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*Journal of Paleontology*, Vol. 58, No. 4. (Jul., 1984), pp. 1062-1073.

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*Journal of Paleontology* is currently published by SEPM Society for Sedimentary Geology.

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*WAKIEWAKIE LAWSONI*, A NEW GENUS AND SPECIES OF  
POTOROINAE (MARSUPIALIA: MACROPODIDAE) OF  
MEDIAL MIOCENE AGE, SOUTH AUSTRALIA

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**ABSTRACT**—A new genus and species of potoroine macropodid is described from strata of medial Miocene age in South Australia. The new form, *Wakiewakie lawsoni*, is notable mainly in its extremely elongate last premolar and the hypertrophy of the mandibular foramen and masseteric canal of the mandible that apparently housed an unusually large anterior insertion of the masseteric muscle, an apparently concomitant deepening of the ascending ramus of the mandible and development of a very short lower muzzle. The taxon not only adds to the evolutionary breadth shown by this subfamily, but appears to be one of the few potoroine genera of biochronological potential for Miocene faunas of Australia.

The fossils are part of the Kutjamarpu Local Fauna, found in the Wipajiri Formation at Lake Ngapakaldi on the eastern margin of the Lake Eyre basin. A specimen from the Ngapakaldi Local Fauna that occurs in the subjacent Etadunna Formation at Lake Pitikanta may be related to the Kutjamarpu form; no descendants have been identified in younger assemblages as yet, however.

INTRODUCTION

FIVE genera and ten species of potoroine macropodids are known in the modern Australian fauna (Ride, 1970). Of these *Hypsiprymnodon*, *Potorous*, *Bettongia*, and *Aepyprymnus* are found in faunas of Pleistocene and Pliocene age (Turnbull and Lunelius, 1970; Ride, 1964; Marshall, 1973), to which may be added the extinct genus *Propleopus* (Woods, 1960; Ride, 1964; Archer, Bartholomai and Marshall, 1978; Pledge, 1981). *Caloprymnus* has but a Pleistocene fossil record (Tedford, 1967a). Potoroines of Miocene age are rare, with one purported genus *Gumardee* Flannery, Archer and Plane (1982), known from the Riversleigh Local Fauna of Queensland (Tedford, 1967b). Stirton, Tedford and Miller (1961) tentatively identified the genus *Bettongia* in the Ngapakaldi Local Fauna from strata of the Etadunna Formation of medial Miocene (ca. 14 m.y.) age at Lake Pitikanta on the eastern margin of the Lake Eyre Basin, South Australia (Figure 1). As presently known, this is the oldest certain member of the Potoroinae (sensu Kirsch, 1968, and as used here). As discussed by Case (1984), the Ngapakaldi form probably does not pertain to the genus *Bettongia*, but is related to that genus, as well as to the new genus and species, *Wakiewakie lawsoni*, herein described from the Kutjamarpu Local Fauna. The Kutjamarpu Local Fauna is found in strata of the Wipajiri For-

mation of late Miocene age (ca. 12 m.y. old) that unconformably overlies the Etadunna Formation at Lake Ngapakaldi, ca. 2 km north of Lake Pitikanta (Stirton, Tedford and Woodburne, 1967).

The remains described here were obtained during the 1971 field season, conducted as a joint project by the South Australian Museum, Adelaide, and the University of California, Berkeley, from locality V-6213 = RV-7231 (fossil localities of the University of California, Berkeley, and Riverside, respectively). General comments on the stratigraphic relationships, geographic and chronologic range of Cenozoic mammals of Australia can be found in Stirton, Tedford and Woodburne (1968), Archer and Bartholomai (1978), Rich and Thompson (1982), and Rich et al. (1982). All measurements are in millimeters. Dental terminology is traditional (e.g., the last premolar is designated as P3, the molars numbered 1–4). Classification follows Kirsch (1968). UCMP refers to the University of California, Berkeley; UCR to the University of California, Riverside; SAM P to paleontological collections of the South Australian Museum, Adelaide; QM F to the paleontological collections of the Queensland Museum, Brisbane.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Subclass THERIA Parker and Haswell, 1897

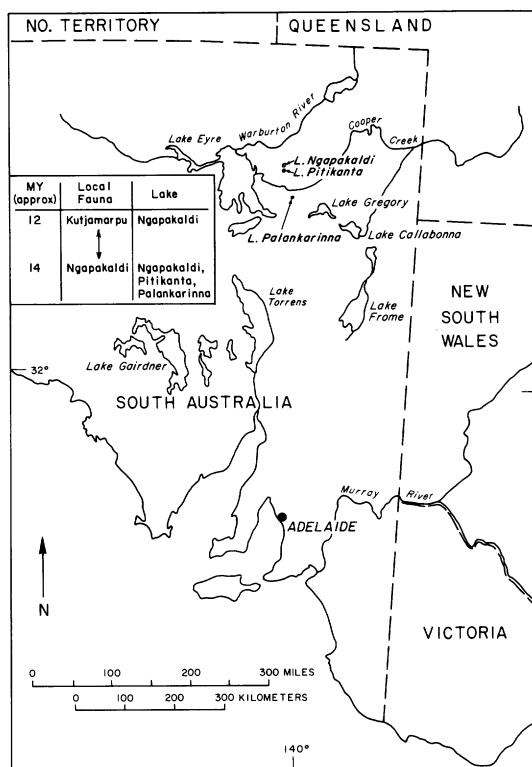


FIGURE 1—Map of southern Australia showing localities discussed in the text, and a chart of their chronological sequence, geographic, and temporal distribution in terms of the radiometric time scale. The arrow indicates that the Wipajiri Formation (containing the Kutjamarpu Local Fauna) at Lake Ngapakaldi physically overlies the Etadunna Formation (containing the Ngapakaldi Local Fauna).

Infraclass METATHERIA Huxley, 1880  
 Order DIPROTODONTA Owen, 1866  
 Family MACROPODIDAE Owen, 1839  
 Subfamily POTOROINAE Trouessart, 1898  
 Genus WAKIEWAKIE n. gen.

Figures 2, 3; Table 1

*Type species.*—*Wakiewakie lawsoni* n. sp.

*Diagnosis.*—That of the type species until other species are described.

*Etymology.*—Onomatopoetic rendition of an early morning cry commonly heard at the field camp in the sand hills adjacent to Lake Ngapakaldi during the 1971 field season. Gender is considered to be masculine.

#### WAKIEWAKIE LAWSONI n. sp.

*Holotype.*—SAM P17897, left mandible lacking the ascending ramus and angle, with partial alveolus for  $I_1$ ;  $P_3$ ,  $M_1$ – $M_3$  present.

*Type locality.*—UCMP locality V-6213 (=UCR RV-7231), east side of Lake Ngapakaldi (Figure 1), eastern margin of Lake Eyre Basin, South Australia; grid coordinates 644491, grid zone 5, Kopperamanna 4-mile topographic series, SH-54-1; 1:250,000.

*Horizon and age.*—Unit 3 of Wipajiri Formation (Stirton, Tedford and Woodburne, 1967), Kutjamarpu Local Fauna, of late Miocene age (ca. 12 m.y.).

*Referred specimens.*—UCMP 99888,  $RP^3$ , lacking roots; UCMP 66854, anterior  $\frac{1}{2}$ ,  $RP^3$ , lacking roots and base of crown.

*Etymology.*—In honor of Paul F. Lawson, MBE, of the South Australian Museum, Adelaide, who, since 1953 participated in, and made many critical and important contributions to, the scientific successes enjoyed by members of field excursions into the Australian desert led by the late R. A. Stirton, and subsequently by his students, in the search for fossil mammals.

*Diagnosis.*—Differs 1) from all Macropodidae in the combination of  $P_3$  being about as long as the combined length of  $M_1$ – $M_3$ ; the horizontal ramus of the mandible being as deep as the combined length of  $M_1$ – $M_3$ ; the steep angle at which  $I_1$  rises from the horizontal ramus of the mandible. Differs from all Macropodinae in the above as well as in 2) the bunolophodont character of the lower molars, and 3) in the high number of finely constructed ribs on  $P_3$ . Differs from all Potoroinae in 1) and 3) above, as well as in the (except for *Propleopus*) distinctly sloping versus vertically standing labial surfaces of the protoconid and hypoconid, the relatively and actually lower crown height of the lower molars and the steep angle (nearly  $90^\circ$ ) at which the ascending ramus rises from the horizontal ramus of the mandible.

Differs from *Hypsiprymnodon* in 1) and 3) above, plus the alignment of  $P_3$  as a continuation of the molar row, in the rectilinear outline of  $P_3$  and  $P^3$ , and the even lateral profile of these teeth; in the broad, uncompressed trigonid of  $M_1$ , and in the absence of a strong pre-protocristid, and of a strong pre-metacristid, and the apparent absence of a

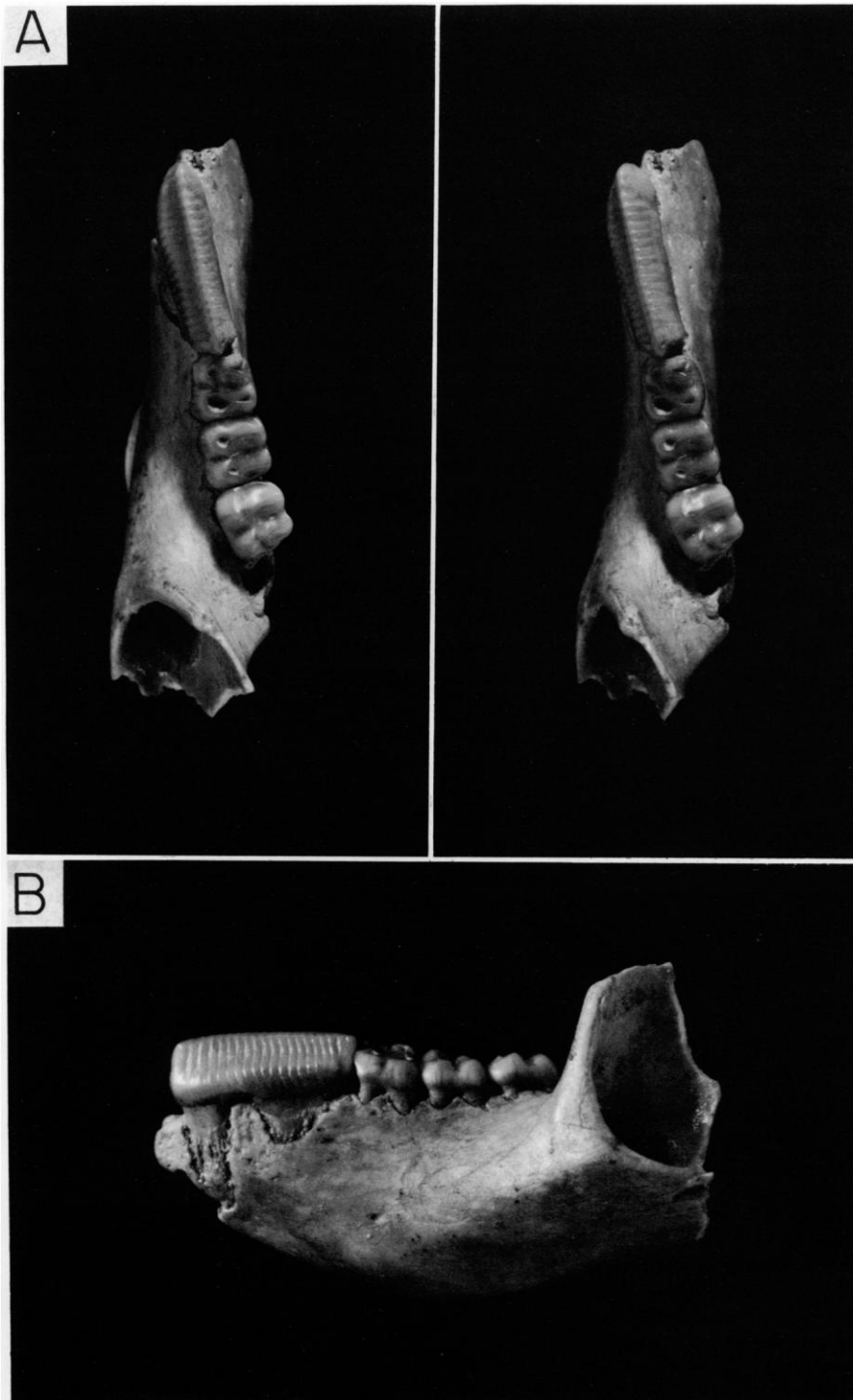


FIGURE 2—*Wakiewakie lawsoni* n. gen., n. sp. *A*, stereopair of occlusal view of holotype dentition, SAM P17897, LP<sub>3</sub>–M<sub>3</sub>. *B*, labial view of holotype lower mandible. All about  $\times 2.5$

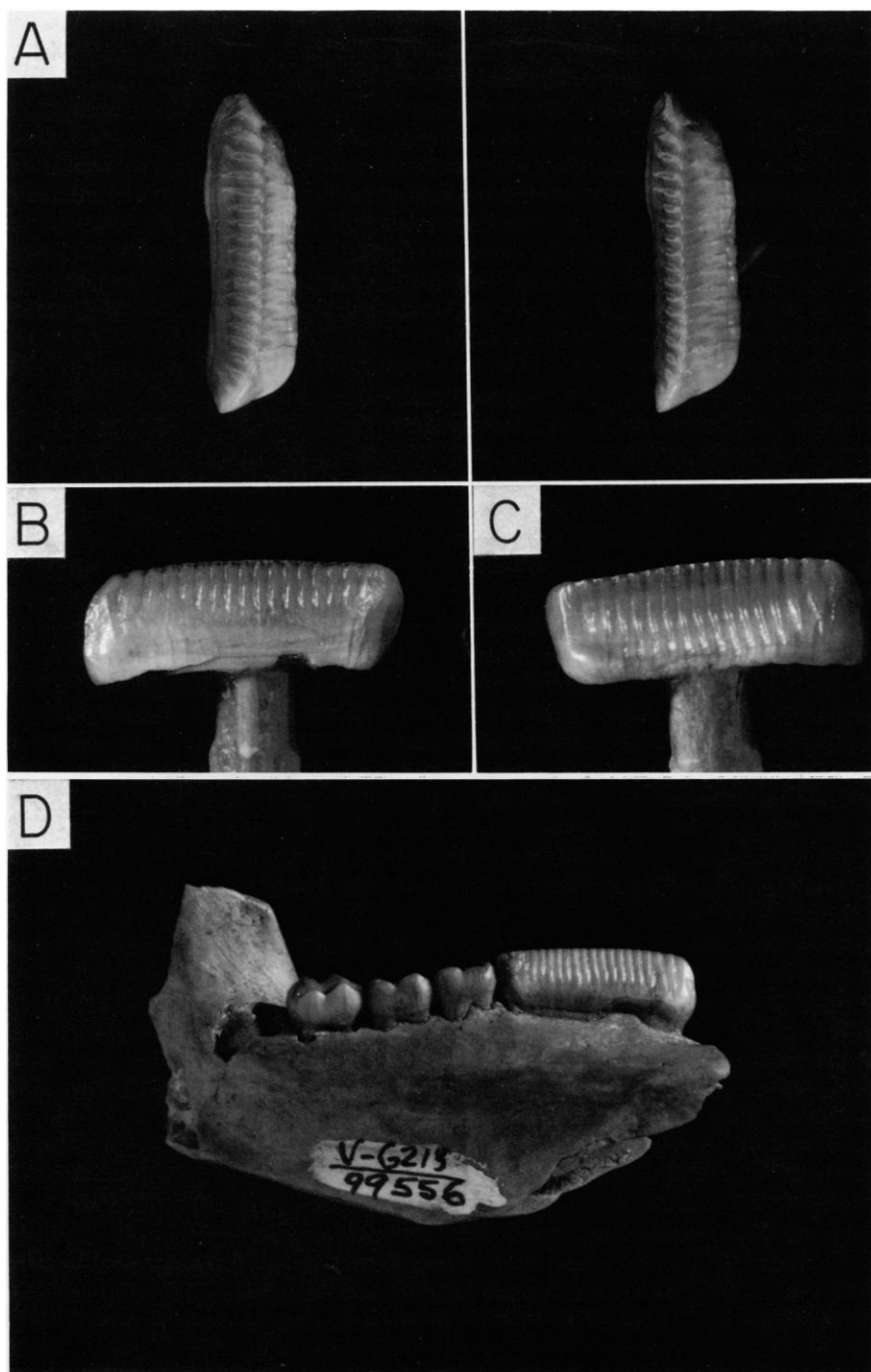


FIGURE 3—*Wakiewakie lawsoni* n. gen., n. sp. *A*, stereopair of occlusal view of referred specimen, UCMP 99888, RP<sup>3</sup>. *B*, labial view of UCMP 99888. *C*, lingual view of UCMP 99888. *D*, lingual view of holotype mandible, SAM P17897. *A*, *B* and *C* are about  $\times 4.3$ ; *D* is about  $\times 2.5$ . V-6213 is the U.C. Berkeley locality number; 99556 is the number initially given to the specimen for clerical purposes which now will be applied to the cast of this specimen, to be housed in the U.C. Berkeley Museum of Paleontology.

TABLE 1—Measurements (in millimeters) of *Wakiewakie lawsoni* n. gen., n. sp.

Specimen	Side	Tooth	Length	Width		Height, metaconid	
				Anterior	Posterior	Anterior	Posterior
SAM P 17897	L	P <sub>3</sub>	11.0	2.9	2.6	—	—
	L	M <sub>1</sub>	3.8	3.1	3.4	1.8 (b)	—
	L	M <sub>2</sub>	4.0	3.5	3.6	2.1	—
	L	M <sub>3</sub>	4.35	3.7	3.6	2.1	—
Length: M <sub>1</sub> –M <sub>3</sub> :			10.0				
							Height
							Anterior Posterior
UCMP 99888	R	P <sup>3</sup>	10.0	2.8	2.7	3.5	3.3

parconid on M<sub>1</sub>; in the more squared up occlusal outline of the lower molars; in the short symphyseal region of the horizontal ramus of the mandible anterior to P<sub>3</sub>. Probably differs also in having a short cranial and mandibular snout, and in the absence of P<sub>2</sub> and P<sup>2</sup> in the adult state.

Most of the above also would differentiate *Wakiewakie* from *Propleopus*, in addition to its much smaller size relative to that Pliocene and Pleistocene genus. In the relatively low crown height and sloping labial surface of its lower molars, however, *Propleopus* is more comparable to *Wakiewakie* than any other Pliocene or younger potoroine (see Woods, 1960; Ride, 1961; Archer, Bartholomai and Marshall, 1978, for a discussion of *Hypsi-primnodon* and *Propleopus*).

Differs from *Potorous* in 1) and 3) above, in the shorter and proportionately wider proportions of the lower molars, and in the much shorter lower diastema. Probably also differs in having a short snout in the cranium.

Differs from *Caloprymnus* in 1) and 3) above, as well as the lesser hypsodonty of the lingual and labial cuspids on the lower molars, in the fact that M<sub>3</sub> is larger than M<sub>2</sub>, and that lower molars are only slightly longer than wide, and in the much shorter mandibular muzzle. The short P<sub>3</sub> of *Caloprymnus*, with only a very few, large-sized ribs is a striking difference relative to *Wakiewakie*. *Wakiewakie* probably also differs from *Caloprymnus* in having a much shorter cranial snout (see also Finlayson, 1932).

Differs from *Aepyprymnus* in 1) and 3) above, as well as the lesser development of labial and lingual molar cuspids and associated ridges and crests, and the shorter molar proportions. *Wakiewakie* probably also dif-

fers from *Aepyprymnus* in having a shorter cranial snout (see also Wakefield, 1967).

Differs from *Bettongia* in 1) and 3) above.

Differs from *Gumardee* in P<sup>3</sup> having many more, and much more finely constructed, labial and lingual ribs, and lacking a lingual and labial basal expansion of the crown in its anterior half, lacking the conspicuous lingual and labial emargination posterior to that and (probably) in lacking the distinct lingual cusp that apparently attached to the posterior end of the premolar blade.

**Mandible.**—The holotype mandible is broken anterior to P<sub>3</sub> and posterior to the anterior margin of the masseteric fossa (Figure 2B). P<sub>3</sub>–M<sub>3</sub> are preserved, as is the alveolus for M<sub>4</sub> and that for the root of I<sub>1</sub> (Figure 2A, 3D). As seen in lateral view (Figure 2B), the mandible is very deep dorsoventrally (11.2 mm below M<sub>1</sub>; 10.4 mm below M<sub>3</sub>). The ventral margin rises steeply anteriorly (at an angle of about 40° relative to a line drawn at the alveolar edge from P<sub>3</sub>–M<sub>3</sub>). To judge from the lingual surface of the ramus (Figure 3D), where the alveolus for I<sub>1</sub> is displayed, the bone terminated only 3 mm anterior to P<sub>3</sub>, at which point the incisor would have emerged from its alveolus. This is consistent with the anteriorly steeply rising ventral margin of the mandible anterior to its deepest point. *Wakiewakie lawsoni* must have had a very short lower jaw anterior to P<sub>3</sub>, and a concomitantly very short snout.

Posteriorly, the lateral surface of the horizontal ramus is broadly convex in cross section, and flares posterolabially from the longitudinal axis of the tooth row at an angle of about 25°, as seen from above (Figure 2A). The body of the ramus encloses a very large masseteric canal that is about 5 mm high,

and 4 mm wide, as seen in oblique antero-medial view. The canal extends anteroventrally from the mandibular foramen of the masseteric fossa for about 21 mm relative to the anterior margin of the fossa. Thus, the canal, and presumably the masseteric muscle it contained, penetrated forward in the body of the ramus to a point below the anterior root of  $P_3$ .

The lingual surface of the ramus is nearly flat (Figure 3D), except as it becomes linguallly convex around the alveolus for the root of  $I_1$ . The lingual surface of the ramus is breached in this area, but remnant textures on the surrounding bony surface indicate that the symphysis extended posteroventrally to a point below the posterior quartile of  $P_3$ . The symphysis thus was relatively extensive posteriorly. A small, and circular (typically potoroine) mandibular foramen opens on the lingual surface of the mandible, ventral to the postalveolar shelf that bounds the alveolus of  $M_4$ .

The ascending ramus of the mandible is not preserved, except for its base, anterior to the masseteric fossa. To judge from this, the ascending ramus rose from the horizontal ramus of the mandible at an angle of nearly 90°; this is greater than for any other known potoroine.

As mentioned above,  $I_1$  is not represented, other than by inference as determined from the shape and orientation of the alveolus for its root. Judging from this,  $I_1$  must have been an elongate, slender tooth, that extended anterodorsally at an angle of about 40° relative to the alveolar border of  $P_3$  as seen in lingual view, and must have emerged from the ramus about 3 mm anterior to  $P_3$ . The diastema between  $I_1$  and  $P_3$  must have been about that long, therefore. Inasmuch as the ramus is not preserved anterior to  $P_3$ , there is little direct information as to the presence or absence of teeth between  $I_1$  and  $P_3$ . A small pit (Figure 2A) anterolingual to the anterior root of  $P_3$  seems to represent a nutrient foramen rather than a (?partially) resorbed alveolus for an anterior premolar. These data suggest that the diastema anterior to  $P_3$  was very short in *Wakiewakie* and that its mandible had a short muzzle, as well as a short cranial snout.  $P_2$  (?) and  $P^2$ ) appears to have been absent in the adult state.

$P_3$ . — This is an elongate, bladed tooth with

a nearly horizontal dorsal profile in lateral view (Figures 2B, 3D). In occlusal view (Figure 2A), the crest of the blade is straight and essentially continues the alignment of the molar teeth; it adjoins the mid-anterior surface of  $M_1$ . The labial surface of  $P_3$  slants ventrolaterally at a greater angle than that at which the lingual surface slants ventrolingually; the lingual surface thus is somewhat steeper. A distinct cingulum-like bulge is present at the labial base of the tooth, but a comparable feature is not so well developed linguallly. The crown of the tooth is highest (or extends farther ventrally) at its anterior end (4.0 mm tall, versus 2.38 mm posteriorly). It is supported by two roots, the posterior of which is about 5.6 mm long and underlies about half the total length of the tooth (see Table 1).

$P_3$  is about as long as the combined length of  $M_1$ – $M_3$  (see also Table 1). It is thus relatively, even if not actually, the longest such tooth known for any of the fossil or Recent Macropodidae. The labial surface (Figure 2B) is ornamented by 20 narrow vertical ribs that are separated by equally narrow valleys and terminate in a point at the dorsal blade of the tooth. The first five are essentially vertical, the next nine are slightly sinusoidal and curve distinctly posteriorly at the base of the crown. The following five ribs are essentially vertical. The last curves anteroventrally, parallel to the posterior border of the tooth, and truncates the bases of the two next anterior ribs. The 19 or more lingual ribs (the enamel is broken away at the posterolingual corner of the tooth; Figure 3D) are generally similar to the labial ribs. As for the labial set, the first lingual rib is essentially vertical. In contrast, lingual ribs two to nine slant slightly anteroventrally, and the remaining posterior ribs slant increasingly posteroventrally as the rear of the tooth is approached. The posterobasal curvature shown by some labial ribs is not seen in their lingual counterparts.

$M_1$ – $M_3$ . — These are short, relatively broad, low crowned (Table 1) bunolophodont teeth (Figures 2, 3D).  $M_1$  and  $M_2$  are broader posteriorly than anteriorly;  $M_3$  is broader anteriorly, but in all cases the difference is slight. All molars are slightly longer than wide but again the difference is not great (Table 1). Enamel has been breached by wear on  $M_1$  (Figure 2A) so that a broad, irregularly shaped

labial area and a narrower and transversely directed lingual area of dentine has been exposed on both the protolophid and hypolophid. This reflects the originally bunoid configuration of the protoconid and hypoconid in contrast to the more lophate condition of the meta- and entoconid. Similar conditions are seen in  $M_2$  and  $M_3$  ( $M_3$  being but slightly worn, with dentine exposed only—and as a small point—at the protoconid).  $M_3$  is thus nearly unworn and shows that the molar teeth of *Wakiewakie* were extremely low crowned, in contrast to all Pliocene and younger members of the Potoroinae in which, although of bunolophodont construction, the molar teeth still are significantly higher crowned.

The lingual surface of each tooth is flatter in occlusal view and steeper than the labial. This is due to the presence of an anterior and posterior ridge on both the metaconid and entoconid, in contrast to the protoconid and hypoconid, where the ends of the cuspids are more rounded and slope less steeply to the base of the crown.  $M_1$  is an exception, with a flat labial surface of the protoconid. All molars show, or appear to have had prior to occlusal or interdental wear, the following features: 1) a short preprotocristid that extends anterolingually from the protoconid (in  $M_1$  this is aligned with the posterior end of the blade of  $P_3$ ); 2) a low and slightly developed anterior cingulum that is continuous with the ridged, curvilinear, anterior edge of the metaconid and also extends labially, across the preprotocristid; 3) a postprotocristid that meets a prehypocristid in the labial third of the crown and separates a broad, shallow lingual occlusal valley from a sharp, deep labial crevice; 4) a posthypocristid that is continuous with the posterior cingulum and the ridged, curvilinear posterior edge of the entoconid which, together, separate a transversely aligned pocket that is completely enclosed between the posterior cingulum and the hypolophid. The protoconid and hypoconid also are connected by low transverse crests to the metaconid and entoconid, respectively. In  $M_1$  the protolophid appears to have converged posterolingually toward the hypolophid; in  $M_2$  and  $M_3$  the two lophids are essentially parallel, and transversely directed.

To judge from the alveoli, which suggest

that  $M_4$  had an anterior root that was bifurcated, but only a single posterior root, this tooth was much smaller than  $M_3$ , as in Potoroinae in general, but uncommon in the Macropodinae, wherein  $M_4$  is about the same size as  $M_3$ .

$P^3$ .—The last upper premolar is represented by two specimens, UCMP 99588, a complete  $RP^3$  crown that lacks roots, and UCMP 66584, an anterior one-half  $RP^3$  that also lacks roots and the base of the crown. UCMP 99588 is otherwise complete and unworn (Figure 3). It is very similar to  $P_3$  of the holotype in size, shape, degree of ornamentation, and lateral profile. It differs in that the blade crest curves labially at its posterior end, is as broad posteriorly as anteriorly, has a stronger lingual basal cingulum-like bulge in the posterior quarter of the tooth, lacks a posterobasal curvature in any labial or lingual rib, and in that its labial ribs do not extend as far toward the base of the crown (they terminate above the basal  $\frac{1}{3}$  of the lingual surface). There are 17 lingual (Figure 3C) and 17 labial ribs (Figure 3B). No upper molars surely identifiable as pertaining to *Wakiewakie lawsoni* have been recognized in the collections of the Kutjamarpu Local Fauna available at UCR.

*Discussion.*—*Wakiewakie lawsoni* differs from all other Macropodidae in the 1) combination of  $P_3$  being nearly as long as the combined length of  $M_1$ – $M_3$ , the horizontal ramus of the mandible being as deep as the combined length of  $M_1$ – $M_3$ , and the steep angle at which  $I_1$  rises from the horizontal ramus of the mandible. *W. lawsoni* differs from all Macropodinae in the above as well as in the bunolophodont character of the lower molars, in the high number of finely constructed ribs on  $P_3$ , and in the strongly developed masseteric canal that extends anteriorly to a point below the anterior root of  $P_3$ . These differences are taken to support referral of *Wakiewakie* to the Potoroinae.

*W. lawsoni* differs from all other known Potoroinae in the combination of characters indicated as 1) above and 2) in the high number of finely constructed ribs on  $P_3$ , the sloping rather than vertically standing labial surfaces of the protoconid and hypoconid (except for *Propleopus*), the low crown height of the lower molars, the steep angle (nearly 90°) at which the ascending ramus rises from the



horizontal ramus of the mandible, and the extremely large and anteriorly penetrating mandibular canal of the horizontal ramus.

Additional differences between *Wakiewakie lawsoni* and the other potoroine genera have been cited in the diagnosis. Thus is clear that *Wakiewakie* is most closely aligned with the genus *Bettongia*, which, with *Aepyprymnus*, contains species with a relatively large, bladed, finely (ca. 18/cm) and evenly serrated premolar. The more bunodont molars of *Bettongia* and the distinctly and completely enclosed post-hypolophid pocket on the lower molars in *Bettongia*, in contrast to *Aepyprymnus*, further focus on the potential relationship between *Bettongia* and *Wakiewakie*.

Within the genus *Bettongia*, *Wakiewakie* appears to be most similar to *B. penicillata* as suggested by the following data: P<sub>3</sub> of *Wakiewakie lawsoni* deepens (if slightly) anteriorly; molar proportions of the fossil species are but slightly longer than wide; where unworn, as in M<sub>2</sub> and M<sub>3</sub>, a distinct, completely enclosed, and relatively transversely elongate pocket is displayed between the hypolophid and the postcingulum. In other species of *Bettongia* (see Wakefield, 1967; Lundelius and Turnbull, personal commun.) the premolar blade is essentially straight and equally deep from front to back; the proportions of the lower molar teeth seem to be somewhat more rectangular, i.e., longer than wide; and the post-hypolophid pocket is at least no more well developed than, and generally less so than, in *B. penicillata*.

The above are suggestive of *Wakiewakie lawsoni* being more like *Bettongia penicillata* than any other species or genus of Potoroinae (see also Diagnosis). At the same time, the molars of *Wakiewakie* are virtually identical to those of the taxon identified tentatively as *Bettongia* sp. by Stirton, Tedford and Miller (1961), from the Ngapakaldi Local Fauna; however the premolar of *Wakiewakie* still is about twice as long as that of the Ngapakaldi form (nominated as a new genus by Case, 1984) and that in species of *Bettongia*. Both the Kutjamarpu and Ngapakaldi forms, however, differ from all Pliocene and younger members of that genus (as well as from other potoroines of any genus, with the possible exception of *Propleopus*) in the much lower

actual and relative crown height of the lower molars, and the sloping labial surfaces of the protoconid and hypoconid (see Case, 1984). In virtually every other Pliocene and younger member of the subfamily these teeth are actually approximately twice the comparative crown height as displayed by *Wakiewakie* and the Ngapakaldi form. Even though the latter does not seem directly ancestral to the Kutjamarpu species because of its still much smaller and shorter, but at the same time much stouter, lower premolar, it is the only form to which *W. lawsoni* is comparable in terms of its molar dentition, and thus could be considered to be roughly derivative from the Ngapakaldi species (see Case, 1984, for a description of the Ngapakaldi taxon). Study of the phyletic relationships of *Wakiewakie* and its allies shows promise of yielding information that will aid in ranking biochronologically the fossil faunas in which they are found.

*General comments on the Potoroinae.*—All of the preceding discussion has been directed at taxa traditionally allocated to the Potoroinae (sensu Kirsch, 1968), composed of species that possess relatively low-crowned bunolophodont upper as well as lower molar teeth, a mandibular canal that penetrates anteriorly well within the body of the horizontal ramus (to below P<sub>3</sub>), and other characters of the cranium and soft anatomy cited in Pearson (1950). A fuller diagnosis of the Potoroinae versus the Macropodinae is presented in Case (1984). This diagnosis, which stresses, in part, the presence in the Potoroinae of bunolophodont upper and lower molars, restriction of the enamel of the lower incisor to its ventral surface, and the penetration of the masseteric canal to a position below the premolar (rather than terminating more posteriorly, below the intermediate molars), clearly separates taxa traditionally considered as potoroines (see above named genera) from those traditionally allied with the Macropodinae. On the other hand, Flannery, Archer and Plane (1982) propose an innovative expansion of the morphological breadth of the Potoroidae (Potoroinae as used here) to encompass forms with definitely lophodont lower molars, bunolophodont upper molars, large, multiserrate premolars, and a masseteric canal that penetrates only as far

anteriorly as  $M_3$  ( $M_2$  of the terminology used here). Under that proposal, the Potoroidae of Flannery, Archer and Plane (1982) contains two major radicles, the Potoroinae and Bulungamayinae. The former contains the taxa traditionally considered as rat-kangaroos, while the latter is represented by extinct Miocene taxa with lophodont lower molars and the other features cited above.

For the purposes of the present paper, the bulungamayine taxa (*Wabularoo*, Archer, 1977; *Bulungamaya* Flannery, Archer and Plane, 1982; Riversleigh Local Fauna, ca. 12 m.y. old, Queensland) are considered members of the Macropodinae (as utilized here) and will not be discussed further. On the other hand Flannery, Archer and Plane (1982) nominate *Gumardee* from the Riversleigh Local Fauna as a potoroine rat-kangaroo, and this is discussed more fully below.

Although it has not been the purpose of the present paper to differentiate all potoroine genera from one another, a perusal of the literature cited above supports the thesis that, within limits, the molar morphology of the Potoroinae is far more stable than that of the premolars, at least at the generic level. At the same time, the Pliocene and younger genera show a number of distinctive changes in molar morphology, relative to those of the Miocene—if *Wakiewakie* and its probable cousin from the Ngapakaldi Local Fauna ("*Bettongia*"; see Case, 1984) are considered representative of the earlier taxa. The genera of Pliocene or younger age show an increased crown height, a steeper labial surface of the lower molars and longer molar proportions (except for *Propleopus*), a suppression of the labial portion of the anterior cingulum of the lower molars and (except for *Bettongia*) development of a more open hypolophid pocket on the lower molars. Of course, certain specializations also are shown in the molar morphology of the Pliocene and younger taxa (the retention of the paraconid, development of a pre-metacristid, and transverse narrowing of  $M_1$  in *Hypsiprymnodon* is perhaps the most striking combination of characters; Ride, 1961; Woods, 1960), but the general changes in molar morphology noted above appear to be pertinent here and to fit well within the range of morphology shown by all of the Miocene and younger potoroines discussed thus far.

On the other hand, the potoroine affinity proposed for *Gumardee pascuali*, a taxon newly named from the Riversleigh Local Fauna, Queensland (Miocene, ca. 12 m.y. old; Flannery, Archer and Plane, 1982) is questioned here. These authors note that *Gumardee* differs from all macropodids (=macropodines as used here) in having "bunodont" molars and a greatly reduced  $M^5$  ( $M^4$  as used here), and from potoroids (potoroines as used here) in having a distinct labial and lingual cingulum and a large number (11) of ridgelets (ribs) on  $P^3$ . Note, however, that although designated as "finely" serrated by those authors, premolar serrations in *Gumardee* are actually much coarser than in *Bettongia*, *Aepyprymnus*, *Wakiewakie*, *Hypsiprymnodon* and *Propleopus*. However, other traditional potoroines (*Caloprymnus*, *Potorous*) have premolars that are more coarsely serrated than in *Gumardee*. Thus, density of premolar serrations alone is insufficient to unequivocally allocate individual specimens to the Potoroinae. At the same time, certain traditional macropodines e.g., *Dorcopsis*, *Wallabia bicolor*, etc., have a greater density of premolar serrations than do *Caloprymnus* or *Potorous*, even though not as dense as in *Gumardee*. Except in extreme cases (extremely high density; *Bettongia*, *Aepyprymnus*, *Wakiewakie*—Potoroinae, versus very low density of premolar serrations; *Macropus*, etc.,—Macropodinae) caution appears to be called for when assessing subfamilial affinity of individual kangaroo specimens on the basis of this aspect of premolar morphology. Other aspects of premolar morphology are discussed below. These, as well as features found in the molar dentition, are here interpreted as favoring allocating of *Gumardee* to the Macropodinae.

As shown in Flannery, Archer and Plane (1982) and in a plastic cast of the holotype, QM F10646, graciously made available to J. A. Case, the upper molars of *Gumardee* are relatively low-crowned teeth of subquadrate occlusal outline.  $M^1$ – $M^3$  are in a late stage of wear, with broad expanses of dentine exposed on all surfaces, especially lingually.  $M^4$  is distinctly less worn, as compared to the other teeth, however. The labial surfaces of the teeth are flattened and show remnants of longitudinal ridges on either side of the paracone and metacone, in  $M^1$ – $M^3$ , at least (as noted

also by Flannery, Archer and Plane, 1982). These teeth, especially  $M^1$ , show small stylar cusps on opposite sides of the labial valley that separates the paracone from the metacone. The above features on  $M^1$ – $M^3$ , the apparently sublophodont (but not “bunodont”) original condition of those teeth (as judged from the wear patterns and their similarity to those shown by upper molars of *Dorcopsoides fossilis* from the ca. 10 m.y. old Alcoota Local Fauna, Northern Territory, also represented by unworn teeth), and the fact that the anterolingual root is flat lingually and so extensive posteriorly as to nearly mask from lingual view the posterior root of these teeth, are features in which *G. pascuali* is essentially identical to *D. fossilis* (see Woodburne, 1967).

$P^3$  in *D. fossilis* also is very similar to that of *G. pascuali*. Both possess 1) elongate shape, 2) labial and lingual cingula and 3) posterior emargination on each side before the rear of the tooth expands transversely and, at that point, bears a posterolingual cusp as well as the cusp present at the rear of the premolar blade. The blade is ornamented with as many as six ribs (Woodburne, 1967), less than in *G. pascuali*, and otherwise differs from  $P^3$  of *G. pascuali* in having a stronger labial and lingual rib at the anterior-most ridge, which is situated at the anterior-most quarter of the tooth. Also in distinct contrast to *G. pascuali*, *D. fossilis* lacks additional ribs anterior to this point. On the other hand, these differences are comparable to those displayed by other genera and species of Miocene and certain younger Macropodinae that have sublophodont and/or low crowned upper molars, more lophodont but still relatively low crowned lower molars, and large, moderately to complexly ornamented premolars. Examples of Miocene age are *Wabularoo*, *Balbaroo*, *Bulungamaya* (Riversleigh Local Fauna; Archer, 1977; Flannery, Archer and Plane, 1982), and *Dorcopsoides* and *Hadronomas* (Alcoota Local Fauna; Woodburne, 1967). Taxa of Pliocene and younger age include *Dorcopsis* Turnbull and Lundelius, 1970; Hamilton Local Fauna, Victoria, (to Recent); *Dendrolagus* Plane, 1967a, Awe Local Fauna, New Guinea (to Recent); *Protemnodon* (various Pliocene and Pleistocene faunas; Stirton, 1963; Bartholomai, 1973; Plane 1967b), and *Wallabia* (various Pliocene to Recent faunas; Bartholomai, 1972, 1978). In this context,

the overall shape and size of  $P^3$ , the presence of labial and lingual basal cingula, and the morphology of  $M^1$ – $M^3$  are here believed to support referral of *Gumardee pascuali* to the Macropodinae.

For example, Flannery, Archer and Plane (1982) believe that the relatively bunodont character of the upper molars is sufficient to warrant excluding *G. pascuali* (only upper dentition known) from *Wabularoo naughtoni* (Archer, 1977), also from the Riversleigh Local Fauna, but known only from the lower dentition, in which the molars are lophodont. Inspection of such taxa as *Dorcopsoides fossilis*, however, indicates that Miocene macropodines may have such an association, with the lophodonty of the lower molars exceeding that of the upper teeth (e.g., Woodburne, 1967). This does not suggest that *G. pascuali* is to be referred to *W. naughtoni*. Arguments against that in Flannery, Archer and Plane (1982), such as  $P_3$  of *W. naughtoni* being larger than, but having fewer ridges than, that of *G. pascuali* support their taxonomic separation.

The main argument in favor of allocating *G. pascuali* to the Potoroinae thus is the reduced nature of the last molar, a state almost universally restricted to the subfamily. On the other hand, the other morphologic features in QM F10646 either are here considered to be equivocal or to combine to argue in favor of its allocation with the Macropodinae, other members of which—*Dorcopsoides*, *Dorcopsis*, *Dorcopsulus*, *Hadronomas*, *Protemnodon*, *Wallabia bicolor*—are generally agreed to belong to that subfamily. [Woodburne, (1967) once argued in favor of allocating *Dorcopsoides*, *Dorcopsis* and *Dorcopsulus* to the Potoroinae, based largely on these taxa having retained a relatively large mandibular canal in which the masseteric muscle inserted within the body of the horizontal ramus of the mandible (to about  $M_2$ ). Subsequently, however, others (Kirsch, 1968; Bartholomai, 1972, 1978) argued for including *Dorcopsoides*, *Dorcopsis* and *Dorcopsulus* in the Macropodinae (see also Hayman and Martin, 1974; Kirsch, 1977; Richardson and McDermid, 1978; Peacock et al., 1981, for criteria developed from analysis of blood sera, chromosome number and karyotypes, allozyme electrophoresis, and repetitive DNA sequences to indicate that *Dorcopsis*, *Dor-*

*copsulus* and *Wallabia* should be allied with the Macropodinae).]

For the moment, allocation of *G. pascuali* to the Potoroinae is not followed here; the characters cited by Flannery, Archer and Plane (1982) are not compelling but are, in fact, more persuasive of the opposite conclusion. Under this interpretation, the Potoroinae continue to be characterized, in part, by species that have bunolophodont, low crowned upper as well as lower molars, variously specialized, but still generally large-sized premolars, and a masseteric canal that penetrates far into the body of the horizontal ramus of the mandible (to about P<sub>3</sub>). See Case (1984) for additional comment and a definition of the Potoroinae.

#### ACKNOWLEDGMENTS

I am especially grateful to the late R. A. Stirton, of the Museum of Paleontology, University of California, Berkeley, for his keen, and unflagging efforts to secure a reliable pre-Pleistocene record of the Australian marsupial fauna. Hand-in-hand with "Stirt" and his students and colleagues since 1953, the cooperative support of Paul F. Lawson, MBE, South Australian Museum, has been unequalled in importance in securing the record of Cenozoic mammal faunas in Australia of which students of the subject can now avail themselves. Specimens collected in the present report were obtained during a cooperative expedition between the South Australian Museum, Adelaide, and the University of California, Berkeley, in 1971. Participation of P. F. Lawson and Winston Head of the South Australian Museum was graciously supported by W. Grant Ingliss, then Director of the South Australian Museum, and subsequently Head of the Department of Environment of South Australia. U.S. participants, under the direction of W. A. Clemens, University of California, Berkeley, were M. O. Woodburne (U.C. Riverside), C. R. Campbell (Berkeley) and M. Archer (School of Zoology, University of New South Wales, Australia). Funding to support the studies reported here was provided by National Science Foundation Grants GB-28864 (to W. A. Clemens) and GB-35488 (to M. O. Woodburne). Publication costs were borne by the author.

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MANUSCRIPT RECEIVED MAY 9, 1983

REVISED MANUSCRIPT RECEIVED OCTOBER 11, 1983