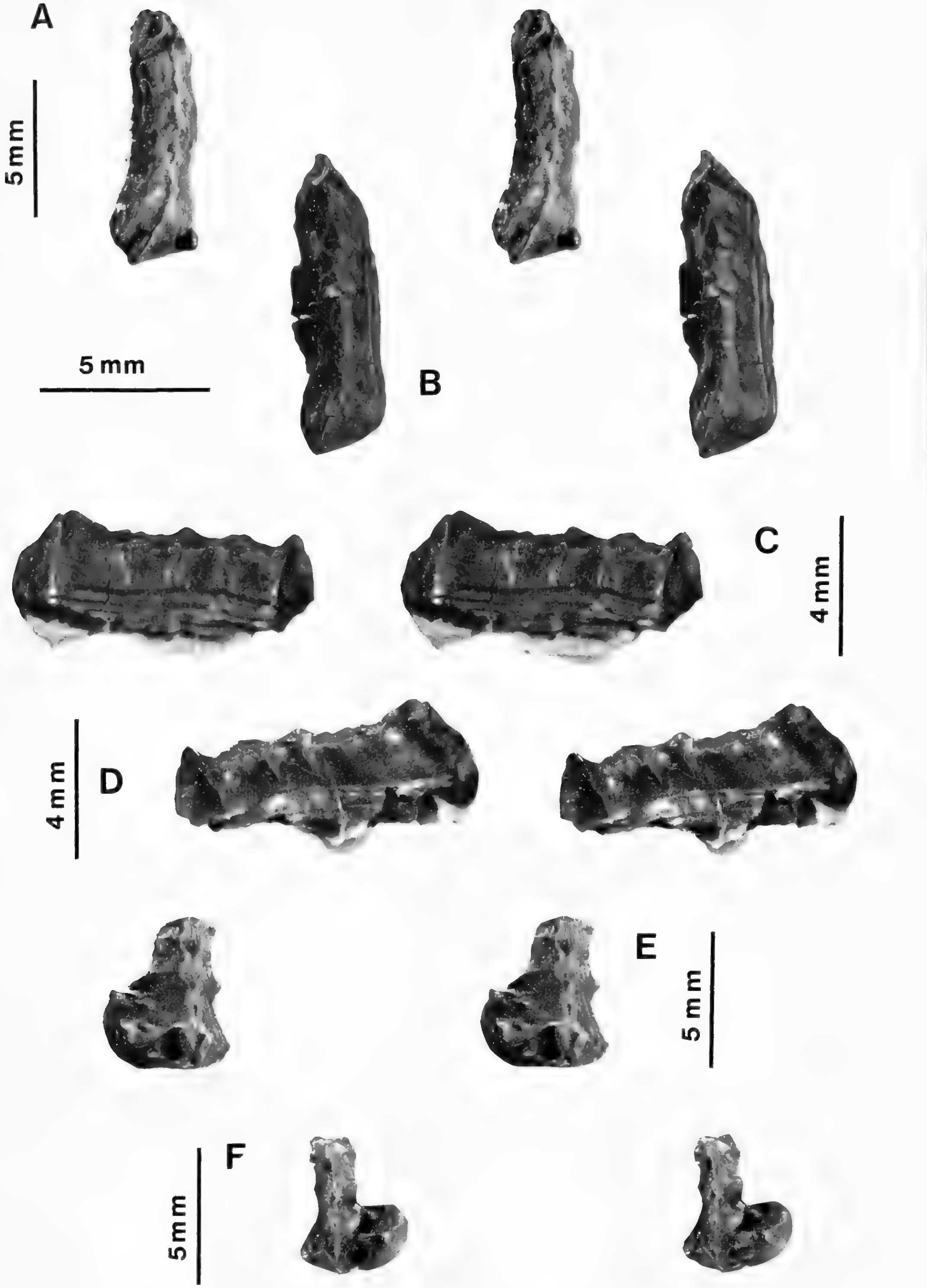

FIG. 8. Stereophoto pairs of various specimens of *D. wintercookorum* (A–D) and specimens referred cf. *Dendrolagus* (E, F). **A,** NMV P157477, right P_3 shown in crown view at approx. ×4.2. **B–D,** NMV P158462, right P_3 shown in crown

wintercookorum, and the P^3 has a different morphology.

Discussion—Turnbull and Lundelius (1970) recognized the presence of *Dorcopsis* in the Hamilton local fauna on the basis of a nearly complete lower molar and two fragmentary lower molars, three complete and nine fragmentary upper molars, and a fragmentary P^3. The upper molars described by Turnbull and Lundelius are similar to those of the holotype of *D. wintercookorum,* but no comparison with the lower molars can be made. The P^3 (PM 4436) differs markedly from those described here for *D. wintercookorum* and in some ways resembles the P^3's referred below to cf. *Dendrolagus* sp. Turnbull and Lundelius (1970) originally referred PM 4436 to *Dorcopsis* sp. This is continued here. This specimen differs from the P^3 of the other specimens of *Dorcopsis wintercookorum* in possessing a broad, bladelike posterolingual cuspid that approaches the main crest at a 60° angle (not 90° as in *D. wintercookorum*) and in its broad lingual cingulum. Except for the angle, in these characteristics it resembles the premolar fragments here assigned to cf. *Dendrolagus* sp., but it shows no sign of a labial (buccal) cingulum or, perhaps more significantly, the bladelike labial crest that *Dendrolagus* usually shows. The existing sample of these *Dendrolagus*-like specimens is too fragmentary to permit adequate description of a new species.

Dorcopsis wintercookorum and *Dorcopsis* sp. are the only species of *Dorcopsis* known from Australia, all living species and other possible fossil occurrences (Woodburne, 1967) being restricted to New Guinea. The presence of *Dorcopsis* in southern Australia during the early Pliocene suggests that species of the genus were at that time widespread and that they have subsequently become extinct in all but the northern, more tropical end of their former range, probably in response to climatic change.

Dendrolagus **Müller and Schlegel, 1839**

cf. *Dendrolagus*

(fig. 8E,F; table 1)

Material—NMV P157483, posterior part of left P^3 (fig. 8E); NMV P157481, posterior portion of right P^3 (fig. 8F); NMV P160154, anterior part of right P^3.

Description—The P^3 fragments NMV P157483 and NMV P157481 possess a broad bladelike posterolingual cusp and a broad lingual cingulum. Although broken, a piece of a labial cingulum can be seen on NMV P157483. A posterobuccal cusp is present on NMV P157481. NMV P160154 possesses a broad lingual and narrower labial cingulum. No distinct anterior cusp is present on the blade as in some species of *Dendrolagus* (e.g., *D. lumholtzi*).

Discussion—These specimens have been tentatively referred to a species of *Dendrolagus,* rather than to a species of *Sthenurus, Simosthenurus,* or *Procoptodon,* on the basis of the presence of a posterobuccal cusp on the P^3, which is separated from the posterior end of the blade much more than is seen in any other genus of macropodid. In addition, they often possess a narrow labial cingulum and a broad lingual cingulum. The posterolingual cusp is broad and bladelike, intersecting the main crest at nearly 90°. These premolar fragments differ from those of the sthenurines mentioned above in possessing a lower lingual cingulum and less crenulate enamel.

The Hamilton fossils assigned to cf. *Dendrolagus* are most similar to *Dendrolagus bennettianus* among living species in the involvement of the posterior-lingual blade of its P^3 in the formation of a posterior cingulum and a poorly defined cingular basin behind the blade. It is smaller than any living *Dendrolagus.* The posterior width of P^3 is 4.2–4.9 mm. The narrowest posterior width for P^3 known in any living species of *Dendrolagus* is 8.3 mm for a specimen of *D. lumholtzi* (Groves, 1982). The P^3, which is smaller than that of any named species other than *D. bennettianus,* is very similar, however, to P^3 fragment(s) assigned to cf. *Dendrolagus* from the early Pliocene Bow local fauna (Flannery & Archer, 1984).

Thylogale **Gray, 1837**

Thylogale ignis **n. sp.**

(figs. 9–11, 12A; table 3)

Holotype—NMV P157480, a barely worn right P^3 (fig. 9A).

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(B), buccal (C), and lingual (D) views at approx. ×5.9. **E,** NMV P157483, posterior portion of a left P^3 shown at approx. ×4.1. **F,** NMV P157481, posterior portion of a right P^3 shown at approx. ×4.1.

Referred Specimens—**I^2**—PM 4733, left (pl. XXV C in Turnbull & Lundelius, 1970).

I^3—NMV P54055, right (fig. 9D); NMV P162890, left; NMV P162891, right; NMV P162892, right; PM 4731, right (pl. XXII A,B in Turnbull & Lundelius, 1970).

P^2—NMV P54078, left (fig. 9C).

P^3—NMV P54146, right; NMV P158471, left; NMV P157478, left; NMV P162893, left; PM 17514, left (fig. 9B).

M^1—NMV P54086, right (fig. 9E).

M^2, M^3, or M^4—PM 16802, right (fig. 9F); PM 17526, ¾ left upper molar.

I_1—NMV P26419, left (fig. 10A); NMV P158455, right; NMV P160133, right; NMV P160150, right; NMV P160152, left; NMV P160160, right; NMV P160180, left; NMV P160213, left; NMV P160665, right; NMV P162894, left; NMV P175472, left; PM 4444, left (figured by Turnbull & Lundelius, 1970, pl. XXV D); PM 16805, left.

P_3—NMV P54111, left; NMV P54139, right; NMV P157479, right; NMV P157482, left; NMV P160132, left; NMV P160224, right (fig. 10B).

M_1—NMV P54100, right; NMV P158472, right (fig. 10C); NMV P159847, left; NMV P160188, left; NMV P162895; PM 4430, right; PM 4438, left (figured by Turnbull & Lundelius, 1970, pl. XXVI A–D); PM 17520, right.

M_2—PM 4564, right (figured by Turnbull & Lundelius, 1970, pl. XXIII B–E).

$M_{2\text{-}4}$—NMV P158432, right (figs. 10D, 11A).

M_3 or M_4—NMV P26420, right; PM 4576, right (figured by Turnbull & Lundelius, 1970, pl. XXIV A–D).

Type Locality and Age—See the Introduction for details.

Diagnosis—*Thylogale ignis* can be distinguished from other species of *Thylogale* in the following ways. *Thylogale thetis, T. stigmatica,* and *T. brunii* have a more posteriorly positioned groove on I^3, a better developed cingulum on P^3, and a markedly broader protolophid on M_1 than occurs in *T. ignis.* The molars are broader, the protolophid of the M_1 is slightly wider, and the anterior cingulum is shorter in *T. billardierii* than in *T. ignis* (table 3). *T. ignis* differs from *T. christenseni* in being larger and having a lower posterolingual cusp on the P^3 and in having a proportionately shorter P^3 and P_3 relative to the molar series.

Etymology—*Ignis* means fire in Latin and is a reference to the vulcanism that resulted in the burial of the Hamilton site beneath a lava flow.

Description—**I^3**—In the five known specimens of I^3 of *T. ignis,* the groove present on the labial face of the tooth is situated between 1.0 and 1.5 mm from its posterior edge. The tooth (fig. 9D) is almost identical in morphology to that of *T. billardierii.*

P^2—The P^2 of *T. ignis* (fig. 9C) is shorter than P^3; its crest is less prominent and is basically like the P^2 of *T. stigmatica.*

P^3—This tooth consists of a main blade and a posterolingual cusp (fig. 9B). The posterolingual cusp is much lower than the main blade of the tooth. The main blade consists of anterior and posterior cusps with three smaller cuspules between them. The posteriormost cuspule is indistinct and tends to merge with the posterior cusp. A distinct lingual cingulum is absent but a small ridge is present basally on the lingual and buccal sides of the tooth.

M^1—The single M^1 in the collection is unworn (fig. 9E). Its parastyle is small and the protoloph is poorly developed. The anterior cingulum is restricted to the labial half of the tooth. The midlink, postparacrista, and premetacrista are well developed. The metaloph is strongly developed and a very slight postlink is present on its rear face. The posthyposcrista and postmetacrista form a "U"-shaped posterior cingulum. This tooth is indistinguishable in morphology from that of *T. billardierii* but differs from that of *T. stigmatica, T. brunii,* and *T. thetis* in having the anterior cingulum further restricted to the buccal side of the tooth.

M^2, M^3, or M^4—This tooth (fig. 9F) has a *Thylogale* morphology and is tentatively assigned to *T. ignis.* Its procingulum is broad and prominent, and the anterior moiety is wider than the posterior.

I_1—The I_1 of *T. ignis* (fig. 10H) is virtually indistinguishable in size and morphology from that of *T. billardierii.* The enamel is restricted to the labial side of the tooth except for the flanges of enamel present on the ventral and dorsal margins.

P_3—The P_3 is formed of a simple blade (fig. 10B) that is slightly deflected lingually at its posterior end. The blade of the tooth is formed by anterior and posterior cuspids with three smaller cuspules between them. A small cingulum is present around the base of the tooth. The P_3 is slightly broader than that of *T. billardierii.*

Lower Molars—The M_1 is fully lophodont in form, although the protolophid is much narrower than the hypolophid (fig. 10C). The cristid obliqua and paracristid are well developed, and well-defined pre- and postmetacristids are present. No posterior cingulum or ornamentation is present on the rear face of the hypolophid. The anterior cin-

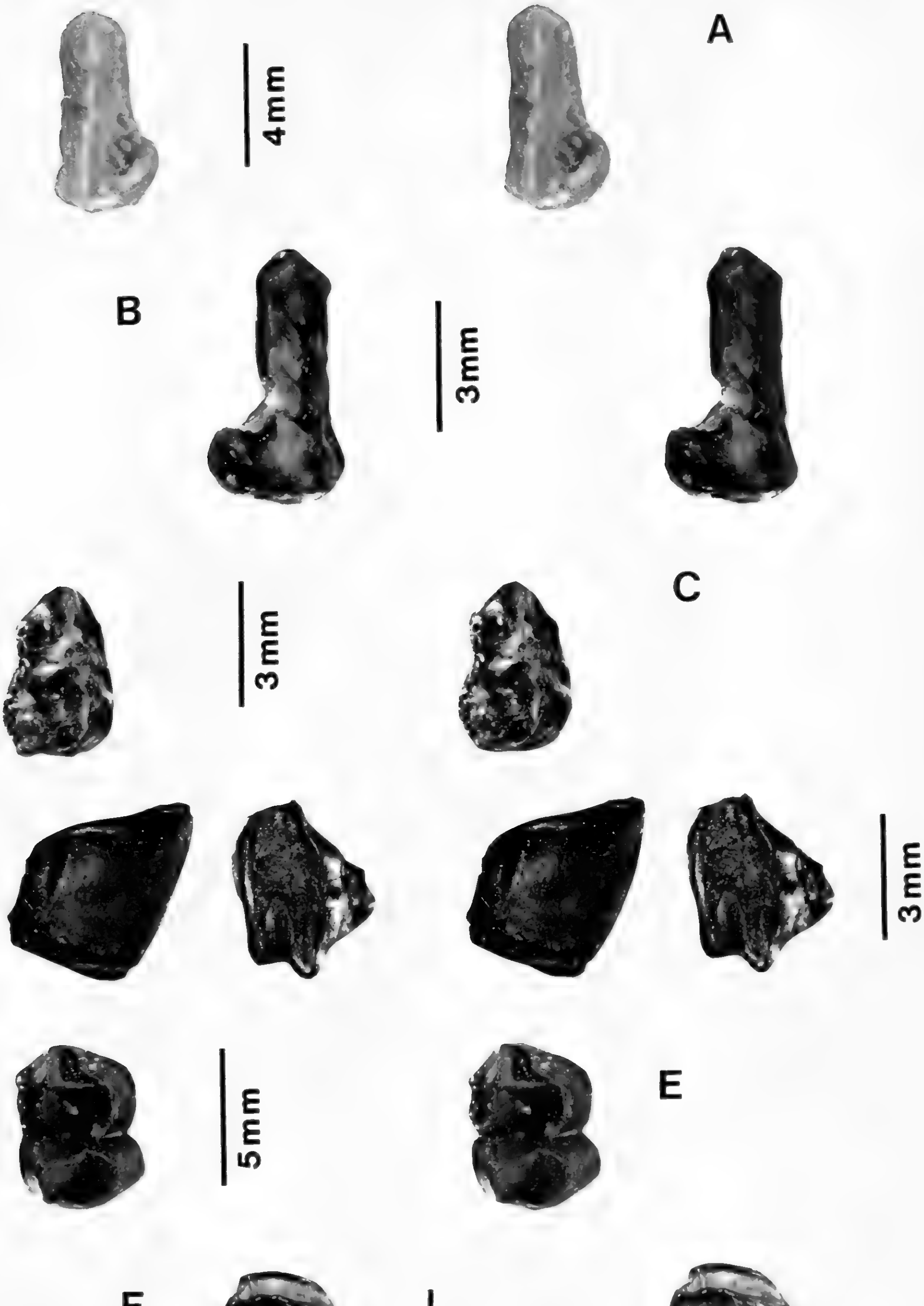

FIG. 9. Stereophoto pairs of various teeth assigned to *Thylogale ignis*. All are shown in crown view and D is also shown in buccal view. **A,** NMV P157480, the holotype, a nearly unworn right P^3 shown at approx. ×4.1. **B,** PM 17514, left P^3 shown at approx. ×5.7. **C,** NMV P54078, left P^2 shown at approx. ×5.7. **D,** NMV P54055, right I^3 shown in buccal (left) and crown (right) views at approx. ×6.0. **E,** NMV P54086, right M^1 shown at approx. ×3.8. **F,** PM 16802, right upper molar (M^2, M^3, or M^4) shown at approx. ×3.9.

FIG. 10. Stereophoto pairs showing some of the lower teeth of *T. ignis.* The cheek teeth are all shown in crown (occlusal) view. **A,** NMV P26419, left I_1 shown in dorsal (left) and ventral (right) views at approx. ×2.3. Insert shows

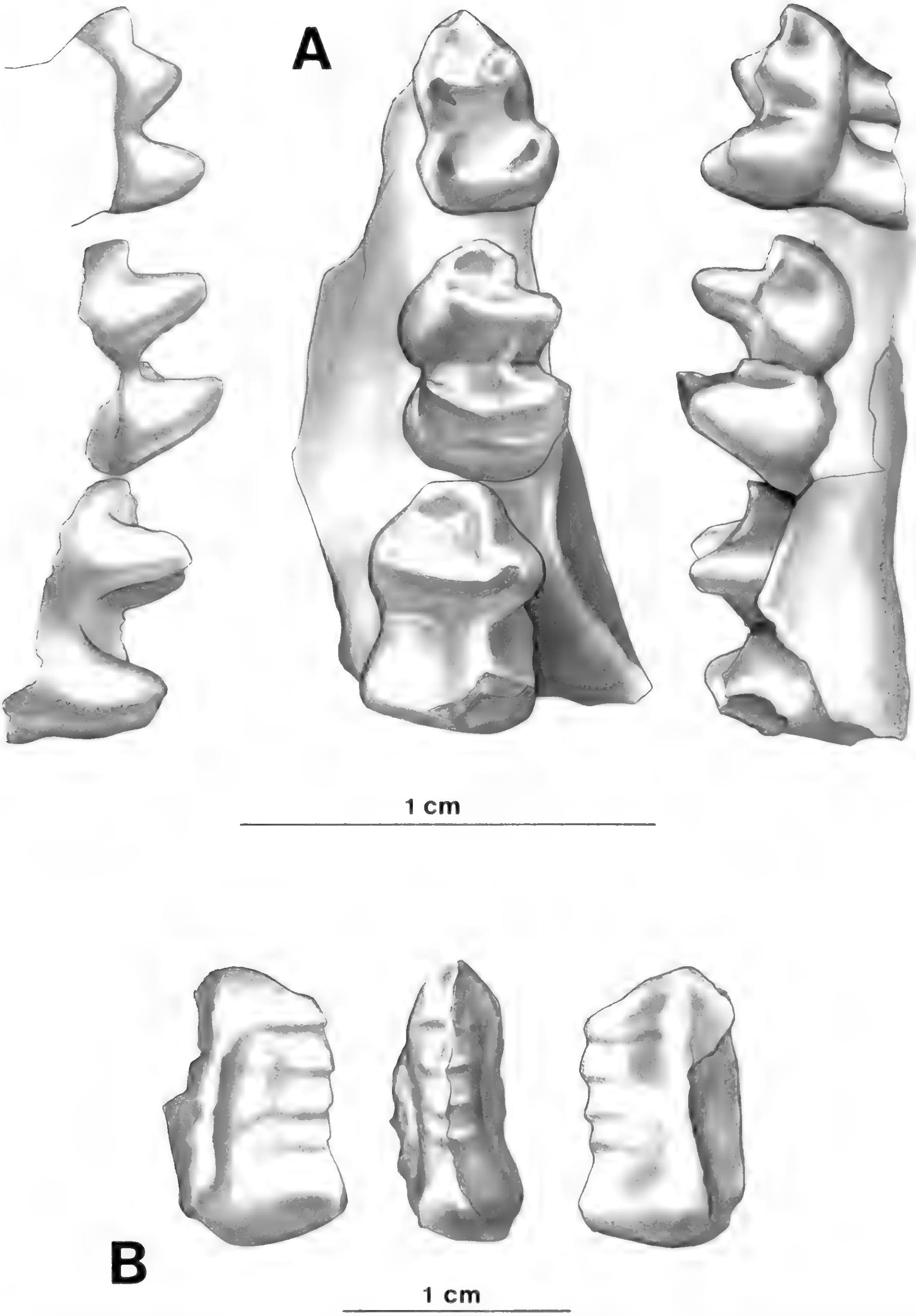

FIG. 11. Drawings of specimens of *T. ignis* (A) and *Kurrabi pelchenorum* (B), part of the holotype specimen. **A,** NMV P158432, the right mandibular fragment preserving M_{2-4} is drawn at approx. ×6.4. Left to right are lingual, crown, and buccal aspects. **B,** NMV P158425, the P_3 from the holotype specimen shown, left to right, in buccal crown, and lingual views at approx. ×3.6. The rest of the type is illustrated in Figure 12.

←

detail of the forming wear facet at the tip of the tooth. **B,** NMV P160224, right P_3 shown at approx. ×4.3. **C,** NMV P158472, right M_1 shown at approx. ×4.4. **D,** NMV P158432 with M_{2-4}, right mandibular fragment shown at approx. ×3.0.

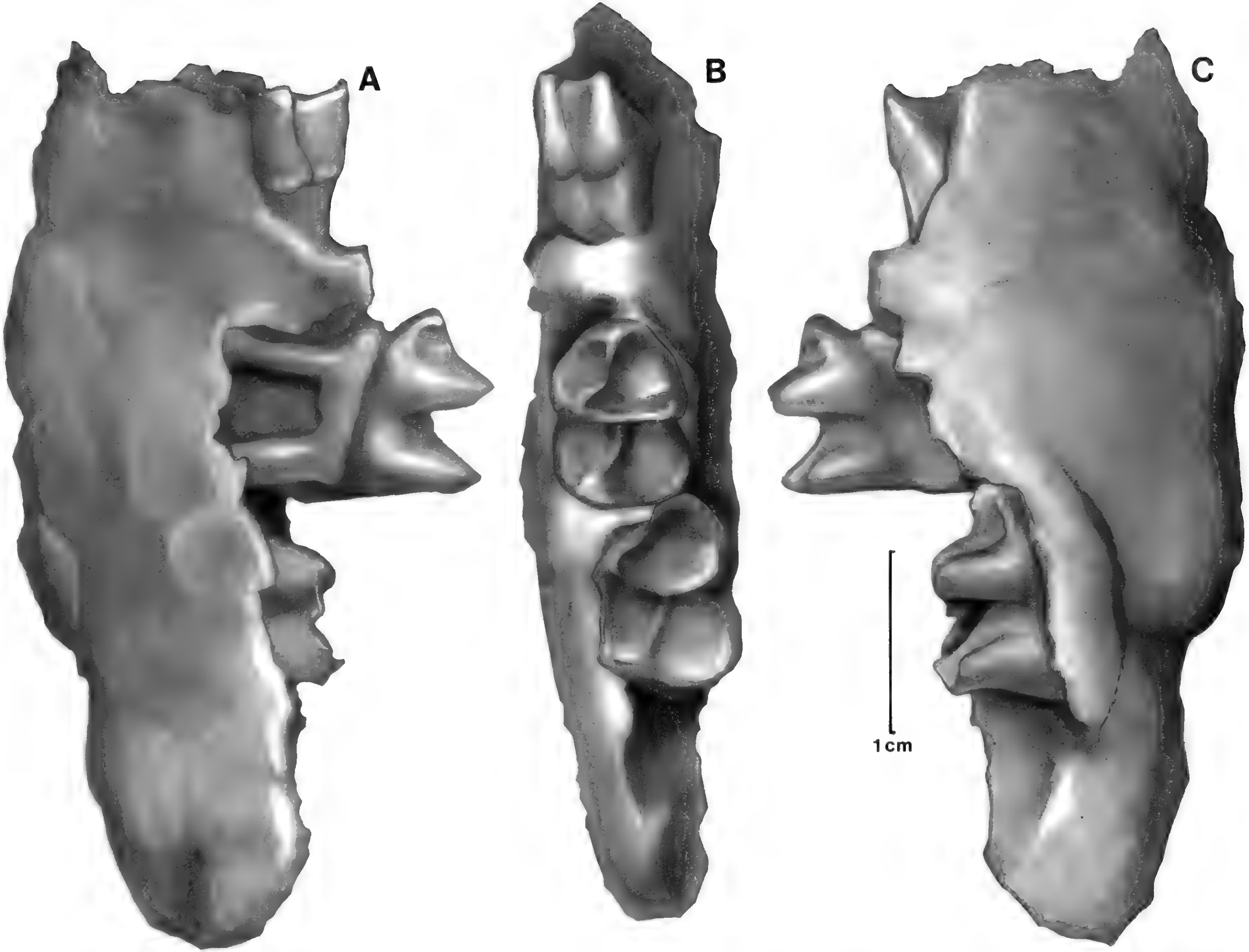

FIG. 12. Drawings of the holotype specimen of *Kurrabi pelchenorum*, NMV P158425, a partial left mandible with three molar teeth, shown at approx. ×2.3. (The P_3 is illustrated in fig. 11B.) The M_2 has been rotated out of its normal position to lie within the mandible below the alveolar margin with its occlusal surface facing anteriorly. M_3 and M_4 are in their proper positions, the latter being unerupted within its crypt.

Table 3. Measurements (mm) of three species of *Thylogale*.

		Length				Anterior width				Posterior width			
		$\bar{X}$	R	SD	N	$\bar{X}$	R	SD	N	$\bar{X}$	R	SD	N
T. ignis	P^3	6.4	6.2–6.8	.27	4	2.1	1.8–2.3	.216	4	2.1	1.6–2.6	.41	4
T. billardierii		6.5	6.0–7.4	.46	13	2.1	1.9–2.4	.139	13	3.4	3.0–3.8	.24	13
T. christenseni		6.5	6.3–6.7	.17	4	2.2	2.0–2.3	.126	4	2.7	2.6–2.8	.10	4
T. ignis	P_3	6.8	6.5–7.1	.28	4	2.2	2.1–2.2	.050	4	3.5	3.2–3.8	.25	4
T. billardierii		5.9	5.1–6.6	.41	13	1.8	1.6–2.0	.111	13	2.1	1.9–2.6	.19	13
T. christenseni		5.4	5.1–5.9	.27	9	1.7	1.6–1.8	.09	9	1.7	1.6–1.8	.09	9
T. ignis	M^1	5.5	—	—	1	3.9	—	—	1	4.4	—	—	1
T. billardierii		4.7	4.5–4.8	.15	5	3.8	3.4–4.1	.255	5	4.0	3.8–4.2	.18	5
T. christenseni		4.0	3.9–4.2	.15	3	2.7	2.6–2.8	.1	3	2.8	2.8–2.9	.06	3
T. ignis	M_1	4.8	4.7–4.9	.08	4	2.6	2.4–2.8	.173	4	3.2	3.0–3.4	.17	4
T. billardierii		4.0	3.9–4.1	.07	5	2.4	2.3–2.7	.167	5	2.9	2.3–2.7	.08	5
T. christenseni		3.5	3.4–4.5	.06	4	1.8	1.6–1.9	.13	4	2.0	2.0–2.1	.05	4
T. ignis	M_2	5.0	—	—	1	2.9	—	—	1	3.4	—	—	1
T. billardierii		4.7	4.3–5.0	.18	10	3.2	2.9–3.4	.183	10	3.5	3.2–3.8	.19	10
T. christenseni		3.8	3.6–4.0	.13	26	2.5	2.3–2.8	.13	23	3.7	2.4–2.9	.16	24
T. ignis	M_3	5.8	—	—	1	3.6	—	—	1	—	—	—	—
T. billardierii		5.3	5.0–5.7	.25	11	3.8	3.4–4.2	.272	11	—	—	—	—
T. christenseni		4.1	3.8–4.4	.18	28	3.0	2.8–3.5	.15	26	—	—	—	—
T. ignis	M_4	6.9	—	—	1	4.3	—	—	1	4.3	—	—	1
T. billardierii		6.1	5.6–6.4	.29	10	4.5	4.0–5.2	.378	10	4.5	3.7–5.3	.42	10
T. christenseni		4.6	4.3–4.8	.14	22	3.4	3.2–3.8	.19	21	3.4	3.1–3.8	.20	21

$\bar{X}$ = mean, R = range, SD = standard deviation, N = sample size.

gulum is extremely narrow and elongate compared to that of other species of *Thylogale*.

One specimen, NMV P158132, has M_{2-4} preserved in order of position (figs. 10D, 11A).

M_2 differs from M_1 in being larger, in having the lophids subequal in width, and in having the pre- and postmetacristids reduced in size. The anterior cingulum is also shorter and broader.

M_3 differs from M_2 in being larger and in having the anterior cingulum broader and shorter.

M_4 is larger than M_3 but otherwise is very similar. These teeth are indistinguishable from those of *T. billardierii* apart from being slightly more elongate and narrower (table 3).

Discussion—Turnbull and Lundelius (1970) previously recognized a species of *Thylogale* in the Hamilton fauna on the basis of a partial I^2 and I^3, an upper molar, probably M^3, M^4, or M^5, and four partial upper molars, a partial lower premolar, three lower incisors, and isolated lower molars. Because of uncertainty regarding the association of isolated teeth, they refrained from naming a new species. The new material justifies the naming of a new species. The I^3, P^3, and M^1 show characters that differ from all known species of *Thylogale*. Although only three molars are certainly associated in a jaw fragment, the other teeth appear to represent a single species because of size, relative abundance, and morphology.

Ride (1957) notes that *T. billardierii* differs from all other species of *Thylogale* in having the labial groove of I^3 situated farther anteriorly, which is the condition in *T. ignis*. This character state is regarded as plesiomorphic within macropodids as it is widespread in other macropodine genera. Several other primitive character states are seen in *T. billardierii* and *T. christenseni* as well as in the newly described *T. ignis*, which are not seen in other species of *Thylogale*. These characters, such as the form of the M_1 and the morphology of the M^1 and P^3, appear to point to a dichotomy of advanced and primitive species within *Thylogale*. The polarity of these features and the relationships of the species of *Thylogale* are discussed extensively in Flannery (1989).

Kurrabi **Flannery and Archer, 1984**
Kurrabi pelchenorum **n. sp.**
(figs. 11B, 12–14; table 4)

Holotype—NMV P158425, partial left dentary containing P_3 (removed; fig. 11B), hypolophid of M_2, complete M_{3-4} (fig. 12).

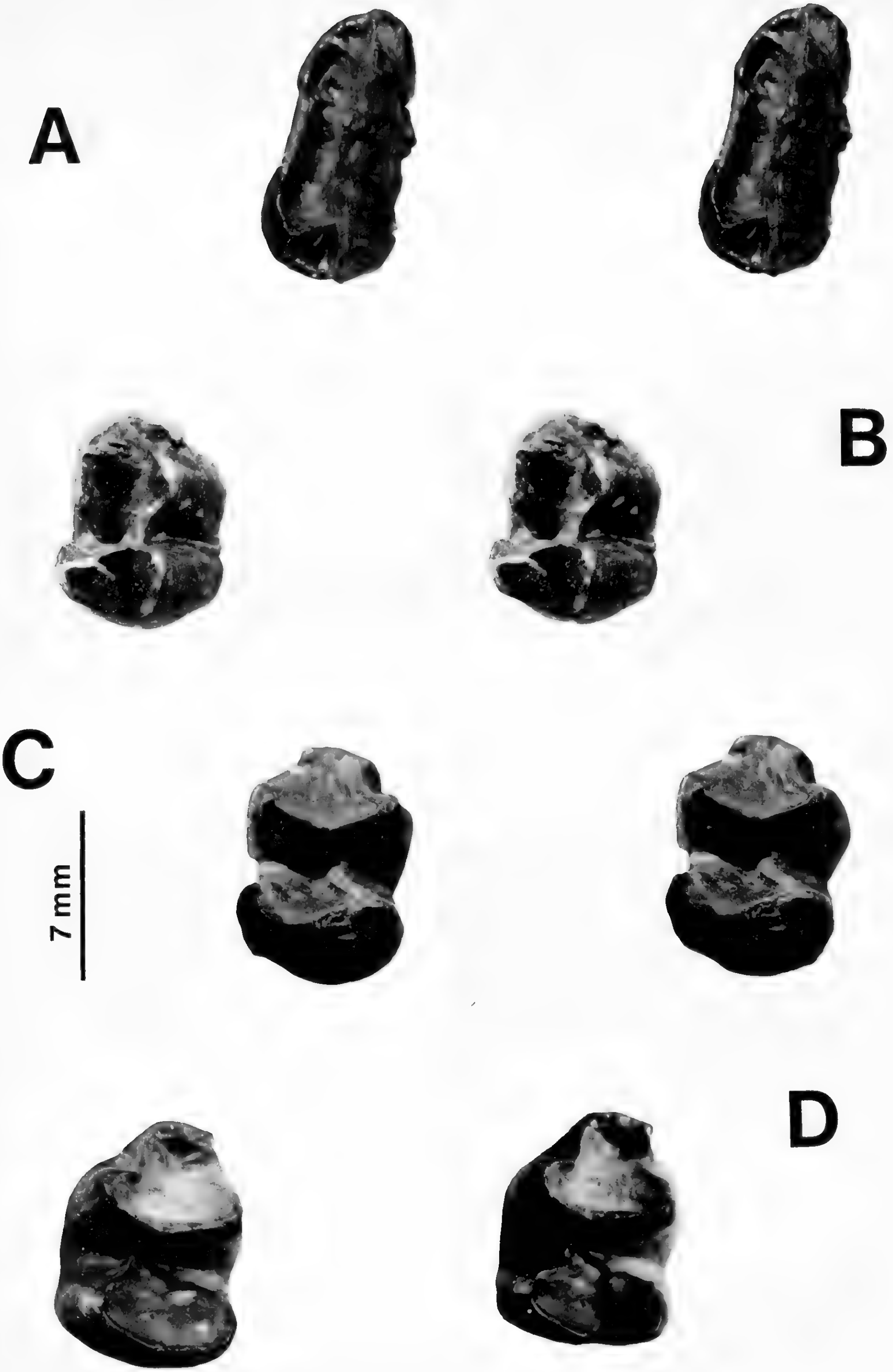

FIG. 13. Stereophoto pairs of four specimens referred to *Kurrabi pelchenorum,* shown in crown views. **A,** NMV P160209, left P^3. **B,** NMV P160190, right M^1. **C,** NMV P160494, right M_2. **D,** NMV P158634, left M_4.

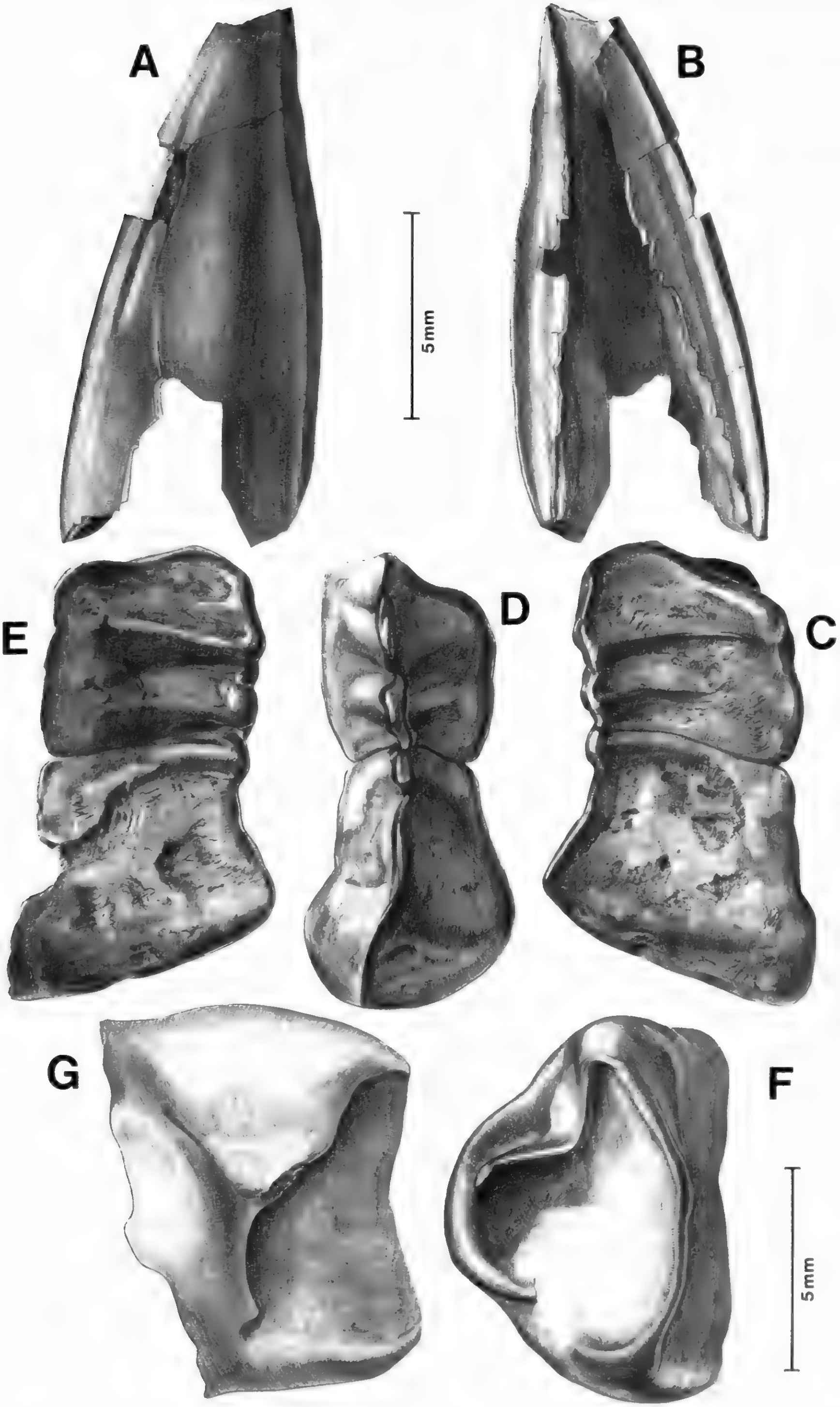

FIG. 14. Drawings of two teeth of *Kurrabi pelchenorum* (A, B and F, G) and one of *Protemnodon* sp. (C–E). **A, B,** PM 17508, left I_1. **C–E,** PM 16818, right P_3. **F, G,** PM 17507, protolophid, right lower molar, probably M_3, M_4, or M_5.

TABLE 4. Measurements (mm) of teeth referred to *Kurrabi pelchenorum*.

		P_3	M_1	M_2	M_3	M_4	M_5
NMV P158425 (type)	L	11.3	—	—	11.1	12.9	—
	AW	4.1	—	—	7.2	8.1	—
	PW	4.8	—	7.1	7.1	8.3	—
NMV P160494	L	—	—	10.1	—	—	—
	AW	—	—	7.3	—	—	—
	PW	—	—	7.4	—	—	—
NMV P158634	L	—	—	—	—	11.3	—
	AW	—	—	—	—	7.3	—
	PW	—	—	—	—	7.7	—
NMV P54105	AW	—	—	—	—	—	8.5
NMV P160368	PW	—	—	—	8.7	—	—

		P^3	M^1
NMV P160209	L	11.4	—
	AW	4.8	—
	PW	5.6	—
NMV P160190	L	—	8.7
	AW	—	5.6
	PW	—	5.6

L = length, AW = anterior width, PW = posterior width.

REFERRED SPECIMENS—NMV P160209, left P^3 (fig. 13A); NMV P160190, right M^1 (fig. 13B); NMV P54120 and NMV P160179, anterior part of protoloph of upper molars; NMV P54192, anterior portion of right I_1; PM 17508, left I_1 (figs. 14A,B); NMV P54195, protolophid of left M_2; NMV P160210 and NMV P160494 (fig. 13C), right M_2's; NMV P158632, protolophid of left M_3; NMV P160368, hypolophid of left M_3; NMV P54113, right M_4; NMV P158634, left M_4 (fig. 13D); NMV P54105, protolophid of left M_5; NMV P158058, right M_3, M_4, or M_5; PM 17507, right lower M, probably M_3, M_4, or M_5 (figs. 14F,G).

TYPE LOCALITY AND AGE.—See the Introduction for details.

DIAGNOSIS—*Kurrabi pelchenorum* can be distinguished from *K. mahoneyi* in possessing shorter premolars and lower crowned molars. The P^3 of *K. pelchenorum* also differs from that of *K. mahoneyi* in possessing a better-developed lingual cingulum and in having an anterior edge that slopes more gently to the crown base. *K. pelchenorum* differs from *K. merriwaensis* in possessing lower crowned molars with a better-developed lingual cingulum and a more gently sloping anterior margin.

ETYMOLOGY—Named for Mr. and Mrs. George Pelchen, the previous owners of the property containing the fossil site, who aided us greatly during our early periods of fieldwork at the Hamilton site.

DESCRIPTION—**P^3**—The P^3 (fig. 13A) is composed of a main crest, with anterior and posterior cusps, a lingual cingulum, and a posterolingual cusp. Between the anterior and posterior cusps of the main crest are two well-defined ridgelets and a third, less well-defined one. A posterior fossette and well-developed lingual cingulum are present.

Upper Molars—The only known M^1 is unworn (fig. 13B). The protoloph is almost undeveloped, the paracone and protocone forming distinct cusps. The anterior cingulum is formed of the preparacrista and is poorly developed, ending lingually anterior to the protocone. The midlink is well developed, and an extremely well-developed postparacrista is present, forming a longitudinal shearing blade. The metaloph is well developed. A postlink is present, situated slightly nearer the metacone than the metaconule on the rear face of the metaloph. The posthypocrista is strongly developed and forms a posterior cingulum with a much more weakly developed postmetacrista. Only two anterior fragments of more posterior upper molars are known. One of them possesses a slight forelink.

I_1—The I_1 (figs. 14A,B) is almost identical in morphology to that of *K. mahoneyi*. The buccal side is extensively enameled, and the dorsal and ventral flanges of enamel are present on the lingual face, reaching approximately one-quarter of the way up the tooth.

P_3—The P_3 (fig. 11B) in the holotype has a simple bladelike crest, with a slight posterolingual flexion. The posterior cuspid is the highest point on the crest and the anterior cuspid the lowest. Three ridgelets, decreasing in size anteriorly, are present between the cuspids. The anterior edge of the crest slopes in a similar manner (though not so steeply) as in the P^3.

Lower Molars—M_2 is represented by two isolated right teeth (fig. 13C) and a protolophid, in addition to the fragmented hypolophid in the holotype. There is no posterior cingulum present. The M_3 is represented in the holotype by a complete, barely worn tooth. The anterior cingulum is low, relatively narrow, and anteroposteriorly short. The paracristid originates at the apex of the protoconid, is concave buccally, and terminates in the medial part of the anterior cingulum. The protolophid and hypolophid are subequal in width. The cristid obliqua originates just below the apex of the hypoconid and terminates slightly labiad of the center of the rear face of the protolophid. The rear face of the hypolophid is nearly vertically oriented and no posterior cingulum or other ornamentation is present. An unerupted M_4 is part of the holotype. It differs from M_3 only in being larger. Several isolated M_4's are present; one of them (fig. 13D) compares closely to that of the holotype.

DISCUSSION—*Kurrabi pelchenorum* is closest in morphology to *K. merriwaensis* from the Bow local fauna. It differs from the latter species primarily in possessing lower crowned molars with weaker links, which may suggest habitat differences. One molar, NMV P158058, a right M_3, M_4, or M_5, may represent an extreme variant of *K. pelchenorum* or possibly an additional species. It differs from the specimens more certainly assigned to *K. pelchenorum* in having the lophids placed closer together and, at least on M_5, in having weaker links. It is possible that the hypolophid reported by Turnbull and Lundelius (1970) as belonging to a species of *Troposodon* (NMV P26422) also represents the hypolophid of an M_4 of *K. pelchenorum.*

A dentary fragment (Melbourne University Geology Department No. 2014), initially assigned as a sthenurine kangaroo (Stirton, 1957) but later considered to be a species of either *Setonix, Dendrolagus, Dorcopsis,* or *Dorcopsulus* (Tedford, 1966), was reported from the marine sediments of Forsyth's Bank, Grange Burn, near Hamilton. Forsyth's Bank is approximately 1 km downstream from the Hamilton site (site 8 on Gill's map of the area; Gill, 1957, text fig. 3) and represents an earlier time period. [? Miocene or earliest Pliocene?] This specimen is similar in M_3 morphology to the holotype of *K. pelchenorum* (the only comparable tooth between the specimens) and the other species of the genus. However, it differs in being larger (see table 4), and the alveoli for the roots of P_3 indicate that it was a much larger tooth absolutely and relative to molar size than P_3 in *K. pelchenorum.* It differs from the other species of *Kurrabi* in having lower crowned molars. It probably represents yet another distinct species in this genus, but in any case it is not part of the Hamilton fauna.

Protemnodon Owen, 1874
Protemnodon sp.
(figs. 14C–E, 15; table 1)

MATERIAL—NMV P160372, a left M^1 (figs. 15A–E); PM 4429, left M^2 (figured by Turnbull & Lundelius, 1970, pl. XXVIII A–E, as a dP^3); NMV P162896, anterior fragment of left P^3 (figs. 15F–I); PM 16818, nearly complete left P_3 (figs. 14C–E).

DESCRIPTIONS—The P^3 fragment contains the anterior cusp and the two anteriormost cuspules on the main blade and the anterior portion of the lingual cingulum. The lingual cingulum terminates lingual to the anterior cusp and is composed of a series of tubercles, which correspond to the lingual ridgelets originating at the cusp and cuspules of the main crest.

The M^1 is barely worn and is low-crowned. The protoloph is poorly developed, as is the midlink. The preparacrista joins a poorly developed anterior cingulum, which extends only two-thirds the width of the tooth. A well-developed postparacrista is present. The metaloph is broader and better developed than the protoloph. The pre- and postmetacristae are well developed as is the posthypocrista. A weakly developed postlink is present on the rear face of the metaloph, placed slightly closer to the metacone than the hypocone. The M^2 has been described in Turnbull and Lundelius (1970), where it was considered to be a dP^3.

The P_3, like that of *Kurrabi pelchenorum,* has a simple bladelike crest with a slight posterior labial flexure. There are three weak ridges ahead of the posterior cuspid. They extend from the crest to the base and decrease slightly in size posteriorly rather than anteriorly as in *K. pelchenorum.* The tooth minus its anterior cusp is as long as the complete tooth of *K. pelchenorum.*

DISCUSSION—The M^1 is most similar to that of *Protemnodon otibandus* among named macropo-

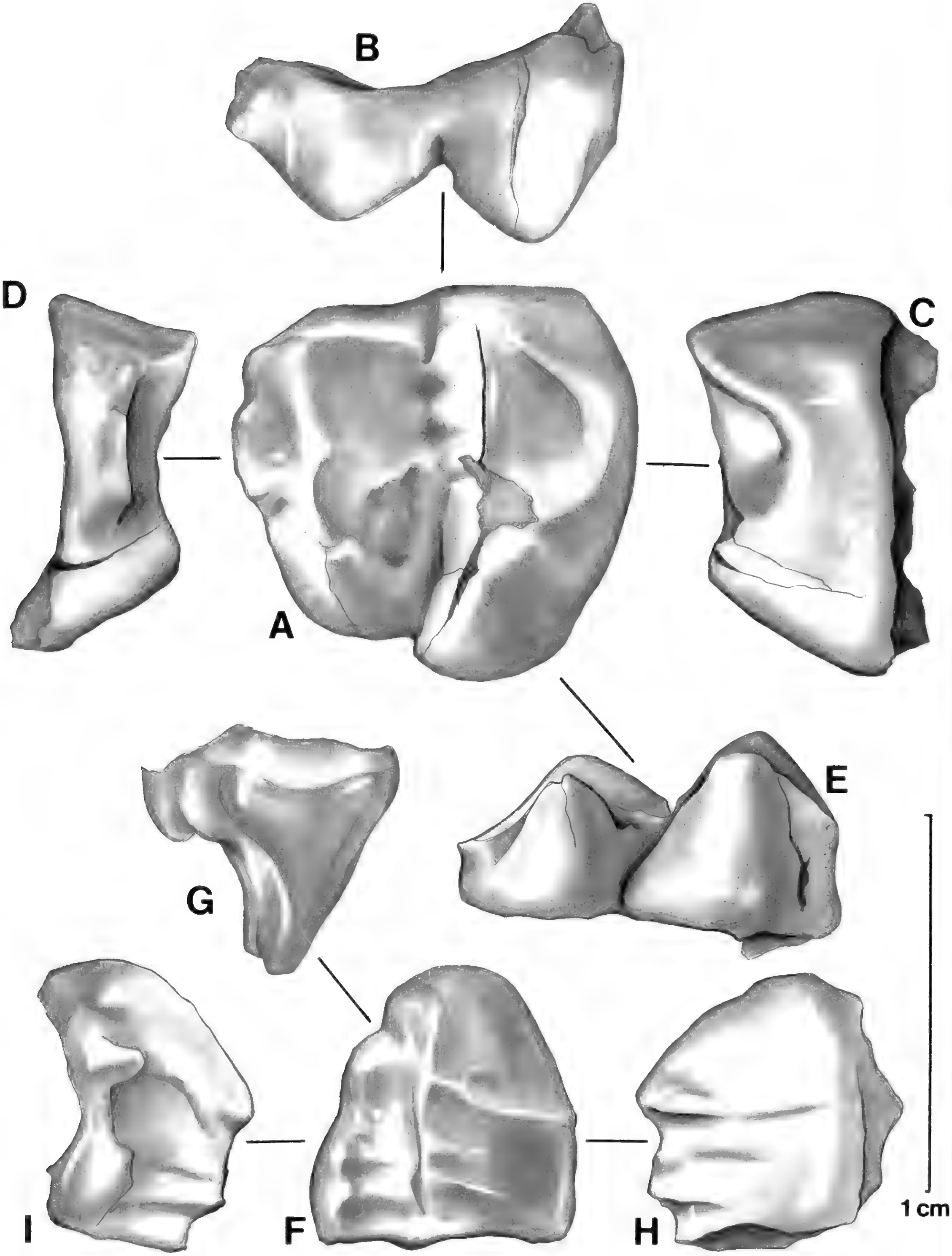

FIG. 15. Drawings of two specimens referred to *Protemnodon* sp. **A–E,** NMV P160372, left M^1 shown in crown (A), buccal (B), posterior (C), anterior (D), and lingual (E) views. **F–I,** NMV P162896, left P^3 shown in crown (F), anterior (G), lingual (H), and buccal (I) views.

doids. However, it differs from *P. otibandus* in being proportionately broader and in having the anterior cingulum more restricted lingually. The premolar fragments indicate that a distinct anterior cusp is present, as in most species of *Protemnodon,* and that the P^3 possesses a broad lingual cingulum. While probably representing a new species, more complete material is needed before it can be named.

Macropus **Shaw, 1790**

Macropus **(*Notamacropus*) sp.**

(fig. 16A; table 1)

MATERIAL—NMV P54112, hypolophid of a right lower molar.

DESCRIPTION—The specimen is a completely unworn hypolophid, probably from an unerupted tooth. The occlusal edge is much narrower than the base of the crown. The midlink is well developed, originating at the apex of the hypolophid. The accessory link is a sharp raised crest that extends anterolingually from a point just lingual to the cristid obliqua to the point where it is broken away. The hypoconid is taller than the entoconid.

DISCUSSION—The specimen can be recognized as representing a species of *Macropus* because it possesses a strongly posteriorly convex hypolophid. The posterior face of the hypolophid is unornamented except for an extremely shallow groove. This differs from the condition in species of *Macropus* (*Macropus*), where a deeper groove or fossette is invariably present. An accessory link buccal to the midlink is present in the Hamilton tooth. This has not been observed in species of *Macropus* (*Osphranter*) or *M.* (*Macropus*) but occurs occasionally in species of *M.* (*Notamacropus*) (see *M.* (*N.*) *agilis siva* in Bartholomai, 1975). Its small size is also suggestive of a species of *Macropus* (*Notamacropus*) (see Dawson & Flannery, 1985).

This tooth fragment is the only evidence of a truly hypsodont macropodid in the Hamilton fauna. Although it is determinable to the subgeneric level, it cannot be assigned to a species.

Wallabia **Trouessart, 1905**

cf. *Wallabia*

(fig. 16B; table 1)

MATERIAL—NMV P54208, a single unworn left P^3.

DESCRIPTION—NMV P54208 consists of a blade and a posterolingual cusp. Anterior and posterior cusps are present on the blade, with three distinct cuspules and their ridgelets and a weaker fourth cuspule between them. The posterolingual cusp is connected to the main crest by two ridges, one that extends around the posterior end of the tooth, the other that goes directly to the main crest, intersecting it at 90°. A broad, well-developed lingual cingulum is present and a weak buccal one. This tooth appears to be indistinguishable in size and morphology from that of *Wallabia bicolor.*

DISCUSSION—This specimen can be distinguished from the P^3 of all potoroids and macropodine species of the genera *Dorcopsulus, Dorcopsis, Lagorchestes, Onychogale,* and *Macropus* and the species of *Thylogale billardierii, T. ignis,* and *T. christenseni* by possessing a well-developed lingual cingulum. It lacks the distinct lingual crest seen on the P^3 of sthenurine kangaroos. The tooth is smaller than that of species of *Protemnodon.* The main blade is more distinctly ridged than that of species of *Macropus* (*Osphranter*) and lacks the posterobuccal cusp often seen in species of *Dendrolagus.* Although possibly belonging to a form close to *Setonix, Thylogale, Prionotemnus, Macropus* (*Notamacropus*), or *Petrogale,* it is here tentatively assigned to *Wallabia,* because it is most similar in morphology to the P^3 of *W. bicolor.* The doubt surrounding the taxonomic status of this specimen, and the poorly understood fossil record of the species of *Wallabia,* makes further analysis pointless.

Macropodinae gen. indet. 1

An isolated premolar probably represents a P_2 or P_3 of a macropodine (NMV P158431). It consists of an enlarged posterior cuspid that stands slightly above the rest of the tooth, an anterior cuspid, and three cuspules in between. This tooth resembles the P_2 of *Lagorchestes conspicillatus* except that it possesses an extra cuspule.

Macropodinae gen. indet. 2

The enamel cap of a large right I_1 (NMV P160165; fig. 16C) may represent a species near *Dorcopsulus.* It is too large to belong to *D. wintercookorum.* It has a slight flange of enamel ventrolingually and is elongate, curving upward anteriorly.

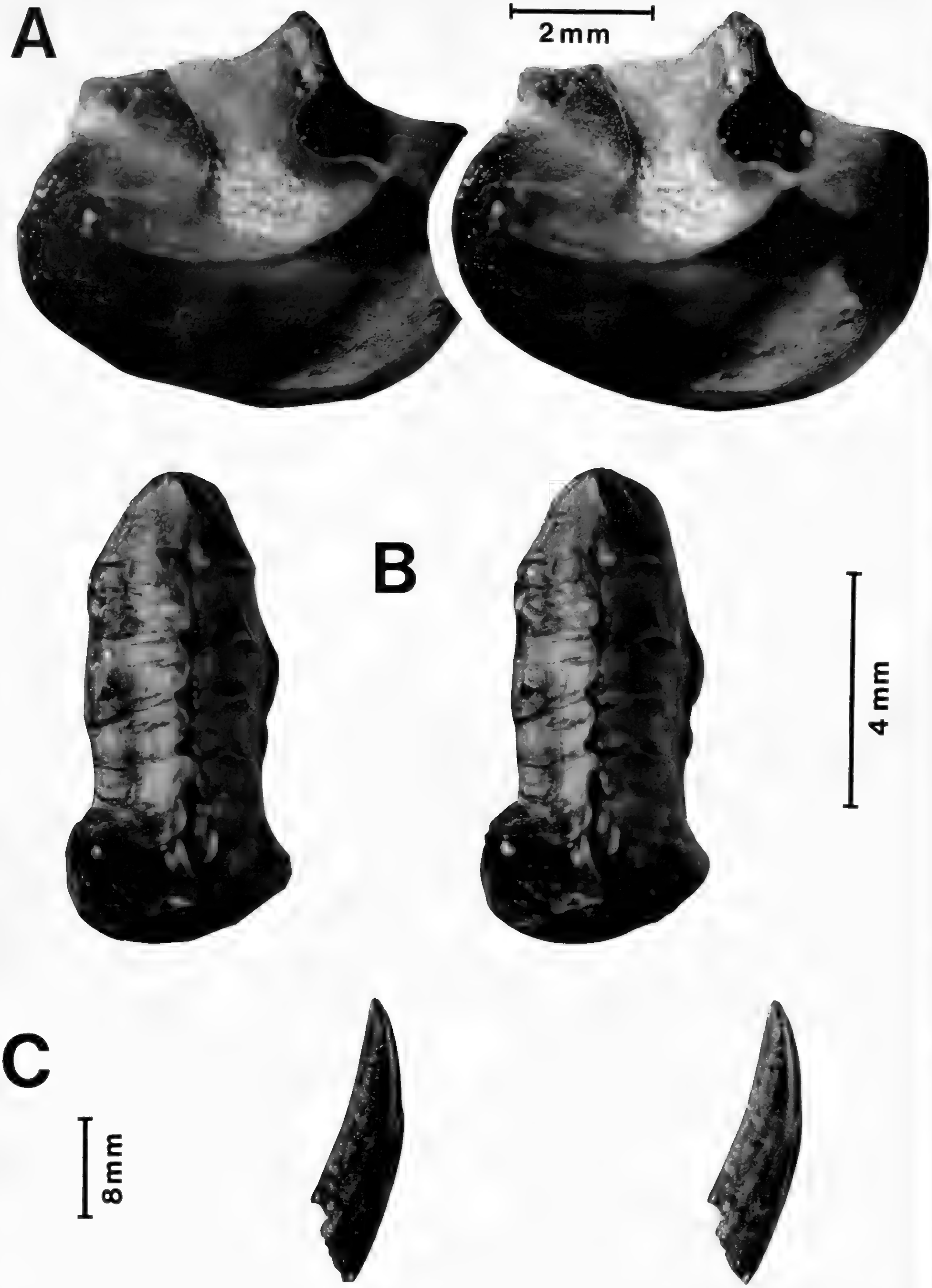

FIG. 16. Stereophoto pairs shown in crown view. **A,** *Macropus* (*Notamacropus*) sp., NMV P54112, hypolophid of a right lower molar. **B,** *Wallabia* sp., NMV P54208, left P^3. **C,** Macropodidae gen. indet. 2, NMV P160165, right I_1.

Discussion

Four of the Pliocene fossil localities of Australia–New Guinea have been radiometrically dated. These are Hamilton, southwestern Victoria (4.46 ± .1 Ma); Bluff Downs, northeastern Queensland (dated to at least 4.0 ± .12 Ma; Archer & Wade, 1976); Dog Rocks, southcentral Victoria (>2.1 Ma; Rich et al., 1982); and Awe, Papua New Guinea, with four dates that indicate an age of between 4.5 and 7.6 Ma (Plane, 1967; Hoch & Holm, 1986). However, Page and McDougall (1972) indicate that the dates for this site older than 3.1 Ma may have resulted from incomplete degassing of radiogenic argon at the time of eruption.

These assemblages make it possible to examine the biotic and climatic change during the Pliocene. Any attempt to use the habitat preferences and requirements of the living relatives of the Hamilton fauna to reconstruct the paleonenvironment faces the possibility that there has been evolutionary change in the tolerances of the animals. The first report on the Hamilton fauna (Turnbull & Lundelius, 1970) interpreted the fauna as a rain forest assemblage. The recovery of more material requires that this conclusion be reexamined. Modern representatives of many of the Hamilton taxa are rain forest inhabitants, although they do not all live in the same kind of rain forest.

The genera *Hypsiprymnodon, Dorcopsis, Dendrolagus,* and *Strigocuscus* have modern representatives that are almost wholly rain forest dwellers. However, the various living species of *Dorcopsis* live in high mountain forests, lowland rain forest, mossy montane forests, and midmontane forests. Living species of *Dendrolagus* live mainly in montane rain forests, and *Hypsiprymnodon* is confined to rain forest, preferring the wetter areas (Johnson & Strahan, 1982). The modern New Guinea species *Strigocuscus gymnotus* is primarily a rain forest animal but has been found in areas of regrowth, mangrove swamps, and woodland savannah (Menzies & Pernetta, 1986).

The living species of *Thylogale* live in diverse environments. *T. thetis* and *T. stigmatica* are found in rain forests and wet sclerophyll forests (Ride, 1970). Other species of *Thylogale* live in high montane forests (*T. brunii*) or in a variety of habitats (*T. billardierii*). Pseudocheirids are also found in a wide variety of habitats, but, as pointed out in the initial report, there are three taxa of this family in the Hamilton fauna, and the only areas that contain as many taxa today are rain forest situations in New Guinea and Cape York Peninsula.

The living petaurids live in treed areas such as tall forest or tall woodland but not rain forest. Only one of the pygmy possums, *Cercartetus caudatus,* inhabits rain forest. *Burramys* today inhabits alpine or subalpine heath (Calaby et al., 1971; Gullan & Norris, 1984; Mansergh, 1984). The harsh environment of the living *Burramys* is in strong contrast to those of all the other Hamilton taxa. *Burramys triradiatus* from Hamilton differs morphologically from later species and probably differed in its physiological characters as well.

Wallabia bicolor prefers wet or dry sclerophyll forests but is found in rain forests, woodland, and heath. The two macropodids with no close living relatives, *Protemnodon* and *Sthenurus,* have Pleistocene relatives distributed over much of Australia in association with taxa that are not rain forest forms. The various living species of *Macropus* inhabit a wide variety of habitats but are not rain forest forms. This is the earliest record of *Macropus,* which suggests the presence of open, perhaps grassy areas.

A consideration of the entire Hamilton mammalian assemblage suggests the presence of very diverse habitats in the area. If the living representatives of the Hamilton taxa have not undergone drastic changes in their habitat requirements, the environment must have been much more varied than is seen anywhere today. The Hamilton fauna is one of only two known faunas to have both *Trichosurus* and *Strigocuscus,* whose ranges do not overlap today (Flannery et al., 1987). This is an example of a disharmonious association similar to those found in Pleistocene assemblages in Australia and other parts of the world (Lundelius, 1983). The environment appears to have been more of a mosaic than is seen today, with patches of forest, both rain forest and other wet forests, and open areas.

A limited palynological and macroplant analysis has been carried out for Hamilton. Charred stumps of the gymnosperm *Phyllocladus* are present in growth positions directly under the basalt (figured by Turnbull & Lundelius, 1970, p. 9). In addition, the pollen of *Podocarpus, Dacrydium, Phyllocladus, Casuarina, Halophagus, Nothofagus,* Murtaceae, and Poacaea have been found (Ladd, pers. comm.). Species of *Phyllocladus* and *Dacrydium* are no longer found on mainland Australia. These data further indicate that some rain forest patches were present at the site during the early Pliocene. Today the Hamilton area, where not cleared, supports a *Eucalyptus camaldulensis* woodland.

Palynological studies in the Murray Basin by Martin (1991) indicate a drying trend from the mid-Miocene (about 12 million years ago) to the early Pliocene (about 6 million years ago). A brief return to more humid conditions is indicated by the reappearance of gymnosperm and *Nothofagus* pollen, which is interpreted as rain forest, until just after 5 million years ago. This is very close to the age of the Hamilton fauna. The variable percentages of *Nothofagus* and gymnosperm pollen from various localities is interpreted as an indication of a rain forest mosaic.

It appears from the existence of the diverse mammalian rain forest assemblages at Hamilton 4.46 million years ago that the restricted modern Australia–New Guinea mammalian rain forest fauna is a relict of a formerly much more widespread biota. Faunas such as Bow and Bluff downs from eastern and northern Australia, which represent woodland or riparian habitats, suggest that the rain forest that is thought to have been continuous along the east coast in earlier Tertiary time had begun to fragment by Early Pliocene. Rain forest isolates may have been in existence long enough for considerable endemism to have developed by the Early Pliocene. The small remaining areas of southern Australian rain forests today have no unique mammals; however, the Hamilton fauna includes some species such as *Milliyowi bunganditj,* which are not known elsewhere and may represent southern rain forest endemics. The genus *Burramys,* which is now restricted to montane heaths at higher elevations, seems to have undergone some evolutionary change since the late Pliocene (Turnbull et al., 1987).

Other Hamilton species may provide clues to the origins of extant forms. The presence of *Thylogale ignis* at Hamilton suggests that the ancestors of *T. billardierii* were rain forest dwellers that survived shrinkage of their habitat by adapting to life in the surviving wet sclerophyll areas. *Macropus* (*Notamacropus*) sp. may represent yet another such species, as *M.* (*N.*) *parma,* like *T. billardierii,* is restricted to southeastern Australia, and both living species are found in rain forests and wet sclerophyll forests.

Conclusions

1. The Hamilton local fauna provides the earliest record for species of the genera *Simosthenurus, Troposodon, Milliyowi, Propleopus, Kurrabi, Thylogale,* and *Macropus* (*Notamacropus*), as well as possibly *Dendrolagus* and *Wallabia.*

2. The Hamilton local fauna contains taxa representing diverse habitats. The fauna may contain elements restricted to the Pliocene southern rain forests.

3. The macropodids from Hamilton show that the macropodoid assemblage typical of the more mesic modern environments of Australia–New Guinea was already present by the Early Pliocene.

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Appendix

Fossil macropodoid specimens from Hamilton in the collections of the Museum of Victoria and the Field Museum that are not discussed in either this text or in Turnbull and Lundelius (1970), because we could not be certain of their generic or specific identity, are listed here, identified as best we can.

Potoroidae:

near *Hypsiprymnodon*. PM 50907, 50935, 50939, 50993

near *Potorous*. PM 50950

near *Milliyowi*. PM 4492

Macropodidae: Macropodinae:

near *Dorcopsis*. NMV P26418; PM 4431, 4433, 4434, 4482, 4484, 4485, 4565, 4572, 4573, 4713, 4755, 16803, 16818, 16824, 16825, 16835, 16837, 16838, 17509, 17515, 17526, 17527, 17539, 50768, 50776, 50889, 50942

near *Dendrolagus*. PM 16811, 16812

near *Thylogale*. PM 4432, 4451, 4452, 4483, 4562, 4574, 4586, 16809, 16833, 17513, 17514, 17518, 17520, 50765, 50937, 50945

near *Kurrabi*. PM 50892, 50894, 50895, 50925, 50926

near *Protemnodon*. NMV P160166; PM 17507, 17508, 17510, 17521

near *Macropus*. PM 16806, 50940

near *Wallabia*. PM 16826, 50772

indet. Macropodid.

Upper incisors: NMV P54022, 54120, 54129, 157471, 158441, 160149, 160151, 160154, 160156, 160172, 160219, 160222; PM 50896

Lower incisors: NMV P54187, 54190, 157472, 158445, 160130, 160145, 160148, 160158, 160160, 160214; PM 16804, 16813, 16821, 17517, 50890

Upper molars: NMV P54001, 54002, 54003, 54012, 54025, 54030, 54031, 54037, 54041, 54044, 54054, 54071, 54073, 54092, 54101, 54117, 54118, 54119, 54121, 54127, 54141, 54145, 54148, 54152, 54155, 54157, 54162, 54171, 54174, 54196, 54206, 158072, 158446, 158447, 158448, 158450, 158456, 158457, 158458, 158459, 158460, 158461, 158463, 158464, 158466, 158469, 160129, 160134, 160135, 160136, 160138, 160139, 160145, 160155, 160163, 160173, 160175, 160176, 160183, 160185, 160187, 160189, 160191, 160192, 160195, 160196, 160197, 160200, 160201, 160206, 160208, 160216, 160369, 160370; PM 16809, 17516, 17519, 50764, 50769, 50775, 50777, 50898

Lower molars: NMV P54001, 54026, 54033, 54042, 54043, 54049, 54053, 54056, 54060, 54062, 54067, 54072, 54091, 54096, 54106, 54116, 54135, 54142, 54143, 54156, 54160, 54163, 54173, 54179, 54195, 54198, 54202, 158019, 158022, 158071, 158434, 158467, 158468, 160131, 160137, 160140, 160141, 160144, 160146, 160148, 160161, 160162, 160167, 160168, 160169, 160170, 160171, 160174, 160177, 160193, 160198, 160202, 160203, 160204, 160205, 160212, 160215, 160218, 160220, 160317, 160371, 160429; PM 16812, 16814, 16824, 16825, 16833, 16834, 17502, 17503, 17512, 17516, 50770, 50775, 50936

Premolars and fragments: NMV P54028, 54056, 54078, 54150, 54169, 157476, 158440, 159788, 160142, 160164, 160182, 160195, 160367; PM 16815, 16834, 16839, 17522, 50773, 50774, 50891, 50940, 50941, 50946, 50947

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