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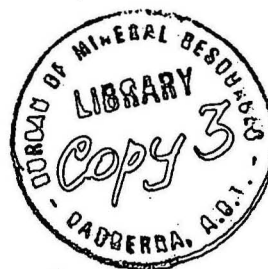
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BUREAU OF MINERAL RESOURCES,
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Record No. 1973/22



MID-TERTIARY THYLACOLEONIDAE
(Marsupialia Mammalia)

by

W.A. Clemens and M. Plane.

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MID-TERTIARY THYLACOLEONIDAE (MARSUPIALIA, MAMMALIA)

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and Bureau of Mineral Resources, Canberra, Australia

ABSTRACT -- Fossils recovered from the Wipajiri Formation in northeastern South Australia and the Camfield Beds of north-central Northern Territory, Australia, document two previously unknown taxa of the Thylacoleonidae, Marsupialia. Wakaleo oldfieldi n. gen. and n. sp., a member of the Kutjamarpu local fauna, and W. vanderleueri n. sp., a member of the Bullock Creek local fauna, demonstrate that the evolution of the Thylacoleonidae was well underway by the middle of the Tertiary.

INTRODUCTION

Among the mammals of Australia the marsupial lions, species of Thylacoleo, have especially piqued the interest of paleobiologists. Until recently the fossil record of this extinct genus, sole member of the Thylacoleonidae, was limited to material from late Cenozoic deposits. In 1967 a Bureau of Mineral Resources field party, led by M. Plane, recovered

a fragmentary mandible of a thylacoleonid from the Camfield Beds (Bullock Creek local fauna) in the Northern Territory. Subsequently, in 1971, a joint South Australian Museum - Museum of Paleontology, University of California field party, directed by W. A. Clemens and M. O. Woodburne, discovered specimens of a thylacoleonid in the Wipajiri Formation (Kutjamarpu local fauna) in South Australia. These fossils of mid-Tertiary, most likely Miocene, age appear to represent two species of a genus clearly distinct from Thylacoleo.

The stratigraphic relationships of the Camfield Beds and Wipajiri Formation have been described by Stirton, Tedford, and Woodburne (1968). In order to facilitate our current research projects and, hopefully, those of others, we are here presenting descriptions of these taxa and brief resumé's of their stratigraphic and phylogenetic significance. The following abbreviations have been employed: Prefixes to catalogue numbers -- CPC, Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra; SAM, South Australian Museum; SAMUC, temporary field designation employed by joint South Australian Museum - Museum of Paleontology, University of California, field party of 1971 (ultimately all material will be given SAM or UCMP catalogue numbers); UCMP, Museum of Paleontology, University of California, Berkeley. Prefix to locality designation: UCMP loc. V-, locality catalogue of the Museum of Paleontology, University of California, Berkeley. Unless otherwise indicated all measurements are in millimeters.

SYSTEMATIC PALEONTOLOGY

Order Marsupialia

Family Thylacoleonidae

Wakaleo, n. gen.

Diagnosis. -- Dentition smaller than that of Thylacoleo carnifex.

Ratio of crown length of P_3 : M_1 less than 1.5. P_3 supported by two roots of approximately equal size. M_1 talonid longer than trigonid. Additional probably diagnostic characters: M_2 and M_3 present; each supported by two roots. Upper molars apparently arranged distal to P^3 in typical tribosphenic pattern.

Type species. -- Wakaleo oldfieldi, n. sp.

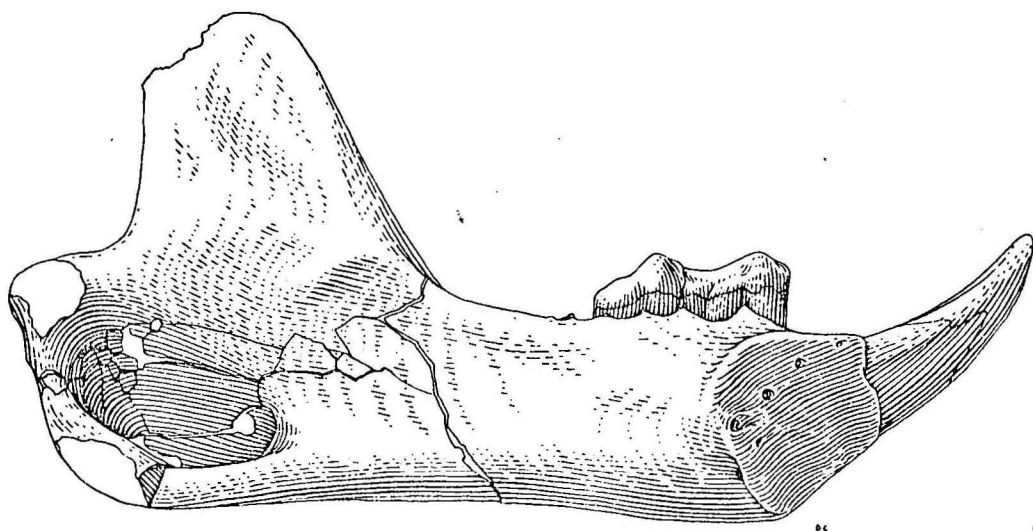
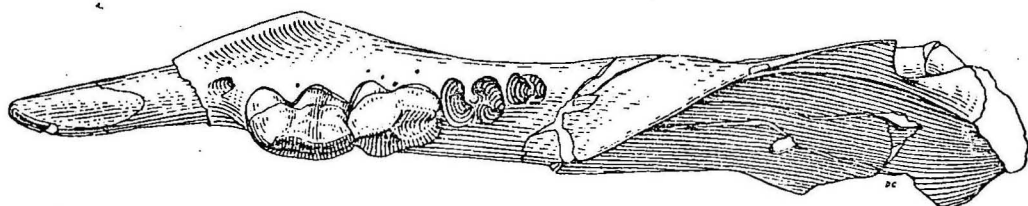
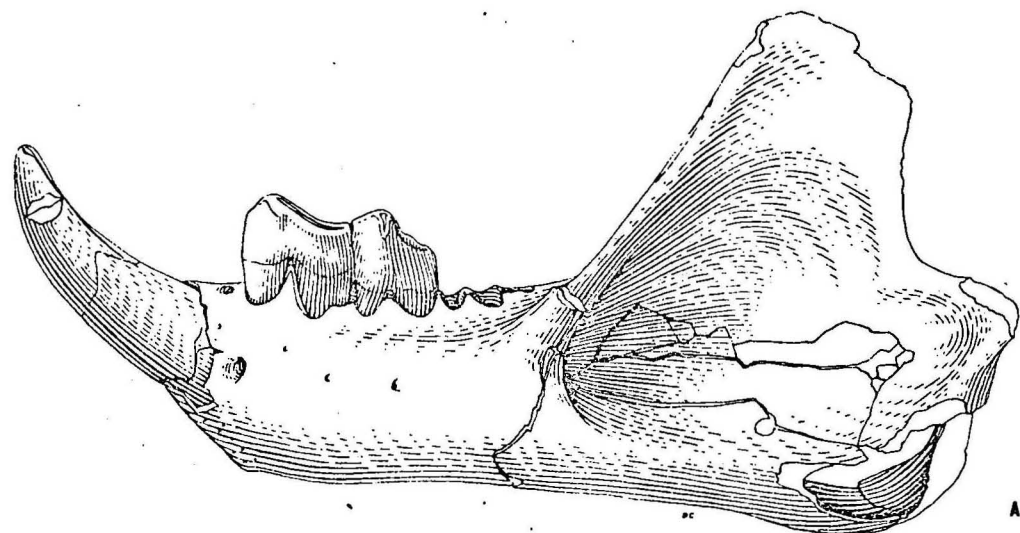
Geologic range. -- Wipajiri Formation and Camfield Beds, tentatively assigned a Miocene age by Stirton, Tedford and Woodburne (1968).

Etymology. -- Waka, Dieri aboriginal dialect, small or little; Leo, Latin, lion.

Wakaleo oldfieldi, n. sp.

Pl. 1, figs. 1-3, 7-9; Text-fig. 1

Diagnosis. -- Animals with smaller molars and dentary bones than those allocated to Wakaleo vanderleueri, n. sp. M_1 with strong anterior and weak labial trigonid ridges descending from the apical cusp and separated by a flat to slightly convex surface. Additional possibly diagnostic characters: P_3 , absolutely and relative to M_1 , smaller. M_1 talonid basin of oval outline.



Text-Fig. 1

Type specimen. -- SAM P 17925 (field designation SAMUC 438), a left dentary containing the caniniform incisor, P_3 , M_1 , and alveoli for M_2 , M_3 , and a single-rooted tooth between the caniniform and P_3 .

Type locality. -- Leaf locality, UCMP loc. V-6213, eastern strand of Lake Ngapakaldi, Tirari Desert, South Australia. Additional locality data for this, the type locality of the Kutjamarpu local fauna, have been published by Stirton, Tedford and Woodburne (1967).

Referred specimens. -- UCMP 102678 (field designation SAMUC 186), isolated fragment of anterior half, right P_3 . UCMP 102677 (field designation SAMUC 277) isolated, right M_2 .

Etymology. -- We gratefully acknowledge the hospitality and assistance of Mr. Bryan Oldfield of Etadunna Station, his family and his parents that have contributed greatly to the success of paleontological field work in the Tirari Desert.

Description and comparisons. -- Unless otherwise indicated morphological data on Wakaleo oldfieldi are drawn from SAM no. P 17925.

Relative to that of Thylacoleo carnifex, the horizontal ramus of the dentary is shallow dorsoventrally. Major mental foramina are present ventral to the anterior end of P_3 and the posterior end of M_1 . Both labially and lingually a large number of smaller foramina open on the dorsolateral surfaces of the dentary near the alveoli of P_3 and M_1 . Anteriorly the masseteric fossa ends in a deep pocket just behind M_3 . A distinct line of flexion separates the depressed area of insertion of the deep masseter from a flatter area on which part of the temporalis inserted. What remains of its base suggests the condyle was a transversely wide, cylindrical

structure closely comparable to that of T. carnifex. The long axis of the base of the condyle is oriented approximately perpendicular to the sagittal plane (as determined from the symphyseal surface). Although its base was destroyed by erosion, clearly the pterygoid fossa was well developed in a posterolabial direction. What remains suggests the angular process was as strongly inflected as its counterpart in T. carnifex. Except for a triangular boss, the internal surface of the coronoid process is featureless.

The caniniform incisor -- provisionally designated I_1 -- is large with an asymmetrically oval cross-section at the alveolar rim. In a small sample of T. carnifex the cross-section of I_1 is also asymmetrical but is broadest dorsally. In Wakaleo the greatest breadth is ventral to the midpoint. Enamel invests only the apical portion of I_1 ; in life it might have been more extensive. Mesially the enamel is developed into distinct dorsal and ventral ridges demarking the area of contact with the other incisor. The intervening area is concave. Along the dorsolabial margin of the incisor, the enamel is drawn out into a distinct flange. The facet beveling the tip of I_1 extends about halfway down this flange. Unlike T. carnifex in which the posterodorsal margin of the I_1 alveolus is opposite or posterior to the anterior root of P_3 , on the mandible of Wakaleo this alveolar margin is in front of P_3 .

Between I_1 and P_3 and on the dorsal surface of the symphysis is an alveolus for a small, single-rooted tooth. This is the only major departure from a predicted dentition of an ancestor of T. carnifex, which has two, single-rooted, button-like teeth in this area.

The crown of P_3 slopes posteriorly from its apex over the anterior root, which unlike T. carnifex, is only slightly smaller than the posterior. Another ridge from the apex extends anteroventrally swinging lingually toward the base of the crown. Posterior to the apex a lingual concave area is delimited anteriorly and posteriorly by rounded ridges and is continued by a groove onto the lingual side of the posterior root. Except for a short, vertical, rounded ridge just behind the apex, the labial side is an essentially uninterrupted convex surface. The wear facet along the crest of the tooth posterior to the apex slopes ventrolabially at an angle of approximately 30° from the horizontal. Woods (1956, p. 135) reported that in T. carnifex the wear facet of P^3 slopes, "making angle of approximately 60° with the horizontal, decreasing in aged individuals". Other than size, P_3 of W. oldfieldi differs primarily from that of T. carnifex in the relatively great enlargement of the posterior part of the crown and supporting root.

The trigonid of M_1 is elevated over the oval talonid basin, which is distinctly larger than the talonid of M_1 in T. carnifex. Three ridges converge at the apical cusp of the trigonid (metaconid of Woods 1956). The anterior is a continuation of the cutting edge of P_3 and carries an extension of the labial wear facet. Labially a low vertical ridge marks the back of the trigonid. The wear facet on the posterolabial side of this ridge covers the labial side of the talonid. Vertical convolutions mark both sides of the posterior half of the ridge extending posteriorly from the trigonid apex and encircling the lingual side of the slightly pebbled talonid basin. Anteriorly the end of the crown is concave. It abuts against and interlocks with a major part of the crown of P_3 . In contrast the posterior end of M_1 is nearly flat and the interdental wear facet is on the lingual half of the crown.

M₂ and the smaller M₃ are missing from SAM P 17925 but their alveoli show these molars were two-rooted and decreased in size posteriorly. An isolated right lower molar, UCM P 102677, is of the proper size and morphology to be an M₂ of Wakaleo oldfieldi. Its two roots are long, deeply grooved along their opposing faces, and, the posterior particularly, slightly twisted. Interpretation of the morphology of the crown is made difficult by its advanced stage of wear and postmortem breakage with loss of several fragments. Anteriorly the crown is flat, unlike M₁, and has a large, interdental wear facet. An apical trigonid basin is situated lingual to the midline of the tooth. The rim of the basin appears to have been continuous and lacking distinct cusps. A large wear facet on the labial slope of the trigonid breaches the enamel in two, circular areas.

The talonid basin of M₂ is large and, except posteriorly, its rim is unbroken. The large wear facet on its labial slope is slightly offset lingually from the facet on the labial side of the trigonid. A facet on the posterior slope of the trigonid extends ventrally along the lingual side of the basin. Particularly on its labial side there is evidence that the talonid basin originally had a rugose, pebbled floor similar to that of M₁.

Probably the wear facet on the labial slope of the trigonid is attributable to contact with the lingual or posterolingual sides of the metacone of M¹. The facet on the labial surface of the talonid and the facet on the posterior side of the trigonid extending down into the talonid basin are most easily interpreted as results of occlusion with the paracone and protocone, respectively, of M². If these interpretations are correct it

follows that at least M^1 and M^2 were situated behind P^3 in the arrangement typical of a tribosphenic dentition.

Wakaleo vanderleueri n. sp.

Pl. 1, figs. 4-6; Text-fig. 2

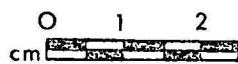
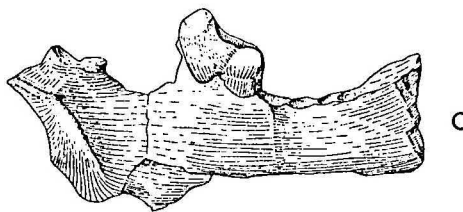
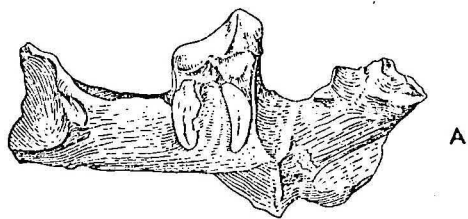
Diagnosis. -- Animals with larger molars and dentary bones than those allocated to Wakaleo oldfieldi. M_1 with strong anterior and labial ridges descending from the apical cusp and separated by a concave surface. Additional possibly diagnostic characters: P_3 , absolutely and relative to M_1 , larger than that of W. oldfieldi. M_1 talonid basin of subrectangular outline.

Type specimen. -- CPC 13527, a right mandibular fragment containing M_1 , alveoli for M_2 and M_3 and part of the alveolus of I_1 .

Type locality. -- Small Hills locality, Bullock Creek, 16 miles southeast of Camfield Homestead, northcentral Northern Territory. Additional locality data presented by Plane and Gatehouse (1968) and on file in the Bureau of Mineral Resources.

Etymology. -- Named in honor of Mr. Paul Vanderleuer of Camfield Station to record our appreciation of the help and hospitality he extended to members of the Bureau of Mineral Resources.

Description and comparisons. -- CPC 13527 includes a portion of the lingual wall of the horizontal ramus of a right mandible extending from the anterior end of the masseteric fossa to the posterior end of the symphysis: M_1 ; the complete alveoli for M_2 and M_3 , both of which have two roots; the lingual halves of both alveoli of P_3 ; and the proximal end of the lingual wall of the alveolus for the caniniform incisor.



Text-Fig. 2

The molar series is reduced to three, two-rooted teeth. M_1 , which shows only the very earliest stages of wear, is roughly rectangular with the anterior third of the crown tapering mesially. The apical cusp of the trigonid, believed to be the metaconid, is located slightly lingual to the midline approximately one third of the way back from the front of the tooth. From the apical cusp a strong ridge descends anterolabially to form a functional continuation of the blade of P_3 . It shows a slight wear facet on its labial slope. A second ridge descends labially from the apical cusp perpendicular to the midline of the tooth. It fades and swings slightly posteriorly as it approaches the base of the crown. The enamel in this area is broken (Pl. 1, fig. 4). This ridge has two small wear facets on its leading edge. A third ridge descends medially from the apical cusp for 1.5 mm then turns posteriorly and descends to form the lingual edge of the talonid basin. The labial edge of the basin is delineated by a ridge originating on the trigonid just behind and ventrolabial to the apical cusp. Both ridges fade as they approach the interdental wear facet on the posterior end of the molar. The talonid basin is sub-rectangular, deepest medially and pebbled or ornamented with ridgelets oriented perpendicular to the ridge circumscribing the basin. At the anterior end of the crown the form of the concave, triangular interdental wear facet indicates a close interlocking of M_1 and P_3 .

STRATIGRAPHIC RELATIONSHIPS AND AGE

The difficulty of determining the age of Australian non-marine formations containing mammalian fossils has been emphasised several times, for example, Stirton, Tedford and Miller 1961 and Stirton, Tedford and Woodburne 1968. It should be stressed once again that the first, and to our minds most significant goal pertaining to the geochronological arrangement of prehistoric terrestrial faunas is the establishment of a reliable, relative, intra-Australian sequence. Statements concerning the age of local faunas in terms of the Lyellian time scale for the Cenozoic, which is itself in a state of flux, currently can be no more than first approximations.

The Bullock Creek and Kutjamarpu local faunas are known from sites over 800 miles apart. Clearly there is no possibility of establishing a physical stratigraphic succession of the fossiliferous strata. We must rely on evolutionary changes for our interpretation of their relative chronology.

The strata of the Wipajiri Formation form the filling of a channel cut into rocks of the Etadunna Formation. Thus the Kutjamarpu local fauna, preserved in rocks of the Wipajiri Formation, is of more recent age than the Ngapakaldi fauna that is represented at several widely separated localities in the Etadunna Formation. The stages of evolution of the members of the Kutjamarpu and Ngapakaldi faunas corroborate this assignment of relative age.

Determination of the relative ages of the Kutjamarpu and other South Australian and Victorian local faunas has been accomplished through utilization of the stages of evolution within the diprotodontid subfamily Zygomaturinae. The only zygomaturine represented in the Kutjamarpu local fauna, Neohelos

tirarensis, is more primitive than Zygomaturus keani or Z. gilli from the Palankarinna and Beaumaris faunas and more primitive than Kolopsis torus from the Alcoota fauna. Thus the relative age of the Kutjamarpu local fauna is post-Ngapakaldi, on the basis of physical stratigraphy, and pre-Palankarinna, Beaumaris or Alcoota, on the basis of stage of zygomaturine evolution.

The Bullock Creek zygomaturine diprotodontid belongs to the genus Neohelos but is larger and morphologically more advanced than N. tirarensis from the Kutjamarpu local fauna. In many features it approaches the genus Kolopsis represented in the Alcoota and Awe faunas and probably is ancestral to this genus. The evidence points to a post-Kutjamarpu and pre-Alcoota age for the Bullock Creek local fauna. The morphological differences between Wakaleo oldfieldi and W. vanderleueri, viewed in terms of different stages of thylacoleonid evolution, corroborate the assignment of a greater age to the Kutjamarpu local fauna relative to the Bullock Creek local fauna. Stirton, Tedford and Woodburne (1968) reviewed the record of Australian Tertiary deposits containing terrestrial mammals and concluded the Bullock Creek and Kutjamarpu faunas were probably of Miocene age. Our work has not resulted in any refinement of this approximate age assignment.

PHYLOGENY OF THE THYLACOLEONIDAE

Until the discovery of Wakaleo in the Bullock Creek and Kutjamarpu faunas the fossil record of the Thylacoleonidae consisted of representatives of the species of Thylacoleo found in deposits of late Cenozoic age

(Gill 1954, Woods 1956, Bartholomai 1962). The dentition of Thylacoleo differs from those of other diprotodontid marsupials in the enlargement of a caniniform incisor set close to a greatly elongated, trenchant premolar and reduction in size and number of the molars. Although at a more primitive stage of evolution, the dentition of Wakaleo illustrates that these patterns of dental modification were established and evolving synchronously during the temporal range of the Kutjamarpu and Bullock Creek faunas.

In most respects Wakaleo oldfieldi appears to exhibit a complex of characters that would be appropriate for a direct ancestor of Thylacoleo. The only feature possibly barring it from inclusion in this lineage is the reduction of the teeth between the caniniform incisor and the trenchant premolar to one, single-rooted tooth. Two, single-rooted teeth are present in this region of the dentition of T. carnifex. With only one specimen available it is impossible to determine if, in the absence of a second tooth, the type of Wakaleo oldfieldi is typical of the population or represents an extreme in dental variation. Even if W. oldfieldi is shown to be characterized by the presence of but one of these single-rooted teeth, this does not necessarily bar it from the ancestry of Thylacoleo. Kurten (1963) has interpreted the fossil record of the Felidae as demonstrating the reestablishment of M_2 , a molar thought to be lost in all Miocene felids, in the dentitions of a part of the populations of the modern northern European lynx (Felis lynx).

Wakaleo vanderleueri could be a direct descendant of W. oldfieldi and, in turn, also a member of the ancestry of Thylacoleo. In comparison to the Kutjamarpu thylacoleonid, W. vanderleueri is an animal with a slightly

larger dentition and dentary. The difference in dental dimensions is in part due to an increase in size of P_3 . Morphological differences of M_1 cited in the diagnoses of the species of Wakaleo are not great. In view of the variation observed among M_1 's of Thylacoleo carnifex they are of questionable significance and we have considered the possibility that the Kutjamarpu and Bullock Creek thylacoleonids are representatives of one species. However, when the geographic separation of the sites and the difference in their age, indicated by the associated zygomaturine diprotodontids, are added to the morphological differences, recognition of two species within the genus Wakaleo appears warranted.

Unfortunately the fossils from the Bullock Creek and Kutjamarpu faunas provide little information about the homologies of the caniniform tooth and the enlarged, trenchant tooth of the lower dentition. We have followed Woods (1956) and others in identifying the former as I_1 , but cannot offer additional data substantiating this identification. Also we follow earlier workers in designating the enlarged, trenchant tooth as P_3 . The morphology of the dentition of Wakaleo does not rule out the possibility that it might be M_1 but shows that it cannot be a more posterior molar. A fragmentary skull of an animal that is probably a thylacoleonid was found in the Etadunna Formation and is now being studied by one of us (Clemens). The fossil once contained an enlarged P^3 followed by four molars and provides additional justification for the identification of the trenchant teeth of thylacoleonids as P^3_3 .

The Kutjamarpu and Bullock Creek thylacoleonids are regarded as representing two new species of a new genus. A hypothesis that thylacoleonid phylogeny consisted

of one lineage culminating in Thylacoleo is much less likely to be correct than one calling for a plexus of lineages. In the framework of the latter model, the species of Wakaleo demonstrate a grade in thylacoleonid evolution whether or not they were directly involved in the ancestry of Thylacoleo.

ACKNOWLEDGEMENTS

The research reported here is a direct outgrowth of a project initiated by the late Professor R. A. Stirton twenty years ago. Our great indebtedness to Stirt is gratefully acknowledged. It is also a pleasure to acknowledge Dr. Grant W. Ingles, then Director of the South Australian Museum; Mr. Paul Lawson, who has made major contributions to our field work; Mr. Neville Pledge and the Board of the South Australian Museum who made possible the organization and operation of the joint South Australian Museum - Museum of Paleontology project in 1971. This and subsequent laboratory work were funded by grants from the National Science Foundation (GB 28864) and the Annie M. Alexander Endowment. Dr. M. O. Woodburne, who discovered the type of Wakaleo oldfieldi; Mr. Michael Archer; and Mr. Colin Campbell were largely responsible for the success of our 1971 field work. Text-fig. 2 was prepared by Mr. George Matveev; the other illustrations are the work of Mr. David Cook. Permission to publish this report was granted by the Director of the Bureau of Mineral Resources.

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Text-figure legends:

TEXT-FIG. 1 -- Wakaleo oldfieldi n. gen. and n. sp., holotype, SAM P 17925,
UCMP loc. V-6213. A, labial; B, occlusal; C, lingual views.

TEXT-FIG. 2 -- Wakaleo vanderleueri n. sp., holotype, CPC 13527. A, labial;
B, occlusal; C, lingual views.

Plate legend:

EXPLANATION OF PLATE 1

All figures drawn to the same scale. Fracture surfaces darkened.

FIGS. 1-3 -- Wakaleo oldfieldi n. gen. and n. sp., P₃ and M₁ of holotype,
SAM P 17925. 1, labial; 2, occlusal; 3, lingual views.

4-6 -- Wakaleo vanderleuri n. sp., M₁ of holotype, CPC 13527.
4, labial; 5, occlusal; 6, lingual views.

7-9 -- Wakaleo oldfieldi n. gen. and n. sp., isolated right M₂,
UCMP 102677. 7, labial; 8, occlusal; 9, lingual views.

TABLE 1. -- Dimensions (in mm) of specimens of Wakaleo oldfieldi n. gen.
and n. sp. and W. vanderleueri n. sp.

	<u>W. oldfieldi</u>	<u>W. vanderleueri</u>
	SAM P 17925	CPC 13527
P_3		
Length	12.4	13.5-15.3 (range of estimates)
Maximum width over		
Anterior root	6.2	---
Posterior root	7.8	---
M_1		
Length	10.4	11.7
Width (trigonid)	8.7	7.9+
Width (talonid)	7.2	7.7
M_{2-3}		
Total length of alveoli	13.7	14.5
Dentary		
Depth below anterior root P_3	23	---
Depth below anterior root M_2	22	---
	UCMP 102677	
M_2		
Length	7.5	
Width (trigonid)	6.3	
Width (talonid)	6.1	

0 1 2
cm

