COMMONWEALTH OF AUSTRALIA

DEPARTMENT OF NATIONAL DEVELOPMENT
BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

BULLETIN No. 85

# Tertiary Diprotodontidae from Australia and New Guinea

BY

R. A. STIRTON and M. O. WOODBURNE
University of California

and

M. D. PLANE
Bureau of Mineral Resources

*Issued under the Authority of the Hon. David Fairbairn,*
*Minister for National Development*
1967

COMMONWEALTH OF AUSTRALIA

DEPARTMENT OF NATIONAL DEVELOPMENT
MINISTER: THE HON. DAVID FAIRBAIRN, D.F.C., M.P.
SECRETARY: R. W. BOSWELL, O.B.E.
BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS
DIRECTOR: J. M. RAYNER, O.B.E.

THIS BULLETIN WAS PREPARED FOR PUBLICATION IN THE GEOLOGICAL BRANCH
ASSISTANT DIRECTOR: N. H. FISHER

*Manuscript received: 7 September 1965*
*Issued: 15 May 1967*

*Published by the Bureau of Mineral Resources, Geology and Geophysics*
*Canberra A.C.T.*

**ALEX. B. DAVIES, Government Printer, Western Australia**
**(Printed in Australia)**

# FOREWORD

Vertebrate remains from Australia were first studied over a century ago by Sir Richard Owen; and thereafter systematic work was carried on only sporadically, until in 1953 the late Professor R. A. Stirton of the University of California at Berkeley came to South Australia and started an intensive field and laboratory study of the vertebrate faunas of that State. He and his co-workers have continued the study, extending it into the Northern Territory as a consequence of finds by geologists of the Bureau of Mineral Resources, of which the Alcoota fauna is perhaps the richest so far.

Professor Stirton also paid a visit to New Guinea to inspect the finds in the Watut Valley, first discovered by N. H. Fisher in 1935 when he was Government Geologist in the Territory, and extended recently by M. D. Plane of the Bureau of Mineral Resources. As a result of this visit, Stirton and the Bureau made arrangements for Plane to study the fauna at Berkeley.

Stirton and his co-workers R. H. Tedford, M. O. Woodburne, and Plane have introduced a new rigour into the study of vertebrate palaeontology in Australia, with which the Bureau is happy to be associated. Geologically, fossil mammals are of great importance because they provide a clue—sometimes the only clue—to the Cainozoic history of Australia. This volume records work on an extinct group of marsupials which, as the final paper in the collection shows, forms an evolutionary series that can be applied directly to the dating of Australian Tertiary rocks.

J. M. RAYNER
*Director.*

Page vi is blank.

# CONTENTS

Page

The Diprotodontidae from the Ngapakaldi Fauna, South Australia; by R. A. Stirton .... 1

A Diprotodontid from the Miocene Kutjamarpu Fauna, South Australia; by R. A. Stirton 45

Three new Diprotodontids from the Tertiary of the Northern Territory; by M. O. Woodburne 53

Two new Diprotodontids from the Pliocene Otibanda Formation, New Guinea; by M. D. Plane .... .... .... .... .... .... .... .... .... .... .... .... 105

New species of *Zygomaturus* and additional observations on *Meniscolophus*, Pliocene Palankarrina Fauna, South Australia; by R. A. Stirton .... .... .... .... .... .... 129

A phylogeny of Diprotodontidae and its significance in correlation; by R. A. Stirton, M. O. Woodburne, and M. D. Plane .... .... .... .... .... .... .... .... 149

## BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

## BULLETIN 85

## CORRECTIONS

p. 5: Type locality of *N. tedfordi* should be V5858, not V6213.

p. 50, third line from bottom: $M_4$, not $M_3$.

p. 66, Table 5, column 6: height of hypo-, not hyper-.

p. 138: Size of figure 2(2. keanei) is X$\frac{2}{3}$, not X1.

p. 152, para. 2, line 2: *P. azael*, not *P. azeal*.

p. 159: The paper by Striton, Tedford, and Woodburne was still in press when this Bulletin was issued.

## *Abbreviations*

AM—Australian Museum, Sydney
BMNH—British Museum (Natural History)
BMR—Bureau of Mineral Resources, Canberra
CPC—Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra
GSQ—Geological Survey of Queensland
MUDG—Geology Department, University of Melbourne
NMV—National Museum of Victoria, Melbourne
QM—Queensland Museum
SAM—South Australian Museum
UCMP—University of California, Museum of Paleontology

Unless otherwise stated, all measurements are in millimetres.

# THE DIPROTODONTIDAE FROM THE NGAPAKALDI FAUNA, SOUTH AUSTRALIA

by

R. A. STIRTON

## CONTENTS

Page

INTRODUCTION .... .... .... .... .... .... .... .... .... .... .... 3

Genus *Ngapakaldia* nov.

*Ngapakaldia tedfordi* gen.nov.et sp.nov. .... .... .... .... .... .... .... 4

*Ngapakaldia bonythoni* sp.nov. .... .... .... .... .... .... .... .... 26

Genus *Pitikantia* nov.

*Pitikantia dailyi* gen.nov.et sp.nov. .... .... .... .... .... .... .... 30

REFERENCES .... .... .... .... .... .... .... .... .... .... .... 34

APPENDIX: Glossary of terms used. .... .... .... .... .... .... .... .... 35

## SUMMARY

Two new genera, including three species, of the marsupial family Diprotodontidae from the late Oligocene or early Miocene Etadunna Formation are described ; they are the smallest diprotodontids known. They are referred to the subfamily Palorchestinae. One excellent specimen reveals nearly all the cranial features including the auditory region. As in the wombats the extension of the squamosal ventrally excludes the alisphenoid from the auditory region. Perhaps the most conspicuous feature in the cranium is the great expansion of epitympanic sinus into the squamosal dorsally and into a squamosal tuberosity ventrally. There is no direct evidence in these genera of their derivation from ancestral marsupials with tribosphenic molars. It is evident that the family Diprotodontidae was well established at this time.

# INTRODUCTION

The first evidence of a small diprotodontid in the Etadunna Formation was a median phalanx found on the surface at Lake Palankarinna in 1953 by the expedition of the South Australian Museum and Museum of Paleontology, University of California, into that area. The specimen was recognized as being different from the fossil mammalian remains collected in the Woodard Quarry, but its identity remained obscure until 1957, when R. H. Tedford, Brian Daily, and P. F. Lawson found foot bones associated with teeth at Lake Pitikanta.

The abundance of these creatures in the fauna was revealed by the 1958, 1961, and 1962 expeditions. In localities UCMP V5774 at Lake Pitikanta and V5858 at Lake Ngapakaldi, specimens have been found from 3 to 15 feet apart. In fact parts of skeletons of two individuals have been found where they were buried together. None of the specimens found by our parties is a complete skeleton, although parts of the postcranial skeleton are included with nearly every find. Some parts, like the feet and caudal vertebrae, are remarkably complete. It has become increasingly evident that the remains of these small diprotodontids are as common in some areas of the Etadunna Formation as is the huge *Diprotodon optatum* at Lake Callabonna.

Unfortunately most of the specimens have been found in the surface weathering zone of the grey-green claystone or of the white calcareous mudstone and consequently are badly fractured and partly destroyed by the growth of gypsum crystals. These fragments are scattered over the surface or are disintegrated. The most completely preserved parts are the rather compact footbones and caudal vertebrae. Occasionally more complete bones and teeth of the shattered specimens are found under the surface and in place. The weathered zone usually ranges from a few to 15 inches in thickness. This of course has made collecting and preparation extremely difficult. The best specimens were found in the Ngapakaldi Quarry, where the grey-green claystone was not affected by weathering.

Time has not permitted a full description of the skeleton at this time; therefore only the crania, mandibulae, and teeth are included in this report. Description of the postcranial elements must await full preparation and restoration of the broken parts: there is enough material to make a composite restoration of the most common species. The generic diagnoses as presented are not necessarily exclusively diagnostic but are combinations of characters in relation to other genera.

### *Acknowledgments*

This research was sponsored by the South Australian Museum and the Museum of Paleontology at the University of California. I am particularly grateful to the Director of the South Australian Museum, Dr Peter Crowcroft, and to his museum staff for their continued encouragement and active participation. Those deserving of special recognition are Mr Paul F. Lawson and Mr Harry J. Bowshall, who did much of the organization of the expeditions and entered enthusiastically into the field work. Dr Brian Daily, Department of Geology, University of Adelaide, has also contributed in many ways and his counsel has been much appreciated. Without the able assistance of my colleagues, Drs Richard H. Tedford, Michael O. Woodburne, and Alden H. Miller, the specimens could not have been found and collected. The illustrations were skilfully rendered by Mr Owen J. Poe (1 to 4, and 6), and Mrs Jaime P. Lufkin (5).

The 1958, 1961, and 1962 expeditions were generously financed by the United States National Science Foundation grants G5632 and G15957.

## Genus NGAPAKALDIA nov.

*Genotypic Species—Ngapakaldia tedfordi* sp.nov.

*Generic Diagnosis.* Highest point on cranium on sagittal crest 60·0 anterior to lambdoidal crest; dorsal profile of rostrum nearly horizontal; infraorbital foramen above $P^3$; masseteric tuberosity of zygomatic arch at level of maxillary tooth row; squamosal expanded laterally to accommodate large epitympanic sinus; greatly reduced postglenoid process.

Tip of $I^1$ extends below occlusal level of $I^2$ and $I^3$, occlusion on posterior surface of $I^1$. Alveolus for vestigial canine. $P^3$ with parametacone, steep decline of posterior crest continuous to lowest point of posterior cingulum; small protocone but no parastyle or hypocone. Transverse median valleys sharply V-shaped in $M^1$ and $M^2$, more widely V-shaped in $M^3$ and $M^4$; no indication of midlink-like structure.

Digastric fossa of mandible short, fades out below $M^4$, is confluent with pterygoid fossa posteriorly; no digastric sulcus or process.

Lower incisors widely lanceolate, only slightly upturned anteriorly, roots long and not vertically deep. $P_3$ much wider across talonid than across main cuspid. Lower molars with wide U-shaped transverse median valleys; no indication of midlink-like structure.

## NGAPAKALDIA TEDFORDI* sp.nov.

*Holotype.* Cranium nearly complete but without left nasal and premaxilla, ends of right nasal and premaxilla, paroccipital processes, and most of pterygoids; left radius complete; left ulna with proximal end missing; left manus complete including carpals, metacarpals, phalanges, and sesamoids; right metacarpal III with proximal phalanx; left pes nearly complete with tarsals, metatarsals (distal condyles of metatarsal I and II missing), phalanges (distal phalanx of digit IV mostly restored, both phalanges of digit I missing), and only two sesamoids; right proximal phalanx of digit I; caudal vertebrae 7, 9 to 15, 17, and 19–29; haemal arches between vertebrae 6–7, 7–8, 9–10, 10–11, and 11–12. SAM P13851.

*Paratypes.* Maxillae and premaxillae with right $I^2$ missing but otherwise with incisors and cheekteeth present on both sides; left mandible with dentition complete, but with condyle and upper part of coronoid missing; part of skeleton; UCMP 57256. Left maxilla with $M^1$–$M^3$; part of skeleton; UCMP 69817. Right $I^2$, root of left $I^1$;

---

* Named for Dr Richard H. Tedford, Department of Vertebrate Paleontology, American Museum of Natural History, New York,

part of skeleton; UCMP 69814. Right $I^2$, left $I^3$, three vertebrae and some foot bones; UCMP 60985. Left $P^3$, $M^3$ and $M^4$; part of skeleton; UCMP 69815. Right $I^1$; footbones; UCMP 60977. Right and left $I^2$, right $I_1$; UCMP 60979. Left $M^1$; parts of skeleton; UCMP 69812. Right $M_1$; left $M_2$; bone fragments; UCMP 57286. Left $I^2$; right $I^2$ and $I^3$; footbones; UCMP 57257.

*Referred specimens.* Lake Pitikanta.—Nasals; left premaxilla with $I^1$ to $I^3$; right $I^1$ to $I^3$; part of left maxilla with $P^3$ to $M^4$; both petrosals; left mandible including symphyseal area and both incisors, left $M^2$ to $M^4$; part of skeleton; loc. V5774–UCMP 57254. Left ?$P_2$ and ?$DP_3$; loc. V5774–UCMP 69821. Premaxillae with right $I^1$, $I^2$ and $I^3$; right $P^3$, $M^1$ and part of $M^2$; left $P^3$, part of $M^2$, $M^3$ and $M^4$; both lower incisors; left $P_3$, $M_1$, $M_2$, posterior moiety of $M_3$, and $M_4$; right $P_3$, posterior moiety of $M_1$, $M_2$, and $M_3$; loc. V5774–UCMP 57271. Left $M^4$; loc. V5774–UCMP 69811. Left $P_3$, anterior moiety of $M_1$, $M_2$ to $M_4$; loc. V5774–UCMP 57290. Right $I^2$ and $I^3$; left $I_1$; left $I_1$; left $M_3$; loc. V6150–UCMP 60982. Left $I_1$, most of right $I_1$; other fragments; loc. V6151–UCMP 60983. Lake Kanunka.—Most of right $M_2$ and other fragments; loc. V5855-UCMP 57283.

*Specific Diagnosis.* Length of cranium from occipital condyles to anterior edge of $I^1$ 234·0; sagittal crest about 3·0 wide; depth of rostrum anterior to $P^3$ 49·0; length of rostrum as measured anteriorly from orbit about 92·0; diastema between $I^3$ and $P^3$ about 43·0; depth of zygomatic arch 25·5.

Anteroposterior length of $I^2$ averages about 10·6; height of crown about 7·3, anteroposterior length of $I^3$ averages about 6·2, height of crown 5·4. $P^3$ longer than wide, anteroposterior length 9·6, width 8·6. Average length of $M^3$ 15·0, average width of anterior moiety 12·5, average width of posterior moiety 11·4.

Width of lower incisor across talonid about 11·1; diastema between $I_1$ and $P_3$ 38·8, $P_3$ much longer than wide, length about 8·9, width about 6·4. Length of $M_1$ average about 12·0, width of anterior moiety about 8–0, width of posterior moiety about 8·9.

*Type Locality.* Ngapakaldi Quarry, UCMP Loc. V6213. Top of grey-green claystone unit below white calcareous mudstone, in only exposures of Etadunna Formation along eastern shore of Lake Ngapakaldi (mapped only in early pastoral sheets), a large saltpan about 5 miles long (NE–SW) and 2·5 miles at widest place (NW–SE); locality about 3 miles north-east of south-west end of lake and about 4 miles north of Lake Pitikanta, about 22 miles west of Birdsville Track and an equal distance north of Cooper Creek in Tirari Desert east of Lake Eyre, South Australia. Approximate grid coordinate 642488, grid zone 5, Marree Sheet, 1:506,880; Australian Army H.Q., Cartographic Co., 1942.

The quarry is in the only area of banklike exposures on the eastern shoreline. The 6-foot bank exposes about 2 feet of grey-green claystone, overlain by 2 feet of white calcareous mudstone, and is capped with sand which is cemented by gypsum. All the specimens from this immediate area and from the grey-green claystone have been referred to the UCMP locality V5858.

Age—?late Oligocene. Fauna—Ngapakaldi.

*Description*

*Cranium.* The cranium of the holotype SAM P13851 is slightly larger than in the common wombat *Vombatus hirsutus* Perry, although it differs in shape and proportions. One of the most conspicuous features in *Ngapakaldia* is the great lateral expansion of the squamosal below the parietal. The distance of 96·2 between the dorsomesial edges of the zygomatic sulci is 8·2 greater than the midsagittal measurement of 88·7 from the frontoparietal suture to the lambdoidal crest. The greatest width of the cranium, however, is across the zygomatic arches about 10·0 anterior to the glenoid surface. This is more than half of the total length of the cranium (see table of measurements). Another proportion, more like that in the wombats and the koala, and in contrast to the macropodids, is in the rostrum as measured from the lacrimal foramen to the anterior edge of $I^1$, being about three-eighths of length of the cranium. In this regard the rostrum has been considered as terminating dorsally at the frontonasal suture and laterally at the anterior base of the jugal arch.

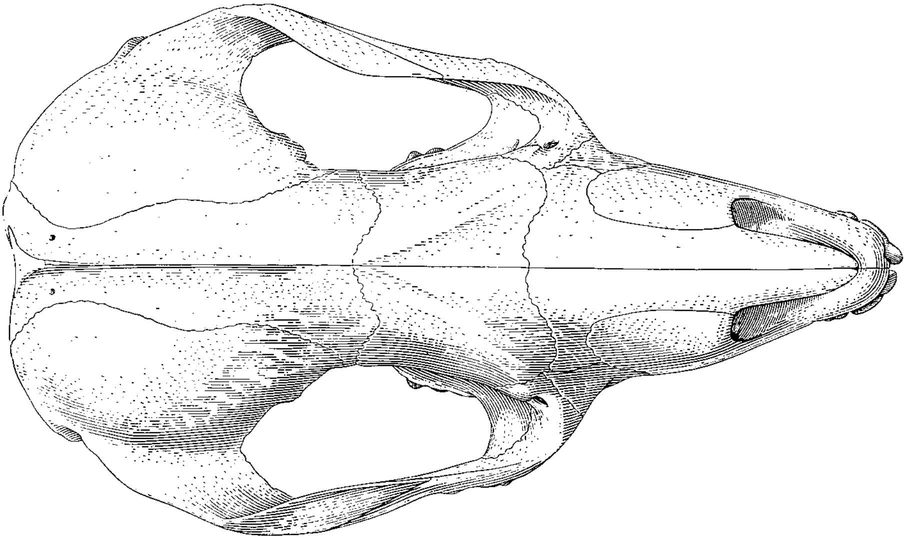


**Fig. 1.—*Ngapakaldia tedfordi* gen. nov. et sp. nov. Part of holotype, SAM P13851, one-half natural size. Cranium with anterior ends of nasals and premaxillae restored from UCMP specimens 57254 and 57271. All fractures and broken areas are eliminated, and where one side is better preserved than the other restoration has been rendered. Dorsal view.**

The highest point on the cranium appears to have been on the sagittal crest about 60·0 anterior to the lambdoidal crest. The crest is broken and partly missing in that area, but fortunately there are contacts for two fragments that closely approximate the height at that point. From the highest point the dorsal profile slopes gently forward across the slight depression of the frontals to the frontonasal suture. The nasal profile is horizontal except for the slight downward curvature of the terminal 15·0 anteriorly. The posterior part of the sagittal crest curves down to the lambdoidal crest.

The narial aperture is 28·2 deep and 45·8 wide. It is therefore relatively wider but much shallower than in the macropodids, and relatively narrower but deeper than in the wombats. In contrast to the kangaroo and koalas the nasals bypass the premaxillae anteriorly and extend down about 4·3 into the narial aperture.

The *nasals* are approximately 82·0 long in UCMP 57254. Their anterior extremity is not preserved in the holotype. In the holotype they have a combined width of 48·7 posteriorly as measured from the juncture of the premaxilla, frontal, and nasal bones on each side across the rostrum. The nasals come to a sharp point anteriorly where they display the downward curvature. Although the left premaxilla and nasal are also missing in the holotype, they have been restored from the right side and from UCMP 57256 and 57254. The narial notch is 30·0 behind the anterior end and approximately 17·5 anterior to P$^3$. The combined nasals are 26·0 wide at that point but somewhat narrower posteriorly before the nasopremaxilla suture curves down over the side of the rostrum to a position above the anterior edge of the zygomatic base of the jugal and 37·8 behind the narial notch. The suture then runs horizontally for a distance of 8·7 back to its contact with the frontal. At that point it is separated from the lacrimal by a space of 5·0, by the end of a narrow strip of the premaxilla and an even narrower extension of the maxilla. The nasofrontal sutures from each side are then directed slightly dorsoposteriorly to the midline. The posterior lateroventral expansion of the nasals is conspicuously different from that in the macropodids and somewhat more like that in most other marsupials.

A dorsal triangular surface of the *frontals* is only slightly depressed. This area, which is so conspicuously depressed in other diprotodontids, is bounded anteriorly by the nasofrontal suture and laterally by the dorsal frontal crests. These crests converge posteriorly on the midline at the frontoparietal suture. The crests are mostly restricted to the frontal bone, but also continue back along the midline of the parietals where they are separated by a narrow groove. These crests are not partly composed of the parietal laterally as in the macropodidae. They are about 4·0 wide and slightly grooved. Anteriorly they terminate 10·7 posterodorsally from the lacrimal tuberosity. From the crests the frontals curve outward and downward into the orbital fossa to the frontopalatine suture on the median wall of the groove at the inner side of the maxillary shelf. There is no postorbital process, nor even a postorbital prominence.

The frontoparietal suture, from the midline, curves anteriorly then posteroventrally to its contact with the squamosal and alisphenoid. At that juncture the fronto-alisphenoid suture descends apparently to the upper edge of the orbitosphenoid, then as the fronto-orbitosphenoid suture runs forward around the anterior end of the orbitosphenoid and down to the frontopalatine suture. The course of the frontopalatine suture anteriorly is slightly upward then nearly horizontal just above the sphenopalatine foramen where it contacts the lacrimal. There is no sutural contact of the frontal and maxilla in this area as in the macropodids and wombats. The frontolacrimal suture then ascends anterdorsally out of the interorbital area just dorsal to lacrimal tuberosity to reach the posterior rostral wing of the maxilla. There appears to be a very small ethmoid foramen in the frontal 9.0 above the sphenopalatine foramen.

The *premaxillae* are rather bulbously expanded laterally just behind the narial notch; consequently the lateral borders of the narial aperture are also somewhat expanded laterally. The border is rounded and about 5.5 thick. The length from the posterior narial border to the posterior extremity of the nasopremaxillary suture is 39.0. The greatest depth of the premaxilla 10.0 behind the narial notch is about 29.0. The width of the anterior end of the palate across the premaxillae at the posterior edge of $I^3$ is 28.0 in UCMP 57256, and 25.0 in UCMP 57271. In UCMP 57256, also, the incisive foramen is 23.0 long and approximately 6.0 wide, but in UCMP 57271 it is 16.7 long and 3.5 wide. Tracing the maxillo-premaxillary suture has been difficult because of the fractured surface and fusion of the bones. Nevertheless the position of the suture on the left lateral surface where the premaxilla is missing but the maxillary part of the suture is preserved appears to be much more like that in the koala than in the wombats or the macropodids. My tracing of the suture is included in the description of the maxilla.

The area occupied by the *maxilla* can be stated most accurately by tracing its sutural contact with the adjacent bones. The length of the suture of the two maxillae along the midline of the palate in UCMP 57256 is 62.0. The maxillopalatine suture on the palate curves uniformly posterolaterally to within 5.0 of the alveolar border of $M^3$, then runs posteriorly parallel to the alveolus of $M^4$ across the lateral end of the transverse palatine ridge (torus) to follow the ventrolateral edge of the interpterygoid fossa.

Seven millimetres behind the postpalatine ridge the suture crosses over laterally into the lower end of the pterygopalatine fossa. Passing around the posterior end of the maxillary ridge, it extends anterodorsally to bisect the sphenopalatine foramen, then on to bisect the maxillary foramen. Just in front of the maxillary foramen it turns upward to contact the lacrimal. It then continues anteriorly for 4.5 as the ventral maxillolacrimal suture to reach the jugal 16.0 below the lacrimal foramen.

The maxillojugal suture within the orbit is 11.0 below the orbital rim. It runs laterally and ventrally and crosses the arch diagonally 6.5 behind the masseteric process. It then crosses the lateral base of the process to extend anterodorsally for a distance of 30.0 across the anterior part of the arch to a point 13.0 directly behind the infraorbital foramen. There it turns dorsally and finally hooks back to contact the lacrimal. The slightly curved dorsal maxillolacrimal suture is 16.0 long. It reaches the frontal 10.2 directly above the lacrimal foramen. The maxillofrontal suture is only 3.2 in length. A narrow posterodorsal extension of the maxilla and a similar but wider extension of the premaxilla is as in the wombats, but, in contrast to an arrangement seen in the macropodids, blocks the posteroventral expansion of the nasal from contact with the lacrimal.

The maxillo-premaxillary suture, from its contact with the frontal, is directed 8.5 anteriorly and from there runs anteroventrally. It passes 6.5 above and then 11.2 anterior to the infraorbital foramen and finally down near the edge of the palate, 7.5 anterior to $P^3$, where it appears to run forward lateral to the diastemal crest in UCMP 57256. In UCMP 57271 it appears to cross the diastemal crest 16.2 behind $I^3$ then crosses anteromesially to the middle of the lateral border of the incisive foramen. From there it runs posteriorly along the lateral wall of the foramen to curve around the posterior end of the foramen, where it runs slightly forward then back to the midline.

The maxillary palate is only slightly arched transversely, but on each side of the midline, starting opposite the anterior end of $M^1$ and probably extending forward to the incisive foramina, is an irregular depressed area. In *Macropus* and *Phascolarctos* a similar depression starts opposite the posterior end of $M^2$. It probably offers better anchorage for the hard palate opposite the long diastemal crests. There are three small foramina on the left and two on the right side of the maxillary surface of the palate. These are directed anteriorly. There is no maxillary fenestration. Within the lowest part of the orbital fossa the maxillary shelf is prominent and forms a ridge that curves down to terminate behind $M^4$. On the posteromedian side of that ridge is the posterior palatine foramen, the canal from which runs anteromesially to open as the anterior palatine foramen under the anterolateral end of the transverse palatine ridge on the maxillopalatine suture opposite the anterior moiety of $M^4$. The large sphenopalatine foramen is 13.5 directly behind the larger maxillary foramen. The infraorbital foramen is 15.0 above $P^3$ and 21.0 anterior to the orbital rim. The canal connecting the infraorbital and maxillary foramina is nearly horizontal and 31.0 in length. A wide fossa probably for the origin of the buccinator muscle lies above $M^1$ and the anterior moiety of $M^2$. The masseteric tuberosity of the arch is directed posteroventrally and extends only 5.4 below the maxillojugal suture. It is slightly higher than the well-worn occlusal surfaces of $M^2$ and $M^3$ in the holotype and in UCMP 57256.

The palatine bones are exposed on the posterior surface of the palate, in the choana, in the side and much of the roof of the interpterygoid fossa, in the anterior part of the pterygoid cavity, in the mesial side of the pterygopalatine fossa, and as a narrow strip of bone from that fossa forward mostly in the groove along the inner base of the maxillary ridge to and slightly beyond the maxillary foramen. There apparently is no orbitopalatine foramen. The surface of the palatines on the palate is 31.0 transversely and 29.0 anteroposteriorly. The length was measured from the posterior edge of the transverse palatine ridge along the midline. There are three anterior palatine foramina near the transverse palatine ridge on the right side, and only one on the left. The ridge is about 4.0 high and slightly convex anteriorly. There is a small foramen in each palatine, one 4.8 and the other 6.2 lateral to the midline, but there are no palatine fenestrations.

The choanal aperture, which is opposite $M^4$, is 23.5 wide and 13.2 deep. The anterior walls of the interpterygoid fossa formed by the palatine laminae come together in the roof of the fossa at the midline, overlapping part of the basisphenoid and obscuring the basispheno-presphenoid suture.

The hamular process of the pterygoid is broken off and the pterygopalatine suture is mostly obscured by fusion and cracks in the bones. Nevertheless pterygoid laminae appear to form the posterior walls of the interpterygoid fossa, then ascend to form a thin sharp crest that runs back to, and apparently past, the large entocarotid foramen and groove back to the median lacerate-ovale foramen. The mesial wall of the pterygoid cavity is formed by the pterygoid.

Anterodorsally the *alisphenoid* is in a 27.0 sutural contact with the frontal. The alisphenosquamosal suture runs posteroventrally to the groove emerging from the median lacerate-ovale foramen. The alisphenoid apparently roofs most of the pterygoid cavity, and the pterygoidal wing of the alisphenoid extends down to the alisphenopterygoidal suture in the pterygoid cavity. There is an opening for a small transverse canal in the pterygoid cavity. The ridge forming the posterior border of the infratemporal fossa is prominent ventrally but fades out posterodorsally where it reaches the alisphenosquamosal suture. The pterygoideus ridge, with prominent processes, passes from the anterodorsal surface to the alisphenoid across the suture onto the squamosal.

Not all the sutures of the orbitosphenoid are distinct. It does seem apparent, however that the anterior lacerate, optic, and rotundum foramina are confluent. There appears to be no alisphenoid canal.

The *lacrimal* is prominent and extends deep into the orbital fossa to a point 6.0 above the anterior end of the sphenopalatine foramen. Its greatest expansion onto the facial surface is about 6.0. At its upper end is an elongate lacrimal tuberosity which is diagonally directed anteroventrally. The lacrimal foramen lies within the edge of the orbit; it is 5.0 long and 2.8 wide, and is oriented in the same direction as the tuberosity.

Another conspicuous feature in the cranium is the nearly transverse surface of the zygomatic arch in front of and mostly below the orbit. This surface is composed mostly of the *jugal* but is also formed in part by the maxilla. This base of the arch marks a sharp demarcation of the rostrum from the remainder of the cranium. The lateral and most of the anterior parts of the thick orbital wall, about 5.0 thick, are formed by the jugal. The jugal reaches its greatest vertical depth of 32.0 on the lateral surface of the arch between the orbit and the masseteric process. Posteriorly it curves gently downward and becomes shallower as the squamosal part of the zygomatic arch becomes deeper. The jugal extends back to form a limited part of the anterior surface of the glenoid fossa. The insertion area of the masseter lateralis profundus reaches its greatest depth of 17.8 above the masseteric tuberosity. It is arched in outline, is consistently 5.8 below the squamosojugal suture, and fades out near the posterior end of the bone.

The *parietals* are rather wide anteriorly, and although the parietosquamosal suture is somewhat irregular the bones become narrower posteriorly. The midline measurement, from the anterior end of the interparietal to the frontal, is 74.2. From the midline anteriorly, the frontoparietal suture runs anterolaterally then curves back over the side of the cranium to reach the squamosal 33.7 below the sagittal crest. At 12.8 a contact of the frontal and squamosal blocks the parietal from reaching the alisphenoid. The sutures in this area on the right side are mostly obscured

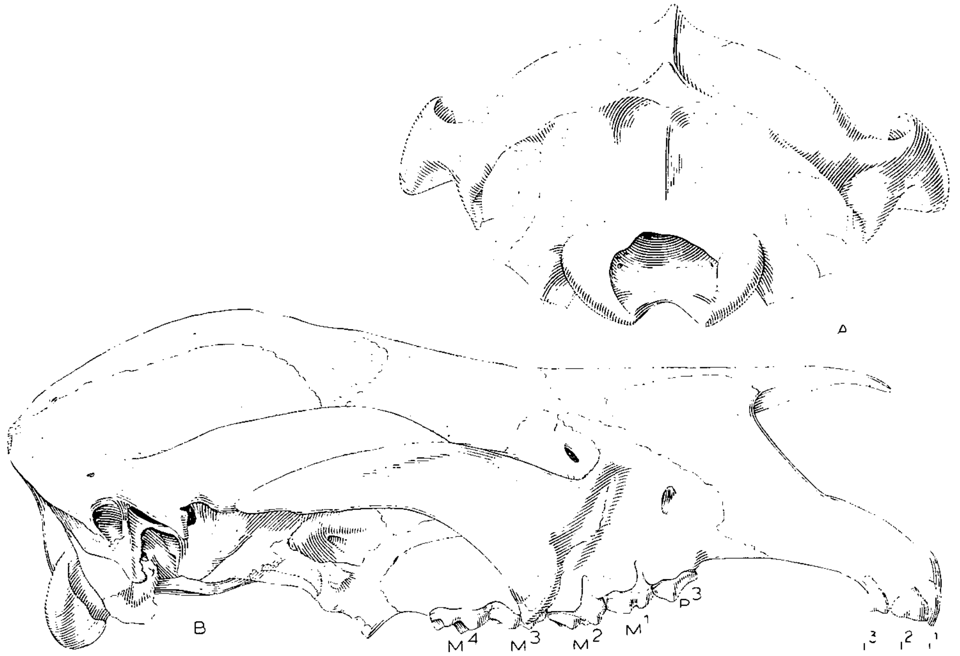


**Fig. 2.**—*Ngapakaldia tedfordi* **gen. nov. et sp. nov. Part of holotype, SAM P13851. Cranium, one-half natural size.** *A*, **posterior view.** *B*, **lateral view, with broken edges of cheekteeth restored from UCMP 57254.**

by fractures. The brain case is 57.0 wide between these lowest points of the squamosal anteriorly. From that point the parietosquamosal suture runs 25.8 posterodorsally toward the upper edge of the brain case, then its course is nearly parallel to the sagittal crest for a distance of 23.3, where it curves in toward the crest, then laterally, to reach the lambdoidal crest 9.5 from the midline.

The *interparietal* is wedge-shaped. Its width along the lambdoidal crest is 20.0, and it terminates about 17.0 anteriorly, where it is pinched in between the parietals.

The lambdoidal crest overhangs the supraoccipital to the extent that in direct dorsoventral view only the posterior ends of the condyles can be seen. From the apex of the anterior curvature at the midline the crest curves posterolaterally to the outer end of the interparietal, then slightly anteriorly and ventrally down to the tip of the mastoid process. Thus the occiput is broadly rounded.

The sutures between the *mastoid* and adjacent bones cannot be traced accurately. Nevertheless there is evidence of its exposure on the posterior wall of the auditory region below and mostly mesial to the petrosal. The squamosomastoid suture appears to cross the lambdoidal crest 6.5 above the tip of the mastoid process. The process is only slightly demarcated on the lambdoidal crest, is separated from the paroccipital process by a shallow depression of the crest, and is preserved only on the right side. On the occiput a thin strip of the mastoid extends to a distance of 35.0 dorsally and somewhat medially from the tip of the mastoid process. There appears to be no mastoid foramen.

The lambdoidal crest is about 36.0 above the edge of the foramen magnum. The *supraoccipitals* and *exoccipitals* do not appear to be separated by a suture. The rectus capitis dorsalis depressions of the supraoccipital are deep on each side of the midline crest below the lambdoidal crest. The depressions fade out ventrally, but the midline crest extends down nearly to the edge of the foramen magnum. The paroccipital processes are broken off. They are separated from the condyle by sulci 9.0 wide. There are two small condyloid foramina in the condyloid sulcus that passes posteromedially from the posterior lacerate foramen.

The length of the *basioccipital* from the edge of the foramen magnum to the basioccipito-basisphenoid suture is 30.8. Its width opposite the posterior ends of the petrosal is 31.5, and at the basioccipito-basisphenoid suture 26.0. Elongate basioccipital sulci 6.0 wide lie on each side of the midline. On the lateral side of each sulcus is a long, flat, 5.5-wide insertion surface for the rectus capitis muscle. The posterior lacerate foramen is at the posteromedian corner of the petrosal. It

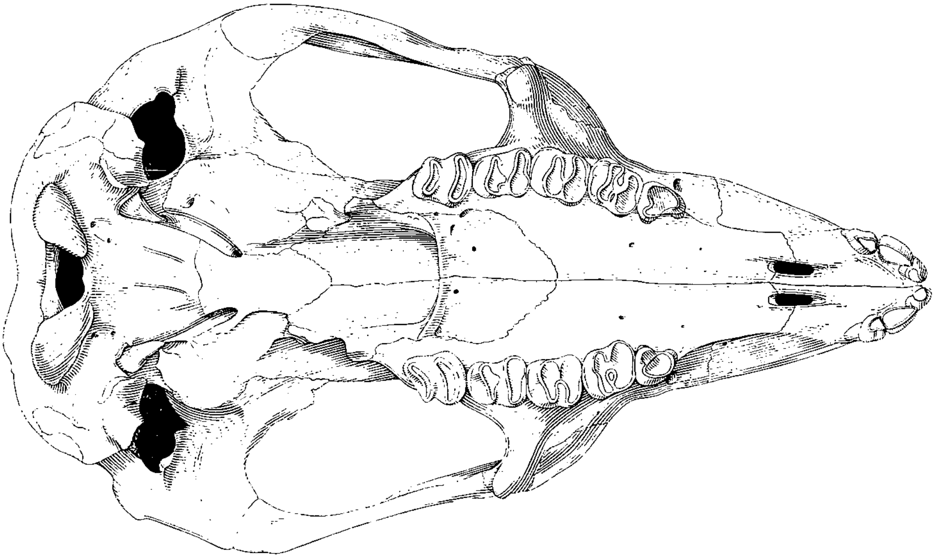


**Fig. 3.**—***Ngapakaldia tedfordi*** **gen. nov. et sp. nov. Part of holotype, SAM P13851. Ventral view of cranium with restorations as indicated in Figs 1 and 2. One-half natural size.**

is narrowly confluent with the posterior carotid foramen, which is on the contact of the petrosal with the basioccipital and 7.9 behind the anterior end of the petrosal. The median lacerate foramen is located at the anterolateral apex of the petrosal. The median lacerate and the ovale foramina are confluent.

Anteriorly the *basisphenoid* is overlapped by laminae of the palatines in the interpterygoid fossa. The extent of its normal exposure is not known because the thin edges of the palatine laminae are partly broken away. In ventral view its smooth surface is only slightly convex transversely.

The *squamosals* are prominent because of their great lateral expansion. They are rounded both dorsoventrally and anteroposteriorly. The zygomatic arch is 39.2 anteroposteriorly across its dorsal basal sulcus. The sulcus, between the zygoma and the lateral surface of the cranium, slopes down anteriorly, where it is about 12.0 wide transversely. It is, however, narrower posteriorly. The zygoma curves gently outward and forward to reach the jugal, which it overlaps in sutural contact for a distance of 62.0; but it does not wedge into the jugal. Its anterior tip is about 13.0 behind the orbit. The upper edge becomes very sharp anteriorly and there is no postorbital process. Its greatest depth is at the anterior edge of the glenoid, where it measures 18.0.

The squamoso-alisphenoid suture extends posteroventrally, from its lowermost contact with the frontal, to the median lacerate-ovale foramen near the anterior end of the petrosal. This arrangement excludes the alisphenoid from the auditory region by a massive squamosal tuberosity; consequently the suture is far anterior to the base of the zygomatic process of the squamosal. The glenoid is flat; it curves down on the massive squamosal tuberosity on the mesial side and its transverse measurement is more than twice the anteroposterior dimension. There is, however, no mesial glenoid process as in the wombats. The lower end of the mesial glenoid surface is above but continuous down onto the large ventral squamosal tuberosity. Between the horizontal glenoid surface and the thin postglenoid process is a long, narrow, transverse, postglenoid sulcus. The tympanic evidently was separated from the glenoid surface by the anteroposterior width of the sulcus. The postglenoid process descends to a sharp point 13·2 below the horizontal glenoid surface. It is widely grooved on the median side and has a less conspicuous groove on the posterior side. There is a wide postglenoid arch between the small postglenoid process and the ventral squamosal tuberosity; consequently there is no evidence of a styliform groove nor a ventral opening of the eustachian canal.

The rather rounded postzygomatic crest (postzygomatic crest, Cope, 1880, p. 453; subsquamosal ridge, Gregory, 1910, p. 224; parietal crest, Stirton, 1963, p. 109) between the lambdoidal crest and the posterior end of the zygoma is 13·5 in length. The postsquamosal foramen (fissure) is 5·0 above the postzygomatic crest and 9·0 anterodorsally from the lambdoidal crest where the latter passes the end of the postzygomatic crest. A small subsquamosal foramen is on the upper margin of the postzygomatic crest at the posterior end of the zygomatic process. There is no supratympanic process, anterior epitympanic fossa (supratympanic sulcus; supratympanic fossa), nor postzygomatic foramen as seen in *Macropus*.

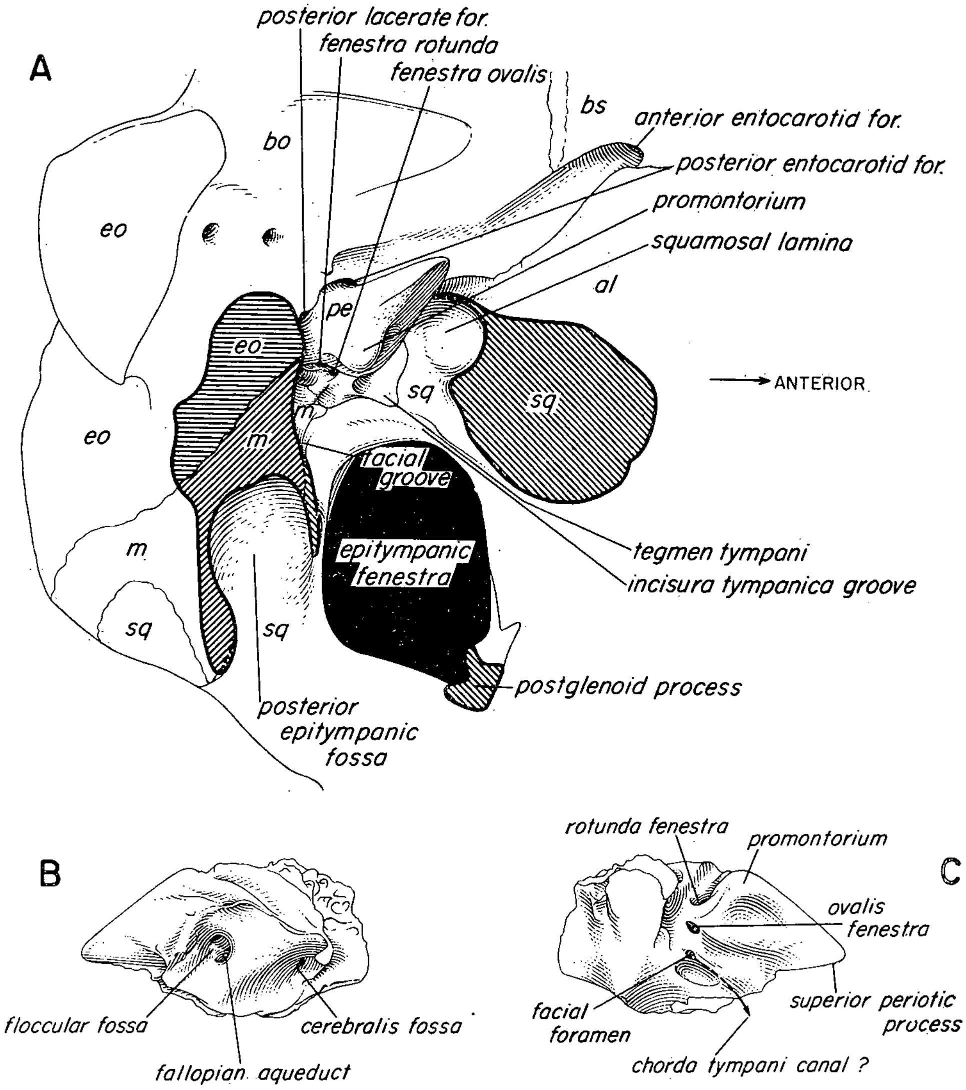


**Fig. 4.**—*Ngapakaldia tedfordi* **gen. nov. et sp. nov.** *A*, **ventral view of left half of basicranium of holotype, SAM P13851.** *B*, **medial view, and** *C*, **lateral view, of right petrosal of UCMP 57254. One and a half times natural size.**

*Auditory region.* Off the posteromedian corner of the rather delicate and tenuous postglenoid process, in the area of the superficies meatus of the squamosal, is a large nearly round epitympanic fenestra in *Ngapakaldia*, which opens into an enormous dorsal epitympanic sinus. The sinus ramifies out into numerous accessory pockets under the squamosal. Mesially it is limited by the closely appressed vertical wall of the squamosal and parietal at their sutural contact within the cranium at the edge of the braincase; anteriorly it extends into the posterior part of the zygoma, and ventrally into the large ventral tuberosity of the squamosal. Actually the epitympanic sinus in *Ngapakaldia* might be conveniently divided in anterior, posterior, dorsal, and ventral parts. The function of this great sinus and others like it in mammals is not certainly known. Its size accounts for the great lateral expansion of the squamosal as viewed from above, and the enlarged squamosal tuberosity below.

The epitympanic fenestra on the left side measures 18·8 transversely, and 14·8 anteroposteriorly; but the opening on the right side is slightly larger. The lateral, posterior, and median edges are smoothly rounded. The fenestra, evidently, was covered ventrally by the tympanic, which was not fused to the surrounding bones and consequently has been lost. The loss of the tympanic was probably facilitated by the 17·8 width of the superficies meatus area of the squamosal between the postglenoid process and the paroccipital wing of the squamosal, the anterior base of the paroccipital, and the mastoid process. Possibly the course of the dorsal cerebral vein was along the groove on the mesial surface of the postglenoid process and passed into the anterior part of the fenestra.

Just behind the epitympanic fenestra, and separated from it dorsally by a 2·4 ridge, is the posterior epitympanic fossa, which occurs as a 17·0 deep blind pocket in the squamosal. It has been called 'the hind part of the epitympanic sinus' by Van der Klaauw (1931, p. 82). This structure also occurs in the wombats, phascolarctids, dasyurids and peramelids, and is partly formed in some of the potoroids and macropodids. The posterior epitympanic fossa in *Ngapakaldia* penetrates mesially and posteriorly under the lambdoidal crest where its walls are formed by the paroccipital wing of the squamosal and the mastoid. Laterally it opens under the postzygomatic crest. The anteroposterior dimension of the fossa is about 12·0 and transversely 19·0. The dorsal epitympanic sinus, and the posterior epitympanic fossa probably were confluent above the tympanic and communicated with the epitympanic recess through a rather wide supratympanic foramen (fissure).

The tympanic cavity of the middle ear is smaller than the posterior epitympanic fossa. It is widely open ventrally but partly underhung anteriorly by a posteromesial extension of the ventral squamosal tuberosity. Most of the roof of the anterior part of the cavity is formed by the squamosal, which has a thin lamina extending down on to part of the dorsolateral surface of the petrosal. Posteriorly a triangular tegmen tympani of the petrosal is in the roof of the cavity. Laterally the epitympanic recess is bounded by an anteroposterior ridge forming the mesial end of the superficies meatus of the squamosal. Posterolaterally the small incisura tympanica cavity is on the squamoso-tegmen tympani suture. That cavity is about 2·5 wide and its roof is composed of the squamosal and the tegmen tympani of the petrosal. It opens by a narrow groove anteriorly into the lateral edge of the expanded anterior part of the tympanic cavity. Posteriorly it is bounded by the mastoid and evidently in part ventrally by the crista tympanica. The wide arch between the ventral squamosal tuberosity anteriorly and the squamosal and mastoid posteriorly measures 11·8 and is 7 mm below the mesial ridge of the superficies meatus. This as well as the wide lateral part of the superficies meatus area of the squamosal indicates that the tympanic was relatively large in *Ngapakaldia*.

The epitympanic recess, or attic, not clearly recognizable in the posterodorsal surface of the tympanic cavity, in which the ossicles occur, is small and mostly below an incisura tympanic groove. Transversely it was not more than 4·0, and probably less. The ossicles, of course, are missing. The length of the crista tympanica, or mesial projection of the external auditory tube into the cavity of the middle ear, is not known. Any extension would reduce the size of the epitympanic recess and perhaps indicate small ossicles.

The petrosus part of the periotic is well exposed on its ventral and lateral sides in the holotype cranium. Study of the bone, however, is greatly facilitated by the right and left petrosals of UCMP 57254, which show all views of the bone. Dorsolaterally the petrosal is in squamous sutural contact with a lamina of the squamosal in the tympanic cavity; mesially it is closely appressed to the basisphenoid; and posteriorly it is coalesced with the mastoid, and in contact with the exoccipital.

Ventrally the sharply pointed bladelike superior periotic process projects anteriorly and slightly mesially to the posterior end of the entocarotid carotid groove. The tip lies at the posteromesial border of the median lacerate foramen and laterally is separated from the posterior extension of the pterygoid and the squamosal by a deep, 3·0 wide fissure. The rather elongate, sharp, ventral edge extends back to the promontorium (housing the first coil of the cochlea), which is expanded laterally below the ovalis fenestra. The ventral edge and the promontorium are somewhat variable in width and shape in the two specimens SAM P13851 and UCMP 57254.

In UCMP 60981, referred (below, p. 31) to the new genus *Pitikantia*, the ventral surface expands widely to the mesial side below the internal auditory meatus; it is therefore more bulbous at the posterior end than in *Ngapakaldia*.

The lateral surface of the petrosal in *Ngapakaldia* is concave anterior to the promontorium and above the ventral border. The promontorium is somewhat bulbous just anterodorsal to the ovalis fenestra, then becomes constricted ventrally, and finally again becomes somewhat expanded at the posterior end of the ventral crest in the holotype SAM P13851 and in UCMP 57254.

As stated in the description of the tympanic cavity, a triangular tegmen tympani of the petrosal roofs the posterior part of the tympanic cavity. The tegmen tympani forms most of the mesial crest of the incisura groove. It is also involved mesially in the posterior extension of the anterior part of the tympanic cavity. It is above the ossicles, and posteriorly it coalesces with the mastoid.

The tiny facial foramen, where the Fallopian aqueduct opens into the middle ear, is 2·0 anterodorsal to the ovalis fenestra in *Ngapakaldia*. After emerging from the aqueduct into the tympanic cavity, the facial nerve is probably directed posteriorly, but its course across the middle ear cannot be traced accurately in our specimens; however, there is a wide groove that passes ventrally on the anterior face of the mastoid and exoccipital in the position for the stylomastoid foramen. The ovalis fenestra is about 0·7 in diameter. Only the edge of the rotunda fenestra can be seen in direct lateral view; it is exposed on the posterior surface and in a more ventral position than the ovalis fenestra. Furthermore, the rotunda fenestra is at the contact of the petrosal with the exoccipital.

Apparently the main branch of the internal carotid artery passed anteriorly from the area of the posterior lacerate foramen, giving off a branch that passed through the posterior entocarotid foramen, in a rather wide groove at the contact of the petrosal and basioccipital. Anterior to the petrosal the groove is even wider, 4·0, where it curves anteromesially to enter the basisphenoid through the anterior entocarotid foramen.

Confluent with the facial foramen, on the lateral surface of the petrosal, is the opening of a tiny canal under the lateral surface of the petrosal. Its course can be traced directly anteriorly by an elevation of the petrosal surface. This may be the course of the chorda tympani branch of the facial nerve.

On the mesial side the large internal auditory meatus (floccular fossa) is about 2·0 horizontally and 3·0 vertically and the fundus is about 2·0 deep. In the dorsal part of its fundus is the tiny mesial opening of the Fallopian aqueduct. A small ventral opening in the fundus connects with the cochleae. There seem to be no other openings in the fundus; if they are present they are very small and obscured with matrix. The meatus is bordered ventrally and posteriorly by rounded overhanging lips of the mesial prominences. Anterodorsally the lip is almost totally reduced. There is a shallow depression above the dorsal prominence. Behind the posterior prominence is a large cerebralis fossa that is separated from the exoccipital by a crescentic crest of the petrosal.

The dorsal crest of the superior periotic process is 6·8 long and very sharp. Mesial to the posterior end of the crest is a narrow crescentic fossa which appears to have a tiny opening in its fundus that may connect with the fundus of the internal auditory meatus, but this is not demonstrable without making thin sections of the petrosal. This fundus might be the subarcuate fossa, but if so it is extremely small; otherwise there is no evidence of a subarcuate fossa.

*Measurements of Cranium* (unless otherwise indicated taken from holotype)

| | |
|---|---|
| Length from condyles to anterior edge of I$^1$ (composite from SAM P1385 and UCMP 57256, 57271) | 234·0 |
| Length of rostrum from lacrimal foramen to anterior edge of I$^1$ (composite from SAM P1385 and UCMP 57256, 57271) | 93·0*a* |
| Length from lacrimal foramen to lambdoidal crest | 141·4 |
| Length from frontoparietal suture along midline to lambdoidal crest | 88·7 |
| Length of nasals (composite of SAM P1385 and UCMP 57254) | 82·2*a* |
| Length of diastema I$^3$ to P$^3$ (composite from SAM P1385 and UCMP 57256, 57271) | 47·7*a* |
| Width of zygomatic arches 20·0 anterior to end of jugals | 137·1 |
| Width between upper edges of infraorbital foramina | 54·7 |
| Width between masseteric processes of arches | 116·2 |
| Greatest width of occiput | 92·0 |
| Narrowest measurement between interorbital areas across frontoparietal suture | 48·7 |
| Width between lacrimal tuberosities | 67·0 |
| Width across condyles dorsally | 51·0 |
| Width of palate between inner edges of M$^3$ | 42·0 |
| Width of palate between posterior lingual roots of P$^3$ | 31·0 |

*a* Approximate.

| | |
|---|---|
| Width of palate 11·0 anterior to $P^3$ | 27·3 |
| Width of palate between third incisors (UCMP 57271) | 16·3 |
| Width of choanal apertures | 27·5 |
| Width of narial apertures | 42·0 |
| Depth of narial apertures | 28·3 |
| Height of cranium above metacone of $M^2$ | 65·0 |
| Height of cranium above anterior edge of glenoid fossa | 92·0 |
| Height of rostrum 11·0 anterior to $P^3$ | 47·5 |

*Upper teeth.* The outer outline of the upper *incisor* series from $I^1$ to $I^3$ is convex. Wear on the occlusal surface of $I^2$ and $I^3$ is horizontal, whereas on $I^1$ it is on the posterior surface. Consequently the tip of $I^1$ extends below the occlusal surfaces of the other incisors. The crown of $I^2$ is nearly vertical, whereas $I^3$ slants somewhat anteriorly. All of the roots are open at the base but the openings are much smaller in $I^2$ and $I^3$ than in $I^1$.

$I^1$ is the smallest in its anteroposterior and transverse dimensions, but the length of the enamel surface in the three specimens in which it can be measured ranges between 16·3 (approximately) and 13·2. This is about twice that of $I^2$, and in $I^3$ it is even shorter. In cross-section the crown of $I^1$ is ovate. The crown is strongly curved. The root extends back into the premaxilla along the midline of the narial passage to a point opposite the base of the ascending lateral border of the narial aperture. This is well exemplified in UCMP 57271. In UCMP 57254 the end of the root is 14·5 anterior to that position.

The crown of $I^2$ is larger than $I^3$. In the occlusal view it is nearly triangular with the base of the triangle at the posterior end; however, the posteromesial corner is oblique. The labial surface is convex dorsoventrally and less so anteroposteriorly. There is a slight dorsoventral groove in the middle of the labial surface. Anteriorly $I^2$ appresses against the posterolabial side of $I^1$. The root of $I^2$ is anchored back under the lateral premaxillary border of the narial passage; it is not as strongly curved and much shorter than the root of $I^1$.

The coronal dimensions of $I^3$ are smaller than in $I^2$ but larger than in $I^1$. The occlusal outline is also triangular, but in contrast to $I^2$ the base of the triangle is at the anterior end. The labial surface, although smaller, is much like that in $I^2$. The dorsoventral groove, however, is more pronounced. The root is nearly straight and terminates near but just above the end of the root of $I^2$; its length, which is about 12, is less than in $I^2$.

A small alveolus, evidently for a vestigial *canine*, occurs on the maxillo-premaxillary suture at the edge of the palate. The alveolus curves upward and backward into the maxilla. There is evidence of it in all the specimens in which that area is preserved. Its position in the diastema, however, is variable. In the holotype that area is preserved only on the right side. In UCMP 57256 it is 17·0 from $P^3$ and 23·0 from $I^3$ on both sides; in UCMP 57271, 18·3 from $I^3$ on the right side.

$P^3$ has a high parametacone and a much lower protocone, and there is one anterior and one posterior root. Unfortunately these teeth are heavily worn in the holotype, but their occlusal outline and some indication of the cusps are preserved. The protocone is demarcated by commissures labially. In unworn and slightly worn teeth like UCMP 57271 sharp crests descend from the anterior and posterior ends of the parametacone and the anterior crest is much the longer. It measures 7·9. The posterior crest declines steeply from the cusp to the posterior cingulum. It is 4·3 long. There is only a slight depression on the posterior part of the labial surface. There is no indication in *Ngapakaldia* of an inception of the five-cusped pattern seen in *Zygomaturus* and some of the other genera.

The upper molar series together with $P^3$ form a convex labial outline and the lingual borders are slightly concave. $M^1$ is the smallest, and $M^2$ is smaller than $M^3$. In three specimens, $M^4$ is longer than $M^3$, and in two, $M^3$ is longer than $M^4$. Comparable measurements of the protoloph and metaloph are also variable. In some specimens the protoloph is wider, but in others the greatest width is across the metaloph. In $M^4$, however, the metaloph is much narrower than the protoloph. When the molars are in their normal position but with the cranium turned over (palate up) the paracone and metacone are higher than the protocone and hypocone because the teeth are tilted toward the palate. Actually, however, there is little if any difference in the height of the lophs and cusps on $M^2$ and $M^3$, but on $M^1$ the metaloph is higher than the protoloph and on $M^4$ the protoloph is higher than the metaloph. There are two roots in front and one behind.

The molars are sharply bilophodont with no indication of commissures on or near the anteroposterior midline on the anterior or posterior surfaces of the lophs. The lophs are convex anteriorly. There is no midlink as in *Palorchestes.* The transverse median valley is more sharply V-shaped on $M^1$ and $M^2$ than on $M^3$ and $M^4$. The labial mouth of the valley is narrow, because a rather sharp postparaconal crest is continuous from base to crest of the posterior surface of the protoloph. On the lingual end of the loph a postprotoconal ridge is rather rounded but does not extend high into the valley. The intervening part of the posterior surface of the protoloph is widely depressed anteriorly. The prominence of the postparaconal crest and of the postprotoconal ridge decreases from $M^1$ to $M^4$. On the other hand the depression between these structures becomes wider and more anteriorly directed from $M^1$ to $M^4$. A slight cusp is developed at the posterolingual base of the protocone on $M^1$ and $M^2$ in some specimens, but appears to be missing on $M^3$ and $M^4$. A low cingulum extends across the anterior end of each molar. There are small parastyles on $M^1$ and $M^2$, but on $M^3$ and $M^4$ they are only slightly indicated. There is no lingual or labial cingulum and no mesostyle. The posterior cingulum, starting from the posterolingual base of the hypocone, curves around the posterior end of the tooth to terminate about half way down the posterior surface of the metacone. A wide posthypoconal ridge does not extend up to the cingulum. The depression on the posterior surface of the metaloph is wider than the one on the protoloph except on $M^4$ and in some specimens on $M^3$. The enamel surface in UCMP 69817 is finely crenulate and apparently in others it is smooth.

*Mandible.* Superficially the mandible is more like that in the kangaroos, and less like that in the wombats or the koala. The symphysial region, however, is more upturned and less elongate than in the kangaroos. The U-shaped symphysial sulcus is 4·0 deep about 18·0 behind the incisor alveolus in UCMP 57254, and the diastemal crests are 14·0 apart nearer to the incisors. The length of the symphysis varies from

58·9 to 46·5 in the four specimens in which it was observed; its greatest depth is 15·0 in UCMP 57256, and it is not fused. The ventral surface is convex, not grooved along the sutural line, and the surface of the bone is smooth. The subalveolaris fossa, on each side of the short spina mentalis, is 3·0 in diameter; it is about 2·0 deep in UCMP 57256. There is no transverse torus. The diastemal crests are rather sharp except directly in front of $P_3$. The mental foramen is round and 7·5 anterior to $P_3$ and 5·5 below the diastemal crest in UCMP 57256.

The ventral outline of the ramus is convex between the posterior end of the symphysis and the anterior end of the angular ridge. There is no digastric process nor sulcus. The digastric fossa is short, fades out below $M^4$, and is confluent with the pterygoid fossa posteriorly. The posterior part of the angular ridge medial to that part of the pterygoid fossa and the angle are missing, therefore the total mesial extension is not known. The depth of the ramus is included in the table of measurements. The pterygoid fossa is deep; its greatest width is about 15·0, and its length approximately 32·0. It does not extend under the coronoid nor masseteric fossa. The mandibular foramen is on its upper border, about 24·0 directly back of $M_4$, on the same level as the cheekteeth.

The masseteric fossa is moderately deep, but instead of forming a pocket anteroventrally it becomes shallow and passes out onto the lateral surface of the ramus where it is confluent with the digastric fossa as in the koala. Within the masseteric fossa are two tiny masseteric foramina that open through to the inferior dental

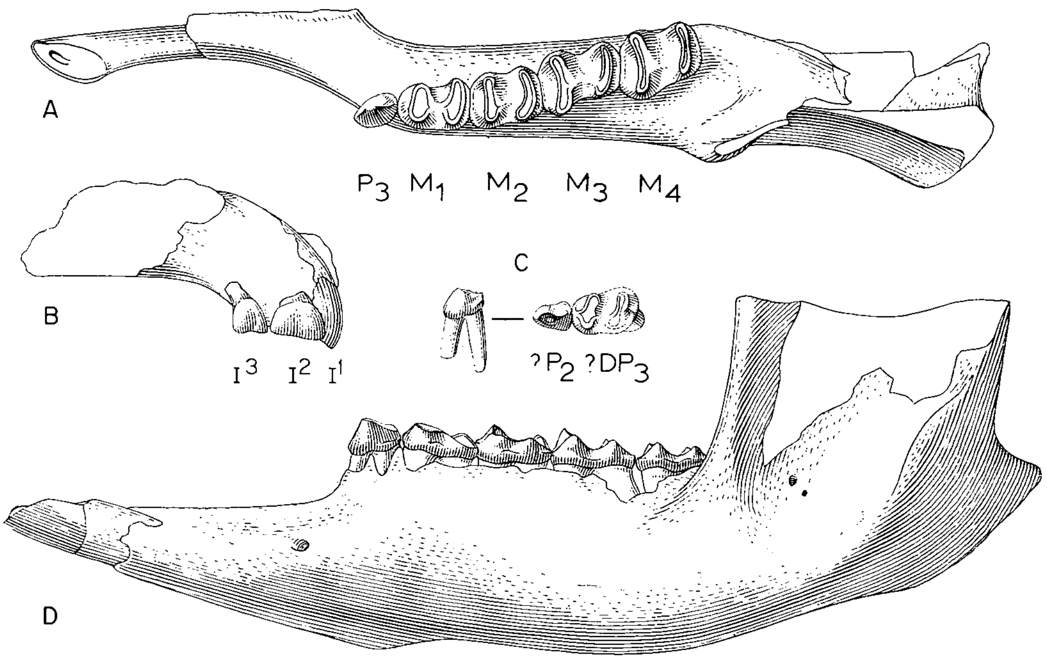


**Fig. 5.—*Ngapakaldia tedfordi* gen. nov. et sp. nov. Three-fourths natural size. *A*, UCMP 57254, mandible with occlusal view of teeth ; $P_3$ unworn, taken from UCMP 57271 ; $M_1$ taken from UCMP 57256 ; labial ends of anterior moieties on $M_2$, $M_3$ and $M_4$ restored. *B*, UCMP 57271, part of premaxilla, lateral view. *C*, UCMP 69821, $?P_2$ and $DP_3$, occlusal view, $DP_3$ partly restored ; labial view of $?P_2$. *D*, UCMP 57256, lateral view of mandible, no restoration.**

canal about 16·0 anterior to the mandibular foramen. As in other diprotodontids there is a posterior masseteric eminence, but this does not extend over the edge of the masseteric fossa. The postalveolar shelf descends slightly posteriorly from the alveolus of $M_4$, but is level transversely. Its inner border curves uniformly posterolaterally to the mesial side of the coronoid. Insofar as it is known the anterior crest of the ascending ramus is between 2·5 and 5·0 thick transversely as measured 27·0 above the hypoconid of $M_4$. The width from the alveolar edge of $M_4$ across the lateral sulcus to the anterior edge of the ascending ramus is about 13·4 in UCMP 57254, and in 57256 it is 12·2. Where the occlusal surfaces of $P_3$ to $M_4$ are in a horizontal position the anterior crest of the ascending ramus slopes about 2° to 3° posteriorly. The vertical diameter of the foramen is 5·5 in UCMP 57256, and transversely it is 4·0. The condyle, the mandibular notch and the top of the coronoid are not represented in our material.

*Lower teeth.* The lower incisors are widely lanceolate. Their ventrolateral surfaces are widely convex transversely, and from the base of the enamel curve gently upward anteriorly, where their tips come in contact at the midline. The occlusion surface is from the anterior tip lateroposteriorly to the posterolateral flange. They occlude on the posterior surfaces of the median upper incisors and horizontally across the coronal surfaces of $I^2$ and $I^3$. The roots are rather ovate in cross-section and diminish gradually in size back to the open end. The length of the root in UCMP 57254, an animal with slightly worn cheekteeth, is 33·0, whereas in UCMP 57271, with unworn cheekteeth, the length is 32·5. It seems, therefore, that if additional growth of the tooth takes place because of the open end, it takes place in the root. It should be noted, however, that within the open end the growth of dentine has largely restricted the size of the inervation canal, and thus the tooth differs from hypsodont ever-growing teeth, whose enamel extends back to the open end.

The only specimen possibly representing $P_2$ and $DP_3$ is two teeth, UCMP 69821, that contact on their appression surfaces. They were found with UCMP 57254 and included under the same field number. This has been particularly puzzling because in the mandible of 57254 the cheekteeth anterior to $M_2$ are missing. Furthermore, the edges of the alveoli for the missing molariform teeth have been destroyed. At the posterior end of the diastemal crest there is a small round alveolus 3.0 across. The space between the anterior or edge of that alveolus and anterior cingulum of $M_2$ is 24.1. In UCMP 57276 and 57271 in which $P_3$ and $M_1$ are in place this measurement is 22.5 and 19.2. Therefore in 57254 it is assumed that this space was occupied by a $P_3$ and an $M_1$, although the teeth would have had to be larger than in 57276. The space necessary for the two teeth of 69821, as measured on the teeth, is 17.5; furthermore the divergence of the roots of $P_2$ is not wide enough to fit down into the alveolus of 57254. In addition the $P_2$ of 69821 does not occlude with $P^3$ of 57254, so this does not agree with its being a $P_3$.

$P_2$ is a simple premolariform tooth, not appreciably different from $P_3$ except for its smaller size. The main cuspid is worn through to the dentine on its posterior crest and is slightly forward of centre. There is a steep anterior crest. The trigonid is 0.7 wider than the transverse measurement of the main cuspid. It is horizontally

Table 1: *Ngapakaldia tedfordi*: Measurements of Upper Teeth

| $I^1$ | Length of enamel | Ant. post. length of crown | Transverse width of crown | Length of root below enamel |
|---|---|---|---|---|
| | Lake Ngapakaldi | | | |
| UCMP 60977 | 13·2 | 6·1 | 4·2 | ? |
| ,, 57254 | ? | 6·1 | 4·6 | 24·2 |
| | Lake Pitikanta | | | |
| UCMP 57271 | 14·0*a* | 6·8 | 5·0 | 21·9 |
| $I^2$ | Height of crown | Ant. post. length | Transverse width | |
| | Lake Ngapakaldi | | | |
| UCMP 57256 | ? | 9·9 | 6·0 | Well worn |
| ,, 57257 | ? | 10·3 | 6·2 | Well worn |
| ,, 19814 | ? | 9·5*a* | 6·3 | Well worn |
| ,, 60985 | ? | 12·2*a* | 7·7 | Well worn |
| ,, 60979 | 7·5 | 10·3 | 6·3 | Unworn |
| | Lake Pitikanta | | | |
| UCMP 60982 | 6·9 | 11·2 | 6·2 | Slightly worn |
| ,, 57271 | 7·5 | ? | 6·6 | Slightly worn |
| ,, 57254 | ? | 10·2 | 7·0 | Well worn |
| $I^3$ | Height of crown | Ant. post. length | Transverse width | |
| | Lake Ngapakaldi | | | |
| UCMP 57256 | 5·0 | 6·3 | 5·3 | Well worn |
| | Lake Pitikanta | | | |
| UCMP 57254 | ? | 6·1 | 5·6 | Well worn |
| ,, 57271 | 5·5 | 6·3 | 6·0 | Slightly worn |
| ,, 57267 | 5·7 | 6·2 | 6·0 | Slightly worn |
| ,, 60982 | 5·4 | 6·2 | 5·5 | Moderately worn |
| $P^3$ | Height para-metacone | Length | Width | |
| | Lake Ngapakaldi | | | |
| SAM P13851 | ? | 10·2 | 9·2*a* | Well worn |
| UCMP 57256 | 7·0 | 10·2 | 8·9 | Slightly worn |
| ,, 69815 | 6·6 | 9·2 | 8·4 | Slightly worn |
| | Lake Pitikanta | | | |
| UCMP 57271 | 7·6 | 9·8 | 9·2 | Unworn |
| ,, 57254 | 5·6 | 8·8 | 8·2 | Slightly worn |

Table 1:—*continued*

| | Length | Width ant. m. | Width post. m. | Height of proto-cone | Height of para-cone | Height of hypo-cone | Height of meta-conid | |
|---|---|---|---|---|---|---|---|---|
| M$^1$ | | | Lake Ngapakaldi | | | | | |
| SAM P13851 .... | 13·4 | ? | 11·5 | ? | ? | ? | ? | Well worn |
| UCMP 57256 .... | 13·5 | 11·0 | 10·8 | ? | ? | ? | ? | Well worn |
| „ 69813 .... | 13·0 | 11·1 | 11·7 | 5·8 | 5·5 | 7·1 | 6·1 | Unworn |
| „ 69812 .... | 12·7 | 10·3 | 10·9 | ? | 5·7 | 6·0 | 5·9 | Unworn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 12·3 | 10·0 | 10·7 | ? | ? | ? | ? | Well worn |
| „ 57271 .... | 12·3 | 10·3 | 10·5 | ? | 5·1 | 5·1 | 5·1 | Unworn |
| M$^2$ | | | Lake Ngapakaldi | | | | | |
| SAM P13851 .... | 15·0 | ? | 12·8 | ? | ? | ? | ? | Well worn |
| UCMP 57256 .... | 13·9 | 11·8 | 11·2 | ? | ? | ? | ? | Well worn |
| „ 69813 .... | 14·7 | 12·6 | 12·6 | 6·9 | 5·9 | 7·8 | 6·4 | Unworn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 13·8 | 12·2 | 11·7 | ? | ? | ? | ? | Well worn |
| „ 57271 .... | 14·0*a* | ? | 11·7 | ? | ? | 6·1 | 5·4 | Unworn |
| M$^3$ | | | Lake Ngapakaldi | | | | | |
| SAM P13851 .... | 15·0 | ? | ? | ? | ? | ? | ? | Well worn |
| UCMP 57256 .... | 14·8 | 12·6 | 11·0 | ? | ? | ? | ? | |
| „ 69813 .... | 15·8 | 12·8 | 11·9 | 6·9 | 6·3 | 7·3 | ? | Unworn |
| „ 19815 .... | 14·7 | 12·5 | 11·3 | ? | ? | ? | ? | Moderately worn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 14·8 | 12·4 | 11·5 | ? | ? | ? | ? | Well worn |
| „ 57271 .... | 15·0 | 12·2 | ? | 5·7 | 5·8 | 6·1 | ? | Unworn |
| M$^4$ | | | Lake Ngapakaldi | | | | | |
| SAM P13851 .... | 14·6 | 13·9 | 10·7 | ? | ? | ? | ? | Well worn |
| UCMP 57256 .... | 15·2 | 13·0 | 9·8 | ? | ? | ? | ? | Well worn |
| „ 19815 .... | 15·0 | ? | 9·9 | ? | ? | 4·9 | ? | Slightly worn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 15·2 | 12·9 | 10·8 | ? | ? | ? | ? | Well worn |
| „ 57271 .... | 14·2 | 12·4 | 10·1 | 5·7 | 5·5 | 5·7 | 5·5 | Unworn |
| „ 69811 .... | 13·3 | 12·9 | 11·2 | 6·0 | 5·8 | 5·7 | 6·2 | Unworn |

*a* Approximate.

crested anteroposteriorly and from its posterior end cingulumlike structures descend on each side where they have a tendency to curve anteriorly. At the juncture of the talonid and main cuspid on the labial side the enamel surface is somewhat depressed.

The probable $DP_3$ is well worn and part of the posterior moiety on each side is missing. The anterior end is somewhat pointed, much as in $M_1$, just labial of the midline of the tooth, with the paralophid extending down to the tip. The protolophid is oblique and the metalophid appears to be somewhat so. The posterior end of the tooth is rounded. The tooth is slightly longer than $M_1$; in UCMP 57286 and 57271.

$P_3$ is a rather simple premolariform tooth with a high main cuspid. The talonid is much wider than the transverse measurement across the main cuspid. The basal outline then is somewhat triangular. The talonid is further indicated by a depression of the enamel that runs obliquely from the posterolingual base of the main cuspid up to the posterior crest. The enamel is even less depressed on the posterolabial side. The anterior crest of the main cuspid is uninterrupted and there is no anterobasal cuspid. There are an anterior and a posterior root.

Table 2: *Ngapakaldia tedfordi*: Measurements of Lower Teeth

| $I_1$ | Length of enamel crown | Width at labial talonid | Length of root | Vertical depth of root | |
|---|---|---|---|---|---|
| | | Lake Ngapakaldi | | | |
| UCMP 57256 | ? | 10·4 | 11·3 | ? | Well worn |
| „ 60979 | ? | 12·0 | ? | ? | Unworn |
| | | Lake Pitikanta | | | |
| UCMP 57254 | ? | 10·3 | 33·0 | 9·5 | Well worn |
| „ 57271 | 21·7 | 11·3 | 32·5 | 11·4 | Slightly worn |
| „ 60983 | 19·3 | 11·0 | 29·2 | 10·0 | Slightly worn |
| „ 60982 | 22·8 | 12·0 | ? | 10·6 | Slightly worn |

| | Length | Width of talonid | Height | |
|---|---|---|---|---|
| $P_2$ | | Lake Pitikanta | | |
| UCMP 69821 .... .... | 7·4 | 5·3 | 6·3 | Slightly worn |
| $P_3$ | | Lake Ngapakaldi | | |
| UCMP 57256 .... .... | 9·1 | 6·4 | 6·8*a* | Moderately worn |
| | | Lake Pitikanta | | |
| UCMP 57271 .... .... | 8·8 | 6·5 | 8·4 | Unworn |
| „ 57290 .... .... | 8·7 | 6·4 | ? | Moderately worn |

Table 2:—*continued*

| | Length | Width ant. m. | Width post. m. | Height of protoconid | Height of metaconid | Height of hypoconid | Height of entoconid | |
|---|---|---|---|---|---|---|---|---|
| DP$_3$ | | | Lake Pitikanta | | | | | |
| UCMP 69821 .... | 12·4 | 7·6 | ? | ? | ? | ? | ? | Well worn |
| M$_1$ | | | Lake Ngapakaldi | | | | | |
| UCMP 57256 .... | 12·7 | 8·1 | 9·7 | ? | ? | ? | ? | Well worn |
| ,, 57286 .... | 12·0 | 7·8 | 8·8 | 5·7 | 6·9 | 5·3 | 5·8 | |
| | | | Lake Pitikanta | | | | | |
| UCMP 57271 .... | 11·2 | 7·7 | 8·3 | 6·9 | 4·9 | 5·7 | 4·8 | Unworn |
| ,, 57290 .... | ? | 8·3 | ? | ? | ? | ? | ? | Well worn |
| M$_2$ | | | Lake Ngapakaldi | | | | | |
| UCMP 57256 .... | 13·3 | ? | 11·2 | ? | ? | ? | ? | Well worn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 12·9 | ? | 10·0 | ? | 5·0 | ? | 5·1 | Slightly worn |
| ,, 57271 .... | 13·7 | 9·5 | 9·3 | 6·2 | 7·3 | 5·7 | 6·4 | Unworn |
| ,, 57290 .... | 14·2 | 10·4 | 10·3 | ? | ? | ? | ? | Well worn |
| M$_3$ | | | Lake Ngapakaldi | | | | | |
| UCMP 57256 .... | 14·3 | 11·1 | 11·2 | ? | ? | ? | ? | Well worn |
| ,, 57286 .... | 14·6 | ? | 11·6 | 7·7 | ? | 6·8 | 6·2 | Unworn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 14·3 | 11·2 | 10·6 | ? | 5·4 | ? | 5·6 | Slightly worn |
| ,, 57271 .... | 13·9 | 10·7 | 10·2 | 7·2 | 6·3 | 6·2 | 5·8 | Unworn |
| ,, 57290 .... | 15·0 | 11·5 | 11·0 | ? | ? | ? | ? | Well worn |
| ,, 60982 .... | 13·9 | 11·4 | 10·8 | 7·4 | 6·9 | 6·8 | 6·1 | Unworn |
| | | | Lake Kanunka | | | | | |
| UCMP 57283 .... | 12·8 | ? | 10·4 | ? | 7·0 | 5·7 | 6·3 | Unworn |
| M$_4$ | | | Lake Ngapakaldi | | | | | |
| UCMP 57256 .... | 14·4 | 10·8 | 10·3 | ? | ? | ? | ? | Well worn |
| | | | Lake Pitikanta | | | | | |
| UCMP 57254 .... | 14·6 | ? | 11·3 | ? | 5·9 | ? | 5·1 | Slightly worn |
| ,, 57271 .... | 14·7 | 11·0 | 9·6 | 6·4 | 6·9 | 6·3 | 6·2 | Unworn |
| ,, 57290 .... | 14·8 | 11·8 | 10·3 | ? | ? | ? | ? | Well worn |

*a* Approximate.

The *lower molars* together with $P_3$ lie in a straight line. $M_1$ is the smallest and $M_2$ is smaller than $M_3$. In all the specimens measured $M_4$ is longer than $M_3$, but the width of $M_3$ is always greater than in the last molar. As in the upper molars, the lower molars are sharply bilophodont. The crests are gently curved with the posterior surfaces being convex. There is no suggestion of commissures on or near the midline of the tooth separating the lophid into pretrite and post-trite parts.

The protoconid, because of its more bulbous expansion anteriorly, is slightly larger than the metaconid. Except for the bulbous expansion of the protoconid the tribosphenic pattern of the trigonid pattern is missing. A cingulum extends across the anterior base of the tooth. It ascends the metaconid in some teeth but bypasses the base of the protoconid. There is no stylar cuspid on the cingulum. The transverse median valley is widely U-shaped with no suggestion of a metalophid, but the floor of the valley is slightly elevated a little more than a third of the distance in from the labial side. The metaconid and entoconid are slightly more widely separated than the protoconid and hypoconid. There is a posterior cingulum but no evidence of a hypoconulid. A slight labial cingulum is present which crosses the mouth of the transverse median valley, and in some specimens this can be traced forward to a connexion with the anterior cingulum.

$M_1$ differs from the other molars in its relatively and actually shorter oblique protolophid. Consequently the anterior end of the tooth is angulate toward the anterolabial corner.

### NGAPAKALDIA BONYTHONI* sp.nov.

*Holotype.* Badly weathered specimen. Most of cranium with rostrum and upper incisors of both sides, left cheekteeth $P^3$ to $P^4$ all fractured and partly missing, right $P_3$; both lower incisors and symphysis crushed and fractured, left mandibular ramus with $P_3$ to $M_4$ fractured; parts of humerus; right and left radius and ulna; left manus, most of right manus; left femur; parts of tibia and fibula; left pes nearly complete; part of right pes; parts of pelvis, some caudal vertebrae. SAM P13863.

The holotype evidently at one time was a nearly complete skeleton, but it was discovered in a deep zone of weathering of the grey-green claystone, where the expansion and contraction of the clay as well as the growth of gypsum crystals have almost destroyed the specimen. Most of the skeleton had disintegrated and the part remaining was so severely fractured that it was extremely difficult to collect and prepare. Apart from a few fragments of another specimen questionably referred, this is our only specimen of this important species from the Ngapakaldi fauna.

*Referred Specimen.* This is questionably referred. Lake Pitikanta. Well worn left $I^1$; fragment of left $I_1$; posterior end of $M^3$; foot bones. Loc. V5774-UCMP 57263.

*Specific Diagnosis.* Length of cranium from occipital condyles to anterior edge of $I^3$ estimated at 287.0; sagittal crest 5.0 wide; depth of rostrum anterior to $P^3$ about 60.0; length of rostrum measured anteriorly from orbit about 130.0; diastema between $I^3$ and $P^3$ about 60.5; depth of zygomatic arch 30.0.

---

* Named for C. Warren Bonython, member of Board of Directors, South Australian Museum.

Anteroposterior length of $I^2$ 13.0, height of crown about 7.4. $P^3$ wider than long, width 11.6, anteroposterior length 11.2. Length of $M^3$ 19.5, width of anterior moiety, approximately 17.2; width of posterior moiety approximately 16.2.

Width of lower incisor across talonid about 15.2. Diastema between $I_1$ and $P_3$ about 54.5. $P_3$ slightly longer than wide, length 9.8, width 8.8. Length of $M_1$ 15.4, width of anterior moiety 10.8, width of posterior moiety 12.0.

*Type Locality.* Eastern shore, UCMP loc. V5879. In weathered surface of upper part of grey-green claystone of Etadunna Formation; along eastern shore of Lake Ngapakaldi, 1165 feet north and 8° west of Ngapakaldi Quarry V5858, but in same stratigraphic unit, about 3 miles north-east of south-west end of lake and about 4 miles north of Lake Pitikanta, about 22 miles west of Birdsville Track and an equal distance north of Cooper Creek in Tirari Desert east of Lake Eyre, South Australia. Approximate grid coordinate 642488, grid Zone 5, Marree Sheet, 1:506880; AHQ Cartographic Co., 1942.

*Age.* ? Late Oligocene or early Miocene. *Fauna.* Ngapakaldi.

*Description*

*Cranium.* Most of the left side and the back part of the cranium have been destroyed, but the rostrum is represented on both sides. The dorsal surface is preserved back to the orbit and partly beyond on the left side. The right zygomatic arch and most of the palate also remain. All the upper incisors are retained as well as the left cheekteeth from $P^3$ to $M^4$. The cheekteeth however are severely fractured, and the crowns mostly destroyed. The crown of the right $P^4$ is well preserved except for a section missing on the labial surface; fortunately, however, that can be accurately restored from the left $P^3$.

The total length of the cranium from the anterior curvature of the median incisors to the lambdoidal crest is estimated as 287.0. The holotype is preserved to a point just behind the base of the zygomatic process of the squamosal and this length is about 260.0, which is in marked contrast to the approximate total length of 234.0 in *N. tedfordi.* The infraorbital foramen is located above $P^3$ in both species. The squamosal appears not to have been as expanded laterally as in *N. tedfordi,* but the evidence is not conclusive. The sagittal crest is 5.0 wide. Position of the narial notch is much like that in *N. tedfordi.* There is no indication of a depressed dorsal profile of the rostrum. The depth of the rostrum in front of $P^3$ is about 60.0, and its length as measured anteriorly from the orbit is approximately 130.0. Length of the diastema between $I^3$ and $P^3$ is 60.5. The depth of the zygomatic arch is about 30.0. Otherwise the specimen is too incomplete or distorted for reasonable measurements or estimations of other cranial proportions. Nevertheless the characters that can be observed in the teeth, and despite the greater size the proportions of the specimen, seem to justify placing *N. bonythoni* and *N. tedfordi* in the same genus. Except for their greater size the upper incisors are morphologically like those of *N. tedfordi.* The alveolus for a vestigial canine is located 31.2 posterior to $I^3$.

$P^3$ in *N. bonythoni* differs from *N. tedfordi* not only in its larger size and different proportions, but in a greater lingual expansion of the protocone and in a more posterolabial direction of the posterior crest of the parametacone. The posterior

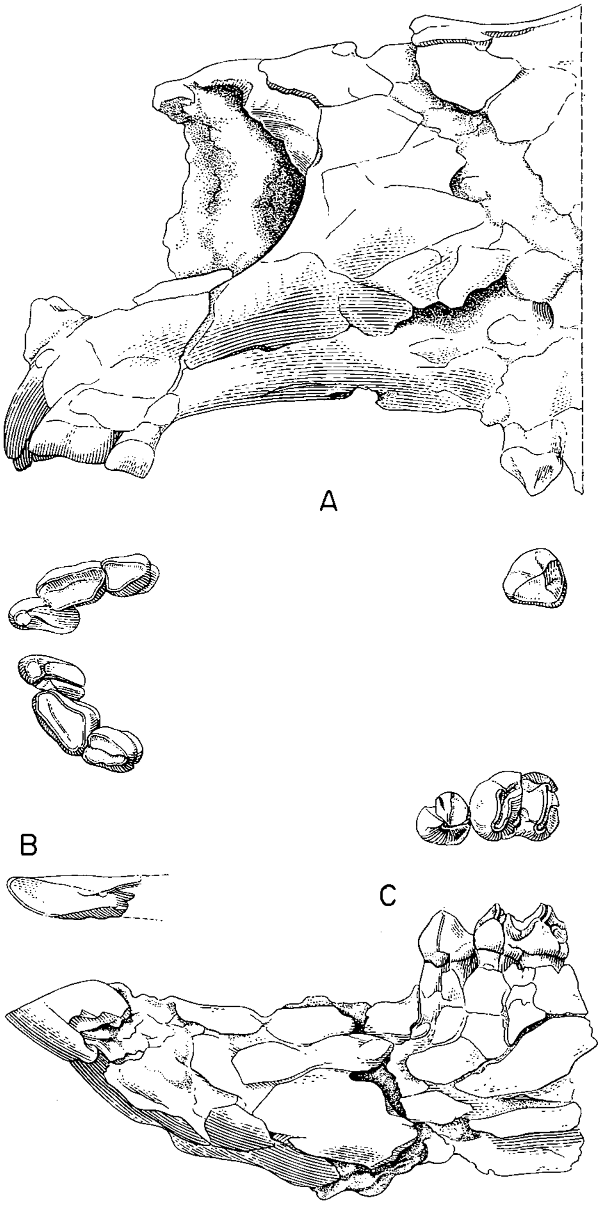


Fig. 6.—*Ngapakaldia bonythoni* sp. nov. Part of holotype, SAM P13863, three-fourths natural size. *A*, lateral view of rostrum, incisors and $P^3$ ; occlusal view of incisor and $P^3$. *B*, occlusal view of lower incisor. *C*, occlusal view of $P_3$ and $M_1$; lateral view of incisor $P_3$ and $M_1$.

crest measures 5.6 whereas the anterior crest is 9.0. As a consequence of the obliquity of the posterior crest there is a relatively wider depression of the posterior surface than in the smaller *N. tedfordi.* The labial surface is more convex than in the smaller species and there is a suggestion of a stylarlike ridge on the labial surface of the parametacone.

The length of the tooth row from $P^3$ to $M^4$ measures 89.0. Unfortunately the crowns of the upper molars are badly damaged, but except for their larger size they do not appear to have differed from *N. tedfordi.*

When the lower incisors were first observed, they were thought to be widely spatulate, but a more careful study has revealed that like *N. tedfordi* they are rather widely lanceolate. Although *N. bonythoni* is much larger, the ventrolateral enamel surface displays no greater convexity than in the smaller species. The roots of both incisors are crushed, and therefore the shape cannot be determined accurately; but the left root has been exposed and even in its dorsoventral measurement, in its crushed condition, at the open end it is about 11.7. The transverse dimension cannot be determined.

The length of the $I_1$ to $P_3$ diastema is about 52.5. In contrast to *N. tedfordi*, $P_3$ is slightly wider than long. The talonid therefore is very wide and the tooth is nearly triangular in outline. The anterior crest of the main cuspid is steeper than the posterior crest, but they are equal in length and are aligned anteroposteriorly. The posterior cingulum shelf is prominent on the lingual side but only slightly developed on the labial side. The rather rounded posterior cingulum terminates at the lingual and posterolabial sides of the main cuspid. The posterior basal outline as viewed from above is V-shaped.

The length of the lower tooth row from $P_3$ to $M_4$ is 84.5. All the lower molars are fractured, but are not as severely damaged as the upper cheekteeth. The lengths given in the measurements are probably correct except for $M_3$, and it is reasonably accurate. Except on $M_1$ the widths of the moieties are estimated from the preserved parts. In $M_1$ the anterior end is relatively and of course actually wider, and not as angulate anterolabially as in *N. tedfordi.* Otherwise, except for their larger size, the molars do not appear different from the small species.

Table 3: *Ngapakaldia bonythoni*, SAM P13863: Measurements of Upper Teeth

| | Length of enamel crown | Ant.-post. length of crown | Transverse width of crown | Length of root below enamel |
|---|---|---|---|---|
| $I^1$ .... .... | 16·3*a* | 7·3 | 5·4 | 31·8*a* |

| | Height of enamel crown | Ant.-post. length of crown | Transverse width of crown | |
|---|---|---|---|---|
| $I^2$ .... .... | 7·2 | 13·0 | 7·6 | Moderately worn |
| $I^3$ .... .... | 6·2 | 8·2 | 6·4 | Moderately worn |
| $P^3$ .... .... | 7·7 | 11·2 | 11·6 | Moderately worn |

Estimates indicated by *a*

Table 3:—*continued*

| | Length | Width ant. moiety | Width post. moiety | |
|---|---|---|---|---|
| M$^1$ .... .... | 15·5*a* | ? | 14·3*a* | Distorted and partly missing |
| M$^2$ .... .... | 17·4*a* | 15·0*a* | 14·8*a* | Partly missing |
| M$^3$ .... .... | 19·5 | 17·0*a* | 16·2*a* | Partly missing |
| M$^4$ .... .... | 21·0*a* | ? | ? | Mostly missing |

Table 4: *Ngapakaldia bonythoni*, SAM P13863: Measurements of Lower Teeth

| | Length of enamel crown | Width at labial talonid | Length of root | Vertical depth of root | |
|---|---|---|---|---|---|
| I$_1$ | 26·3*a* | 16·0*a* | 40·0*a* | ? | Moderately worn |

| | Length | Width of talonid | Height | |
|---|---|---|---|---|
| P$_3$ .... .... | 9·8 | 8·8 | 8·9 | Unworn |

| | Length | Width ant. m. | Width post. m. | Height pr$^d$ | Height hy$^d$ | Height en$^d$ | |
|---|---|---|---|---|---|---|---|
| M$_1$ .... | 14·6 | 11·4*a* | 12·2 | 6·1 | 5·6 | 5·8 | Slightly worn |
| M$_2$ .... | 18·1 | 13·8*a* | 14·5*a* | ? | 6·7*a* | ? | Slightly worn |
| M$_3$ .... | 19·2*a* | ? | ? | ? | 8·6*a* | ? | Slightly worn |
| M$_4$ .... | 21·0*a* | 17·0*a* | 15·0*a* | ? | 7·9 | ? | Slightly worn |

Estimates indicated by *a*.

## Genus PITIKANTIA nov.

*Genotypic Species: Pitikantia dailyi* sp.nov.

This first identifiable diprotodontid from the Ngapakaldi fauna was discovered by Dr Brian Daily at Lake Pitikanta on the 1957 expedition. Diprotodontids are common in the fauna; therefore it was totally unexpected that after considerable collecting this specimen would be the only clearly identifiable representative of a new genus.

*Generic Diagnosis.* Occlusal wear of I$^1$ on same horizontal plane as on I$^2$ and I$^3$. Posterior crest of P$^3$ ascends steeply just behind parametacone then levels off nearly horizontally on back to lowest point of posterior cingulum; small protocone; no parastyle or hypocone.

Symphyseal sulcus not as widely U-shaped as in *Ngapakaldia*; from lateral view outline of diastemal crest concave, sharply crested throughout; symphyseal region with more upward direction than in *Ngapakaldia*; mental foramen 4.3 anterior to P$_3$.

Lower incisor widely spatulate, ventrolateral enamel surface 16.5 from heel across curvature to anterior edge, transverse width at posterior edge of enamel 7.2; root 13.8 deep dorsoventrally and 7.0 narrow transversely, length from heel of crown 28.3. $P_3$ 0.3 wider across talonid than across main cuspid. Metalophid of $M_1$ forming midlink-like structure; $M_2$ and $M_3$ with only slight anterior expansion of protoconid and metaconid, anterior surface of protolophid directed posteriorly but not deeply depressed as in *Ngapakaldia.*

### PITIKANTIA DAILYI* sp.nov.

*Holotype.* Right upper incisors, $I^1$-$I^3$; left $I^1$ and $I^3$; left $P^3$; part of right mandible with incisor, $P_3$, $M_1$, $M^2$, anterior moiety of $M_3$; left $P_3$; six incomplete tarsals; metatarsals I, III, IV and V; six phalanges. SAM P13862.

*Referred Specimens.* Lake Pitikanta. These are questionably referred. Left $I^2$, part of $I^1$, part of right $I_1$, and other fragments; loc. V6150-UCMP 61029. Right and left petrosals; left manus nearly complete; five lumbar vertebrae; left pelvis, epipubic bone; femur, fibula, and pes nearly complete; caudal vertebrae numbers 5 to 25, with haemal arches connecting each pair of caudal vertebrae between 5-6 and 16-17 inclusive. Loc. V6152-UCMP 60981.

*Specific Diagnosis.* See generic diagnosis until other species are described.

*Type Locality.* Discovery Basin, UCMP loc. V5774. Top of grey-green claystone with boxes extending into lower part of upper white calcareous mudstone of Etadunna Formation, on west side of Lake Pitikanta, about ¼ mile south of north end of lake in little blowout basin, at mouth and extending about 40 yards north of mouth of wide wash that runs back to west through escarpment (see Stirton, Tedford, & Miller, 1961, fig. 2). Lake Pitikanta about 22 miles west of Birdsville Track and 19 miles north of Cooper Creek in Tirari Desert east of Lake Eyre, South Australia. Approximate grid coordinate 645481, grid zone 5, Marree Sheet, 1: 506880; Australian Army, H.Q., Cartograph Co., 1942.

*Age.* ?Late Oligocene or early Miocene. *Fauna.* Ngapakaldi.

#### *Description*

*Pitikantia dailyi* was evidently a short rather wide-faced diprotodontid with wide spatulate lower incisors. Its relationship to the later genera is not yet known.

The labial outline of the upper incisor series is convex. Wear on the occlusal surface of $I^1$, $I^2$, and $I^3$ is on the same horizontal plane. Otherwise these teeth are not appreciably different from those in *N. tedfordi.*

$P^3$ is more like this tooth in *Ngapakaldia* than in any of the later genera, but it differs from *Ngapakaldia* in the construction of the posterior crest. There is a high pyramidal parametacone and a low protocone. Although the anterior crest of the parametacone is longer than the posterior crest, the difference is not as great as in *Ngapakaldia.* Length of the anterior crest is 8.7. The posterior crest ascends steeply just behind the cusp then levels off nearly horizontally to the lowest point of the posterior cingulum. Its length is 5.3. The depression on the labial surface at the juncture of the parametacone and the posterior part of the posterior crest is essentially a groove. This emphasizes the demarcation of the two parts.

---

* Named for Dr Brian Daily, Department of Geology, University of Adelaide.

The depth of the ramus below $M_1$ is 33.0. The symphyseal sulcus appears not to be as widely U-shaped as in *Ngapakaldia*. Another apparent difference is seen in the diastemal crest, the outline of which in lateral view is concave anteroposteriorly, and it is sharply crested throughout. The length of the diastema is 29.8. The depth of the symphysis is 14.3, and its length is about 49.0. It has a more upward direction than in *Ngapakaldia*. The mental foramen is 4.3 anterior to $P_3$ and 5.0 below the diastemal crest.

The ventrolateral enamel surface of the lower incisor is widely convex and measures 16.5 from the heel across the curvature to the anterior edge. The enamel extends 4.8 around on the mesial side. At the posterior edge of the enamel the transverse width is 7.2. The root is also deep dorsoventrally, 13.8, and narrow transversely, 7.0; it becomes even narrower at its distal end, about 3.0. The length of the root from the heel of the crown is 28.3. Its open end is slightly mesial to the anterior end of the mental foramen.

$P_3$ is small: length 8.6; width of talonid 5.4, which is only 0.3 wider than across the main cuspid; height on labial side 7.7. A sharp crest descends from the main cuspid to the anterior end of the tooth, and another crest less steeply declined crosses the talonid to the posterior end. A slight labial depression, a somewhat deeper lingual depression and the end of the steepest decline of the posterior crest distinguish the talonid from the main cuspid. The anterior root is 10.0 long and the posterior root is shorter, but distally is tightly appressed against the anterior root of $M_1$.

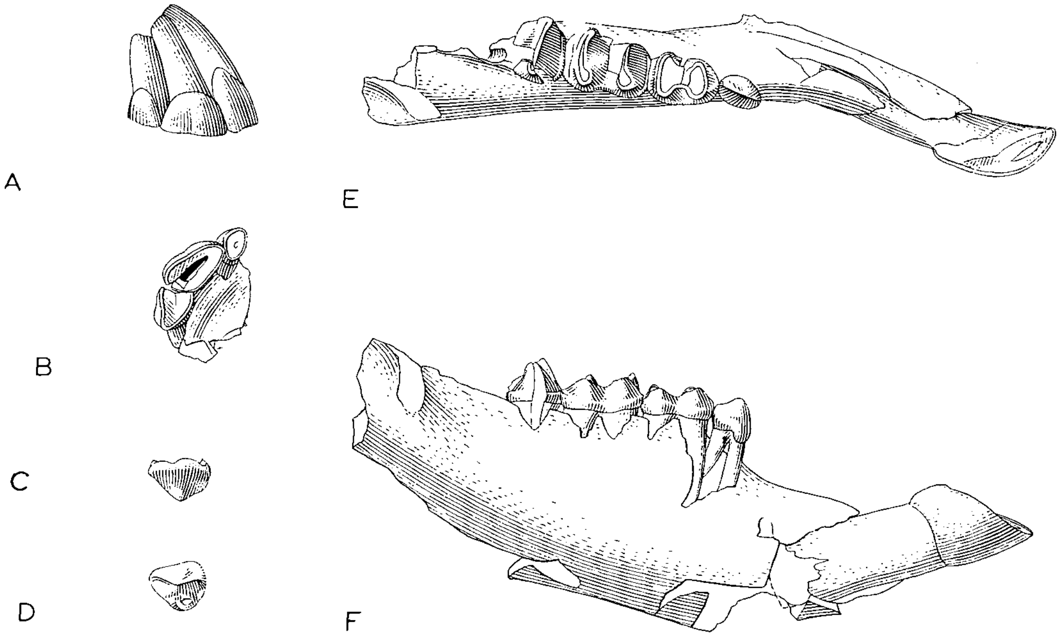


**Fig. 7.—*Pitikantia dailyi* gen. nov. et sp. nov. Holotype, SAM P13862, three-fourths natural size. A, upper incisors, labial view; B, occlusal view. C, $P^3$, labial view; D, occlusal view. E, part of right mandible with occlusal view of teeth; F, part of right mandible, labial view.**

$M_1$ is well worn and part of the anterior surface of the hypholophid is missing. As in most diprotodontid first molars the anterior end of the tooth is somewhat pointed with a rather rounded paralophid crest descending to a position nearly opposite the end of the posterior crest of $P_3$. The protolophid is oblique. The metalophid is distinct and crosses the transverse median valley in a midlink-like structure to the base of the protolophid. The valley is rather widely U-shaped on each side. There is a faint anterior cingulum and a distinct posterior ? cingulum, but no labial or lingual cingulum. Measurements: length 12.8; width of anterior moiety 8.0; width of posterior moiety 8.9.

$M_2$ is moderately worn; the lingual end and part of the posterior surface are missing. It is much like $M_1$ but not pointed anteriorly, and the anterior and posterior cingula are better developed. Furthermore the midlink-like structure is evidently worn off. There is no indication of a paralophid. The posterior cingulum is nearly horizontal transversely. Measurements: length 15.1; width of anterior moiety 10.2a; width of posterior moiety 10.7; height of metaconid 7.0; of entoconid 6.3.

Only the anterior moiety of $M_3$ remains; it is slightly worn. It is very much like $M_2$, but larger. In all the molars the anterior surface of the protolophid is directed posteriorly but is not as depressed as in *Ngapakaldia*, partly because the protoconid and metaconid are only slightly expanded anteriorly. This however is not true of the hypolophid. Measurements: width of anterior moiety 12.0; height of protoconid 7.3; height of metaconid 7.0.

The alveolus for the posterior root of $M_3$ and the alveolus for the anterior root of $M_4$ are preserved.

Table 5: *Pitikantia dailyi*, SAM P13862: Measurements of Upper Teeth

| | Length of Enamel crown | Ant.-post. length of crown | Transverse width of crown | Length of root below enamel |
|---|---|---|---|---|
| $I^1$ .... .... | ? | 7·3 | 5·2 | 16·9 |

| | Height of enamel crown | Ant.-post. length of crown | Transverse width of crown | Length of root below enamel |
|---|---|---|---|---|
| $I^2$ .... .... | 8·3 | 12·2 | 7·1 | Moderately worn<br>15·9 |
| $I^3$ .... .... | 6·7 | 7·8 | 6·0 | Moderately worn<br>10·0 |
| $P^3$ .... .... | 7·8 | 10·3 | 8·7 | Unworn |

Table 6: *Pitikantia dailyi*, SAM P13862: Measurements of Lower Teeth

| | Length of enamel crown | Width at labial talonid | Length of crown | Vertical depth of root |
|---|---|---|---|---|
| $I_1$ .... .... | Moderately worn<br>16·1 | 16·5 | 7·2 | 28·3 |
| $P_3$ .... .... | 8·6 | 5·1 | 5·4 | Unworn |

Table 6:—*continued*

| | Length | Ant. m. | Post. m. | Height pr$^d$ | Height hy$^d$ | Height me$^d$ | Height en$^d$ | |
|---|---|---|---|---|---|---|---|---|
| $M_1$ .... | 12·8 | 8·0 | 8·4 | ? | ? | ? | 6·0 | Moderately worn |
| $M_2$ .... | 14·8 | 9·7*a* | 10·8 | ? | ? | 6·8 | 6·2 | Slightly worn |
| $M_3$ .... | ? | 11·4 | ? | 6·9 | ? | 7·0 | ? | Slightly worn |

Estimates indicated by *a*.

## REFERENCES

Cope, E. D., 1880—On the foramina perforating the posterior part of the squamosal bone of the mammalia. *Proc. Amer. phil. Soc. Phila.*, 18, 452–461.

Gregory, W. K., 1910—The orders of mammals. *Bull. Amer. Mus. nat. Hist.*, 27, 524 pp.

Stirton, R. A., 1963—A review of the macropodid genus *Protemnodon*. *Univ. Calif. Publ. geol. Sci.*, 44 (2), 97–162, 15 figs.

Stirton, R. A., Tedford, R. H., and Miller, A. H., 1961—Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Rec. S. Aust. Mus.*, 14 (1), 19–61, 4 figs.

Van der Klaauw, C. J., 1931—The auditory bulla in some fossil mammals. *Bull. Amer. Mus. nat. Hist.*, 62, 352 pp., 18 figs.

# APPENDIX

It oftens happens that the morphological features of an animal or group of animals are designated by one particular set of names while homologous structures in other animals are named differently. Therefore, in the interests of clarity a list of the terms applied to features of the mandibles and upper and lower dentitions of the diprotodontids described in this series of reports is presented below. Where possible these features have been illustrated in Figures 8, 9, and 10. Inasmuch as only the cranium of *Ngapakaldia tedfordi* is described, a separate listing of its bony elements, foramina, and processes is not included here. Those names will be found in the text.

## *Upper Dentition*

*Incisors:* The three teeth found on either side of the anterior tip of the snout in the premaxillae. They are referred to as $I^1$, $I^2$ and $I^3$.

*Canines:* Evidence of this tooth is found only in *Ngapakaldia.* It is lost in all other diprotodontids. The canine is a small, simple, conical tooth which is implanted in the maxillaries midway between the incisor and the premolar dentitions.

*Premolars:* Only one upper premolar per side is known in the Diprotodontidae. It is found anterior to the four molars and differs conspicuously from them in morphology. This tooth is generally designated as $P^3$ although some authors have listed it as $P^4$.

*Molars:* These are the four bilophodont, nearly square to rectangular teeth which occur on either side of the palate posterior to the premolar. They are usually numbered consecutively posteriorly ($M^1$, $M^2$, $M^3$, and $M^4$).

*Cheekteeth:* Those teeth which have the major grinding function. These consist of the premolar and the molars, and are separated from the non-grinding teeth (incisors and canines) by a long diastema.

*Diastema:* An edentulous space between teeth. In diprotodontids this usually occurs between the incisors and canines, canines and premolars. Where canines are absent, the diastemal crest extends from the incisors to the premolars.

*Crown:* That part of the tooth which bears enamel.

*Root:* That part of the tooth which supports the enamel-bearing crown and is implanted in the bone of the jaw or maxillary.

*Cusp:* A term designating any of the four major denticles of the molar teeth. Premolars may bear from two to five major cusps.

*Protocone:* The primary cusp of the upper tribosphenic mammalian tooth. In diprotodontids this cusp occupies the anterointernal corner of the molar. This term is also used to designate the major lingual cusp in the premolar.

*Parametacone:* The prominent labial cusp in the upper premolar.

*Paracone:* The anteroexternal cusp of the diprotodontid upper molar. In some diprotodontids, the parametacone may become separated into two cusps. The anterior of these is designated the paracone, the posterior the metacone.

*Metacone:* The posteroexternal cusp of the diprotodontid upper molar.

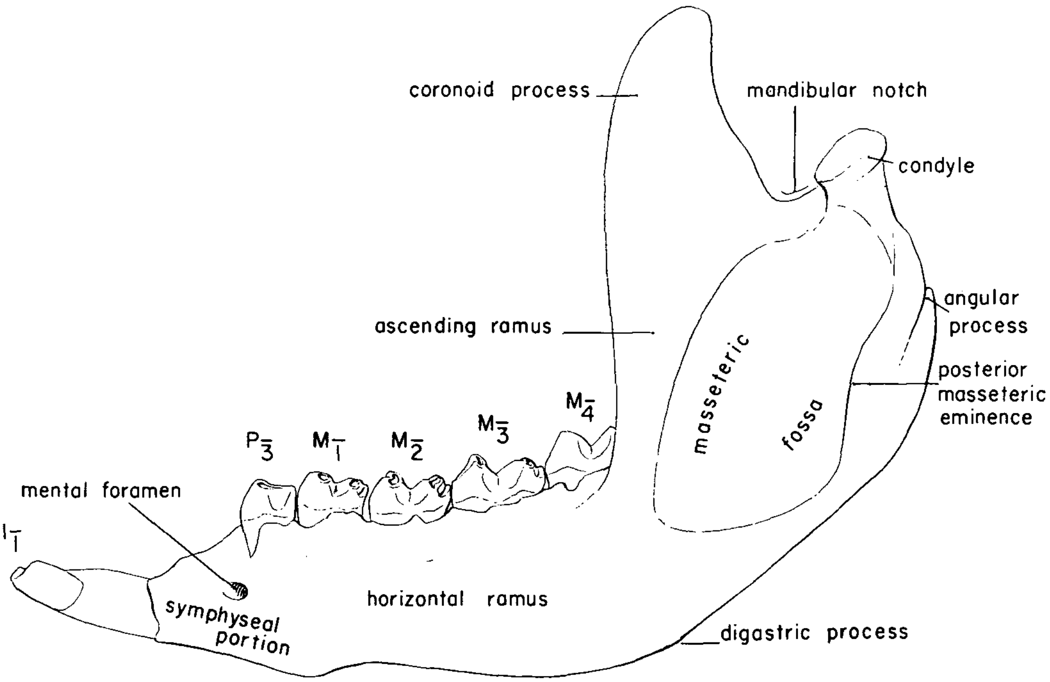


**Fig. 8.—Lateral view of diprotodontid mandible with features labelled according to usage in the text. Composite drawing; includes features found in several genera of diprotodontid.**

*Hypocone:* The posterointernal cusp of the diprotodontid upper molar. This is a topographic name only. Homology to a similarly positioned cusp of placental mammals is not implied. A posterointernal cusp occasionally develops in the upper premolar.

*Protoloph:* The transversely oriented loph of the upper molar in diprotodontids which contains the protocone and paracone. The protoloph is the more anterior of the two lophs of diprotodontid upper teeth.

*Metaloph:* The more posterior of the two lophs of diprotodontid upper teeth; contains the metacone and hypocone.

*Transverse valley:* The valley which separates the protoloph from the metaloph.

*Cingulum:* Any small shelf-like linear structure at the base of the enamel crown. Anterior and posterior cingula are commonly present. Labial and lingual cingula are often limited to the peripheral portions of the transverse valley.

*Stylar cusps:* Usually small cusps developed from the labial cingulum.

*Parastyle:* The stylar cusp anterolabial to the base of the paracone in diprotodontid molars. In premolars, the term parastyle is used to designate a cusp at the anterior tip of the tooth; in some premolars the parastyle may become nearly as large as the paracone.

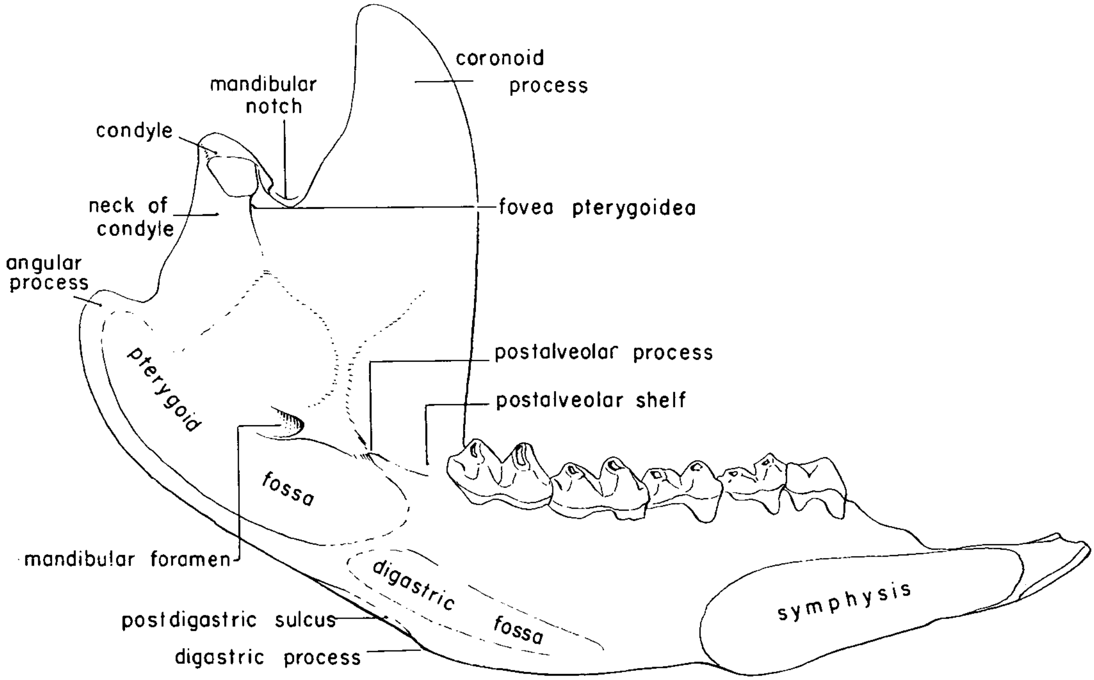


**Fig. 9.—Medial view of diprotodontid mandible with features labelled according to usage in the text. Composite as in Fig. 8.**

*Mesostyle:* A stylar cusp which develops from the singulum at the posterolabial base of the paracone. In molar teeth, the mesostyle is usually found anterior to the transverse valley.

*Metastyle:* The stylar cusp which develops at the posterolabial base of the metacone.

*Anterior moiety:* The portion of a molar tooth anterior to the transverse valley. This includes the protoloph, mesostyle, parastyle, anterior cingulum, and parts of the labial and lingual cingula.

*Posterior moiety:* The portion of the molar tooth posterior to the transverse valley, including the metaloph, metastyle, posterior cingulum, and parts of the labial and lingual cingula.

*Postparaconal ridge:* A longitudinal ridge which extends posteriorly from the apex of the paracone to the transverse valley.

*Premetaconal ridge:* A longitudinal ridge which is confluent with the postparaconal ridge and extends posteriorly from the transverse valley to the crest of the metaloph a short distance from the apex of the metacone.

### *Lower Dentition*

*Incisor:* The single, elongate spatulate to lanceolate tooth which is found at the anterior end of each half of the mandible.

*Premolar:* The single, non-molariform tooth at the anterior end of cheektooth series. This is designated here as $P_3$, other authors may call it $P_4$.

*Molars:* The four bilophodont teeth posterior to the premolar. These are numbered consecutively posteriorly ($M_1$, $M_2$, $M_3$, $M_4$).

*Cuspid:* The counterpart of the cusp of the upper dentition. The suffix -id denotes a feature in the lower dentition.

*Protoconid:* In the molars it is located at the anterolabial portion of the tooth. The term is also sometimes used to denote the major cuspid of the premolars.

*Paraconid:* The anterolingual cuspid of the tribosphenic mammalian molar. It is commonly reduced or lost in phalangeroid marsupials.

*Metaconid:* The posterolingual cuspid of the trigonid in the tribosphenic mammalian tooth. In phalangeroids it occupies the anterolingual portion of the tooth opposite the protoconid.

*Hypoconid:* The posterolabial cuspid in the diprotodontid dentition. This is a topographic term only, and is not meant to imply homology with a similarly placed cuspid in placental mammals.

*Entoconid:* The posterolingual cuspid in the diprotodontid lower molar.

*Main cuspid:* Used to denote the large, nearly central cuspid of the lower premolar in diprotodontids.

*Posterior cuspid:* Used to denote the posterior cuspid in the diprotodontid premolar.

*Protolophid:* The anterior transverse lophid of the lower molar which connects the protoconid and metaconid.

*Paralophid:* In the primitive tritubercular dentition, this term is used to denote a crest which extends anterolabially from the paracone to the parastyle, or to the anterior cingulum. In diprotodontids, particularly in the first lower molars, there is a remnant of this structure which extends from the protoconid to the anterior cingulum.

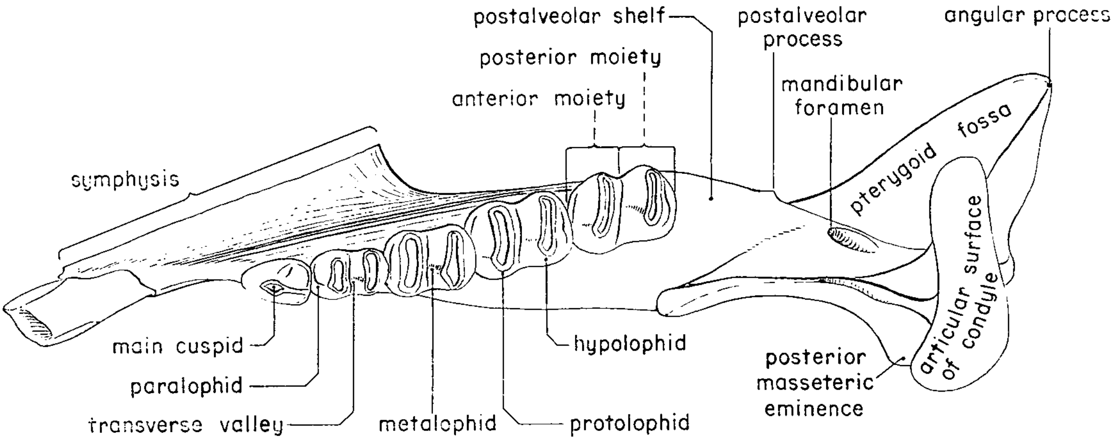


**Fig. 10.—Occlusal view of diprotodontid mandible with features labelled according to usage in the text. Composite as in Fig. 8.**

*Metalophid:* In placental mammals this term denotes an oblique crest which extends anterolingually from the hypoconid toward the metaconid, commonly joining the trigonid on the posterior surface of the protolophid, nearly midway between the protoconid and metaconid. In diprotodontids, a similarly placed structure extends anterolingually from the hypoconid, but usually curves anteriorly before reaching the transverse valley and is thus limited to the labial half of the tooth. Metalophid is used in the diprotodontids as a convenient topographic term. Homology with the structure of the same name in placental mammals has not been proved.

*Hypolophid:* The main transverse lophid posterior to the transverse valley of the diprotodontid lower molar, that connects the hypoconid and entoconid.

*Transverse valley:* The valley which separates the protolophid from the hypolophid.

*Mesostylid:* A small stylar cusp which developed at the posterolabial base of the protoconid in some diprotodontids.

*Cingulum:* As in the upper dentition.

*Anterior moiety:* That portion of the tooth anterior to the transverse valley.

*Posterior moiety:* That portion of the lower molar tooth posterior to the transverse valley.

### *Mandible*

*Mandible:* The lower tooth-bearing element which articulates with the cranium.

*Jaw:* Another name for mandible.

*Symphysis:* The vertical median plane at which the right and left mandibles are joined together.

*Symphyseal region:* The portion of the mandibles in which the symphysis occurs. This is generally that anterior to the premolar and posterior to the incisors.

*Horizontal ramus:* The major portion of the mandible; it is horizontally elongate and bears the premolar and molar teeth.

*Ascending ramus:* The vertical portion of the mandible which rises from the horizontal ramus and articulates with the glenoid fossa of the cranium, and to which the temporal musculature is attached.

*Coronoid process:* That portion of the ascending ramus dorsal to the articular condyle.

*Condyle:* The transversely elongate process with a generally flat, sinuous dorsal surface which lies posterior to the coronoid process and dorsal to the angle of the mandible. The condyle articulates with the glenoid fossa of the cranium.

*Neck:* The transversely narrow base of the condyle.

*Mandibular notch:* The dorsally concave excavation in the lateral profile of the mandible between the condyle and the body of the coronoid process.

*Masseteric fossa:* An excavation on the lateral surface of the ascending ramus posterior and generally ventral to the tooth-row.

*Posterior masseteric eminence:* A flangelike process developed at the posterior edge of the masseteric fossa.

*Angular portion:* The broad, flat medial expansion at the posteroventral edge of the ascending ramus, posterior to the digastric process.

*Angular process:* The broadly acuminate portion of the mandible which projects posteromedially.

*Masseteric foramen:* A small foramen located just within the anteroventral edge of the masseteric fossa.

*Fovea pterygoidea:* A triangular cavity on the medial surface of the ascending ramus at the anteroventral base of the condyle.

*Postalveolar shelf:* A flat surface on the medial surface of the mandible which extends posteriorly from the molar series and above the pterygoid fossa.

*Postalveolar process:* The spur often developed at the posterior end of the postalveolar shelf.

*Pterygoid fossa:* An anteroventrally elongate cavity on the medial surface of the angular portion of the mandible.

*Digastric fossa:* A shallow anteroventrally elongate cavity near the ventral edge of the medial surface of the mandible anterior to the pterygoid fossa and ventral to the tooth row.

*Digastric process:* A process sometimes developed at the ventral edge of the mandible ventral to the last molar and below the posterior portion of the digastric fossa.

*Postdigastric sulcus:* A shallow, longitudinally elongate excavation on the ventromedial surface of the mandible posterior to the digastric process.

*Mandibular canal:* The canal leading anteroventrally into the body of the horizontal ramus, posterior to the postalveolar process and anterior to the condyle.

*Mandibular foramen:* The aperture through which the mandibular canal leaves the medial surface of the ascending ramus.

*Mental foramen:* The foramen on the lateral surface of the mandible anteroventral to the premolar.

*Genial pits:* A pit or depression found on the ventral surface of the symphyseal portion of each mandible.

*Genial crest:* A variably developed midsagittal crest, chiefly developed on the posterior portion of the symphysis.

*Transverse torus:* A transversely oriented strut of bone at the posterior surface of the symphysis.

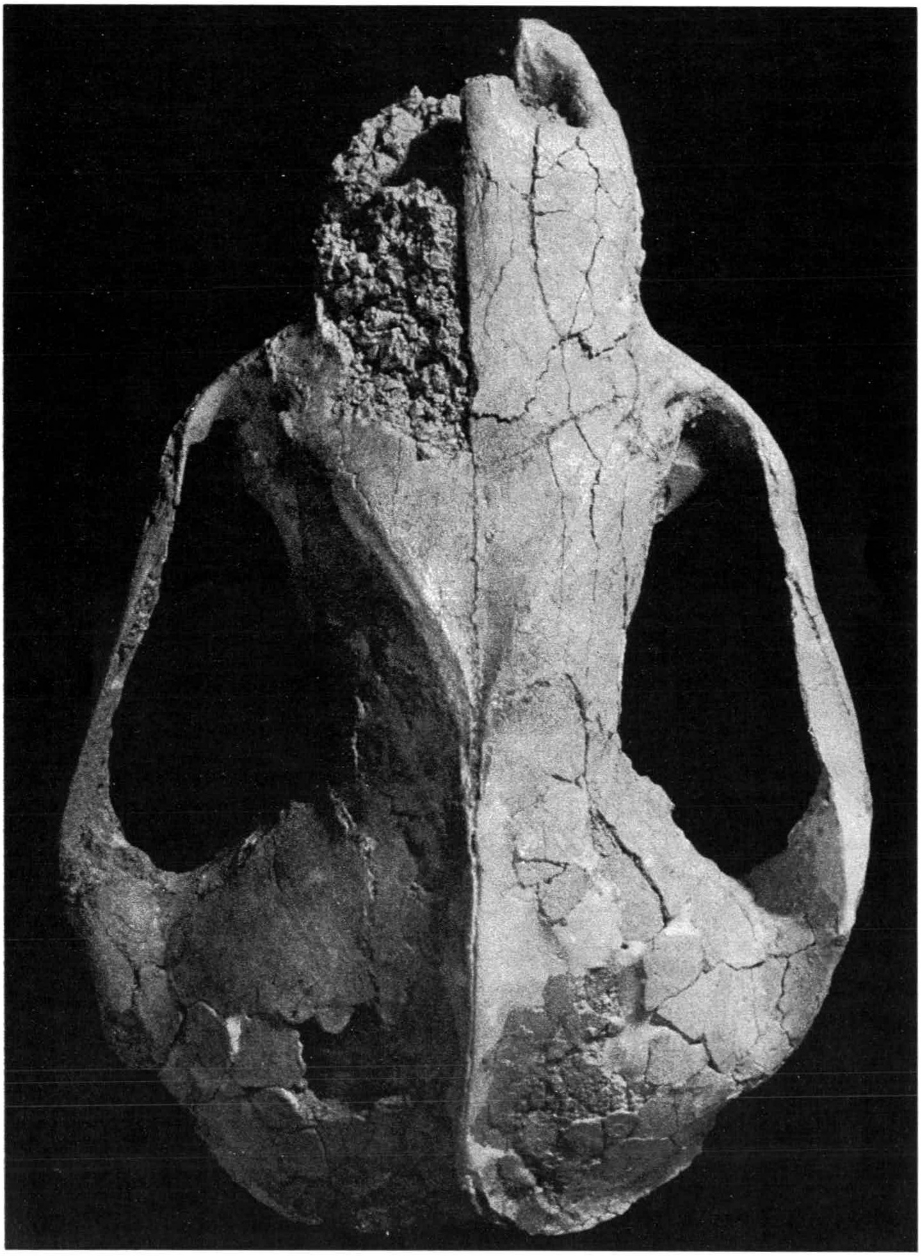


Plate I.—*Ngapakaldia tedfordi* gen. nov. et sp. nov. Part of *holotype*, dorsal view of cranium, three-fourths natural size; SAM P13851.

**Plate II.**—*Ngapakaldia tedfordi* gen. nov. et sp. nov. Part of *holotype*, lateral view of cranium, three-fourths natural size; SAM P13851.

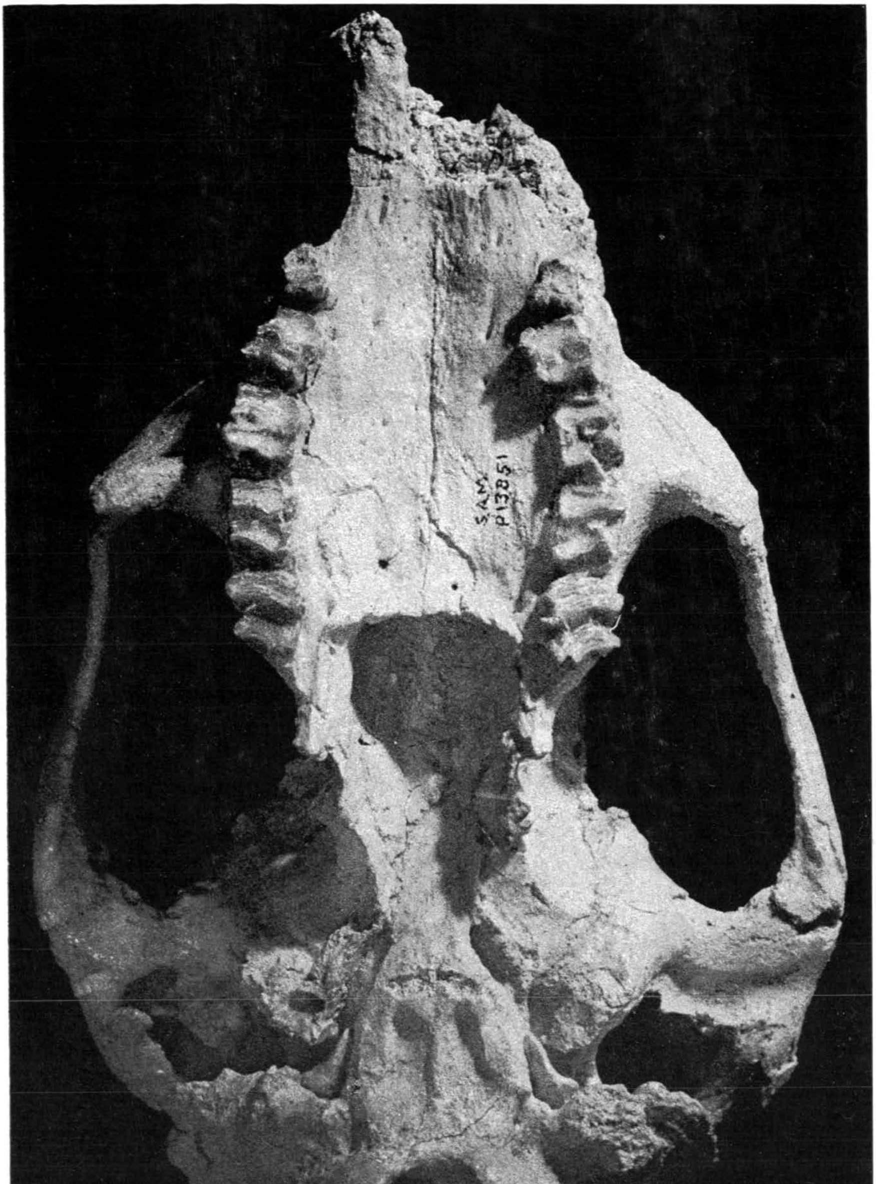


Plate III.—*Ngapakaldia tedfordi* gen. nov. et sp. nov. Part of *holotype*, ventral view of cranium, three-fourths natural size; SAM P13851.

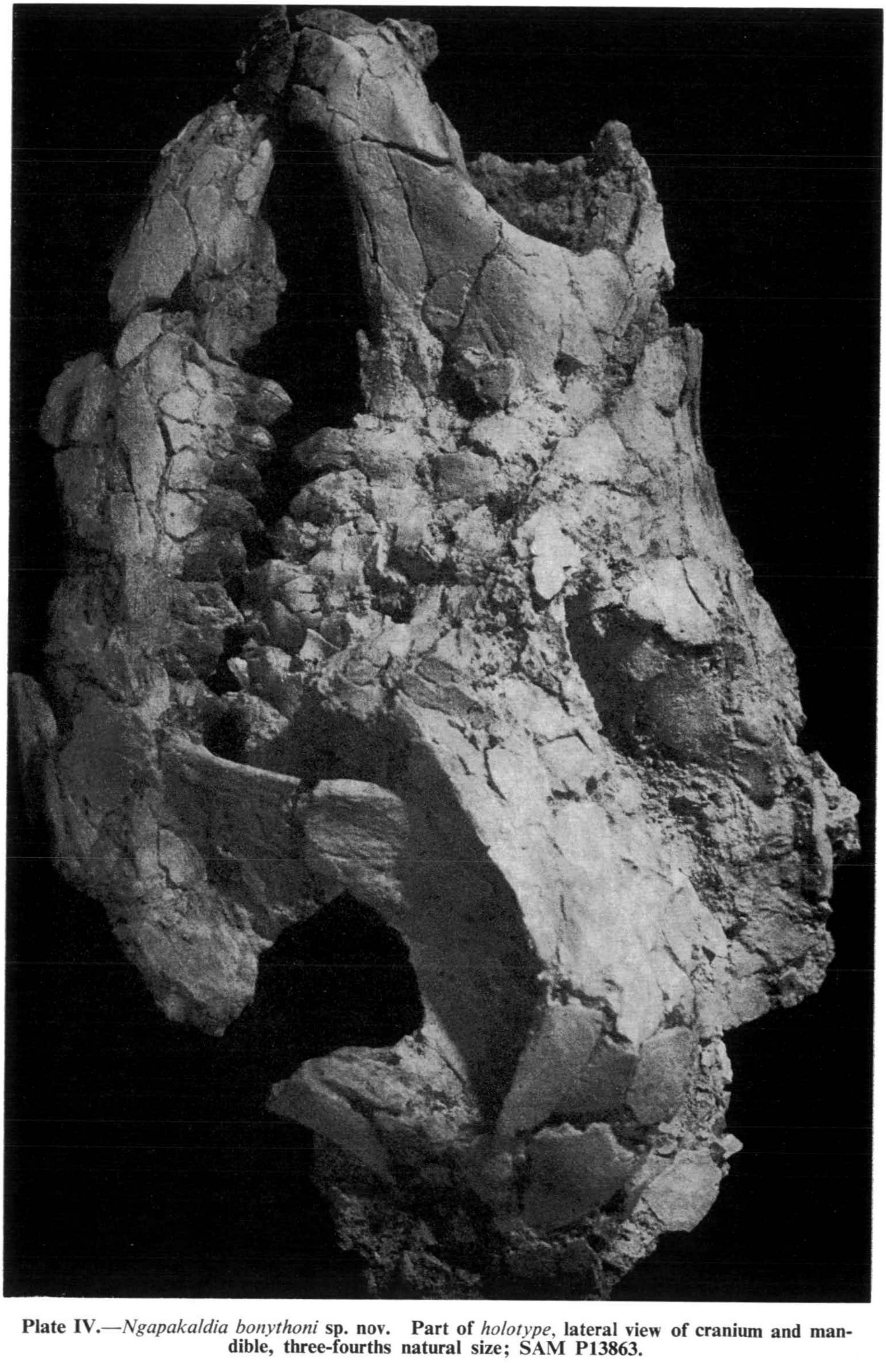


Plate IV.—*Ngapakaldia bonythoni* sp. nov. Part of *holotype*, lateral view of cranium and mandible, three-fourths natural size; SAM P13863.

# A DIPROTODONTID FROM THE MIOCENE KUTJAMARPU FAUNA, SOUTH AUSTRALIA

by

R. A. STIRTON

## CONTENTS

Page

INTRODUCTION .... .... .... .... .... .... .... .... .... .... .... 47

Genus *Neohelos* nov.

*Neohelos tirarensis* gen.nov.et sp.nov. .... .... .... .... .... .... .... 48

REFERENCE .... .... .... .... .... .... .... .... .... .... .... 51

## SUMMARY

A new marsupial genus of the family Diprotodontidae was found in the Wipajiri channel sands that have cut into the Etadunna Formation at Lake Ngapakaldi. The beds are thought to be Miocene in age. The genus is based on five isolated teeth. The upper premolar was quadritubercular with evidence of a parastyle (broken off in the holotype), parametacone, protocone, and a hypocone. This diprotodontid appears to be the oldest known in a phyletic lineage that eventually gave rise to the late Pleistocene *Zygomaturus trilobus* Owen 1859, which had evolved a quinquetubercular upper premolar with the paracone and metacone as separate cusps.

Page 46 is blank.

## INTRODUCTION

Five isolated teeth of a diprotodontid were found in the Wipijari channel sands on the eastern shore line of Lake Ngapakaldi of South Australia in 1962. The fossil assemblage, including several other mammals and lower vertebrates, will be called the Kutjamarpu fauna.

Normally it would not be advisable to name a fossil on such scanty material, but a genus can be diagnosed on the evidence available. Furthermore it falls into an important gap in the phylogeny (see pp. 158-9) between the Ngapakaldi fauna and another from the Northern Territory.

The selection of the holotype has posed another problem. All the other teeth in the sample are more complete than the $P^3$. Nevertheless the $P^3$ was selected as the holotype because the premolars usually are the most diagnostic of the teeth in the genera of the Diprotodontidae, and because the most important characters are revealed in the tooth at hand.

### *Acknowledgments*

This research is part of a joint project between the South Australian Museum and the Museum of Paleontology, University of California. It was mostly financed by the United States National Science Foundation grant G-15957. The illustrations were done by the University Museum of Paleontology staff artist, Owen J. Poe.

## Genus NEOHELOS* nov.

*Genotypic Species. Neohelos tirarensis* sp.nov.

*Generic Diagnosis.* Posterolabial corner of $I^3$ with crown rather expanded, height of enamel covered crown on labial side 11·3. Parametacone of $P^3$ pyramidal, not extended posteriorly, no indication of twinning, height 5·4, transverse basal width across parametacone and hypocone 14·8; apparently there was an isolated parastyle; hypocone not directly behind protocone. Cingulum on $M^1$ and $M^2$ present but not prominent; $M^1$—length at midline 17·3, anterior basal width 15·6, posterior basal width 15·7, height of paracone and of metacone 6·9. $M^2$—length at midline 19·2, anterior basal width 16·9, posterior basal width 16·6, height of paracone and of metacone about 7·5. $M_4$—length at midline 20·7, anterior basal width 15·5, posterior basal width 14·7, height of protoconid and of hypoconid 10·0.

## NEOHELOS TIRARENSIS sp.nov.

*Holotype.* Posterior part of left $P^3$, South Australian Museum No. P13848.

*Paratypes.* Left $I^3$, UCMP 69976; left $M^1$, UCMP 69977; right $M^2$, UCMP 69978; left $M_4$, UCMP 69979.

*Specific Diagnosis.* See generic diagnosis until other species are described.

*Type Locality.* Leaf Locality, UCMP Loc. V6213. Ferruginous conglomeratic sandstone interbedded with dark grey claystone, poorly indurated. Wipijari channel sands on the eastern shore of Lake Ngapakaldi, between Birdsville Track and the shore of Lake Eyre, and between Cooper Creek and the Warburton, South Australia. Channel cut into Etadunna Formation. About 1835 feet north of the Ngapakaldi Quarry, UCMP loc. V5858 (Stirton, Tedford, & Miller, 1961). Approximate grid coordinate 642488, grid zone 5, Marree Sheet, 1:506,880; Australian Army, H.Q., Cartograph Co., 1942.

*Age.* Miocene. *Fauna.* Kutjamarpu.

### *Description*

$I^3$ is a moderately worn tooth; the occlusal pattern has a triangular outline, but the corners are rounded. The enamel has been spalled off on the anterior edge, but is well preserved on the anterolabial and posterolingual sides, where it is 0·7 and 0·3 in thickness at the edges of worn surface.

The anterolabial surface has a slight median groove, but it fades out toward the base of the crown. This surface is somewhat convex dorsoventrally, especially in its posterolabial part, but the anterointernal part of the surface is convex at the base and apparently also near the apex, although nearly flat between. The height of the enamel near the anterointernal corner is 11·3 and near the posterolabial corner it is 10·0. The crown was probably no more than 1·0 higher in an unworn tooth. As seen from the labial view the crown is expanded posteriorly just below the occlusal surface on the posterolabial corner, but is pinched in basally; therefore the length just below the occlusal surface is 9·3 and basally it is 8·4.

---

* νεο, new + ηλος, wart. In reference to the development of the hypocone on $P^3$.

The lingual surface is more irregular. There is a vertical groove between the expanded posterolingual corner and a low rather wide vertical middle ridge. The height of the enamel crown remaining as measured along the middle ridge is 6·6. The lingual surface is somewhat convex anteroposteriorly and its measurement is 9·4.

The transverse width of the anterior end is about 12·7, which allows for the missing enamel on the anterolingual and anterolabial corners. On the anterior surface there is a large ovate appression facet for $I^2$.

The root is nearly round with one dimension of 8·3 and the other 6·9. Its length is 15·7. The end of the root is widely open and has thin sharp edges.

$P^3$ is represented by the posterior part of the tooth including the undivided parametacone of the labial side and the opposing protocone and hypocone. The parastyle is broken off. The transverse basal width across the parametacone and protocone is 14·8. Both cusps are somewhat worn; the parametacone is more so than the protocone. They are connected by a transverse ridge which is crossed by a commissure separating the cusps. The parametacone is pyramidal; it has anterior, labial, and lingual surfaces. It is not lengthened posteriorly nor is there a suggestion of a division of the cusp. The height of the parametacone as measured from the base of the enamel on the labial side is 9·8, but it probably was at least 11·0 in a unworn stage. The width of the broken surface anteriorly and the steep anterior surface of the parametacone remaining indicate that there had been an isolated parastyle in this specimen. Posteriorly a crest extends up from the parametacone to the posterior cingulum. The cingulum, which is continuous from the labial side around to connect with the protocone, is variable in height. There is a strong wide hypocone on the posterolingual corner with a deep trench between it and the base of the parametacone; it is more labial in position than the protocone, and not directly behind it. The protocone is quite rounded and is outlined anterolingually by a sharp crescentic trench which does not cross the posterior cingulum. Anterolabially the protocone is outlined by a shallower trench. The cingulum is not continuous along the lingual base of the protocone. Anteroposteriorly the base of the protocone measures 6·9; its height is 5·4. The posterior root is convex posteriorly and concave anteriorly.

In the slightly worn $M^1$ the lophs are slightly crescentic, as in all diprotodontid molars, and nearly transverse. The anterior moiety, 15·6 wide, lacks 0·1 of being as wide as the posterior moiety 15·7; however, the protoloph just below the lingual cingulum, 14·1, is 0·4 narrower than the same measurement across the metaloph. The depression on the posterior surface of both the protoloph and metaloph is just labial to the anteroposterior midline of the tooth. Occlusion is on the anterior edge of the lophs. The transverse median valley is widely V-shaped. A wide ridge descends from the valley to the tip of the paracone. A distance of 6·6 separates the paracone and metacone, and the protocone and hypocone are 7·1 apart. The height of the paracone and of the metacone are both 6·9. There is a low but well developed parastyle on the anterolabial corner of the tooth. The anterior cingulum extends across the anterior end from the parastyle around to the lingual base of the protocone where it is partly interrupted, but then continues across the lingual end of the transverse median valley to the anterolingual base of the hypocone. It then is interrupted opposite the hypocone, but continues around to the metastyle, where a crest descends to the tip of the metacone. The height of the cingulum averages about 2·5. There is no labial cingulum, but a short vertical groove on the labial side separates the anterior and posterior moieties. The anteroposterior length of the tooth at the midline is 17·3.

$M^2$ is larger but otherwise differs only in some details, outlined below, from $M^1$. The two specimens are essentially in the same stage of wear, and may have belonged to the same animal. The anterior moiety, 16·9 wide, is 0·3 wider than the posterior moiety 16·6. The depressions on the posterior surface of the protoloph and metaloph appear to be slightly more lingually located than in $M^1$. A distance of 7·9 separates the paracone and metacone, and the protocone and hypocone are about 9·3 apart (the hypocone is partly restored). The enamel at the labial base of the paracone and metacone are partly broken away, but their height is approximately 7·5. The cingulum in contrast to $M^1$ appears to have been continuous opposite the hypocone, but it is discontinuous opposite the protocone, and the metastyle is more isolated as a cusp. Height of the cingulum is 3·5. The anteroposterior length of the tooth at the midline is about 19·2 (anterior cingulum partly missing). There is an appression facet for $M^3$.

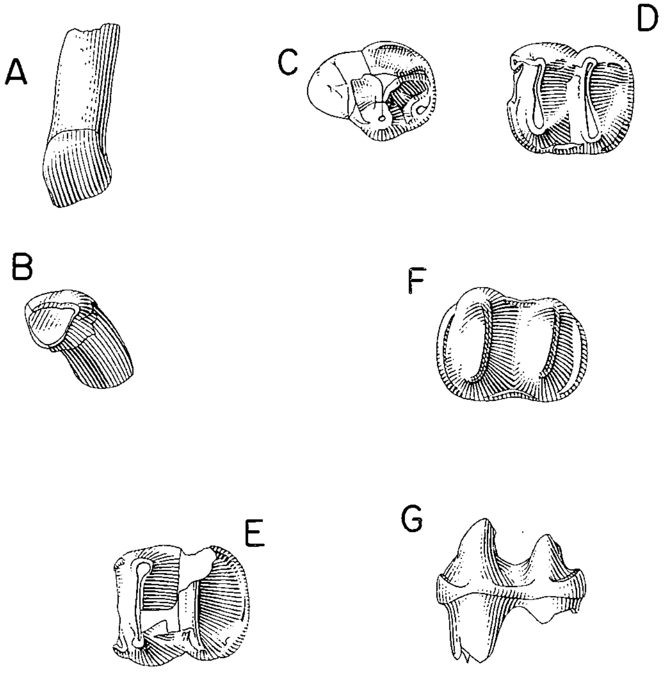


**Fig. 1.** *Neohelos tirarensis*, **gen.nov.et sp.nov. Natural size.**
**A and B, paratype, left $I^3$, UCMP 69976; A, labial view; B. occlusal view.**
**C, holotype, posterior part of left $P^3$, anterior end restored, occlusal view, natural size, SAM P13848.**
**D, paratype, left $M^1$, occlusal view, UCMP 69977.**
**E, paratype, right ?$M^2$, occlusal view, UCMP 69978.**
**F and G, paratype, left $M_4$, UCMP 69979; F, occlusal view; G, labial view.**

The only lower tooth in the collection is an unworn $M_3$. The lophids are slightly crescentic with the concavity anterior. The greatest width of the protolophid is 15·5, and of the hypolophid 14·7. The protolophid crest, which is lowest at the anteroposterior midline of the tooth, slightly overhangs the upper part of the posterior surface. This, however, is not true of the hypolophid. Occlusion is on the posterior edge of the lophids. The protoconid, with a partial anterior crest, is more prominent than the metacone; and the hypoconid, although much smaller than the protocone, is similar to it and much more prominent than the entoconid. The distance between the protoconid and metaconid and between the hypoconid and entoconid is the same, 10·5. The transverse median valley is widely U-shaped. The protoconid and hypoconid are 8·5 apart, and the metaconid and entoconid 9·6. The anterior crest or metalophid extension from the hypoconid is very short, not extending down into the transverse median valley. The height of the protoconid and the hypoconid from the base of the enamel is 10·0, but some enamel may be abraded away at the labial base of the protoconid. It is clear that the tip of the protoconid is higher above the level of the transverse median valley than is the hypoconid. Heights for the metaconid and entoconid cannot be measured because some of the enamel is broken off on the lingual side. The lingual or labial sides, or both, of the four cuspids are convex dorsoventrally. The anterior cingulum is 3·5 high and closely appressed to the base of the protolophid. On the labial side the cingulum is extremely reduced even across the opening of the valley. The posterior cingulum is prominent as a crest that increases in height lingually. It is as high as the anterior cingulum. There probably was no lingual cingulum. The anteroposterior length as measured at the midline is 20·7. The anterior and posterior roots were crescentic in outline; the front one convex anteriorly, and the other convex posteriorly.

TABLE 1. *NEOHELOS TIRARENSIS* sp.nov.: MEASUREMENTS

| | Length of crown | Width of crown | Height of labial surface of crown | Length of root |
|---|---|---|---|---|
| $I^3$ UCMP 69976 .... | 9·3 | 7·9 | 11·3 | 16·0 |
| $P^3$ SAM P13848 .... | ? | 14·8 | 11·7*a* | ? |

| | Length | Width of protoloph | Width of metaloph | Height of metacone |
|---|---|---|---|---|
| $M^1$ UCMP 69977 .... | 17·0 | 15·5 | 15·6 | 6·9*a* |
| $M^2$ UCMP 69978 .... | 19·0*a* | 17·1 | 16·6 | 8·3*a* |

| | Length | Width of Protolophid | Width of metalophid | Protoconid |
|---|---|---|---|---|
| $M_1$ UCMP 69979 .... | 21·0 | 15·8 | 14·7 | 9·9 |

*a*: Approximate.

## REFERENCE

STIRTON, R. A., TEDFORD, R. H., and MILLER, A. H., 1961—Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Rec. S. Aust. Mus.*, 14 (1), 19–61, 4 figs.

# THREE NEW DIPROTODONTIDS FROM THE TERTIARY OF THE NORTHERN TERRITORY, AUSTRALIA

by

MICHAEL O. WOODBURNE*

## CONTENTS

Page
INTRODUCTION .... .... .... .... .... .... .... .... .... .... .... 55

Genus *Pyramios* nov.
*Pyramios alcootense* gen.nov. et sp.nov. .... .... .... .... .... .... .... 57
Genus *Kolopsis* nov. .... .... .... .... .... .... .... .... .... .... 71
*Kolopsis torus* gen.nov. et sp.nov. .... .... .... .... .... .... .... 72
Genus *Plaisiodon* nov. .... .... .... .... .... .... .... .... .... .... 88
*Plaisiodon centralis* gen.nov. et sp.nov. .... .... .... .... .... .... .... 89

REFERENCE .... .. .... .... .... .... .... .... .... .... .... 103

## SUMMARY

Three new diprotodontid genera are described from the Alcoota fauna of the Northern Territory. Each genus is composed of a single species. Two of the genera are broadly related and are part of the lineage leading to *Zygomaturus trilobus* Owen, 1859. The third genus belongs to the lineage leading toward *Meniscolophus mawsoni* Stirton, 1955, *Euryzygoma dunense* Longman, 1921, *Euowenia robusta* DeVis, 1891 and *Euowenia grata* (Owen).

As indicated by the phyletic position of its diprotodontids, the Alcoota fauna is older than the Awe fauna of New Guinea, the fauna from the Sandringham Sands at Beaumaris, Victoria, and the Palankarinna fauna of South Australia; and younger than the Ngapakaldi and Kutjamarpu faunas of South Australia.

On the basis of the present evidence, the best estimation of the age of the Alcoota fauna, in Lyellian terms, is late Miocene or early Pliocene. The sediments containing the Alcoota fossils unconformably overlie laterites which have been developed on Precambrian bedrock. In this area, at least, the conditions necessary for lateritization did not persist later than Miocene time.

---

* Museum of Paleontology, University of California, Berkeley, California.

# INTRODUCTION

A rich concentration of fossil vertebrates has recently been found in Tertiary sediments 4 miles south-west of Alcoota station, Northern Territory. Preliminary collections were taken from the locality in 1962 by Alan E. Newsome, Animal Industries Branch, and Keith A. Rochow, Resident Geologist's Office, Northern Territory Administration, Alice Springs; a preliminary notice of this find was subsequently presented (Newsome & Rochow, 1964). Dr R. A. Stirton, Dr R. H. Tedford, and I were invited to visit the site in 1962 by Dr N. H. Fisher, Chief Geologist, Bureau of Mineral Resources, Canberra; we spent two weeks at the site in August at the close of the 1962 expedition in the Lake Eyre Basin, South Australia. The field season of 1963 was spent at the site making an extensive collection. That party was jointly sponsored by the Museum of Paleontology, University of California, Berkeley, and the Bureau of Mineral Resources. The personnel, other than myself, were Dr John E. Mawby, of the Museum of Paleontology, and James E. Ferguson Stewart of Dardanup, West Australia.

At the present stage of investigation the assemblage, which will be designated as the Alcoota fauna, has been found to consist of several types of birds, a crocodile, a new species of *Thylacinus*, an aberrant ?bandicoot, a small and a large species of macropodid, and four species of diprotodontid. One of these belongs to the Palorchestinae and will not be described here. Each of the other three species represents a new genus. Two of these fall in the lineage leading to *Zygomaturus trilobus*, Owen, 1859, the third is a member of the lineage which contains forms such as *Meniscolophus mawsoni* Stirton, 1955, *Euowenia grata* (Owen), and *Euowenia robusta* DeVis, 1891. The mandibles and upper and lower dentitions of the three species will be described in this report; a full discussion of their crania will be presented. The Alcoota fauna, which seems to be older than the Awe fauna of New Guinea and younger than the Kutjamarpu fauna of South Australia, is either early Pliocene or late Miocene in age (see Stirton, Woodburne, & Plane, this vol., p. 149ff).

The Tertiary sediments which occur at Alcoota consist of a 70-foot sequence of flat-lying siltstone, sandstone and conglomeratic sandstone, which were deposited in a depression in an old lateritized terrain developed on Precambrian metamorphics. The Tertiary sediments definitely postdate the laterite. Remnants of these once widespread sediments now exist as small flat chalcedony-capped mesas at the western edge of a broad plain which lies north and west of the Harts Range and east of the low Precambrian highlands extending south-west from Alcoota. One of the most conspicuous of these erosional remnants is a small pointed hill about 2 miles south-west of the junction of Waite and Ongeva creeks, north-flowing tributaries of the Sandover River.

The red ferruginous fluviatile rocks which make up the bulk of the small pointed hill, as well as the other small mesas in the immediate vicinity, represent the larger portion of the Tertiary deposits of the area. Rocks of this character overlie the green lacustrine fossil-bearing sediments which apparently occur in the deeper part of the Tertiary depositional basin. The fossiliferous portion of the deposit is composed of two lithological units. The lower and more fossiliferous is a pale green fine sandstone 1 foot thick. Immediately overlying this is a 0·8-foot dark olive green siltstone. These beds occur at the base of a small north-easterly rise about 1400 feet at 279° from the small pointed hill. The features of the depositional basin and its Tertiary rocks will be described in more detail in a subsequent publication.

## ACKNOWLEDGEMENTS

Dr N. H. Fisher, Chief Geologist, Bureau of Mineral Resources, Canberra, and Dr R. A. Stirton, Director of the Museum of Paleontology, University of California, Berkeley, have given support in many phases of this project. Alan E. Newsome and Keith A. Rochow gave generously of their time in the spring of 1962 and placed their knowledge at our disposal. Without the assistance given during the 1963 season by John E. Mawby and James E. Ferguson Stewart this project would not have succeeded. Terry Quinlan and others of the Resident Geologist's Office, Alice Springs, contributed much in both time and material in 1962 and 1963. The morale of the field party was kept at a high level by the hospitality so generously extended by Mr and Mrs Ivor Paine of Alcoota station. The illustrations are by Mrs Augusta F. Lucas and Mrs Jaime P. Lufkin, staff artists of the Museum of Paleontology. United States National Science Foundation grant G-15957 enabled this project to be undertaken; appreciation for this support is gratefully tendered.

## Family DIPROTODONTIDAE

### Genus PYRAMIOS* nov.

*Genotypic species: Pyramios alcootense* sp.nov.

*Generic diagnosis:* $I^1$: D-shaped cross-section with curved lateral surface and nearly flat medial surface; in lateral view tooth tapers slightly anteriorly and markedly posteriorly from a thicker portion of the root proximal to the enamel cap; root closed at proximal tip; general radius of curvature of arc of outer surface in lateral view 38·0–50·0. $I^2$: triangular occlusal surface, nearly symmetrical; greatest posterodorsal curvature of outer surface occurs distal to base of enamel; root tapers gradually toward proximal tip. $I^3$: occlusal surface posterolaterally elongate, asymmetrically triangular; broad shallow groove on lateral and posteromedial surfaces. $P^3$: triangular occlusal outline; parastyle small, not sharply separated from rest of crown; tooth two-rooted; single parametacone major labial cusp, small mesostyle and metastyle; protocone major lingual cusp; hypocone absent; parastyle connected to parametacone by crest, and to protocone by lingual cingulum; labial cingulum not present between parastyle and parametacone. $M^1$: parastyle and metastyle prominent, postparaconal crest moderately developed, directed longitudinally, no mesostyle; labial cingulum present, anterior cingulum broad, shelf-like, particularly at anterolingual corner; lingual cingulum elongate with broad sigmoid curve between protocone and hypocone. $I_1$: spatulate, blade oriented at an angle of about 45° to the root; blade conspicuously deeper than immediately adjacent root; root tapers posteriorly from base of crown; posterior edge of lateral surface of enamel sinuous with broad posteriorly projecting lobe in dorsal half and complementary anteriorly projecting recess ventrally; in medial view, rear of enamel cap extends as nearly straight line anteroventrally from dorsal to ventral border of tooth. $P_3$: short, broadly triangular outline; main cuspid connected to anterior apex of tooth by longitudinal crest; no labial indentation posterior to base of main cuspid; no lingual crest from posterior cuspid. $M_1$: no longitudinal crest from protoconid to anterior cingulum; metalophid present; transverse valley V-shaped in lingual view; axes of lophids slant posterodorsally. Jaw: massive; condyle with short anteroposterior width relative to the extremely elongate transverse diameter; articular surface of condyle nearly straight in dorsal view; genial pits broad shallow depressions on ventral surface of symphysis; genial crest absent; angular process and posterior masseteric eminence strongly developed.

### PYRAMIOS ALCOOTENSE, gen.nov. et sp.nov.

(Figs 1–4, Tables 1–6)

*Holotype.* CPC 6749, nearly complete skull lacking only right first and second incisors, left second and third incisor and a portion of the left zygomatic arch.

*Paratypes.* UCMP 66097, basicranium; UCMP 69789, juvenile skull lacking basicranium and rostrum; UCMP 69757, premaxillary and maxillary fragments; UCMP 69753, left premaxillary; UCMP 69754, right premaxillary fragment; UCMP

---

* πυραμις a pyramid, ιος, appearance of; in reference to the pyramidal construction of the principal cusp of the upper premolar.

69756, right premaxillary with I$^{1}$–I$^{3}$; UCMP 65875, left premaxillary with I$^{1}$; UCMP 69755, 69759, 69785, 66195, 69760, 67150, 69726, 69771, eight RI$^{1}$; UCMP 69761, 69763, 69762, 67032, 69772, 69773, six LI$^{1}$; UCMP 69766, 69768, 69769, 69770, four RI$^{2}$; UCMP 69767, 69776, two LI$^{2}$; UCMP 69785, 69774, two RI$^{3}$; UCMP 65844, 69786, 67100, three left I$^{3}$; UCMP 69752, left maxillary fragment with M$^{1}$–M$^{4}$; UCMP 69572, right maxillary fragment with P$^{3}$–M$^{3}$; UCMP 66997, left maxillary fragment with P$^{3}$–M$^{4}$; UCMP 69751, right maxillary fragment with remnants of P$^{3}$–M$^{4}$; UCMP 69724, 69740, 69730, three RP$^{3}$; UCMP 69725, LP$^{3}$; UCMP 69737, left maxillary fragment with roots of P$^{3}$, M$^{1}$; UCMP 67047, 69744, 69573, RM$^{1}$; UCMP 69731, RM$^{3}$; UCMP 69732, 69738, right maxillary fragments with M$^{3}$–M$^{4}$; UCMP 65892, left maxillary fragment with M$^{3}$–M$^{4}$; UCMP 69728, 69736, two RM$^{4}$; UCMP 69746, LM$^{4}$; UCMP 69735, 69726, two fragmentary left upper molars;

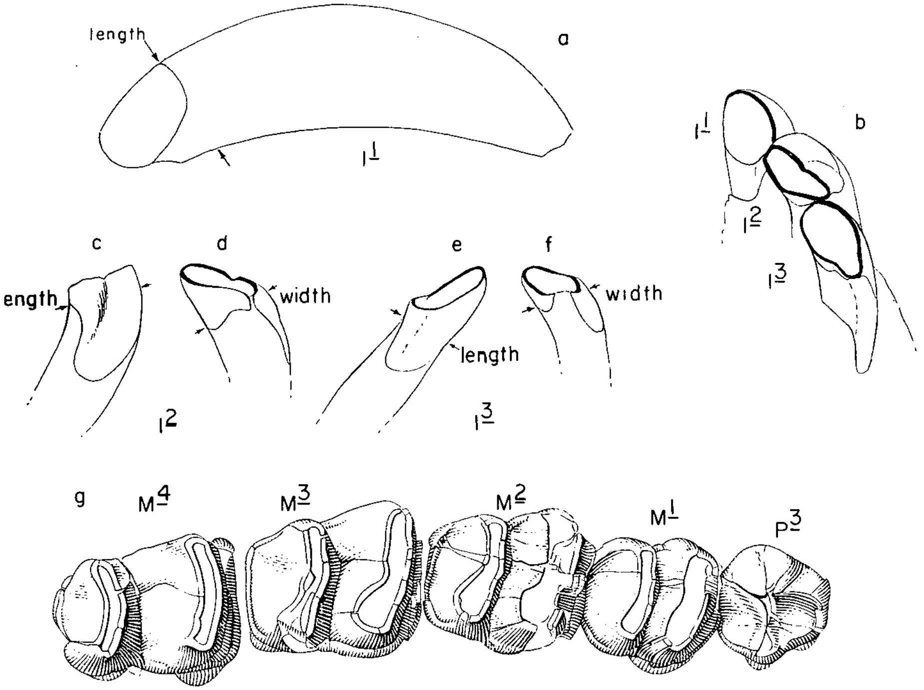


**Fig. 1**

*Pyramios alcootense* **gen.nov. et sp.nov.**

- **a. Lateral view of left upper first incisor, UCMP 69761. x $\frac{3}{4}$.
Length at base of crown (Table 1) measured between arrows.
Width measured perpendicular to length.**
- **b. Occlusal view of left upper incisors, UCMP 69756. x $\frac{3}{4}$.**
- **c. Labial view of left second upper incisor, UCMP 69756. x $\frac{3}{4}$.
Length of crown (Table 1) measured between arrows.**
- **d. Posterior view of left second upper incisor, UCMP 69756. x $\frac{3}{4}$.
Width of crown (Table 1) measured between arrows.**
- **e. Labial view of left third upper incisor, UCMP 69756. x $\frac{3}{4}$.
Length of crown (Table 1) measured between arrows.**
- **f. Posterior view of left third upper incisor, UCMP 69756. x $\frac{3}{4}$.
Width of crown (Table 1) measured between arrows.**
- **g. Occlusal view of right cheek tooth dentition of holotype, CPC 6749. x $\frac{3}{4}$.**

UCMP 65897, a partial right and left $M^4$; UCMP 69729, 69743; two $RI_1$; UCMP 69741, 69733, 69734, 69742, 65886, five $LI_1$; UCMP 69727, $RP_3$; UCMP 69750, $LM_2$; UCMP 69745, $RM_3$; UCMP 69747, partial right lower molar; UCMP 69723, 69749, two left lower molars; UCMP 69571, right jaw with $P_3$–$M_4$; UCMP 69777, right jaw fragment, UCMP 69778, right jaw fragment with $M_2$–$M_4$; UCMP 69781, left jaw and symphyseal portion of right; UCMP 65889, maxillary tuberosity; UCMP 69779, condylar portion of right jaw; UCMP 66237, right condylar portion; UCMP 66996, right jaw with $M_1$–$M_4$; UCMP 69782, right jaw with $P_3$–$M_4$; UCMP 69787, nearly complete left jaw with $P_3$–$M_4$; UCMP 69783, left jaw with $M_1$–$M_4$; UCMP 66972, left jaw with remnant $M_3$–$M_4$; UCMP 69784, right jaw with $M_1$–$M_4$; UCMP 69787, right juvenile jaw with $P_3$–$M_4$.

*Type locality.* Paine Quarry, V-6345, Waite Formation, 4 miles south-west of Alcoota station, 2·1 miles south-west of junction of Waite and Ongeva Creeks, Northern Territory, Australia.

*Age.* Alcoota fauna, early Pliocene or late Miocene.

*Specific diagnosis.* That of the genus until other species are described.

### *Upper dentition*

*Incisors.* Twelve incisors have been measured for Table 1 (see Fig. 1a for method of measurement). The first upper incisor is a moderately compressed tooth which tapers toward each end from a thick middle portion. The cross-section of the tooth near its occlusal surface is an elongate oval. The roughly D-shaped cross-section of the middle portion is maintained for a short distance proximally, then becomes an elongate oval once more. In lateral view the outer surface falls on a arc whose radius is 38·0–50·0. In an unworn tooth the curvature may increase to a radius of 25·0 at its tip. The medial surface of the tooth bears a broad groove, shallow for the most part but becoming deeper toward the tip of the root. The lateral surface is smoothly curved. In some specimens a faint groove is developed in the lateral surface about 6·0 above the ventral border. The enamel cap is found on the dorsal, the dorsal half of the lateral, and only the dorsal corner of the medial surfaces. The occlusal surface is worn nearly flat in most specimens; it is slightly convex anteroposteriorly and slightly concave laterally. In some, the surface is concave anteroposteriorly, with the anterior, enamel covered, portion projecting down beyond the general level of occlusion.

There are six second upper incisors in the sample (Table 1). This (Fig. 1b, c, d) is a broadly triangular tooth in occlusal view; the outer surface bears a well developed groove which rises toward the base of the enamel cap. The occlusal outline is nearly symmetrical, the posterior apex of the triangle being placed nearly midway between the other two corners. The outer surface is strongly curved from enamel cap to root, the greatest curvature occurring at the base of the enamel. All surfaces taper gradually toward the tip. The medial surface of the root, which faces $I^1$ is flat or slightly concave. The posterior surface, facing $I^3$, is convex except for a flat facet just at the base of the crown caused by attrition against the third incisor.

Six third upper incisors (Table 1) have been identified as belonging to this species. The occlusal outline (Fig. 1b) is obliquely elongate; triangular with a strong posterior apex. The anterior surface, which presses against $I^2$, is flat. The lateral surface bears a broad shallow groove near its midpoint. A complementary groove occurs in the medial surface. The anterior and medial surfaces of the shaft are nearly straight. The lateral and posterior surfaces are convex. The shaft tapers toward its tip about 40·0 above the posteromedial base of the crown.

Table 1: Measurements on upper incisors of *Pyramios alcootense*

| | | $I^1$ | | | | $I^2$ | | $I^3$ | |
|---|---|---|---|---|---|---|---|---|---|
| | Side | Length of crown | Transverse width | Length, root | Root closed | Length of crown | Width | Length of crown | Width |
| CPC 6749 | R | .... | .... | .... | ? | .... | .... | 15·2 | 11·1 |
| | L | 20·4*a* | 12·0*a* | .... | ? | .... | .... | .... | .... |
| UCMP 69756 | R | 16·7*a* | 13·1 | 61·5*a* | ? | 13·5 | 11·0 | 11·3 | 10·5 |
| UCMP 65875 | L | 17·4*a* | .... | .... | ? | | | | |
| UCMP 69755 | R | 19·6 | 12·1 | 71·1 | + | | | | |
| UCMP 69759 | R | 17·5 | 10·5 | .... | ? | | | | |
| UCMP 69758 | R | 17·7 | 10·8 | .... | ? | | | | |
| UCMP 66195 | R | 19·9 | 12·0 | 63·4 | + | | | | |
| UCMP 69760 | R | .... | 12·8 | .... | ? | | | | |
| UCMP 67150 | R | 15·1 | 11·5 | .... | ? | | | | |
| UCMP 67032 | L | .... | 13·3*a* | .... | ? | | | | |
| UCMP 69763 | L | .... | 12·1*a* | .... | ? | | | | |
| UCMP 69762 | L | 17·9 | 12·9 | 70·6 | + | | | | |
| UCMP 69766 | R | | | | | 14·0 | 9·6 | | |
| UCMP 69768 | R | | | | | 15·6 | 9·4 | | |
| UCMP 69770 | R | | | | | 12·7 | 8·0 | | |
| UCMP 69767 | L | | | | | 14·3 | 8·9 | | |
| UCMP 69776 | L | | | | | 17·0 | 10·0 | | |
| UCMP 69785 | R | | | | | | | 11·8 | 10·4 |
| UCMP 69786 | L | | | | | | | 12·4 | 10·0 |
| UCMP 67100 | L | | | | | | | 11·5 | 9·1 |
| UCMP 65844 | L | | | | | | | 11·7 | 9·7 |
| Range | | 15·1–<br>20·4*a* | 10·5–<br>13·3*a* | 61·5*a*–<br>71·1 | | 12·7–<br>17·0 | 8·0–<br>10·0 | 11·5–<br>12·4 | 9·1–<br>10·4 |

*a* = approximate; + = root closed; ? = condition not known.

Table 2: Measurements on $P^3$ of *Pyramios alcootense*

| | Side | Height, unworn parametacone | Length | Width | Transverse width, tip parametacone to tip protocone |
|---|---|---|---|---|---|
| CPC 6749 | R | .... | 19·0*a* | 20·8 | 8·9 |
| | L | .... | 20·9 | 20·5*a* | 11·0 |
| UCMP 69789 | R | 9·8*m* | 19·8 | 17·6 | 7·3 |
| | L | .... | 18·8*a* | 16·6*a* | 7·8*a* |
| UCMP 69724 | R | .... | 18·9 | 16·8 | .... |
| UCMP 69740 | R | 12·9 | 18·4 | .... | 6·8 |
| UCMP 69730 | R | .... | 19·1 | .... | 7·8 |
| UCMP 69725 | L | .... | 18·5 | 16·8 | .... |
| UCMP 66997 | L | .... | 17·8*a* | 17·2*a* | .... |
| UCMP 69572 | R | 10·8 | 17·4 | 17·0 | 7·3 |
| Range | | 9·8*m*–<br>12·9 | 17·4–<br>20·9 | 16·8*a*–<br>20·8 | 6·8–<br>11·0 |

*a* = approximate; *m* = moderately worn.

*Premolars.* $P^2$ and $dP^3$ are not known for *Pyramios.* $P^3$ (Table 2, Fig. 1g) is a two-rooted triangular tooth composed of two primary cusps and two poorly developed styles. A longitudinal and a transverse crest divide the crown into unequal quadrants. The longitudinal crest passes from a small parastyle at the anterior end of the tooth, across the apex of the parametacone, and ends at the metastyle. The major lingual cusp, the protocone, is connected by anterior and posterior cingula to the bases of the parastyle and metastyle, respectively. The transverse crest leads from the protocone to the parametacone. The crest continues down the labial surface of the parametacone, and progressively expands into a low rounded mesostyle at the base of the crown. The mesostyle does not have a separate apex, but is continuous with the labial surface of the parametacone. It differs from the more cuspate mesostyles of other phalangeroids. The labial cingulum between the mesostyle and parastyle is absent. That between the meso- and meta-styles is composed of a faint anterior prolongation of the base of the metastyle which dies out just before reaching the base of the mesostyle.

*Upper molars.* Measurements have been made on 10 $M^1$'s (Table 3). This is an elongate, rectangular, bilophodont tooth (Fig. 1g) with two anterior and one posterior root. In the protoloph, the paracone is about the same height as the protocone. In the metaloph, the hypocone is slightly higher than the metacone. The cusps of the metaloph are generally higher than their counterparts in the protoloph. Small parastyles and metastyles are developed at the anterolabial and posterior corners of the teeth, respectively. The width of the protoloph, while variable, is about the same as that of the metaloph. Both are concave posteriorly and oriented anterolabially. In unworn specimens both the protoloph and metaloph develop an anteriorly projecting lip at their respective crests.

The parastyle is connected by a short crest to the paracone. A moderately well developed postparaconal crest descends into the transverse valley from the posterior side of the paracone. This joins to a short premetaconal crest at the anterior surface of the metaloph lingual to the metacone. At the extreme labial edge of the tooth, a small crest curves posteriorly from the apex of the paracone on to the labial cingulum. A similar but less developed crest curves from the apex of the metacone to the anterior base of the metastyle. A labial cingulum is absent at the bases of the paracone and metacone, but is present at the transverse valley. A broad, shelf-like anterior cingulum is continuous from the base of the parastyle around to the anterolingual base of the protocone. Immediately behind this a long, broadly curved lingual cingulum is developed which extends back to the lingual base of the hypocone. Again immediately posterior to this, the posterior cingulum curves around the rear of the tooth to the base of the metastyle.

Second molars, of which there are six measurable specimens (Table 3), are slightly larger than $M^1$. Except that the protoloph is distinctly wider than the metaloph, the metastyle usually less well developed and the postparaconal and premetaconal crest weaker, $M^2$ is essentially like $M^1$. $M^3$ (11 measured specimens, Table 3) and $M^4$ (14 measured specimens, Table 3) taper more posteriorly, and the stylar cusps and postparaconal and premetaconal crests as well as the crests leading

Table 3: Measurements on $M^1$–$M^4$ of *Pyramios alcootense*

| | Side | Length | Width of of protoloph | Width of of metaloph | Height, unworn paracone | Height, unworn metacone | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|
| $M^1$ | | | | | | | | |
| CPC 6749 | R | 24·6 | 21·4 | 20·3 | .... | .... | .... | .... |
| | L | 25·4 | 20·0*a* | 21·4 | .... | .... | .... | .... |
| UCMP 69789 | R | 21·5 | 17·8*a* | 20·1*a* | .... | .... | .... | .... |
| | L | 21·2 | 20·0 | 18·9*a* | .... | .... | .... | .... |
| UCMP 69737 | L | 25·6 | 20·3 | 19·8*a* | .... | .... | .... | .... |
| UCMP 69744 | R | 25·7 | 20·4 | 19·7 | 11·8 | 12·6 | 12·2 | 13·8 |
| UCMP 69753 | R | 21·5 | 17·5 | 17·6 | 8·2 | 9·7 | 10·4 | 12·3 |
| UCMP 67047 | R | 21·5 | 17·2 | 17·2 | 9·7 | 10·8 | 9·4 | 12·2 |
| UCMP 66977 | L | .... | 18·3*a* | 19·1 | .... | .... | .... | .... |
| UCMP 69572 | R | 21·0 | 17·1*a* | 17·9 | .... | .... | .... | .... |
| Range | | 21·0–25·7 | 17·1*a*–21·4 | 17·2–21·4 | 8·2–11·8 | 9·7–12·6 | 9·4–12·2 | 12·2–13·8 |
| $M^2$ | | | | | | | | |
| CPC 6749 | R | 28·8*a* | 24·4*a* | 21·4 | .... | .... | .... | .... |
| | L | 29·4*a* | 24·7*a* | 21·5 | .... | .... | .... | .... |
| UCMP 69789 | R | 24·8 | 21·5 | 20·0 | .... | .... | .... | .... |
| | L | 25·4 | 22·5 | 20·6 | .... | .... | .... | .... |
| UCMP 66997 | L | 26·3*a* | .... | .... | .... | .... | .... | .... |
| UCMP 69572 | R | 24·9 | 20·4 | 19·3 | 8·4*s* | 9·4*s* | 9·7*s* | 10·8*s* |
| Range $M^2$ | | 24·8–29·4*a* | 20·4–22·5 | 19·3–21·5 | 8·4*s* | 9·4*s* | 9·7*s* | 10·8*s* |
| $M^3$ | | | | | | | | |
| CPC 6749 | R | 29·7 | 26·5 | 22·1 | .... | .... | .... | .... |
| | L | 28·8*a* | 25·6 | 21·6 | .... | .... | .... | .... |
| UCMP 69789 | R | 27·6 | 23·5 | 20·8 | .... | .... | .... | .... |
| | L | 28·5 | 23·1 | 20·7 | .... | .... | .... | .... |
| UCMP 69757 | R | 32·9 | .... | 25·3*a* | .... | .... | .... | .... |
| UCMP 69731 | R | 28·0*a* | 19·0*a* | 17·4*a* | 10·8 | 9·0 | 12·3 | 12·5 |
| UCMP 69738 | R | .... | .... | 22·2*a* | .... | .... | .... | .... |
| UCMP 65892 | L | 29·6 | 26·5 | 23·1 | .... | .... | .... | .... |
| UCMP 66997 | L | 27·8 | 23·9 | .... | .... | .... | .... | .... |
| UCMP 69572 | R | 27·6 | 24·0 | 20·5*a* | 10·9 | 10·9 | 11·0 | 10·2 |
| UCMP 69752 | L | 25·5 | 20·6 | 17·6 | .... | .... | .... | .... |
| Range, $M^3$ | | 25·5–32·9 | 19·0*a*–26·5 | 17·4*a*–25·3*a* | 10·8–10·9 | 9·0–10·9 | 11·0–12·3 | 10·2–12·5 |
| $M^4$ | | | | | | | | |
| CPC 6749 | R | 31·3*a* | 23·7 | 20·2*a* | .... | .... | .... | .... |
| | L | 31·3*a* | 25·8*a* | 22·1 | .... | .... | .... | .... |
| UCMP 69789 | R | 29·8 | 22·7 | 19·1 | 10·7 | 11·5 | 10·4 | 11·6 |
| | L | 29·7 | 23·5 | 18·8 | .... | 9·2 | 11·2 | 11·7 |
| UCMP 69757 | R | 35·1 | 26·6*a* | 21·7*a* | .... | .... | .... | .... |
| | L | 34·3 | .... | 22·4*a* | .... | .... | .... | .... |
| UCMP 69732 | R | 25·2 | 20·6 | 16·8*a* | .... | .... | .... | .... |
| UCMP 69738 | R | 31·4 | .... | 20·8 | .... | .... | .... | .... |
| UCMP 65892 | L | 30·3 | 25·8*a* | 20·2*a* | .... | .... | .... | .... |
| UCMP 69736 | L | 32·9 | 24·9 | 21·7 | 12·2 | 8·7 | 14·8 | 13·5 |
| UCMP 69746 | L | 36·4*a* | 28·5*a* | 23·0 | .... | 11·8 | 13·8 | 15·3 |
| UCMP 69728 | R | 32·0 | 25·4*a* | 20·0 | .... | .... | .... | .... |
| UCMP 66997 | L | 27·9*a* | 32·6 | 19·7 | .... | .... | .... | .... |
| UCMP 69752 | L | 25·0 | 20·2 | 16·4 | .... | .... | .... | .... |
| Range, $M^4$ | | 25·0–36·4*a* | 20·2–32·6 | 16·4–23·0 | 10·7–12·2 | 8·7–11·8 | 10·4–14·8 | 11·6–15·3 |

*a* = approximate; *s* = slightly worn cusp.

from the labial ends of the paracone and metacone to the labial cingulum and to the metastylar area, respectively, are less well developed. $M^4$ is longer than, but not as wide as, $M^3$.

In some specimens (UCMP 69789), parastyle and metastyle are developed about equally well on all molar teeth. In all molar teeth, but particularly in $M^1$ and $M^2$, the transverse valley is tightly V-shaped, owing mainly to the posteriorly expanded base of the protoloph. The anterior surfaces of the protoloph and metaloph tend to be concave anteriorly as seen in lateral view. In all molars, the anterior cingulum bears a definite dorsal swelling near the midpoint of the tooth. In $M^1$ and $M^2$ a smaller, second longitudinal crest tends to be developed across the transverse valley about 3·5 lingual to the postparaconal-premetaconal crest.

*Lower dentition*

*Incisors.* (Table 4, Fig. 2a, b.) Seven measurable $I_1$'s have been recovered. The elongate, dorsally curved spatulate tooth tapers posteriorly from the base of the enamel cap toward the tip of the root. The enamel is distinctly deeper vertically than the adjacent root. In unworn and little worn specimens the dorsal edge of the enamel curves anteromedially and ventrally from the bulge at the base of the crown, toward its anterior tip. The enamel-covered portion of the incisor is twisted obliquely so that, as seen in anterior view, a line drawn between its dorsal and ventral edges lies at an angle of about 45° to the vertically oriented shaft.

An elongate groove is developed on the posterior portion of both the labial and lingual surfaces of the shaft. In labial view (Fig. 2a) the posterior edge of the enamel cap has a broadly sigmoid configuration; a deep posterior lobe on the dorsal half and a complementary anterior recess ventrally. On the lingual surface (Fig. 2b) the posterior edge of the enamel extends anteriorly for a short distance from the dorsal edge, then curves ventrally and slightly anteriorly toward the ventral edge. Just before reaching the ventral edge the enamel border turns sharply anteriorly once more for a short distance (about 8·0). Both the dorsal and ventral edges of the shaft curve strongly posterolingually.

*Premolars.* $P_2$ and $dP_3$ are unknown. Only four third premolars (Fig. 2c, d) have been preserved (Table 4). This is a rather low, simple triangular tooth with one anterior and one posterior root. In one unworn specimen (UCMP 69787) the tip of the main cuspid rises about 11·2 above the base of the enamel. As seen in Table 4, the tooth is only about 15 to 25 percent longer than wide. The basal outline is subtriangular. A high main cuspid in the anterior third of the tooth sends off a short crest from its apex to the anterolingual corner of the tooth. This crest then curves posteriorly as a short lingual cingulum. The posterior longitudinal crest joins the apex of the main cuspid to the low median posterior cuspid. There are no transverse crests associated with the posterior cuspid. A short crest also leads posterolingually from the main cuspid to the midlingual base. A small lingual cingulum leads posteriorly from the base of this crest to the base of the posterior cuspid. There are no cingula on the labial surface of the tooth.

Table 4: Measurements on lower incisor and third premolar of *Pyramios alcootense*

| | | $I_1$ | | | $P_3$ | | |
|---|---|---|---|---|---|---|---|
| | Side | Length, base to tip of enamel | Height at base of crown | Width at base of crown | Length | Width | Height of unworn main cuspid |
| UCMP 69729 | R | 34·3*a* | 22·8 | 9·4 | | | |
| UCMP 69743 | R | .... | 20·7 | 11·2 | | | |
| UCMP 69741 | L | .... | 26·4 | 11·1 | | | |
| UCMP 69734 | L | .... | 28·5 | 12·6 | | | |
| UCMP 69733 | L | 35·7*a* | 28·9 | 13·1 | | | |
| UCMP 69742 | L | .... | 25·6 | 10·0 | | | |
| UCMP 65886 | L | .... | 20·7 | 9·8 | | | |
| UCMP 69727 | R | | | | .... | 12·2 | .... |
| UCMP 65971 | R | | | | 15·4 | 11·5 | .... |
| UCMP 69782 | L | | | | 13·5 | 11·5 | .... |
| UCMP 69787 | R | | | | 14·9 | .... | 11·2*a* |
| Range | | 34·3*a*<br>35·7*a* | 20·7–<br>28·9 | 9·4–<br>13·1 | 13·5–<br>15·4 | 11·5–<br>12·2 | 11·2*a* |

*a* = approximate.

*Molars.* Four first lower molars (Table 5) are complete enough to allow measurements to be taken. $M_1$ (Fig. 2c, d) is an elongate, nearly rectangular, bilophodont tooth with one anterior and one posterior root. The protolophid is slightly narrower than the hypolophid. Both are slightly anteriorly concave and directed slightly anterolabially. No sharp paralophid crest connects the protoconid to the anterior cingulum. The transverse valley between the two lophids is slightly sinuous in occlusal view. The metalophid is developed as a low anteriorly directed crest on the anterior face of the hypolophid. The small lingual and labial cingula occur only at the transverse valley. In one specimen (UCMP 69571), a faint crest continues from the anterior cingulum up the anterolabial corner of the protoconid. A similar crest rises up the posterolabial corner of the protoconid and anterolabial corner of the hypoconid from either end of the labial cingulum; a fourth crest rises up the posterolabial corner of the hypoconid from the posterior cingulum. The posterior cingulum bears a small dorsal swelling near its lingual third. This expanded area is joined to the hypolophid by a broad but low longitudinally oriented raised area on the posterior surface of the lophid. In both labial and lingual view the bottom of the transverse valley is V-shaped not U-shaped. The axes of the lophids slant posterodorsally.

*Posterior molars.* With the exception of details noted below, $M_2$, $M_3$, and $M_4$ are essentially larger counterparts of $M_1$. Nine $M_2$'s, eight $M_3$'s, and five $M_4$'s were available for study (Table 5). In $M_2$ and $M_3$, the protolophid is about as wide as the hypolophid, but in $M_4$ the metalophid is definitely narrower. In general the lingual cuspids are higher than their labial counterparts and those of the protolophid are lower than those of the hypolophid. The length and width of each molar are greater than those of the preceding one. The metalophid is more strongly developed at the rear of the dental series and begins to be expressed on the posterior surface of the protolophid in $M_3$ and $M_4$. The swelling near the lingual third of the posterior cingulum becomes better developed and its connexion to the rear of the hypolophid becomes more distinctly crest-like. In little-worn specimens it can be seen that the metalophid begins at the apex of the hypoconid, and is directed anterolingually for about half its length before turning anteriorly toward the bottom of the transverse valley. In the posterior molars the transverse valley becomes less tightly V-shaped than in $M_1$ and the axes of the lophids become progressively more vertical. The total length, $P_3$–$M_4$, is measurable in two specimens. In UCMP 69571 this distance is 119·5; in UCMP 69782, it is about 121·0.

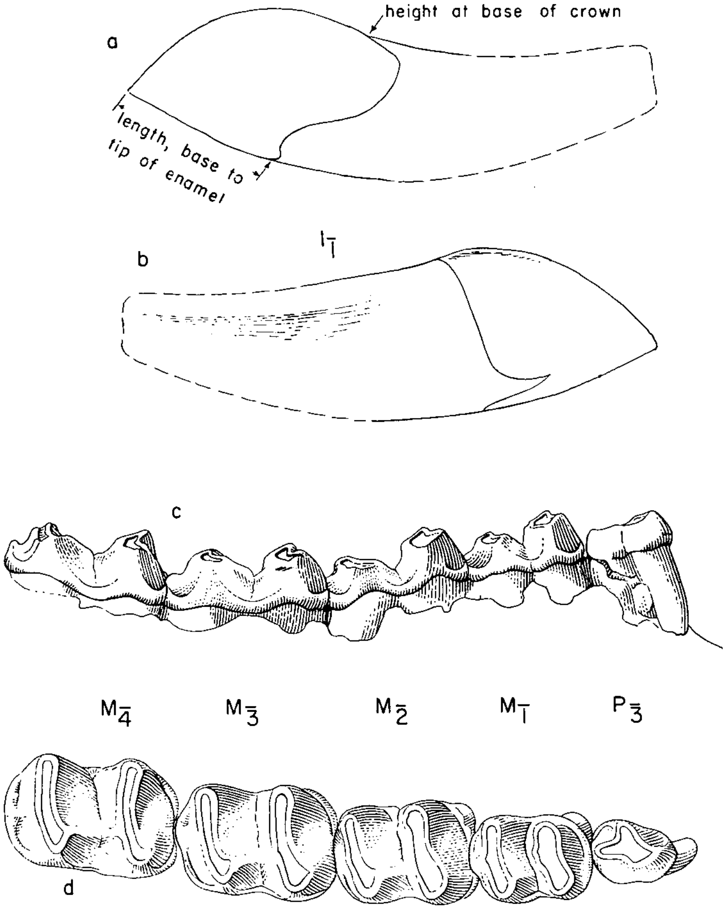


Fig. 2.

*Pyramios alcootense* gen.nov. et sp.nov.

a. Lateral view of left lower incisor, UCMP 69733. x $\frac{3}{4}$. Height at base of crown (Table 4) measured between arrows. Width measured perpendicular to length. Length of enamel measured along ventral edge of tooth.
b. Medial view of left lower incisor, UCMP 69733. x $\frac{3}{4}$.
c. Labial view of right lower cheek tooth dentition, UCMP 69751. x $\frac{3}{4}$.
d. Occlusal view of right lower cheek tooth dentition, UCMP 69751. x $\frac{3}{4}$.

Table 5: Measurements on lower molars of *Pyramios alcootense*

| | Side | Length | Width of protolophid | Width of hypolophid | Height of protoconid | Height of hyperconid | Height of metaconid | Height of entoconid |
|---|---|---|---|---|---|---|---|---|
| $M_1$ | | | | | | | | |
| UCMP 69571 | R | 20·9 | 14·3 | 14·8 | .... | | | |
| UCMP 69872 | L | 21·2 | 15·2*a* | 15·6*a* | .... | | | |
| UCMP 69783 | L | .... | .... | 17·3 | .... | | | |
| UCMP 69787*b* | R | .... | .... | .... | 12·2 | | | |
| Range, $M_1$ | | 20·9–21·2 | 14·3–15·2*a* | 14·8–17·3 | 12·2 | | | |
| $M_2$ | | | | | | | | |
| UCMP 69750 | L | 28·9 | 18·5*a* | 19·1*a* | .... | .... | | |
| UCMP 69571 | R | 24·5 | 17·4 | 16·1 | .... | .... | | |
| UCMP 69778 | R | 28·4 | 19·5 | 19·5*a* | .... | .... | | |
| UCMP 69780 | R | 27·7*a* | 18·8*a* | 18·6*a* | .... | .... | | |
| UCMP 66996 | R | 29·7 | .... | 21·4*a* | .... | .... | | |
| UCMP 69782 | L | 24·4 | .... | .... | .... | .... | | |
| UCMP 69783 | L | 27·7 | 19·0 | 19·9 | .... | .... | | |
| UCMP 69784 | R | 27·3*a* | .... | 18·7*a* | .... | .... | | |
| UCMP 69787*c* | R | 26·3 | .... | 17·9*a* | 12·8 | 10·8 | | |
| Range, $M_2$ | | 24·4–29·7 | 17·4–19·5 | 16·1–21·4*a* | 12·8 | 10·8 | | |
| $M_3$ | | | | | | | | |
| UCMP 69745 | R | 27·8 | 18·0 | .... | 12·9 | 11·6 | 13·8 | 12·8 |
| UCMP 69571 | R | 27·3 | 19·6 | 18·2 | .... | .... | .... | .... |
| UCMP 69778 | R | 32·7 | 23·3 | 23·4 | .... | .... | .... | .... |
| UCMP 69780 | R | 30·1 | 21·2*a* | 21·5*a* | .... | .... | .... | .... |
| UCMP 66996 | R | 36·1 | .... | 24·9*a* | .... | .... | .... | .... |
| UCMP 69782 | L | 27·2 | .... | .... | .... | .... | .... | .... |
| UCMP 69784 | R | 30·0 | 21·3*a* | 21·1*a* | .... | .... | .... | .... |
| UCMP 69787 | R | 31·2*a* | 21·9 | 21·3 | 14·3 | 13·3 | 14·5 | 11·8 |
| Range, $M_3$ | | 27·2–36·1 | 18·0–23·3 | 18·2–24·9*a* | 12·9–14·3 | 11·6–13·3 | 13·8–14·5 | 11·8–12·8 |
| $M_4$ *d* | | | | | | | | |
| UCMP 69571 | R | 30·1 | 20·5 | 19·5 | | | | |
| UCMP 69778 | R | 35·8 | 24·2 | 23·7 | | | | |
| UCMP 69782 | L | 30·5 | 19·8 | 18·3 | | | | |
| UCMP 69783 | L | 34·7 | 32·6 | 23·4 | | | | |
| UCMP 66972 | L | 34·0 | .... | 21·0 | | | | |
| Range, $M_4$ | | 30·1–35·8 | 19·8–32·6 | 18·3–23·7 | | | | |

*a* = approximate.
*b* Only unworn height of protoconid could be measured.
*c* Only unworn height of protoconid and hypoconid could be measured.
*d* Unworn height could not be measured on any of the cuspids.

*Mandible.* (Table 6.) The eleven measured specimens vary through a moderately large range. The teeth in UCMP 69783 are in about the same stage of wear as those in UCMP 69571, yet the jaw of the former is much more robust as well as being about one-third larger. A similar comparison can be made between UCMP 69782, one of the smallest, and UCMP 69784, the largest jaw of *Pyramios alcootense* in the collection. The greater depth of the horizontal ramus of the larger jaws is particularly impressive. Since variations in the configuration and measurements of lower jaws may be related to ontogenetic age it has been useful to treat the specimens according to the following arbitrary arrangement:

Stage 1. $P_3$–$M_2$ fully erupted, teeth unworn.

Stage 2. $P_3$–$M_3$ fully erupted, teeth only slightly worn.

Stage 3. $P_3$–$M_4$ fully erupted. $M_4$ unworn or only slightly worn; wear of other teeth progressively increases toward $P_3$.

Stage 4. $P_3$–$M_4$ fully erupted. Hypolophid of $M_4$ at least halfway worn down. In the tables of jaw measurements which follow, only those specimens in classes 3 and 4 have been included.

Despite the variance of size, the sample displays a unified suite of characters and is treated as a single species. Although jaw size may vary considerably a comparable discrepancy in tooth dimensions is not to be found, suggesting that sexual rather than individual variation is responsible for the observed differences in jaw dimensions.

The deep horizontal ramus presents a nearly flat lateral surface (Fig. 3) from the anterior edge of the ascending ramus to the canine alveolus. A low bulge on the lateral surface extends forward from the leading edge of the horizontal ramus, diminishes anteriorly, and dies out in the dorsal third of the jaw below $M_2$. The flat surface which lies below this anteriorly diminishing convexity expands dorsally below $M_2$ and extends anteriorly to the rear of the symphyseal portion. At this point the lateral surface of the jaw is bent slightly laterally and continues forward to house the lower incisor. The mental foramen, located from about 20·0 to 40·0 below the dorsal edge of the jaw at the anterior root of $P_3$, opens anterodorsally on to the lateral surface of the symphyseal region above the root of the incisor. The ventral profile of the symphysis extends slightly below the general level of the ventral edge of the horizontal ramus. A small digastric process is located at the ventral edge below $M_4$ (121·2 posterior to the rear of the symphysis in UCMP 69784). The ventral profile of the horizontal ramus between the digastric process and the symphysis is only slightly curved.

Posterior to the digastric process the ventral profile of the jaw curves posterodorsally toward the tip of the angular process. If the ventral border of the jaw is oriented horizontally, the posteromedial tip of the angular process would probably be located above the level of the tooth row, and at about the same point as the apex of the posterior masseteric eminence on the lateral surface. The broad posterior surface of the angular region of the jaw is slightly concave. The posterior edge of the ascending ramus is constricted (23·0 to 32·5) at the neck, below the occipital condyle. The condyle expands widely above the neck to a transverse diameter of 88·5 to 94·4 in two specimens. The head of the condyle is asymmetrical; the medial process extends far beyond the longitudinal axis of the ascending ramus. The dorsal surface has its greatest anteroposterior width in at its lateral end. Medially, the flat dorsal surface extends slightly anteriorly and tapers toward its inner tip, which is bent ventrally and slightly posteriorly. In some specimens the *fovea pterygoidea* is a deep triangular excavation on the anteromedial base of the condyle just below the articular surface and medial to the mandibular notch. The fovea is bounded medially by an anterolateroventrally directed strut which buttresses the medial tip of the condyle. As far as can be determined in specimens at hand the anterior half of the masseteric fossa is relatively shallow. As seen in UCMP 69782, the posterior edge of the coronoid process extends anterodorsally from the mandibular notch to at

### Table 6: Measurements on lower mandibles of *Pyramios alcootense*

| | Side | Length of symphysis | Length, dorsal edge of incisor alveolus to rear $M_4$ | Length, dorsal edge of incisor alveolus to postalveolar process | Length, dorsal edge of incisor alveolus to mandibular canal | Length, dorsal edge of incisor alveolus to rear of condyle | Length, $P_3$ to $M_4$ | Length, $P_3$ to postalveolar process | Length, $P_3$ to mandibular canal | Length, $P_3$ to rear of condyle | Length, rear of symphysis to digastric process | Length, anterior root of $P_3$ to rear of mental foramen* | Depth, bottom edge mental foramen below dorsal edge of jaw at $P_3$ | Depth, horizontal ramus below anterior end $M_1$ | Depth, horizontal ramus below anterior end $M_3$ | Length, rear of condyle to anterior edge of ascending ramus | Length, postalveolar process to rear of $M_4$ | Length, mandibular canal to postalveolar process | Anteroposterior width, condyle | Transverse width, condyle | Width, horizontal ramus below rear of $M_3$ | Length, diastem $P_3$–$I_1$ | Stage of maturity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UCMP 69571 | R | .... | .... | .... | .... | .... | 119·5 | 137·5 | 196·5 | 196·5 | .... | —4·9 | 30·7 | 70·0 | 63·6*a* | 81·6 | 15·6 | 23·4 | .... | .... | 38·1 | .... | – |
| UCMP 69777 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 37·9 | .... | .... | .... | .... | – |
| UCMP 69781 | L | 91·6+ | .... | .... | .... | .... | .... | .... | .... | .... | .... | o | 32·5 | 90·4 | 80·6+ | .... | 30·0 | 12·3 | .... | .... | 44·5 | .... | 4 |
| UCMP 66237 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 20·8 | 88·5 | .... | .... | – |
| UCMP 69780 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | —11·3 | 36·5 | 90·8 | 86·5 | .... | .... | .... | .... | .... | 37·8*s* | .... | 4 |
| UCMP 66996 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 79·1 | .... | .... | .... | .... | .... | 51·2*l* | .... | 4 |
| UCMP 69783 | L | 79·4 | 191·7 | 228·3 | 249·4 | .... | .... | .... | .... | .... | .... | +10·6 | .... | .... | .... | .... | 35·0 | 24·3 | .... | .... | 44·5 | 57·6*a* | 4 |
| UCMP 69782 | R | .... | .... | .... | .... | .... | 121·0 | 133·8 | 170·2 | 211·9 | .... | o | 20·7 | 67·1 | 65·1 | 109·4 | 10·9 | 38·1 | .... | .... | 33·4 | 79·8*a* | 4 |
| UCMP 66972 | L | 103·5+ | .... | .... | .... | .... | .... | .... | .... | .... | .... | —3·4 | 24·0 | .... | 75·3 | .... | 37·0 | 31·7*a* | .... | .... | 52·1*l* | .... | 4 |
| UCMP 69784 | R | 129·5+ | 233·2*a* | 262·3*a* | 292·6*a* | 334·5*a* | .... | .... | .... | .... | 121·2 | +2·4 | 39·6 | 95·6 | 95·5 | 132·1 | 32·3 | 36·1 | 19·8 | 94·4 | 44·1 | 103·3 | 4 |
| Range | | 79·4–<br>129·5+ | 191·7–<br>233·2*a* | 228·3–<br>262·3*a* | 249·4–<br>292·6*a* | 334·5*a* | 119·5–<br>121·0 | 133·8–<br>137·5 | 170·2–<br>196·5 | 196·5–<br>211·9 | 121·2 | —11·3<br>to<br>+10·6 | 20·7–<br>39·6 | 67·1–<br>95·6 | 63·6*a*–<br>95·5 | 81·6–<br>132·1 | 10·9–<br>37·0 | 12·3–<br>38·1 | 19·8–<br>20·8 | 88·5–<br>94·4 | 34·4–<br>51·2*l* | 57·6*a*–<br>103·3 | |

*a* = approximate.
\+ = element partly broken, actual measurement would be larger.
*s* = specimen crushed measurement too small.
*l* = specimen crushed measurement too large.

*—: rear of foramen posterior to anterior edge of $P_3$ root.
+: rear of foramen anterior to anterior edge of $P_3$ root.
o: rear of foramen directly under anterior edge of $P_3$ root.

least the level of the condyle. The anterior edge of the ascending ramus leads dorsally or slightly anterodorsally from the body of the horizontal ramus, past $M_4$, at least to the level of the mandibular notch. Beyond this point, information is lacking. The ventral edge of the masseteric fossa lies below the level of the tooth row, generally about on a line with the mental foramen, and leads posterodorsally into the posterior masseteric eminence. The posterior masseteric eminence, best developed in UCMP 69783, is a broadly flange-like structure the apex of which lies about 25·0 above the level of the tooth row. The posterior portion of the masseteric fossa is about 45·0 deep, for this is the distance to which the tip of the eminence extends lateral to the longitudinal axis of the ascending ramus.

Except for a low ridge which extends anteroventrally from the postalveolar process toward the symphysis, the medial surface (Fig. 4) of the horizontal ramus is flat. The surface dorsal to the low ridge slants slightly dorsolaterally toward the

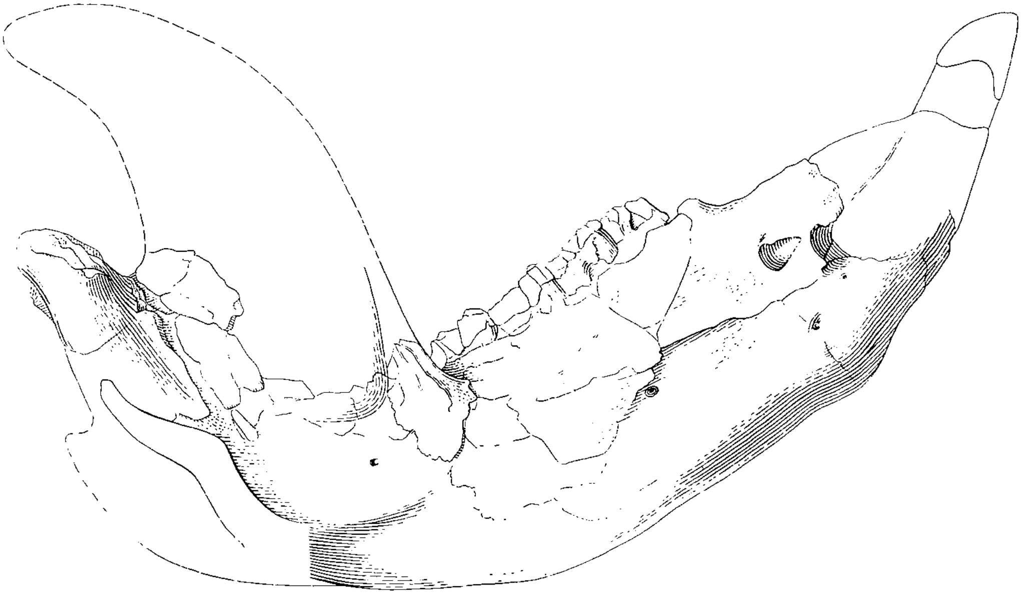


**Fig. 3.**

*Pyramios alcootense* **gen.nov. et sp.nov.**

**Lateral view of right mandible, UCMP 69784. x $\frac{1}{3}$. Unshaded areas bounded by solid lines indicate restoration based on other specimens; dashed lines indicate probable configuration of parts not represented by the available material.**

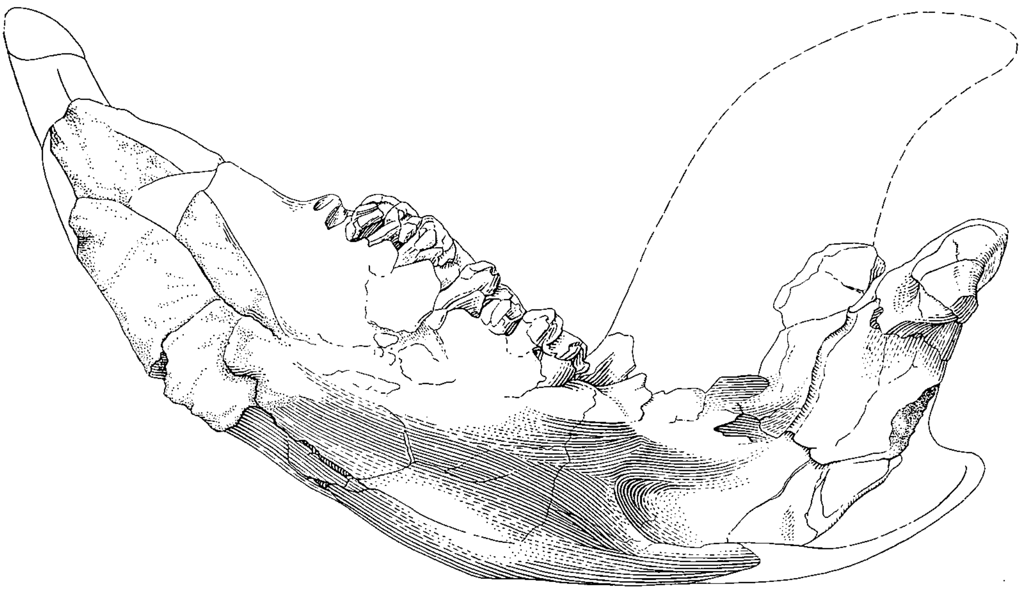


**Fig. 4.**

***Pyramios alcootense*, gen.nov. et sp.nov.**

**Medial view of right mandible, UCMP 69784. x $\frac{1}{3}$. Significance of unshaded and dashed areas as in Fig. 3.**

tooth row. Ventral to the ridge the medial surface is slightly excavated into the digastric fossa. The digastric fossa extends posterior to the small digastric process and is separated by an anterodorsally oriented bony bar from the deep pterygoid fossa. The pterygoid fossa occupies the medial surface of the angular portion of the jaw below and behind the postalveolar shelf. The fossa narrows and becomes shallower toward its posterodorsal extremity below the neck of the condyle. The posterior tip of the angular process is not preserved in any of the jaws of *Pyramios alcootense* available, but it could reasonably be expected to resemble the reconstruction in Figure 4. The postalveolar shelf extends posteriorly from the tooth row and terminates in a postalveolar process 10·9 to 35·0 behind $M_4$. The process is variably expressed. In some specimens it is a slightly pyramidal proliferation of the shelf; in others it is a distinct spur-like projection. The mandibular canal lies 12·3 to 38·1 behind and either on the same level as or slightly dorsal to the postalveolar process. The distinctness with which the foramen is separated by a ventral ridge from the pterygoid fossa is variable.

The dorsal surface of the symphysis is broadly U-shaped and rises anteriorly toward the dorsal edge of the incisor alveoli. The large genial pits are emplaced in the posterior surface of the symphysis, not restricted to the ventral surface.

*Remarks.* Features of *P. alcootense* such as the marked posterior tapering of the root of $I^1$, the simple, pyramidal construction of $P^3$, the relatively strong development of the postparaconal crest on the upper molars, the configuration of the enamel on the lateral and medial surfaces of $I_1$, the relatively broad outline of $P_3$, and the absence of a paralophid crest on $M_1$, demonstrate the strong separation of this species from the other Alcoota diprotodontids. As far as can be determined from the present evidence, *Pyramios alcootense* is the earliest known member of the lineage which contains such forms as *Meniscolophus mawsoni*, *Euryzygoma dunense*, *Euowenia robusta*, and *E. grata*.

## Genus KOLOPSIS* nov.

*Genotypic species.* *Kolopsis torus* sp.nov.

*Generic diagnosis.* $I^1$: D-shaped cross-section with curved lateral surface and nearly flat medial surface; in lateral view, root shows almost no anterior and posterior taper from portion of root proximal to crown; root open at proximal tip; general radius of curvature of outer surface in lateral view 25·0 to 32·0. $I^2$: triangular occlusal surface, nearly symmetrical, less deeply triangular than in *Pyramios alcootense*; greatest curvature of outer surface occurs distal to base of crown; root tapers gradually toward proximal tip. $I^3$: occlusal surface triangular, nearly equidimensional well defined groove on outer surface. $P^3$: low-crowned; occlusal outline subrectangular with moderate elongation of parastyle caused by emargination of lingual base between paracone and protocone; tooth two-rooted; parastyle moderately large, with sharp labial and lingual ridges; generally distinct separation of paracone and metacone by shallow, narrow lingual and labial grooves; paracone and metacone slender; no mesostyle; no metastyle; protocone major lingual cusp, subsidiary to paracone or metacone, connected to paracone by low ridge; base of protocone not expanded posterolabially to form broad close contact with anterolingual base of metacone; hypocone present, smaller than protocone; parastyle separated from paracone by transverse cleft, attached to protocone by small lingual cingulum. $M^1$: parastyle and metastyle prominent; postparaconal crest slightly developed, directed longitudinally; no mesostyle; labial cingulum absent, anterior cingulum not broadened at anterolingual corner of tooth, lingual cingulum shorter than in *P. alcootense*, evenly rounded, convex lingually. $I_1$: moderately spatulate; blade oriented at an angle of about 45° to the root; blade not conspicuously deeper than immediately adjacent root; root vertically thicker than blade proximal to crown; posterior edge of lateral surface of crown a straight line, nearly perpendicular to dorsal edge; in medial view, enamel cap restricted to a thin strip which only just overlaps on to medial surface and parallels dorsal and ventral borders of tooth. $P_3$: moderately short, relatively more elongate than in *P. alcootense*; triangular outline; main cuspid

---

* κολος—shortened, οπσις—appearance; after the moderately short occlusal outline of the upper premolar.

connected to anterior apex of tooth by longitudinal crest; moderate to strong indentation in labial surface just posterior to base of main cuspid; strong lingual crest from posterior cuspid. $M_1$: with sharp remnant paralophid crest from protoconid to anterior cingulum; metalophid absent; transverse valley open, U-shaped; axes of lophids vertical. Jaw: slender; condyle not so transversely elongate relative to its anterior width as in *P. alcootense*; condyle with strongly sigmoid dorsal surface; genial pits small, deep, circular, directed posteriorly from posterior surface of symphysis; genial crest present; angular process and posterior masseteric eminence more moderately developed than in *P. alcootense*.

## KOLOPSIS TORUS* sp.nov.

(Figs 5–6, Tables 7–13)

*Holotype.* CPC 6749, nearly complete skull, lacking only left zygomatic arch, right and left $I^2$ and $I^3$.

*Paratypes.* UCMP 65877, 68779, 68777, three left premaxillaries with $I^1$; UCMP 68778, right premaxillary with $I^1$; UCMP 68776, palate and rostrum with $RI^1$–$I^3$, $LI^1$, $RP^3$, $LP^3$–$M^4$; UCMP 65866, 68781-68783, six $RI^1$; UCMP 68780, 68785–68787, four $LI^1$; UCMP 65894, 66977, 68848, three $RI^2$; UCMP 66999, 68788, two $LI^2$; UCMP 68789, 68790, 68829, 69701, four $RI^3$; UCMP 68830, 66617, two $LI^3$; UCMP 68836, $RP^3$; UCMP 68842, $LP^3$; UCMP 67441, 68831, two maxillary fragments with $RP^3$–$M^4$; UCMP 68834, maxillary fragment with $RP^3$–$M^3$; UCMP 68835, maxillary fragment with $RM^1$–$M^4$; UCMP 70025, palatal fragment with R and $LM^3$–$M^4$; UCMP 66975, 68833, 70022, three maxillary fragments with $RP^3$–$M^1$; UCMP 70024, palatal fragment with $RM^2$–$M^4$, $LM^1$–$M^4$; UCMP 68974, maxillary fragment with $LM^3$–$M^4$; UCMP 68978, maxillary fragment with $LM^1$–$M^4$; UCMP 68981, maxillary fragment with $LP^3$–$M^1$; UCMP 68857, palatal fragment with R and $LM^3$–$M^4$; UCMP 67462; palate and rostrum with R and $LI^1$, $P^3$–$M^4$; UCMP 68856, palatal fragment with $RP^3$–$M^2$, $LP^3$–$M^1$; UCMP 68841, maxillary fragment with $RP^3$–$M^2$; UCMP 67464, palatal fragment with $RP^3$–$M^3$, $LP^3$–$M^1$; UCMP 68854, palatal fragment with R and $LP^3$; UCMP 68855, 67156, two maxillary fragments with $LP^3$–$M^3$; UCMP 68849, maxillary fragment with $LP^3$; UCMP 66974, maxillary fragment with $LP^3$–$M^2$; UCMP 68850, maxillary fragment with $LM^2$–$M^4$; UCMP 68853, maxillary fragment with $LM^2$–$M^3$; UCMP 65867, 68851, 68852, three $LP^3$; UCMP 68838, 65977, two $RM^1$; UCMP 67041, 68985, 68984, 68983, 68980, 68979, 65899, 68972, ten $LM^1$; UCMP 70023, $RM^1$–$M^2$; UCMP 67029, 68846, 68837, three $RM^2$; UCMP 67035, 68847, 67019, 68982, 68844, five $RM^3$; UCMP 68982, 68975, two $LM^3$; UCMP 70026, $LM^2$–$M^4$; UCMP 68845, $RM^3$–$M^4$; UCMP 68843, 65900, 68839, 68940, five $RM^4$; UCMP 68973, 68977, 68976, three $LM^4$; UCMP 68893, juvenile jaw with $RP_3$–$M_2$; UCMP 68892, juvenile jaw with $RP_3$–$M_4$; UCMP 68891, juvenile jaw with $RP_3$–$M_3$; UCMP 68894, jaw with $RP_3$–$M_4$; UCMP 67440, jaw

---

* *torus*-protuberance; after the protuberant nature of the parastyle due to the basal lingual emargination between the parastyle and protocone, and the relatively wide transverse cleft between the parastyle and paracone.

with RM$_1$–M$_4$; UCMP 65984, jaw with RP$_3$–M$_4$; UCMP 66650, jaw with RP$_3$–M$_4$; UCMP 69113, jaw with RM$_2$–M$_4$; UCMP 68898, jaw with RP$_3$–M$_4$; UCMP 68897, jaw fragment with RM$_3$; UCMP 68896, jaw fragment with RM$_3$–M$_4$; UCMP 68895, jaw with RM$_3$–M$_4$; UCMP 70027, jaw with RP$_3$–M$_4$; UCMP 68913, jaw fragment

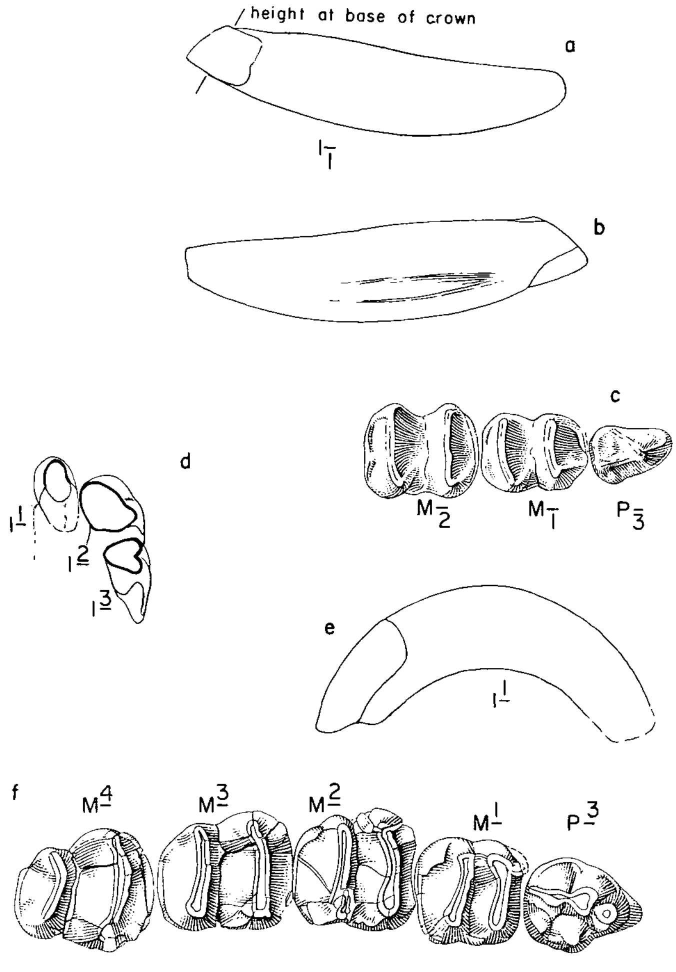


**Fig. 5.**

*Kolopsis torus* **gen.nov. et sp.nov.**

**a. Lateral view of left lower incisor, UCMP 68966. x $\frac{3}{4}$. Height at base of crown (Table 10) measured as shown.**
**b. Medial view of left lower incisor, UCMP 68966. x $\frac{3}{4}$.**
**c. Occlusal view of right P$_3$–M$_2$, UCMP 68893. x $\frac{3}{4}$.**
**d. Occlusal view of left upper incisors, UCMP 68776. x $\frac{3}{4}$.**
**e. Lateral view of left first upper incisor, UCMP 65886. x $\frac{3}{4}$.**
**f. Occlusal view of right cheek tooth dentition of holotype, CPC 6747. x $\frac{3}{4}$.**

with $RM_2$; UCMP 68912, jaw fragment with $RM_4$; UCMP 68900, nearly complete jaw with $RP_3$–$M_4$; UCMP 66464, jaw with $RM_1$–$M_4$; UCMP 67154, fractured jaw with $RM_1$–$M_4$; UCMP 68916, jaw with $RM_3$–$M_4$; UCMP 68515, jaw with $RM_3$–$M_4$; UCMP 68914, jaw with $RM_3$–$M_4$; UCMP 68920, jaw with $RM_3$–$M_4$; UCMP 67149, jaw with $RP_3$–$M_4$; UCMP 70028, juvenile jaw with $RP_3$, $M_2$–$M_4$; UCMP 70029, jaw with $RP_3$–$M_4$; UCMP 70030, jaw with $RM_2$–$M_4$; UCMP 68899, pair of jaws with $RP_3$–$M_4$, $LP_3$–$M_3$; UCMP 70031, paired symphyseal region and left ramus with $RP_3$, $LP_3$–$M_4$; UCMP 70032, paired symphyseal region and left ramus with $LM_2$, $M_4$; UCMP 68917, juvenile jaw with $LP_3$–$M_4$; UCMP 68918, juvenile jaw with $LP_3$–$M_4$; UCMP 67157, jaw with $LM_1$–$M_4$; UCMP 67148, juvenile jaw with $LM_2$–$M_4$; UCMP 68922, jaw with $LM_1$–$M_3$; UCMP 67442, jaw with $LM_1$–$M_4$; UCMP 70033, jaw fragment with $LM_1$–$M_3$; UCMP 68933, jaw fragment with $M_2$–$M_3$; UCMP 65878, jaw fragment with $LM_3$–$M_4$; UCMP 68899, pair of jaws with $RP_3$–$M_4$, $LP_3$–$M_3$; UCMP 70034, jaw with $LM_3$–$M_4$; UCMP 70035, jaw with $LM_2$–$M_4$; UCMP 67153, jaw with $P_3$–$M_2$; UCMP 67155, jaw with $M_1$–$M_4$; UCMP 66523, jaw with $LP_3$–$M_4$; UCMP 68921, jaw with $P_3$–$M_4$; UCMP 65876, jaw fragment with $LM_2$.

*Specific diagnosis.* That of the genus until other species are described.

*Type locality.* Paine Quarry, V-6345, Waite Formation, 4 miles south-west of Alcoota station, 2·1 miles south-west of junction of Waite and Ongeva Creeks, Northern Territory, Australia.

*Age.* Alcoota fauna, early Pliocene or late Miocene.

*Upper dentition*

*Incisors.* Six upper first incisors have been measured for Table 7. See Figure 1a for method of measurement. $I^1$ (Fig. 5d, e) is a thin, laterally compressed, curved tooth which tapers slightly toward the tip and root. Although the curvature is sharper toward the proximal and distal ends, that of the main part of the tooth falls on an arc whose radius varies between 25·0 and 32·0. The medial surface of the tooth is flattened and bears a shallow groove in the outer third. The lateral surface is convex. A small groove is developed in one specimen near the middle of the lateral surface posterior to the enamel cap. Wear produces a chisel-like occlusal surface which is notched in its posterior part. The dorsoventral height of the worn portion of the surface and the extent to which it is notched is variable. At the tip of little worn or unworn specimens such as UCMP 68777, the enamel cap extends around onto the lateral and medial surfaces. In UCMP 68783, the terminal part of a nearly unworn incisor, the enamel cap is at least 40·0 long as measured along the curvature of the anterior surface.

$I^2$ (Table 7) has the broadest occlusal surface (Fig. 5d) of all the incisor teeth. The occlusal surface is subtriangular, with a strong apex near the middle of the posteromedial surface. There is a weakly developed groove in the labial third of the outer surface, which fades out toward the base of the enamel cap. The medial and posterolabial surfaces of the root bear an elongate, shallow concavity which leads posterodorsally toward the tip. The outer surface curves posterodorsally from the tip of enamel to the root. The greatest degree of curvature occurs a little above the base of the enamel.

Table 7: Measurements on upper incisors of *Kolopsis torus*

| | | $I^1$ | | | | $I^2$ | | $I^3$ | |
|---|---|---|---|---|---|---|---|---|---|
| | Side | Antero-posterior length | Trans-verse width | Length of root | Root open | Length | Width | Length | Width |
| CPC 6747 | R | 16·5*a* | 10·7*a* | .... | .... | | | | |
| | L | 17·5*a* | 8·5 | .... | .... | | | | |
| UCMP 67462 | L | .... | .... | .... | *o* | | | | |
| UCMP 65866 | R | 12·3 | 6·8 | 48·2 | *o* | 6·7 | 9·6 | | |
| UCMP 68784 | R | 13·4 | 7·9 | .... | .... | | | | |
| UCMP 68785 | L | 14·4 | 7·6 | .... | .... | | | | |
| UCMP 66977 | R | | | | | 6·7 | 9·6 | | |
| UCMP 65894 | R | | | | | 6·0 | 10·2 | | |
| UCMP 68848 | R | | | | | 7·5 | 12·2 | | |
| UCMP 66999 | L | | | | | 6·6 | 11·0 | | |
| UCMP 68788 | L | | | | | 7·0 | 11·4 | | |
| UCMP 68789 | R | | | | | | | 6·3 | .... |
| UCMP 68790 | R | | | | | | | 7·2 | 7·3 |
| UCMP 68829 | R | | | | | | | 7·1 | 7·1 |
| UCMP 68830 | L | | | | | | | 6·3 | 7·3 |
| UCMP 66617 | L | | | | | | | .... | 6·7 |
| Range | | 12·3–<br>17·5*a* | 6·8–<br>10·7*a* | 48·2 | | 6·0–<br>7·5 | 9·6–<br>12·2 | 6·3–<br>7·2 | 6·7–<br>7·3 |

*a* = approximate; *o* = root open.

The shaft of $I^3$ (Table 7) is the straightest of the upper incisors. The tooth tapers slightly from triangular occlusal surface (Fig. 5d) to the tip of the root. The apex of the occlusal surface is medial. A vertical groove is developed on the mid-lateral and in two specimens on the posteromedial surface. The proximal tip of the root is about 25·0 above the dorsal base of the enamel cap.

*Premolars.* $P^2$ and $DP^3$ are as yet unknown in *Kolopsis*. $P^3$ (Table 8) is a relatively short, low-crowned subtriangular tooth composed of five cusps: the parastyle, paracone, metacone, protocone and hypocone. The greatest width of the tooth is measured across the protocone. The position of the hypocone is considerably more labial than that of the protocone. The tooth thus becomes considerably narrower behind and in front of the protocone. The metastyle is not developed. The posterior longitudinal crest from the metacone joins the posterior cingulum at the posterolabial corner of the tooth. The cusps are relatively low and broad. The parastyle forms a strong anterior projection in the occlusal outline. It is sharply isolated from the rest of the tooth by a chevron-shaped transverse cleft. Posterior to the cleft, an anterolabially directed ridge extends from the apex of the paracone toward the labial cingulum. A labial crest from the tip of the parastyle continues posteriorly as a labial cingulum and connects to the anterolabial base of the paracone. This portion of the labial cingulum is very weak in some specimens; in others it is strongly developed. A more posterior segment of the cingulum connects the base of the paracone to the posterior cingulum. The anterior portion of the lingual cingulum extends from the protocone to the parastyle and continues as a nearly vertical ridge to the tip of the latter. The lingual cingulum also leads posterolaterally from the protocone to the hypocone.

Table 8: Measurements on upper third premolar of *Kolopsis torus*

| | Side | Anteroposterior length | Transverse width | Width between apices of paracone and protocone | Width between apices of metacone and hypocone | Length, tips of parastyle and paracone | Length, tips of paracone and metacone | Length, apices of protocone and hypocone | Height, unworn parastyle | Height, unworn paracone | Height, unworn metacone | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CPC 6747 | R | 18·6 | 15·6 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| | L | 18·6 | 14·7 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 68831 | R | 19·8 | 15·6 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 67441 | R | 19·2 | 15·4 | 6·2 | 6·9 | 5·3 | 3·7 | 5·7 | 4·8 | 7·8 | 7·3*s* | 4·4*s* | 3·4*s* |
| UCMP 66975 | R | 18·1 | 14·2 | 5·5 | 5·2 | 4·9 | 2·7 | 6·7 | 6·5 | 7·6 | 6·7 | 5·5 | 3·4 |
| UCMP 68836 | R | 17·2 | 14·1 | 6·3 | 0* | 5·3 | 3·7 | 0* | 5·2 | 9·4 | 8·8 | 4·7 | 0* |
| UCMP 68776 | R | 18·6 | 15·8 | 6·1 | 6·9 | 5·8 | 3·7 | 6·4 | 6·0 | 9·0 | 8·4 | 4·9 | 4·1 |
| | L | 19·7 | 15·6 | 6·9 | 6·8 | 5·4 | 4·1 | 6·7 | 5·7 | 8·8 | 8·8 | 4·7 | 3·1 |
| UCMP 68856 | R | 17·6 | 14·3 | .... | .... | .... | .... | 6·2 | 5·8 | .... | .... | 4·6 | 3·7 |
| | L | 17·6 | 14·1 | 5·7 | 6·8 | 5·1 | 3·8 | 6·4 | 5·2 | 8·6*s* | 8·1*s* | 5·1 | 3·7 |
| UCMP 68841 | R | 17·1*a* | 13·7 | 6·4 | 6·9 | 5·8 | 2·3 | 6·3 | 5·3 | 8·7 | 8·6 | 4·8 | 3·5 |
| UCMP 67464 | R | 18·6 | 15·8 | 6·3 | 5·8 | 4·5 | 4·6 | 6·4 | 6·1 | 7·7 | 8·4 | 5·8 | 4·1 |
| | L | 18·9 | 16·1 | 6·2 | 6·7 | 5·3 | 4·1 | 7·2 | 6·2 | 9·4 | 9·5 | 5·1 | 3·6 |
| UCMP 68852 | L | 20·2 | 15·5 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 66974 | L | 18·6 | 15·7 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 68849 | L | 20·1 | 15·2 | .... | .... | .... | .... | 6·9 | .... | .... | .... | 5·5 | 4·5 |
| UCMP 68855 | L | 20·5 | .... | .... | 7·5 | 5·7 | 3·3 | .... | 5·8 | 10·0 | 8·2 | .... | 4·2 |
| UCMP 67156 | L | 18·7 | 15·8 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| Range | | 17·1*a*–<br>20·5 | 13·7–<br>16·1 | 5·5–<br>6·9 | 5·2–<br>7·5 | 4·3–<br>5·8 | 2·3–<br>4·6 | 5·7–<br>7·2 | 4·8–<br>6·5 | 7·6–<br>10·0 | 7·3*s*–<br>9·5 | 4·4*s*–<br>5·5 | 3·1–<br>4·5 |

*a* = approximate; *s* = slightly worn; * = UCMP 68836 has no hypocone.

The paracone and metacone tend to be united by a longitudinal crest, but in most specimens the two cusps are clearly separated by a vertical groove on the labial and lingual surface of the ectoloph. The apices of the two cusps are distinctly separate. A strong longitudinal crest continues posteriorly from the metacone to the posterolabial corner of the tooth.

The protocone lies lingual to the paracone. These two cusps are poorly connected by a weak transverse crest which is nearly disrupted by the longitudinal valley at the lingual base of the ectoloph. In UCMP 68836, which also lacks a well defined hypocone, the protocone is positioned on a line midway between the paracone and metacone. In other specimens, the protocone is situated only slightly posterior to the paracone. In unworn specimens the protocone is about as high as the parastyle; both being lower than the paracone and metacone. The hypocone is lower than the protocone.

The hypocone is the smallest of the main cusps on the premolar. It is situated posterolingual to the metacone and posterolabial to the protocone. The hypocone is absent in UCMP 68836; in other specimens it ranges nearly as high as the protocone. The basal occlusal diameter of the hypocone is less than that of the protocone. These two cusps are connected by the lingual cingulum. A second connexion is often made by a low longitudinal crest which extends to the hypocone from the mid-posterior base of the protocone. The hypocone is more sharply separated from the labial cusps than is the protocone. In some specimens a small anterolabial ridge extends from the hypocone into the floor of the longitudinal valley.

*Molars.* M$^1$ (Table 9) is a slightly rectangular tooth (Fig. 5f), being somewhat longer than wide. The tooth is composed of two moieties, the protoloph and metaloph; both are concave anteriorly. The protoloph is transversely narrower than the metaloph; the tooth tapers slightly anteriorly. Anterior to the paracone is a smaller but prominent parastyle. The metastyle, posterior to the metacone, is a distinct cusp and is about the same size as the parastyle. The parastyle is separate from the paracone and bears an anterolingually directed crest which descends to the anterior cingulum and continues around the base of the tooth to the protocone. The metastyle bears a posterolingually oriented ridge which descends to the posterior cingulum and continues around to the posterolingual base of the hypocone.

The postparaconal crest which connects the two lophs is weakly developed. It occurs as a low ridge which descends into the transverse valley just lingual to the paracone on the posterior face of the protoloph. The paracone bears a second, very faint, crest, labial to the postparaconal crest, which descends to the equally weak labial cingulum at the mouth of the transverse valley.

The metacone is similar in size to the paracone, but is somewhat more labial in position. The protocone and hypocone are also similar in size, but the protocone is situated slightly more labially than the hypocone. From each cusp a weak ridge courses posterolabially across the posterior surfaces of the protoloph and metaloph. The crest from the protocone ends in the transverse valley near the midline. That from the hypocone blends into the base of the metaloph anterior to the posterior cingulum, also near the midline of the tooth. The smoothly convex cingulum is prominently developed across the transverse valley between the protocone and hypocone.

Table 9: Measurements on upper molars of *Kolopsis torus*

| | Side | Length | Width of protoloph | Width of metaloph | Height, unworn paracone | Height, unworn metacone | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|
| $M^1$ | | | | | | | | |
| CPC 6747 | R | 18·7 | 16·9 | 17·6 | .... | .... | .... | .... |
| | L | 18·1 | 16·6 | 16·8 | .... | .... | .... | .... |
| UCMP 68776 | R | 19·3 | 17·6 | 18·7 | .... | .... | .... | .... |
| UCMP 68831 | R | 20·5 | 17·9 | 18·4 | .... | .... | .... | .... |
| UCMP 67441 | R | 18·5 | 17·7 | 18·3 | .... | .... | .... | .... |
| UCMP 70022 | R | 19·0 | 16·6 | 17·5 | 6·7 | 6·1 | 7·3 | 8·6 |
| UCMP 65977 | R | 19·5 | 18·0 | 18·5 | .... | .... | .... | .... |
| UCMP 67464 | R | 19·4 | 17·2 | .... | .... | .... | .... | .... |
| UCMP 68981 | L | 17·4 | 16·2 | 16·4 | .... | .... | .... | .... |
| UCMP 70024 | L | 18·7 | 18·0 | 18·5 | .... | .... | .... | .... |
| UCMP 68856 | L | 18·8 | 16·9 | 16·5 | .... | .... | .... | .... |
| UCMP 67156 | L | 19·0 | 18·3*a* | 18·2 | .... | .... | .... | .... |
| Range, $M^1$ | | 17·4–20·5 | 16·2–18·3*a* | 16·4–18·7 | 6·7 | 6·1 | 7·3 | 8·6 |
| $M^2$ | | | | | | | | |
| CPC 6749 | R | 21·5 | .... | .... | .... | .... | .... | .... |
| UCMP 68776 | R | 22·2 | 20·4 | 19·5 | .... | .... | .... | .... |
| UCMP 67741 | R | 21·5 | 20·8 | 19·3 | .... | .... | .... | .... |
| UCMP 68831 | R | 22·3 | 20·6 | 20·5 | .... | .... | .... | .... |
| UCMP 68837 | R | 20·4 | 19·2 | 17·8 | .... | .... | .... | .... |
| UCMP 67029 | R | 22·9 | 20·4 | 18·7 | 8·7 | 9·5 | 10·3 | 9·6 |
| UCMP 70023 | R | 22·2 | 20·7 | 19·9 | .... | .... | .... | .... |
| UCMP 70024 | L | 19·7 | .... | .... | .... | .... | .... | .... |
| UCMP 70026 | L | 20·7 | .... | 19·1 | .... | 9·3 | .... | 10·6 |
| UCMP 68853 | L | 19·5 | .... | 18·0 | .... | .... | .... | .... |
| UCMP 68855 | L | 20·8 | 21·4 | 21·4 | 10·6 | 9·6 | 10·6 | 12·1 |
| Range, $M^2$ | | 19·7–22·9 | 19·2–21·4 | 17·8–21·4 | 8·7–10·6 | 9·3–9·6 | 10·3–10·6 | 9·6–12·1 |
| $M^3$ | | | | | | | | |
| CPC 6749 | R | 23·1 | 20·7 | 18·3 | .... | .... | .... | .... |
| UCMP 68776 | R | 24·2 | 22·8 | 20·4 | .... | .... | .... | .... |
| UCMP 67441 | R | 23·6 | 22·2 | 18·7 | .... | .... | .... | .... |
| UCMP 68831 | R | 24·8 | 23·2 | 20·4 | .... | .... | .... | .... |
| UCMP 70023 | R | 24·8 | 22·8 | 20·2 | .... | .... | .... | .... |
| UCMP 70024 | R | 24·0 | 22·0 | 19·4 | 8·9 | .... | 9·6 | 9·6 |
| | L | 22·4 | 22·2 | 19·3 | 10·2 | 9·2 | .... | 9·5 |
| UCMP 70025 | R | 23·9 | 23·0 | 19·4 | .... | .... | .... | .... |
| | L | 24·5 | 22·8 | 19·9 | .... | .... | .... | .... |
| UCMP 67119 | R | 21·7 | 20·4 | 17·7 | .... | .... | .... | .... |
| UCMP 68974 | L | 22·4 | 21·6 | 19·2 | .... | .... | .... | .... |
| UCMP 68975 | L | 25·0 | 21·5 | 19·2 | 10·7 | 9·4 | 10·8 | 11·4 |
| UCMP 68982 | L | 24·1 | 22·1 | 19·5 | .... | .... | .... | .... |
| UCMP 70026 | L | 23·5 | 21·5*a* | 19·6 | .... | .... | .... | .... |
| UCMP 68855 | L | 24·1 | 22·5*a* | 21·1 | 11·6 | 10·7 | .... | 12·7 |
| UCMP 68853 | L | 21·5 | 20·4 | 18·0 | .... | .... | .... | .... |
| UCMP 68850 | L | 23·4 | .... | 19·5 | .... | .... | .... | .... |
| UCMP 68857 | L | 24·2 | 22·2 | 20·7 | .... | .... | .... | .... |
| Range, $M^3$ | | 21·5–25·0 | 20·4–23·2 | 17·7–21·1 | 8·9–11·6 | 9·2–10·7 | 9·6–10·8 | 9·5–12·7 |

*a* = approximate.

Table 9: Measurements on upper molars of *Kolopsis torus*—continued

| | Side | Length | Width of protoloph | Width of metaloph | Height, unworn paracone | Height, unworn metacone | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|
| $M^4$ | | | | | | | | |
| CPC 6747 | R | 24·6 | 21·4 | 14·8 | .... | .... | .... | .... |
| UCMP 65900 | L | 24·7*a* | 23·3 | 22·0 | .... | .... | .... | .... |
| UCMP 67441 | R | 23·8*a* | 20·7 | 17·4 | 8·4 | 7·8 | 8·7 | 8·9 |
| UCMP 68831 | R | 25·3 | 23·5 | 18·8 | .... | .... | .... | .... |
| UCMP 68974 | L | 22·1 | 22·1 | 17·1 | .... | .... | .... | .... |
| UCMP 70024 | R | 23·9 | 21·2 | 16·1 | 8·7 | 8·1 | 9·7 | 8·9 |
| | L | 22·8 | 31·1 | 17·8 | 9·3 | 8·6 | .... | 8·9 |
| UCMP 70025 | R | 22·8 | 22·8 | 17·2 | .... | .... | .... | .... |
| | L | 22·7 | 22·6 | 17·2 | .... | .... | .... | .... |
| UCMP 68843 | R | 24·8 | 22·0 | 16·4 | 10·7 | 8·4 | 11·3 | 9·6 |
| UCMP 67035 | R | 23·1 | .... | 16·2 | .... | .... | .... | .... |
| UCMP 68839 | R | 25·1 | 22·1 | 17·8 | 10·5 | 7·4 | 10·9 | 9·0 |
| UCMP 68840 | R | 23·2 | 21·6 | 16·8 | 9·6 | .... | 10·5 | 8·4 |
| UCMP 70026 | L | 21·2*a* | 20·1 | 17·5 | 9·2 | 7·6 | 10·1 | .... |
| UCMP 68976 | L | 23·9 | 21·4 | 18·4 | 9·7 | 8·1 | 11·5 | 10·6 |
| UCMP 68977 | R | 23·1 | 21·0 | 17·2 | .... | .... | 10·5 | 7·9 |
| UCMP 68850 | L | 23·1 | 21·9 | 17·5 | .... | .... | .... | .... |
| UCMP 68857 | L | 24·1 | 21·4 | 18·4 | 10·2 | 8·9 | 11·2 | 10·1 |
| Range, $M^4$ | | 21·2*a*–25·3 | 20·1–23·3 | 14·8–22·0 | 8·4–10·7 | 7·4–8·9 | 8·7–11·3 | 8·4–10·6 |

*a* = approximate.

The basic construction of $M^2$ (Table 9) is like that of $M^1$. $M^2$ differs from $M^1$ in the following ways: $M^2$ is higher-crowned; the protoloph and metaloph are about equal in width, the metastyle is smaller than the parastyle; the connexion of the parastyle to the protoloph is more lingual; the parastyle is nearly transversely rather than anterolingually elongate; the postparaconal crest is better developed; the paracone is larger and is more labially placed than the metacone. The posterolabial crest from the protocone is better developed.

$M^3$ and $M^4$ (Table 9) are generally similar to $M^2$. $M^3$ tapers more to the rear than $M^2$ and $M^4$ than $M^3$. The parastyle and metastyle become reduced to the extent that in $M^4$ the metastyle is absent and the parastyle is present only as a small swelling at the labial end of the anterior cingulum. The crest from the hypocone in $M^4$ is nearly absent.

### *Lower dentition*

*Incisor* (Table 10). $I_1$ is a slender laterally compressed strap-like tooth (Fig. 5a, b) composed of a shaft and a terminal enamel cap. The ventral border curves smoothly upward anteriorly. The dorsal edge is concave dorsally except for a bulge in the root posterior to the enamel cap. The tooth is deepest at this point. The dorsal border of the enamel cap is slightly convex. The enamel is not deeper than the posteriorly adjacent root. In cross-section, the dorsal edge of the root is wider transversely than the ventral, and a medial groove just below the mid-depth of the root is parallel to the ventral edge of the tooth.

In contrast to the vertical orientation of the root, the enamel cap is twisted and becomes obliquely spatulate with its upper surface facing dorsomedially. A line drawn between the dorsal and ventral edges of the cap makes an angle of about 45°

with the line drawn between the same edges of the root, which are vertically aligned. The enamel is found chiefly on the lateral side of the tooth. The posterior edge of the enamel forms a nearly straight line directed essentially perpendicular to the dorsal edge, then curves anteroventrally into the ventral border. In some specimens (such as UCMP 68960 and 68969) the posterior border of the cap is composed of an upper and lower posteriorly convex portion, with an intervening concave segment. In little worn or unworn specimens, the dorsal edge of the cap is nearly parallel to the ventral until the distal one-fifth, at which point it curves abruptly downward to meet the ventral edge.

In medial view the enamel is restricted to a thin strip at the dorsal and ventral edge of the tooth. In ventral view, the ventral edge of the tooth is slightly medially concave.

Table 10: Measurements on lower first incisor of *Kolopsis torus*

| | Side | Height at junction of root and crown | Width at junction of root and crown | Length of enamel along ventral edge | Degree of wear of tip | Length, root from rear of enamel to proximal tip | Vertical height at proximal tip of root |
|---|---|---|---|---|---|---|---|
| UCMP 68970 .... | R | 16·6 | 10·7 | .... | .... | .... | .... |
| UCMP 68969 .... | R | 13·5 | 7·9 | 26·3 | *s* | .... | .... |
| UCMP 68963 .... | R | 15·4 | 9·7 | .... | .... | .... | .... |
| UCMP 68962 .... | R | 14·6 | 8·7 | 29·8 | *s* | .... | .... |
| UCMP 68956 .... | L | 15·6 | 8·2 | .... | .... | .... | .... |
| UCMP 68959 .... | L | 14·0 | 8·0 | .... | .... | .... | .... |
| UCMP 65893 .... | L | 15·8 | 8·3 | 22·5 | *m* | .... | .... |
| UCMP 68966 .... | L | 14·3 | 8·4 | .... | .... | 58·9 | 5·3 |
| Range .... .... .... | | 13·5–<br>16·6 | 7·9–<br>10·7 | 22·5–<br>26·3 | | 58·9 | 5·3 |

*s* = slightly worn; *m* = moderately worn.

*Premolars.* P$_2$ and DP$_3$ are unknown. P$_3$ (Table 11) is a short triangular tooth bearing a single central cuspid and a smaller median posterior cuspid (Fig. 5c). The high central cuspid sends off an anterior longitudinal crest to the apex of the tooth and a posterior longitudinal crest to the posterior cuspid. In occlusal view, the labial surface is grooved just posterior to the base of the main cuspid. The groove continues posterolingually toward the apex of the posterior cuspid. The degree of development of the groove, and the associated nearly vertical swelling which occurs labial to the posterior cuspid, are variable. In some specimens (as in UCMP 68892) these features are slightly expressed. In others (as in UCMP 68925) a prominent swelling forms over the labial edge of the posterior root.

The strong lingual crest from the posterior cuspid extends anteriorly as a slight ridge just above the base of the enamel and connects to the base of a prominent crest which is directed posterolingually from the tip of the central cuspid. In some specimens (as in UCMP 68893) a small posterolingual cuspid is developed on the lingual crest at the rear of the tooth. There is only a small anterolabial cingulum, which continues posteriorly from the apex of the tooth to the anterior end of the labial indentation.

Table 11: Measurements on lower third premolar of *Kolopsis torus*

| | Side | Length | Width | Height, unworn main cuspid |
|---|---|---|---|---|
| UCMP 68947 | L | 13·9 | 10·3 | .... |
| UCMP 68940 | R | 15·5 | 11·0 | .... |
| UCMP 68953 | L | 12·9 | 9·3 | .... |
| UCMP 65896a | L | 14·5 | 10·0 | 10·0 |
| UCMP 65896b | L | 14·2 | 10·8 | .... |
| UCMP 68951 | L | 13·2 | 9·8 | 11·2 |
| UCMP 68952 | L | 14·4 | 11·5 | .... |
| UCMP 68921 | L | 14·7 | 11·3 | .... |
| UCMP 67153 | L | 13·6 | 10·7 | .... |
| UCMP 66523 | L | 13·9 | 10·7 | .... |
| UCMP 68899 | R | 15·5 | 10·1 | .... |
| | L | 13·9 | 10·5 | .... |
| UCMP 68918 | L | 13·5 | 9·6 | .... |
| UCMP 68917 | L | 12·3 | 9·9 | .... |
| UCMP 68893 | R | 13·2 | 9·8 | 10·7 |
| UCMP 68892 | R | 13·7 | 9·6 | 10·4 |
| UCMP 68891 | R | 14·3 | 9·1 | .... |
| UCMP 66650 | R | 14·5 | 10·2 | .... |
| UCMP 68934 | R | 14·5 | 9·5 | .... |
| UCMP 70029 | R | 13·7 | 10·1 | .... |
| UCMP 70028 | R | 14·5 | 10·7 | .... |
| UCMP 68900 | R | 14·3 | 10·1 | .... |
| Range | | 12·3–15·5 | 9·1–11·3 | 10·0–11·2 |

*Molars* (Table 12). $M_1$ is an elongate rectangular tooth (Fig. 5c) composed of an anterior and posterior lophid, the protolophid, and the hypolophid. The anterior end of the tooth tapers slightly in front of the base of the protolophid; behind the hypolophid, the tooth is flat. The protoconid connects to the anterior end of the tooth by an anterolingually directed paralophid crest. In unworn and little worn specimens, the crests of the proto- and hypolophid are directed anterolabially across the tooth. The protolophid is narrower than the hypolophid. The metalophid is absent or only slightly developed. An anterior cingulum is present both labial and lingual to the paralophid crest connecting the protoconid to the anterior edge of the tooth. The cingulum on the lingual side of the ridge is stronger than on the labial side. The cingulum on the labial side of the tooth is small; it is found only at the transverse valley. The posterior cingulum connects the posterior base of the hypoconid to that of the entoconid. A slight swelling lingual to the midline marks the point where the greatest depth of cingulum occurs. The lingual cingulum is not present. In lingual view, the floor of the transverse valley is U-shaped. The transverse axes of the lophids are vertical.

$M_2$ is constructed as $M_1$, except that the protoconid is connected to the anterior edge of the tooth only by a very short, weakly developed paralophid crest. The tooth does not extend anteriorly in front of the base of the protolophid as in $M_1$. The anterior cingulum is not divided into a labial and lingual portion, but continues across the anterior basal part of the tooth as a relatively thin ridge. The metalophid is slightly better developed than in $M_1$. It occurs as a faint crest which descends anterolingually from the hypoconid to the floor of the transverse valley. The protolophid and hypolophid are about equally wide. Except for being larger, $M_2$ shows

Table 12: Measurements on lower molars of *Kolopsis torus*

| | Side | Length | Width of protolophid | Width of hypolophid | Height, unworn protoconid | Height, unworn hypoconid | Height, unworn metaconid | Height, unworn entoconid |
|---|---|---|---|---|---|---|---|---|
| $M_1$ | | | | | | | | |
| UCMP 68925 | L | 17·8 | .... | 13·7 | .... | .... | .... | .... |
| UCMP 67153 | L | 18·8 | 14·8 | 14·5 | .... | .... | .... | .... |
| UCMP 66650 | R | 18·0 | 12·5 | 13·8 | .... | .... | .... | .... |
| UCMP 70027 | R | .... | .... | 15·1 | .... | .... | .... | .... |
| UCMP 68892 | R | 17·8*a* | 12·5*a* | 12·5 | 9·5 | 8·4 | 8·1 | 6·1 |
| UCMP 68891 | R | 17·9*a* | 12·3 | 13·0 | 9·1*s* | 7·8*s* | 7·7*s* | 6·4*s* |
| UCMP 65984 | R | 18·2 | 12·8 | .... | .... | .... | .... | .... |
| UCMP 70031 | L | 18·4 | .... | 13·8 | .... | .... | .... | .... |
| UCMP 68922 | L | 18·7 | 12·3 | 13·1 | 9·0 | 8·1 | 7·3 | 6·8 |
| UCMP 67157 | L | 17·7 | 11·7 | 13·6 | .... | .... | .... | .... |
| UCMP 68918 | L | 17·4 | 13·6*a* | .... | .... | .... | .... | .... |
| UCMP 68917 | L | 17·2 | 12·1*a* | 12·8 | .... | .... | .... | .... |
| UCMP 68893 | R | 19·0 | 12·6 | 12·8 | 10·1*s* | 8·6*s* | 8·7*s* | 6·8*s* |
| Range, $M_1$ | | 17·2–<br>19·0 | 12·1*a*–<br>14·8 | 12·5–<br>15·1 | 9·0–<br>10·1*s* | 7·8*s*–<br>8·6*s* | 7·3–<br>8·7*s* | 6·1–<br>6·8 |
| $M_2$ | | | | | | | | |
| UCMP 68925 | L | 20·0 | 14·8 | 15·1 | .... | .... | .... | .... |
| UCMP 66464 | R | 20·9*a* | .... | 16·0 | .... | .... | .... | .... |
| UCMP 70028 | R | 21·4 | 15·6 | 15·3 | 12·2 | 10·2 | 9·8 | 9·3 |
| UCMP 70029 | R | 20·8 | .... | .... | .... | .... | .... | .... |
| UCMP 70030 | R | 21·6 | 15·0*a* | 15·3*a* | .... | .... | .... | .... |
| UCMP 68919 | L | 19·4 | 15·3 | 14·8 | .... | .... | .... | .... |
| UCMP 67153 | L | 21·1 | 16·4 | 15·7 | .... | .... | .... | .... |
| UCMP 68921 | L | 20·9 | 17·3*a* | 16·0 | .... | .... | .... | .... |
| UCMP 66650 | R | 20·2 | 14·8*a* | 15·4 | .... | .... | .... | .... |
| UCMP 70027 | R | 20·5 | .... | 15·5 | .... | .... | .... | .... |
| UCMP 68898 | R | 21·2 | 14·6*a* | 15·4 | .... | .... | .... | .... |
| UCMP 68892 | R | 19·5*a* | 14·1 | 13·8 | 11·6 | 10·4 | 9·2 | 7·7 |
| UCMP 65984 | R | 20·6*a* | .... | 15·0*a* | .... | .... | .... | .... |
| UCMP 70031 | L | 20·0 | .... | .... | .... | .... | .... | .... |
| UCMP 68922 | L | 18·9 | 14·3 | 15·1 | 11·4 | 9·8 | 9·2 | 8·6 |
| UCMP 67157 | L | 18·7*a* | 14·4 | 14·8 | .... | .... | .... | .... |
| UCMP 68918 | L | 19·2 | 15·5 | 14·8 | 10·6 | 9·5 | 9·0 | 7·8 |
| UCMP 67442 | L | 20·3 | 16·1 | 15·5*a* | .... | .... | .... | .... |
| UCMP 68893 | R | 20·0 | 15·0 | 14·3 | .... | .... | .... | .... |
| Range, $M_2$ | | 18·7*a*<br>21·6 | 14·1–<br>17·3 | 13·8–<br>16·0 | 10·6–<br>12·2 | 9·5–<br>10·4 | 9·0–<br>9·8 | 7·7–<br>9·3 |
| $M_3$ | | | | | | | | |
| UCMP 68914 | R | .... | .... | 17·0 | .... | .... | .... | .... |
| UCMP 68925 | L | 22·3*a* | 16·4 | 15·5 | 11·0*s* | 11·2*s* | 9·7*s* | 8·7*s* |
| UCMP 70030 | R | 24·6 | 18·5 | .... | .... | .... | .... | .... |
| UCMP 68924 | L | 23·2 | 18·3 | .... | .... | .... | .... | .... |
| UCMP 70034 | L | 24·7 | 19·2 | 18·1 | .... | .... | .... | .... |
| UCMP 70035 | L | 25·5 | 19·4 | 18·1 | .... | .... | .... | .... |
| UCMP 66650 | R | 22·9 | 17·9 | 17·3 | .... | .... | .... | .... |
| UCMP 69113 | R | 25·8 | .... | 19·7 | .... | .... | .... | .... |
| UCMP 70027 | R | .... | 18·9 | .... | .... | .... | .... | .... |
| UCMP 68898 | R | 22·2 | 17·7 | 17·0 | .... | .... | .... | .... |
| UCMP 67440 | R | 22·6 | 18·3 | 17·4 | .... | .... | .... | .... |
| UCMP 65984 | R | 21·8 | 18·0 | 16·8 | .... | .... | .... | .... |
| UCMP 70031 | L | 24·2 | 19·7 | 17·6 | .... | .... | .... | .... |
| UCMP 67157 | L | 22·1 | 17·8 | 17·5*a* | .... | .... | .... | .... |
| UCMP 68918 | L | 22·1 | 17·0 | 16·2 | 12·1 | 10·8 | 10·2 | 8·5 |
| UCMP 67442 | L | 23·2 | .... | 16·8 | .... | .... | .... | .... |
| Range, $M_3$ | | 21·8–<br>25·8 | 16·4–<br>19·7 | 15·5–<br>18·1 | 11·0*s*<br>12·1 | 10·8–<br>11·2*s* | 9·7*s*–<br>10·2 | 8·5–<br>8·7*s* |

*a* = approximate; *s* = slightly worn.

Table 12: Measurements on lower molars of *Kolopsis torus*—continued

| | Side | Length | Width of proto-lophid | Width of hypo-lophid | Height, unworn protoconid | Height, unworn hypoconid | Height, unworn meta-conid | Height, unworn ento-conid |
|---|---|---|---|---|---|---|---|---|
| $M_4$ | | | | | | | | |
| UCMP 68914 | R | 24·0 | 19·2 | 17·0*a* | 10·7 | .... | 9·6 | 8·6 |
| UCMP 68925 | L | 23·1 | 17·4 | 15·6 | 10·9 | 9·4 | .... | .... |
| UCMP 67149 | R | 25·4 | 20·5 | .... | .... | .... | .... | .... |
| UCMP 68920 | R | 25·3 | 20·7 | .... | .... | .... | .... | .... |
| UCMP 68924 | L | 24·9 | .... | .... | .... | .... | .... | .... |
| UCMP 70034 | L | 25·9 | 19·9 | 18·7 | .... | .... | .... | .... |
| UCMP 70035 | L | 27·0*a* | 20·1 | 18·3 | .... | .... | .... | .... |
| UCMP 67153 | L | 24·1*a* | 18·7 | 17·8 | 11·8 | 11·1 | 10·6 | 9·7 |
| UCMP 66650 | R | 24·1 | 18·7 | 17·3 | .... | .... | .... | .... |
| UCMP 69113 | R | 26·8 | 21·0 | .... | .... | .... | .... | .... |
| UCMP 68934 | R | 22·1 | .... | 16·3 | 11·0 | 9·5 | 10·4 | 8·0 |
| UCMP 70027 | R | 23·8 | 18·9 | 17·7 | 10·8*s* | 9·6*s* | 10·0*s* | 8·6*s* |
| UCMP 68898 | R | .... | 18·4 | .... | 10·0 | .... | 10·1 | .... |
| UCMP 68896 | R | 23·5 | 18·0 | 17·0*a* | 9·8 | 8·8 | 10·1 | 8·8 |
| UCMP 68895 | R | 26·1 | 20·8 | 20·0 | .... | .... | .... | .... |
| UCMP 68984 | R | 22·1 | 18·6 | 16·1 | .... | .... | .... | .... |
| UCMP 68899 | R | 23·6 | 18·6 | 16·4 | .... | .... | .... | .... |
| UCMP 70031 | L | .... | 19·7 | .... | .... | .... | .... | .... |
| UCMP 65879 | L | 23·6 | 19·3 | 16·9 | .... | .... | .... | .... |
| UCMP 70033 | L | 22·5 | 17·3 | 16·4 | .... | .... | .... | .... |
| UCMP 67157 | L | .... | 19·0 | .... | .... | .... | .... | .... |
| UCMP 67442 | L | 23·7 | .... | 17·4 | .... | .... | .... | .... |
| Range, $M_1$ | | 22·1–<br>27·0*a* | 17·3–<br>21·0 | 15·6–<br>20·0 | 9·8–<br>11·8 | 9·4–<br>11·1 | 9·6–<br>10·6 | 8·0–<br>9·7 |

*a* = approximate; *s* = slightly worn.

no other conspicuous differences from $M_1$. Except for being larger and the paralophid being wider than the hypolophid, $M_3$ is like $M_2$. $M_4$ is like $M_3$ except that the width of the hypolophid is even more greatly restricted.

*Mandible.* Measurements of the lower jaw (Fig. 6a, b) are found in Table 13. The greatest depth of the horizontal ramus of the jaw is measured vertically through the point where it is joined by the ascending ramus. Anterior to this, the ventral border of the jaw rises slightly before curving abruptly ventrally to the rear of the symphysis. The symphyseal region then tapers markedly to the alveolus of the incisor. The mental foramen opens ventral and slightly anterior to the anterior root of $P_3$. The digastric process, slightly developed in this species, is not usually visible in lateral view. The ventral edge of the angular portion of the jaw is generally smoothly convex ventrally and rises posterodorsally from the ventral border of the horizontal ramus to the posterior tip of the angle. In lateral view, the ventral border of UCMP 66523 is slightly concave behind the digastric process. This slight concavity is the lateral expression of the postdigastric sulcus, which is more prominently displayed in ventral view as a lingual bowing of the ventral border of the jaw posterior to the digastric process and anterior to the transversely expanded angular process. The ascending ramus rises posterodorsally just behind and below the rear of $M_4$ in mature specimens. In UCMP 68900, in which the ascending ramus is most completely preserved, the anterior edge continues posterodorsally to the tip of the coronoid process. The tip of the process is unfortunately broken off in this specimen; but the posterodorsal orientation of the rear of the process suggests that the tip extended posteriorly to overhang the condyle.

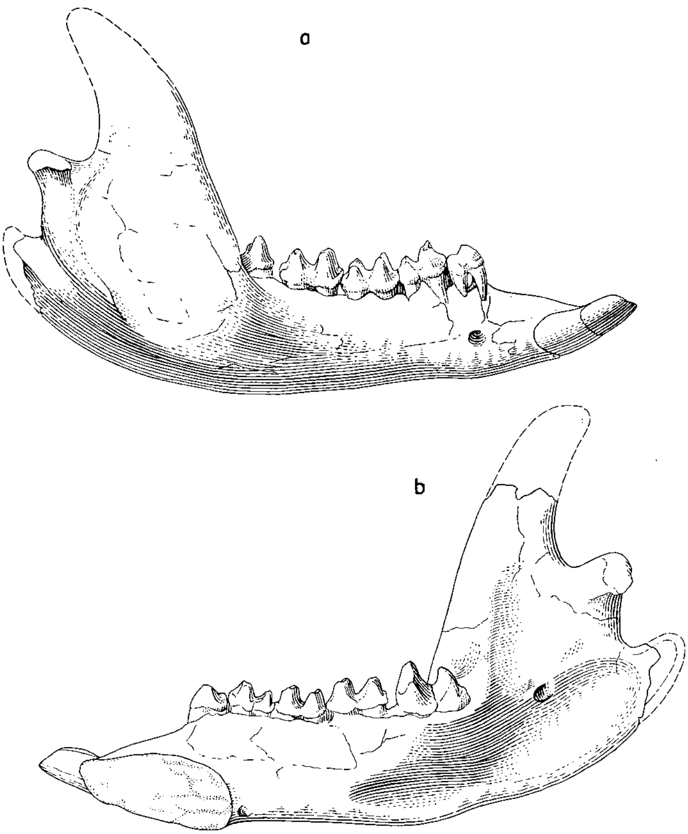


**Fig. 6.**
*Kolopsis torus* **gen.nov. et sp.nov.**

**a. Lateral view of right mandible, UCMP 68900. x $\frac{1}{3}$. Dashed line indicates probable configuration of parts not represented in the available material.**

**b. Medial view of right mandible, UCMP 68900. x $\frac{1}{3}$. Significance of dashed line as above.**

The masseteric fossa is broad and shallow. Its configuration on the lateral surface of the ascending ramus is particularly well developed in UCMP 66464. In this specimen, the dorsal tip of the fossa lies anterior to the mandibular notch and on a level with the condyle. From this point, the anterior edge of the fossa descends, nearly parallel to the leading edge of the ascending ramus, to the rounded anteroventral tip, which lies posterior and slightly ventral to the point where the anterior edge of the ascending ramus merges with the horizontal ramus. The ventral border of the fossa is concave dorsally. It leads posteriorly from the anterior end and expands laterally into the posterior masseteric eminence. The lateral tip of this eminence is vertically below the condyle and slightly above a line drawn across the tips of the molar crowns. The eminence continues dorsally as a crest toward the anterior base of the condyle. The posterodorsal edge of the fossa then leads anterodorsally from the base of the condyle to the dorsal tip of the fossa. The surface of the coronoid process above the masseteric fossa is smooth. The condyle lies above the mandibular

Table 13: Measurements on lower mandibles of *Kolopsis torus*

| | Side | Length, symphysis | Length, dorsal edge incisor alveolus to rear, $M_4$ | Length, dorsal edge incisor alveolus to postalveolar process | Length, dorsal edge incisor alveolus to mandibular canal | Length, dorsal edge incisor alveolus to rear, condyle | Length, $P_3$–$M_4$ | Length, $P_3$ to postalveolar process | Length, $P_3$ to mandibular canal | Length, $P_3$ to rear, condyle | Length, rear of symphysis to digastric process | Length, anterior root of $P_3$ to rear, mental foramen* | Depth, dorsal edge jaw at $P_3$ to ventral edge, mental foramen | Depth, horizontal ramus below anterior and $M_1$ | Depth, horizontal ramus below middle, $M_3$ | Length, rear condyle to anterior edge, ascending ramus | Length, postalveolar process to rear $M_4$ | Length, mandibular canal to postalveolar process | Anteroposterior width condyle across main axis of ascending ramus | Transverse width, condyle | Width, jaw at rear of $M_3$ | Length, diastema $I_1$–$P_3$ | Stage of maturity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UCMP 68925 | L | .... | .... | .... | .... | .... | 100·0 | .... | .... | 138·4 | .... | o | 18·4 | 42·2 | 44·6 | 60·8 | .... | .... | 17·7*a* | .... | 24·5 | .... | 3 |
| UCMP 68900 | R | 63·4 | 145·8*a* | .... | 170·0 | 202·5*a* | 113·7*a* | 136·4*a* | 140·5*a* | 174·7*a* | .... | −9·1*a* | .... | 39·2 | 42·5 | 83·8 | .... | .... | 12·0 | 37·7*a* | 31·6*a* | 27·0*a* | 3 |
| UCMP 66494 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 53·1 | 97·8 | 21·8 | .... | .... | .... | 29·0 | .... | 4 |
| UCMP 70029 | R | 83·[illegible]*a* | 160·0*a* | 182·2*a* | .... | .... | 110·7*a* | 133·4*a* | .... | .... | .... | +3·2 | 18·7 | 49·5 | 50·5 | .... | 22·0 | .... | 15·5 | .... | 30·3 | 44·4*a* | 4 |
| UCMP 68919 | L | 69·[illegible]*a* | 137·8*a* | .... | .... | .... | .... | .... | .... | .... | 72·2*a* | .... | .... | 42·9 | 46·5 | .... | .... | .... | .... | .... | 27·7 | .... | 4 |
| UCMP 70035 | L | .... | .... | .... | .... | .... | .... | .... | .... | .... | 109·5*a* | +5·1 | 15·2 | 50·4 | 50·9 | .... | 19·8 | .... | .... | .... | 29·4 | .... | 4 |
| UCMP 66523 | L | .... | 138·4 | 157·1 | 183·6 | 218·3 | 100·9 | 120·0 | 146·6 | 178·1 | 96·3*a* | +1·2 | 21·4 | 46·8 | 47·7 | 97·2 | 18·1 | 28·2 | .... | .... | 31·3 | 36·4 | 3 |
| UCMP 68921 | L | 78·2 | 151·6 | 161·8 | 192·1 | .... | 112·5 | 120·4 | 150·0 | .... | .... | −1·2 | 21·8 | 49·8 | 52·0 | .... | 8·5 | 28·7 | .... | .... | 32·8 | 38·1 | 4 |
| UCMP 66550 | R | 76·2 | 143·2 | .... | 187·8 | 225·9 | 103·8 | .... | 152·3 | 182·6 | 78·6*a* | −7·3 | .... | 48·5 | 54·5 | 96·8 | .... | .... | .... | .... | 29·3*a* | 34·3 | 4 |
| UCMP 70027 | R | .... | .... | .... | .... | .... | 105·4 | 121·5 | .... | .... | .... | −0·8 | 19·3*a* | 45·4 | 52·7 | .... | 15·5 | .... | .... | .... | 27·8 | .... | 4 |
| UCMP 68898 | R | 67·0 | 141·3 | .... | .... | 158·5 | 103·8 | .... | .... | 161·7 | .... | −3·0 | 18·0 | 42·5 | 42·3 | .... | .... | .... | .... | .... | 28·6 | 36·5 | 4 |
| UCMP 70031 | L | 84·5 | .... | .... | .... | .... | .... | .... | .... | .... | .... | −2·1 | 18·3 | 50·9 | 51·8 | .... | .... | .... | .... | .... | 28·3 | 40·1 | 3 |
| UCMP 68899 | R | 85·7 | .... | .... | .... | .... | 102·7 | 125·4 | 152·5 | .... | .... | +4·6 | .... | .... | 52·5 | .... | 21·3 | 28·1 | .... | .... | 25·5 | .... | 4 |
| | L | 85·7 | .... | 170·2 | 198·0 | .... | .... | 118·1 | 144·3 | .... | .... | .... | .... | .... | 49·8 | .... | .... | 30·8 | .... | .... | 25·7 | 45·5 | 3 |
| UCMP 67442 | L | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 48·6 | 87·8 | 15·8 | 20·8 | 14·0 | 51·4 | 26·2 | .... | 3 |
| Range | | 63·4–85·7 | 137·8*a*–160·0*a* | 157·1–182·2*a* | 170·0–198·0 | 158·5–225·9 | 100·0–113·7*a* | 118·1–136·4*a* | 140·5*a*–152·5 | 138·4–182·6 | 72·2*a*–109·5*a* | −9·1 to +4·6 | 15·2–21·8 | 39·2–50·9 | 42·3–54·5 | 60·8–97·8 | 8·5–21·8 | 20·8–30·8 | 12·0–17·7*a* | 37·7*a*–51·4 | 24·5–32·8 | 27·0*a*–45·5 | |

*a* = approximate.
* —: Rear edge of foramen posterior to anterior edge of anterior root of $P_3$.
\+ Foramen anterior to tooth.

notch. Its dorsal surface is flat; its posterior base descends ventrally and slightly posteriorly to the dorsal edge of the angular process. The process projects posterolingually, at about the level of the alveoli of the teeth, and ends just posterior to the condyle.

In dorsal view, each ramus converges toward the symphysis at an angle of about 10° as measured along the inside of the rami. The ridge between $P_3$ and the rear of the incisor alveolus on the dorsal border of the symphyseal region of each jaw is concave laterally. Between the two ridges, the symphysis is broadly U-shaped transversely; it is shallow anteriorly, but deepens posteriorly. The rear of the symphysis ends in a vertical genial crest which projects posteriorly in the mid-symphyseal line. On each side of the ventral portion of the genial crest is a genial pit. The rami increase in width posteriorly, the greatest thickness being measured across $M_4$. Posterior to $M_4$ the triangular postalveolar shelf projects from the lingual surface of the jaw and ends in a prominent postalveolar process. Posterolabial to the process, the mandibular foramen is found at the dorsal border of the pterygoid fossa.

The labial edge of the flat strap-shaped articular surface of the condyle of UCMP 67442 is directed posterolingually, then curves sharply anteriorly so that it lies perpendicular to the main axis of the ramus. The articular surface traverses most of the condyle in this manner before turning posterolingually again at its lingual tip. The articular surface of the condyle of *Kolopsis torus* is not as transversely elongate as in *Pyramios alcootense*. The mandibular notch merges with the labial fourth of the condyle. The lingual half of the articular surface slightly overhangs anteriorly a shallow *fovea pterygoidea* which is developed on the anterior base of the condyle and is directed lingually and slightly ventrally from the mandibular notch. The angular process projects posterolingually beyond the condyle. Its lingual tip nearly reaches the posterior extension of the longitudinal axis of the tooth row.

In lingual view, the lingual edge of the angular portion of the jaw forms a ridge which merges into the ventral border of the jaw at the anterior end of the pterygoid fossa. The anterior end of this fossa is separate from and just behind the shallower digastric fossa which tapers anteriorly to die out below the anterior end of $M_3$. In some specimens (as in UCMP 66464) the separation between the pterygoid and digastric fossae is conspicuously marked, but separation is usually achieved by a low anterodorsally elongate shelf, formed because the pterygoid fossa is markedly deeper than the digastric. The point of separation of the two fossae is ventral and slightly anterior to the postalveolar process.

A low ridge continues horizontally posteriorly from the postalveolar process to the point where the angular process begins to extend lingually from the posterior base of the condyle. The horizontal ridge indicates the dorsal limit of the pterygoid fossa, and may be designated as the suprapterygoid ridge. The mandibular canal opens posterodorsally as the mandibular foramen, the dorsal and ventral borders of which are bounded by a lingually projecting crest which diminishes posteriorly. The foramen is found at the dorsal edge of the pterygoid fossa and is usually behind and slightly ventral to a small spur of bone which marks the terminus of a ridge which curves posteroventrally from the suprapterygoid ridge.

In ventral view, the ventral border of the jaw bows medially below $M_4$, usually forming a small digastric process, then curves labially into the postdigastric sulcus before swinging posterolingually again as the lingual edge of the angular process. The posterior surface of the angular process is flat in an anterolabial direction. The greatest oblique width of the angular region of the jaw is measured across the posterior surface of the angular process, between the posterior tip of the process and the lateral tip of the posterior masseteric eminence.

Variations in the configuration of the jaw are apparently related to the ontogenetic age of the individual. No variations have been observed which can be definitely correlated with sex. The same arbitrary age classes employed with *Pyramios alcootense* have been used here.

*Specimens of Stage* 1: The horizontal ramus is very slender; ascending ramus relatively not so broad anteriorly as in later stages. Ventral surface of ramus curved as in above basic description. Jaw stockier anteriorly, symphyseal region relatively less elongate than in mature animals; anterior tapering of ramus therefore more abrupt. Anterior end of ascending ramus rises above posterior moiety of unerupted $M_3$.

Masseteric fossa shallow, posterior masseteric eminence not well developed. Proportionally less coronoid process above dorsal end of fossa; anteroventral end of fossa opposite posterior moiety of unerupted $M_3$.

Condyle relatively higher above the tooth row. Condition of angular process unknown. Condition of genial crest is unknown, but genial pits are present in at least one specimen. Greatest width of ramus is across $M_3$ at anterior edge of ascending ramus. Postalveolar shelf and process obscured by bony dental capsule surrounding erupting molars; rear of $M_4$ is slightly above, but at same longitudinal position as mandibular, foramen. Angle of jaw not preserved in specimens at hand. Condyle is incomplete.

Pterygoid fossa seems to be separated from small digastric fossa; point of separation occurs in a line with anterior edge of ascending ramus. Dorsal edge of pterygoid fossa not clearly delineated.

*Specimens of Stage* 2: Much like Stage 1, poor representation in material at hand. Jaw begins to be more elongate; ascending ramus now rises opposite anterior end of unerupted $M_4$, anterior end of masseteric fossa also opposite anterior end $M_4$. Posterior masseteric eminence better developed. Postalveolar shelf and process still obscured. Pterygoid fossa poorly separated from digastric fossa; point of separation now at posterior end of $M_4$.

*Specimens of Stage* 3: Jaw nearing adult proportions; still not as elongate as those in Stage 4, still not as deep through horizontal ramus; ascending ramus still anterior in position relative to teeth. Characters regarding symphysis, angular process, height of condyle are nearly stabilized. Genial crest and pits well developed. Postalveolar shelf and process present, but not as far posterior to $M_4$ as in Stage 4.

As indicated for *Pyramios alcootense* specimens of Stage 4 pertain to adult individuals in which $P_3$–$M_4$ are fully erupted and in which the hyplophid of $M_4$ is at least halfway worn down. The preceding description of the mandible of *Kolopsis torus* was drawn from specimens of this age class; the characteristics of such mandibles will not be repeated here.

It is clear that ontogenetic changes in the configuration of the jaw involve a general increase in size and massiveness. The most conspicuous change is the progressive elongation of the horizontal ramus relative to the anterior edge of the ascending ramus to compensate for the regular addition of new molars from the dental capsule. The length of the symphyseal portion of the jaw also increases, although not as conspicuously. Except for those of the teeth, which are best taken on specimens in an early stage of wear, jaw measurements and proportions taken from immature diprotodonts should be used for comparison only with those other specimens which are of a similar ontogenetic age. In Table 13 only specimens in Stages 3 and 4 have been measured.

*Remarks*

As represented by the material described here, *Kolopsis torus* is clearly smaller and less massive than *Pyramios alcootense.* The features listed in their respective diagnoses indicate that the two genera are rather widely separated phyletically; and indeed they belong to entirely separate lineages.

## Genus PLAISIODON* nov.

### *Genotypic species: Plaisiodon centralis* sp.nov.

*Generic diagnosis:* $I^1$ cross-section of occlusal surface subovate with flat medial side; cross-section of root proximal to crown triangular with broad anterior and narrow posterior surface; pronounced elongate grooves on both lateral and medial surfaces; in lateral view tooth does not taper conspicuously either anteriorly or posteriorly from an enlarged middle portion of the root cap; root is open at proximal tip; general radius of curvature of outer surface in lateral view 38·0–50·0; similar general size to, but less massive than, tooth in *Pyramios alcootense.* $I^2$: asymmetrically triangular occlusal surface, posterior apex nearer to lateral than medial corner of tooth; greatest curvature of outer surface occurs proximal to base of the enamel; root tapers markedly to proximal tip. $I^3$: occlusal surface posterolaterally elongate, slight groove on both outer and posterior surfaces. $P^3$: high-crowned; occlusal outline subrectangular with marked elongation of parastyle caused by lingual basal emargination between parastyle and protocone; tooth two-rooted; parastyle large, high, conical; single labial parametacone as trenchant cusp; no mesostyle; metastyle absent; protocone major lingual cusp, subsidiary to parametacone; hypocone present, smaller than protocone; parastyle separated from parametacone by transverse cleft; no lingual cingulum connecting parastyle to protocone; occlusal diameter of base of hypocone conspicuously less than that of protocone; no labial cingulum. $M^1$: parastyle prominent; metastyle not present as a distinct cusp; postparaconal crest directed posterolabially, continuous with mesostyle; no labial cingulum, anterior cingulum broad and shelf-like, particularly at anterolingual corner; lingual cingulum sharply rectangular, shorter than in *P. alcootense.* $I_1$: moderately spatulate, blade oriented at angle of about 45° with respect to the root; root thicker than blade just proximal to base of crown; posterior edge of lateral surface of enamel as a straight line, nearly perpendicular to dorsal edge;

---

* πλαισιον—an oblong form, οδοντος—tooth; in reference to the shape of the upper premolar.

in medial view, enamel cap restricted to a thin strip which only barely overlaps onto the medial surface and essentially parallels the dorsal and ventral borders of the tooth. $P_3$: elongate, subrectangular to subtriangular outline; main cuspid not connected to anterior apex of tooth by longitudinal crest; indentation in labial surface posterior to base of main cuspid weak or absent; strong lingual crest from posterior cuspid. $M_1$: with remnant paralophid crest from protoconid to anterior cingulum; metalophid present; transverse valley broadly V-shaped; axes of lophids slant posterodorsally. Jaw: massive, condyle not so transversely elongate relative to its anterior width as in *P. alcootense*; condyle sigmoid in dorsal surface; genial pits broad shallow depressions on ventral surface of symphysis; genial crest absent; angular process and posterior masseteric eminence more adequately developed than in *P. alcootense.*

## PLAISIODON CENTRALIS* sp.nov.

(Figs 7–8, Tables 14–20)

*Holotype:* CPC 6748, skull lacking incisor and most of left molar dentition, left zygomatic arch and occiput.

*Paratypes:* UCMP 70021, skull lacking rostrum, sagittal area; UCMP 69955, right premaxillary; UCMP 69954, left premaxillary with $I^1$, $I^3$; UCMP 65894, 69952, 69953, three $RI^1$; UCMP 66612, 69943, 69956, 69957, four $LI^1$; UCMP 69941, 69942, 69947–69949, 69960, six $RI^2$; UCMP 69944, 69946, 69959, three $LI^2$; UCMP 65866, 69935–69937, 69939, 69950, 69958, seven $RI^3$; UCMP 69570, 69921, 69931–69934, 69938, 69940, 69972, nine $LI^3$; UCMP 69914, $LdP^3$, $M^1$; UCMP 69916, 69930, two $RP^3$; UCMP 65627, 69739, 69748, 69911, 69923, five $LP^3$; UCMP 69971, $LM^1$; UCMP 69927, maxillary fragment with $RP^3$; UCMP 69928, maxillary fragment with $RP^3$–$M^1$; UCMP 69569, maxillary with $RP^3$–$M^3$; UCMP 69917, maxillary with $RP^3$–$M^3$; UCMP 69928, maxillary with $RP^3$–$M^2$; UCMP 69913, maxillary with $RP^3$–$M^1$; UCMP 69918, $RM^1$; UCMP 69919, $LM^1$; UCMP 69902, $RM^2$; UCMP 69901, $LM^2$; UCMP 65879, $LM^4$; UCMP 66117, maxillary with $LP^3$–$M^3$; UCMP 69973, maxillary with $LP^3$–$M^4$; UCMP 65622, maxillary with $LM^2$; UCMP 69904, maxillary with $LP^3$–$M^2$; UCMP 69903, maxillary with $LP^3$–$M^4$; UCMP 69907, maxillary with $LP^3$–$M^4$; UCMP 69906, maxillary with $LM^2$–$M^3$; UCMP 69975, maxillary with $LM^2$–$M^3$; UCMP 69912, maxillary with $RM^3$; UCMP 69908, right maxillary fragment; UCMP 69974, maxillary fragment with $RP^3$; UCMP 69905, $LM^4$; UCMP 65880, maxillary with partial $LP^3$, complete $LM^1$ and partial $LM^2$; UCMP 69110, $LP_3$; UCMP 69107, $RP_3$; UCMP 69108, $RM_1$; UCMP 69105, right jaw with $P_3$–$M_3$; UCMP 69104, right jaw with $P_3$–$M_4$; UCMP 67443, right jaw $P_3$–$M_4$; UCMP 69909, left jaw with $M_4$; UCMP 67151, juvenile jaw with $P_3$–$M_4$; UCMP 69964, right jaw fragment with $M_3$–$M_4$; UCMP 67439, left jaw with $M_2$–$M_4$; UCMP 69119, left jaw with $P_3$–$M_4$; UCMP 69120, left jaw with $M_3$–$M_4$; UCMP 66238, right jaw fragment with $M_3$–$M_4$; UCMP 69965, pair of jaws, R and $LM_2$–$M_4$; UCMP 67296, pair of jaws with $P_3$–$M_4$; UCMP 67460, pair of jaws with $P_3$–$M_4$; UCMP 69091, edentulous pair of jaws; UCMP 67438, pair of jaws with $P_3$–$M_4$;

---

* For the occurrence of the species in central Australia.

UCMP 69098, pair of jaws with $P_3$–$M_4$; UCMP 69099, pair of juvenile jaws with $P_3$–$M_4$; UCMP 69100, left jaw fragment with $M_3$–$M_4$; UCMP 69102, right jaw fragment with $M_3$–$M_4$; UCMP 69100, left jaw fragment with $M_3$–$M_4$; UCMP 69102, right jaw fragment with $M_3$-$M_4$; UCMP 69103, left jaw with $P_3$-$M_4$; UCMP 69966, right jaw with $M_3$–$M_4$; UCMP 69967, left jaw with $M_3$–$M_4$; UCMP 69968, right

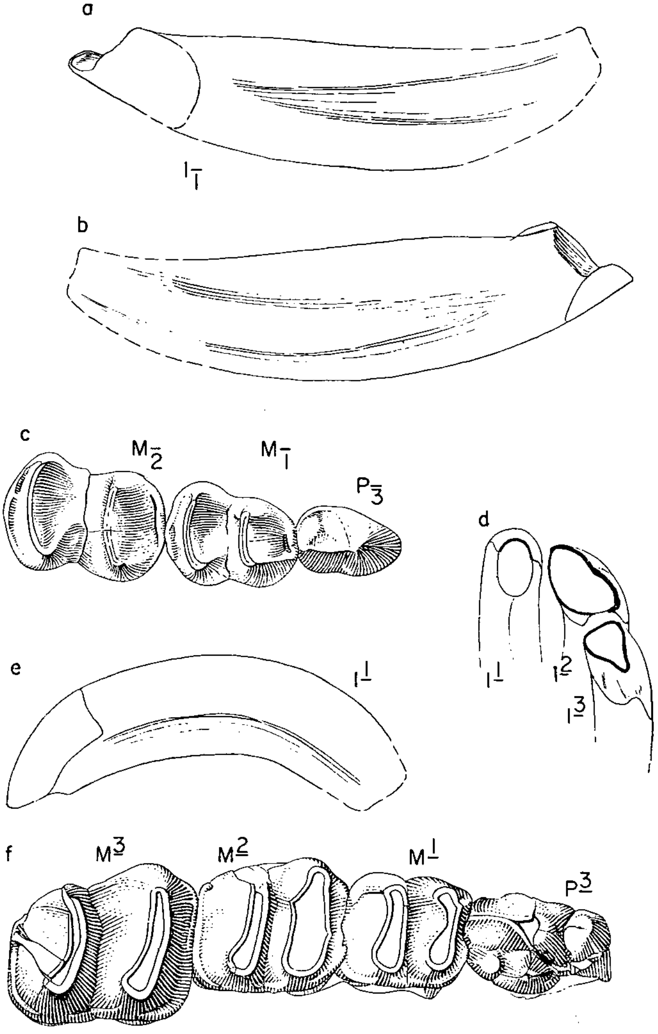


**Fig. 7.**

*Plaisiodon centralis* **gen.nov. et sp.nov.**

- **a. Lateral view of left lower incisor. UCMP 69096. x ¾.**
- **b. Medial view of left lower incisor. UCMP 69096. x ¾.**
- **c. Occlusal view of right $P_3$-$M_2$. UCMP 67157. x ¾.**
- **d. Occlusal view of left upper incisors. UCMP 69957, $I^1$; UCMP 69945, $I^2$; UCMP 69570, $I^3$. x ¾.**
- **e. Lateral view of left upper incisor. UCMP 69957. x ¾.**
- **f. Occlusal view of right cheek tooth dentition of holotype, CPC 6748. x ¾.**

jaw with $M_3$–$M_4$; UCMP 69970, right jaw with $P_3$–$M_4$; UCMP 69969, left jaw with $P_3$–$M_4$; UCMP 69902, 69903, two $RI_1$; UCMP 65623, 69094–69097, five $LI_1$.

*Type locality:* Paine Quarry, V-6345, Waite Formation, 4 miles south-west of Alcoota station, 2·1 miles south-west of junction of Waite and Ongeva Creeks, Northern Territory, Australia.

*Specific diagnosis:* That of the genus until other species are described.

*Age:* Alcoota fauna, early Pliocene or late Miocene.

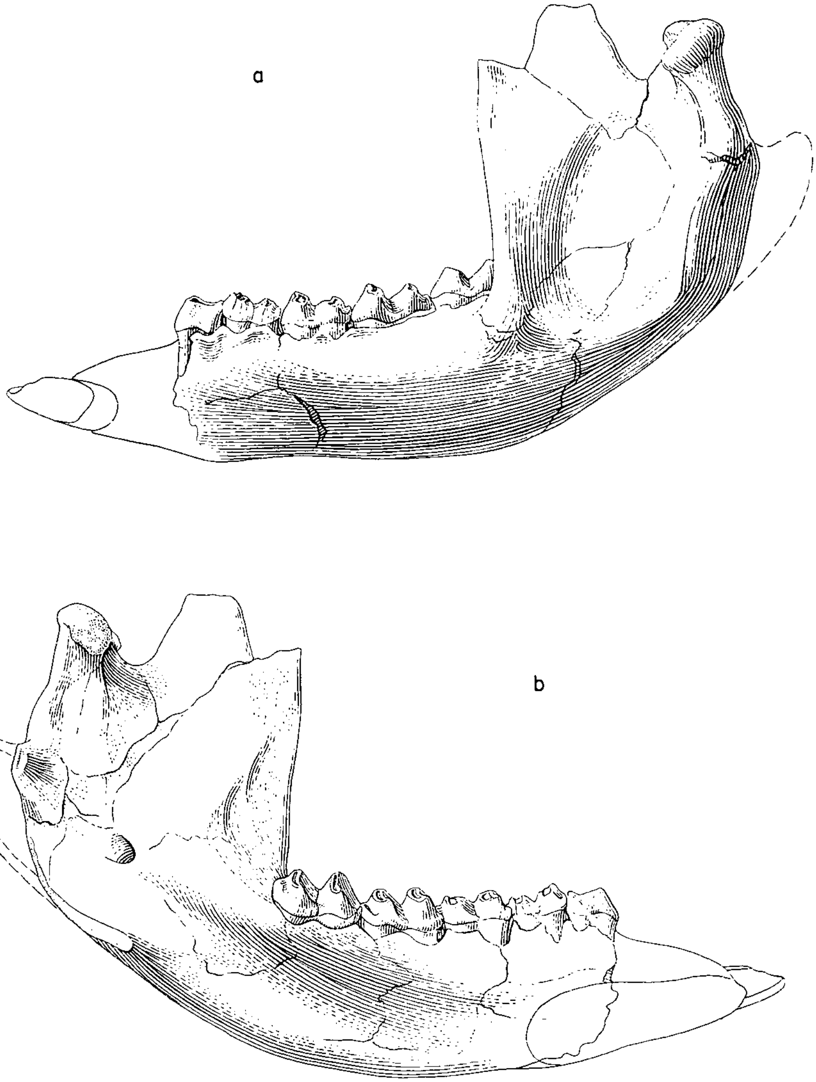


**Fig. 8.**

*Plaisiodon centralis* **gen.nov. et sp.nov.**

**a. Lateral view of left mandible, UCMP 69103. x $\frac{1}{3}$. Unshaded area restored from other specimens.**

**b. Medial view of left mandible, UCMP 69103. x $\frac{1}{3}$. Unshaded area restored from other specimens.**

## *Upper Dentition*

*Incisors.* Four first upper incisors are represented in Table 14. This is an elongate tooth of nearly uniform depth and breadth throughout most of its root. The curvature of the outer surface falls on an arc, the radius of which is 38·0–50·0. The curvature increases somewhat at the tip of both the crown and the root. The outline of the occlusal surface (Fig. 7d) is subovate with a flat medial side. Posterior to the crown, the cross-section of the shaft is subtriangular with a broad dorsal and a narrow ventral surface. Both the lateral and medial surfaces bear deep, elongate grooves which lead from the rear of the crown toward the tip of the root. The root does not taper markedly toward its posterior tip, but remains widely open. The enamel cap occurs chiefly on the dorsal half of the anterior tip of the root and is at least 30·0 long in nearly unworn specimens. At the tip in specimens such as these (UCMP 65894) the enamel extends around to the ventral portion of the medial as well as the lateral surface. Farther back, the medial expression of the enamel is limited to a narrow strip at the dorsal edge of the tooth. In later stages of wear (UCMP 69957) the resistant enamel cap supports a ventrally projecting lip in the anterior portion of the occlusal surface (Fig. 7e).

Table 14: Measurements on upper incisors of *Plaisiodon centralis*

| | | $I^1$ | | | | $I^2$ | | $I^3$ | |
|---|---|---|---|---|---|---|---|---|---|
| | Side | Length, crown | Width, crown | Length, root | Root closed | Length, crown | Width, crown | Length, crown | Width crown |
| UCMP 69954 | L | .... | .... | .... | .... | | | 13·0 | 9·1 |
| UCMP 69953 | R | .... | .... | 66·3+ | no | | | | |
| UCMP 69952 | R | .... | .... | 52·8+ | no | | | | |
| UCMP 66612 | L | 13·4*w* | 10·5 | 49·5+ | no | | | | |
| UCMP 69956 | L | .... | .... | .... | .... | | | | |
| UCMP 69957 | L | 15·3 | 10·9 | 54·5+ | no | | | | |
| UCMP 69942 | R | | | | | 13·3 | 14·2 | | |
| UCMP 69948 | R | | | | | 11·9 | 12·7 | | |
| UCMP 69946 | L | | | | | 14·0 | 11·1 | | |
| UCMP 69945 | L | | | | | 11·7 | .... | | |
| UCMP 69921 | L | | | | | | | 10·5 | |
| UCMP 69940 | L | | | | | | | 9·2 | 11·7 |
| UCMP 69939 | R | | | | | | | 10·3 | 13·0 |
| UCMP 69938 | L | | | | | | | 10·0 | .... |
| UCMP 69937 | R | | | | | | | 11·1 | 16·5 |
| UCMP 65866 | R | | | | | | | 12·1 | 15·1 |
| UCMP 69570 | L | | | | | | | 9·8 | 12·7 |
| UCMP 69972 | L | | | | | | | 11·8 | 15·6 |
| Range | | 13·4*w*<br>15·3 | 10·5–<br>10·9 | 49·5+–<br>66·3+ | no | 11·7–<br>14·0 | 11·1<br>14·2 | 9·2–<br>13·0 | 9·1–<br>16·5 |

*w* = worn, measurement too short.
\+ = measurement would be longer in unbroken specimen.

Only four second upper incisors are suitable for measurement (Table 14). $I^2$ is a massive, strongly curved tooth with an asymmetrically triangular occlusal outline. The medial surface of the crown is slightly convex. The posteromedial apex of the occlusal surface (Fig. 7d) is broadly rounded. The short, flat posterior surface is directed slightly anterolaterally between the posteromedial apex and the posterolateral corner of the occlusal surface. The slightly convex outer, enamel covered, surface bears a nearly vertical groove about 5·0–7·0 anterior to the posterolateral corner. In lateral view, the profile of the outer surface curves markedly posterodorsally. All surfaces of the root converge rapidly to the sharply pointed posterior tip. The greatest curvature of the outer surface occurs dorsal to the base of the enamel. The enamel cap occurs nearly exclusively on the anterior surface of the tooth. Toward the tip, a thin strip of enamel can be found on the anterior edge of the medial and lateral surfaces.

Nine third upper incisors were suitable for measurement (Table 14). $I^3$ is an elongate, gradually tapering, nearly straight tooth. The triangular occlusal surface (Fig. 7d) is posteriorly elongate. A slight groove occurs on both the lateral and medial surfaces. The anterior edge of the crown is broad and flat. The posterior surface is narrow. The root bears a distinct groove on its medial surface. The tip of the root lying about 45·0 above the posteromedial base of the crown, is bluntly pointed. The enamel cap extends up along both the lateral and medial surfaces of the root, but considerably farther on the lateral surface.

*Premolars.* The deciduous third upper premolar is known from one specimen, UCMP 69914. It is an anteroposteriorly elongate, but triangular, tooth with two large labial cusps and one smaller lingual cusp. The tooth is 14·2 long and 9·9 wide. Employing the standard tritubercular terminology, the apex of the 5·8 high paracone is slightly lower than the 7·5 high paracone, and higher than the 4·2 protocone. The paracone and metacone each support an anterior and posterior longitudinal, and a lingual transverse crest. The facets between the crests are essentially flat, giving each cusp a pyramidal aspect. At the bases of their respective cusps, the lingual crests converge toward the apex of the more conical protocone. A small parastyle and metastyle occur at the anterior and posterior corners of the ectoloph, respectively. A short cingulum leads posterolingually from the parastyle to the lingual base of the paracone. The anterior base of the protocone, which projects sharply lingual to the base of the paracone, is devoid of cingula. The smooth, oblique posterior border of the tooth bears a small posterolabially oriented cingulum between the posterior base of the protocone and the metastyle. The labial base of the tooth is composed of two broad arcs, constricted between the paracone and metacone. There is no labial cingulum.

$P^3$ (Table 15) is an elongate, trenchant shearing tooth with a small anterior and a large posterior root. A large conical parastyle (Fig. 7f) is situated at the anterior tip of the tooth and forms a marked prolongation of the labial side of the tooth. The apex of the parastyle leans posteroventrally. The parastyle is separated from the anterior base of the parametacone by a deep transverse cleft. A weak longitudinal crest traverses the anterior face of the parametacone in some specimens, but this does not continue on to the posterior face of the parastyle. A strong cingulum curves posteriorly around the lingual base of the protocone. A small crest descends anterolingually from the apex of the protocone to the lingual cingulum Posteriorly a thin sharp crest curves posterolingually from the base of the protocone, then posterolabially to the apex of the low, conical hypocone. The thin crest on the posterior face of the hypocone expands into the posterior cingulum and curves laterally to the posterolabial corner of the tooth; no labial cingulum is developed. The rear of the posterolabial end of the tooth is flat and triangular in posterior view.

Table 15: Measurements on the third upper premolar of *Plaisiodon centralis*

| | Side | Length | Width | Width, parametacone to protocone | Length, protocone to hypocone | Length, parastyle to parametacone | Height, unworn parametacone | Height, unworn parastyle | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|---|---|
| CPC 6748 .... .... | R | 24·4 | 17·6 | 8·3*a* | 7·8*a* | 8·3*a* | .... | .... | .... | .... |
| | L | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 69923 .... | L | .... | 18·6 | 7·0 | 7·2 | .... | 16·2*s* | .... | 8·5 | 5·6 |
| UCMP 69930 .... | R | 28·4 | 20·3 | 7·7 | 7·5 | 8·1 | 15·8 | 13·0 | 8·6 | 6·6 |
| UCMP 69911 .... | L | 28·0 | 19·8 | 7·2 | 6·5 | 10·4 | 14·5 | 11·7 | 7·8 | 6·4 |
| UCMP 69929 .... | R | .... | 19·2 | 8·0 | 6·5 | .... | 15·5*s* | .... | 8·8*s* | 5·2 |
| UCMP 69928 .... | R | .... | 19·3 | .... | .... | .... | .... | .... | .... | .... |
| UCMP 69927 .... | R | 23·9 | 19·4 | .... | .... | .... | .... | .... | .... | .... |
| UCMP 69917 .... | L | 24·5 | 18·2*a* | .... | .... | .... | .... | .... | .... | .... |
| UCMP 69916 .... | R | 25·3 | 19·1 | .... | .... | .... | .... | .... | .... | .... |
| UCMP 65627 .... | L | 27·6 | 19·7 | 7·9 | 0·0* | 8·6 | 14·3*s* | 11·6 | 7·0*s* | 0·0* |
| UCMP 69568 .... | L | 26·7 | 20·9 | 7·7 | 9·1 | 9·9 | .... | 12·4*s* | 8·0*s* | 6·5 |
| UCMP 69907 .... | L | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 66117 .... | L | 27·4 | 21·8 | .... | 8·5 | .... | .... | 8·7 | 8·7 | 5·0*s* |
| UCMP 69913 .... | R | 28·4 | 19·4 | 7·8 | 6·9 | 9·9 | 15·7*s* | 8·3 | 7·5*s* | 6·2 |
| UCMP 69973 .... | L | 26·7 | 20·6 | .... | .... | .... | .... | .... | .... | .... |
| UCMP 69904 .... | L | 26·5 | 18·1 | 7·9 | 6·7 | 9·2 | 16·0 | 12·3 | 8·4 | 6·0 |
| UCMP 69974 .... | R | 27·1*a* | 21·6 | 6·1 | .... | 6·7 | 18·8 | 13·6*a* | 9·5 | .... |
| Range | | 23·9–<br>28·4 | 17·6–<br>21·8 | 6·1–<br>8·3*a* | 6·5–<br>9·1 | 6·7–<br>10·4 | 14·3*s*–<br>18·8 | 8·3–<br>13·6*a* | 7·0*s*–<br>9·5 | 5·0*s*–<br>6·6 |

*a* = approximate.
*s* = slightly worn.
* UCMP 65627 has no hypocone developed.

The high, narrow trenchant parametacone is a rather blade-like cusp which occupies the greater portion of the labial half of the crown. In a few specimens, there is only the faintest suggestion of incipient splitting of the parametacone into two cusps. This takes the form of a shallow vertical crease in the labial surface of the cusp. No evidence of incipient twinning of the cusp can be found on its lingual surface. A strong shearing crest is developed on the posterior edge of the parametacone. A weak transverse crest extends from the apex of the parametacone to the longitudinal valley which occurs along its lingual base. This valley separates the parametacone from the protocone and the hypocone. A weak transverse crest is developed from the apex of the protocone to the longitudinal valley and joins its counterpart from the parametacone. The protocone and hypocone are much smaller than the parametacone and parastyle. Both the lingual cusps are conical. In some specimens (UCMP 69911) the midpoint of the posterior surface of the protocone is connected to the anterior surface of the hypocone by a short low longitudinal ridge. This crest is in addition to the connexion made between the two cusps by means of the lingual cingulum. In one specimen (UCMP 65627) the hypocone, small in any case, is completely missing. In this tooth, a low elongate ridge extends posteriorly from the mid-posterior base of the protocone for a distance of about 8·0 before merging with the posterior cingulum. The lingual cingulum develops a slight ventrally projecting apex opposite the position of the hypocone, then continues around the tooth as the posterior cingulum.

*Upper molars.* Fourteen upper first molars are in suitable condition to be measured (Table 16). $M^1$ is an elongate rectangular bilophodont tooth (Fig. 7f) with two anterior and one posterior roots. Although the data are inconclusive, the apices of the protocone and paracone lie at about the same distance from the base of the crown. The hypocone and metacone also extend about the same distance from the base. In addition, the cusps of the metaloph are higher than those of the protoloph. The protoloph is as wide as, or in some cases slightly wider than, the metaloph.

A prominent parastyle occurs at the anterolabial corner of the tooth and is connected by a short crest to the paracone. The metastyle usually does not form a distinct cusp, but consists of a basal swelling of the postmetaconal crest. In five specimens a strongly developed postparaconal crest extends from the apex of that cusp into the labial end of the transverse valley. In at least six others, this crest is separated by a sharp anteroventrally directed fissure from the labial end of the paracone. The fissure, although not as well defined as that separating the parastyle from the paracone, extends nearly to the base of the crown as though the cusp-like structure thus defined was a mesostyle derived from the cingulum.

The postparaconal crest, or mesostyle, is directed posterolabially and terminates at the labial end of the transverse valley. There is no premetaconal crest. The protoloph is thus not connected to the metaloph as in *Pyramios alcootense*. There is no shelf-like labial cingulum in *Plaisiodon centralis*. The anterior cingulum is wide, particularly at the anterior base of the protocone, and extends to the anterolingual corner of that cusp. The lingual cingulum begins about 1·5 posterior to this, and is usually sharply rectangular in outline, whereas the structure in *P. alcootense* is longer and broadly curved. The lingual cingulum ends at the anterolingual corner of the hypocone, immediately posterior to which the posterior cingulum continues on around the rear of the tooth to the base of the metastyle.

In the eight second upper molars which could be measured (Table 16), the protoloph is definitely wider than the metaloph. Apart from this, $M^2$ differs from $M^1$ chiefly in being larger and in lacking a mesostyle or posterolabial postparaconal crest. Instead, a shelf-like labial cingulum is formed at the end of the transverse valley and a longitudinally oriented postparaconal crest extends toward the metaloph. In contrast to the condition in *Pyramios alcootense*, there is no corresponding premetaconal crest in *Plaisiodon centralis*. The only other conspicuous difference between $M^1$ and $M^2$ is the weaker development of the para- and metastyles of the latter.

$M^3$ (seven specimens measured, Table 16) and $M^4$ (three measured, Table 16) are larger versions of $M^2$. In addition, the metaloph of $M^4$ is narrower relative to the protoloph than in any other molar of the dental series. The parastyle diminishe progressively from $M^3$ to $M^4$; the metastyle is not retained in $M^4$. The postparaconal crest retains its longitudinal orientation in $M^3$ and $M^4$, but is considerably less distinct than in $M^2$.

*Lower dentition*

*Incisor.* $I_1$ (Table 17) is a relatively massive, laterally compressed tooth (Fig. 7a). The ventral border is a smooth curve, concave dorsally. The dorsal border is also concave dorsally except for a slight bulge posterior to the enamel cap. This bulge is less pronounced than in *Kolopsis.* In little worn or unworn specimens the dorsal border of the enamel cap begins to curve anteroventrally almost as soon as it emerges from the root. The dorsal border of the enamel cap rises abruptly anterodorsally from that of the root. In cross-section, the width of the dorsal part of the root is about equal to that of the ventral half. The two halves are separated near the mid-depth of the tooth by a medial and lateral groove. The lateral groove extends slightly on to the enamel cap. The medial groove begins on the lingual surface of the root above the point where the posterior edge of the enamel cap crosses the ventral border of the tooth. Both grooves deepen progressively backwards. In some specimens the lateral groove is poorly developed. The medial groove is always strongly developed.

The lower incisors of *Kolopsis torus* and *Plaisiodon centralis* differ conspicuously in the manner in which the teeth are twisted. In *P. centralis,* both the root and enamel cap are twisted, but in opposite directions. The only point where the dorsal border of the tooth is vertically above the ventral border in *P. centralis* is in the portion of the root just behind the enamel cap. The amount of twisting of the cap relative to a vertical line is, however, similar to that in *K. torus.*

The greatest posterior extent of the enamel cap occurs on the lateral surface of the tooth. The posterior edge of the cap is a nearly straight line directed anterodorsally, perpendicular to the dorsal edge. On the medial surface (Fig. 7b) the enamel is restricted to a narrow strip at the dorsal and ventral edges of the tooth. In ventral view, the ventral border of the tooth is directed obliquely anteromedially in a straight line, or is slightly convex medially.

Table 16: Measurements on upper molars of *Plaisiodon centralis*

| | Side | Length | Width of protoloph | Width of metaloph | Height, unworn paracone | Height, unworn metacone | Height, unworn protocone | Height, unworn hypocone |
|---|---|---|---|---|---|---|---|---|
| M$^1$ | | | | | | | | |
| CPC 6748 | R | 22·2 | 19·5 | 19·7 | .... | .... | .... | .... |
| | L | 23·1 | 21·3 | 21·7 | .... | .... | .... | .... |
| UCMP 69929 | R | 25·3 | 20·3 | 21·7 | 10·9*m* | 11·7*m* | 12·8*m* | .... |
| UCMP 69928 | R | 22·0 | .... | 20·0*a* | .... | .... | .... | .... |
| UCMP 69913 | R | 26·7 | 21·3 | 20·2 | .... | .... | .... | .... |
| UCMP 69917 | R | 24·7 | 21·3 | 20·2 | .... | .... | .... | .... |
| UCMP 69569 | R | 25·8 | 21·1 | 20·7 | .... | .... | .... | .... |
| UCMP 66117 | L | 24·8 | 22·8 | 21·9 | .... | .... | .... | .... |
| UCMP 69907 | L | 23·6*a* | 18·9*a* | .... | .... | .... | .... | .... |
| UCMP 65880 | L | 25·4 | 21·4*a* | 20·6 | .... | .... | .... | .... |
| UCMP 69904 | L | 24·8 | 20·5 | 21·0 | .... | .... | .... | .... |
| UCMP 69918 | R | 25·0 | 18·2 | 18·3 | 10·6*m* | 11·4*m* | 9·1*m* | 11·5*m* |
| UCMP 69919 | L | 27·6 | 21·7 | 22·1 | 12·4 | 12·1 | 12·4 | 14·6 |
| UCMP 69771 | L | 26·5 | 20·8 | 20·4 | .... | .... | .... | .... |
| Range, M$^1$ | | 22·2–27·6 | 18·2–22·8 | 18·3–22·1 | 10·9*m*–12·4 | 11·4*m*–12·1 | 9·1*m*–12·8*m* | 11·5*m*–14·6 |
| M$^2$ | | | | | | | | |
| CPC 6748 | R | 26·4 | 23·8 | .... | .... | .... | .... | .... |
| UCMP 69929 | R | 28·3 | 24·5 | 23·4 | 10·7*m* | 12·0*m* | 11·4*m* | 13·3*m* |
| UCMP 69917 | R | 28·8 | .... | .... | .... | .... | .... | .... |
| UCMP 69569 | R | 31·3 | 26·4 | 23·7 | .... | .... | .... | .... |
| UCMP 66117 | L | 31·0 | 27·2 | 24·0 | .... | .... | .... | .... |
| UCMP 69907 | L | 26·7*a* | 22·3*a* | .... | .... | .... | .... | .... |
| UCMP 69904 | L | 28·8 | 25·5 | 23·4 | 12·0*m* | 11·2*m* | 11·9*m* | 14·2*m* |
| UCMP 69902 | R | 28·7 | 27·2 | 20·9 | 10·8 | 10·5 | 10·5 | 13·4 |
| Range, M$^2$ | | 26·4–31·3 | 22·3*a*–27·2 | 20·9–24·0 | 10·7*m*–12·0*m* | 10·5–12·0*m* | 10·5–11·4*m* | 13·3*m*–14·2*m* |
| M$^3$ | | | | | | | | |
| CPC 6748 | R | 32·1 | 27·8 | 24·4 | | | | |
| UCMP 69917 | R | 30·6 | 26·1 | 22·1 | | | | |
| UCMP 69912 | R | 31·7 | 26·1*a* | 24·5*a* | | | | |
| UCMP 69569 | R | 34·8 | 29·1 | 24·6 | | | | |
| UCMP 66117 | L | 34·2 | 29·6 | 25·3 | | | | |
| UCMP 69907 | L | 30·0 | 25·3 | 23·2 | | | | |
| UCMP 69906 | L | 31·7 | 30·3 | 26·3 | | | | |
| Range, M$^3$ | | 30·0–34·8 | 25·3–30·3 | 22·1–26·3 | | | | |
| M$^4$ | | | | | | | | |
| UCMP 69907 | L | 31·8 | 27·8*a* | 21·4 | | | | |
| UCMP 69905 | L | 37·2 | 28·4 | 22·1 | | | | |
| UCMP 65879 | L | 34·2 | 26·4 | 22·0 | | | | |
| Range, M$^4$ | | 31·8–37·2 | 26·4–28·4 | 21·4–22·1 | | | | |

No specimens of M$^3$ and M$^4$ were available to give unworn heights of cusps.
*a* = approximate.
*m* = moderately worn lophs.

$P_3$ (Table 18) is an elongate quasitriangular tooth (Fig. 7c). It is not as markedly triangular as in *Kolopsis* and is considerably longer than in *Pyramios*. There is a high median cuspid which sends off a strong longitudinal crest to the smaller posterior cuspid. There is no anterior longitudinal crest as in *Kolopsis*. The indentation in the labial surface of the tooth of *Kolopsis* is poorly developed or absent in *Plaisiodon*. Also, the crest which descends anterolabially from the posterior cuspid in *Kolopsis* is poorly developed in *Plaisiodon*. The labial cingulum, both anterior and posterior to the labial indentation, is either poorly developed or absent. In no case is the base of the crown over the posterior root developed into a prominent swelling.

Table 17: Measurements on lower incisor of *Plaisiodon centralis*

| | Side | Height at junction of root and crown | Width at junction of root and crown | Length of crown along ventral edge | Stage of wear |
|---|---|---|---|---|---|
| UCMP 69093 .... .... | R | 21·2*a* | 12·6*a* | .... | .... |
| UCMP 65623 .... .... | L | 20·5 | 12·2 | .... | .... |
| UCMP 69096 .... .... | L | 19·8 | 10·4 | .... | .... |
| UCMP 69909 .... .... | R | .... | .... | 35·1+ | *s* |
| | L | .... | 10·6 | 35·1+ | *s* |
| UCMP 69105 .... .... | R | 19·1 | 12·9 | .... | .... |
| UCMP 69104 .... .... | R | 18·0 | 10·5 | .... | .... |
| Range | | 18·0–<br>21·2*a* | 10·4–<br>12·9 | 35·1+ | |

*a* = approximate.
*s* = slightly worn crown.
+ = measurement short, would be longer in unworn specimen.

A moderately strong lingual crest from the posterior cuspid extends anteroventrally as a slight ridge above the base of the enamel. Unlike that in *Kolopsis*, this ridge is separated from the posterolingual crest of the main cuspid. The crest is not as sharp as in *Kolopsis*. The anterolabial cingulum is absent.

Table 18: Measurements on lower third premolar of *Plaisiodon centralis*

| | Side | Length | Width | Height of main cuspid |
|---|---|---|---|---|
| UCMP 69107 .... .... .... | R | 20·1 | 13·4 | .... |
| UCMP 69110 .... .... .... | L | 19·4 | 12·7 | .... |
| UCMP 69105 .... .... .... | R | 16·6 | 11·4 | .... |
| UCMP 69104 .... .... .... | R | 16·6 | 10·7 | .... |
| UCMP 67151 .... .... .... | R | 17·4 | 11·3 | 13·4*s* |
| UCMP 67119 .... .... .... | L | 17·4 | 12·7 | .... |
| UCMP 67296 .... .... .... | L | 18·6 | 11·7 | .... |
| UCMP 67460 .... .... .... | L | 19·8 | 12·3 | .... |
| UCMP 69098 .... .... .... | L | 19·1 | 11·7 | .... |
| UCMP 69099 .... .... .... | R | 20·9 | 11·4 | .... |
| | L | 19·1 | 10·8 | .... |
| UCMP 69103 .... .... .... | L | 18·8 | 12·8 | .... |
| UCMP 69970 .... .... .... | R | 21·2 | 14·6 | .... |
| Range .... .... .... .... | | 16·6–<br>21·2 | 10·7–<br>14·6 | 13·4*s* |

*s* = slightly worn crown.

*Lower molars* (Table 19). $M_1$ is an elongate rectangular tooth (Fig. 7c) composed of an anterior and posterior moiety separated by a transverse valley. The anterior moiety is made up of a protolophid, which connects the labial protoconid to the lingual metaconid. The protoconid connects to the anterior cingulum by a strong anterolingually directed paralophid crest. In little worn or unworn specimens the crests of the lophids are directed anterolabially across the tooth. The protolophid is transversely narrower than the hypolophid. The metalophid is not well defined; it extends anterolingually from the hypoconid to the floor of the transverse valley.

Table 19: Measurements on lower molars of *Plaisiodon centralis*

| | Side | Length | Width of protolophid | Width of hypolophid | Height, unworn protoconid | Height, unworn hypoconid | Height, unworn metaconid | Height, unworn entoconid |
|---|---|---|---|---|---|---|---|---|
| $M^1$ | | | | | | | | |
| UCMP 69105 | R | 20·1 | 14·7 | 14·8 | .... | .... | .... | .... |
| UCMP 69104 | R | 22·4*a* | 14·4 | 14·7 | .... | .... | .... | .... |
| UCMP 67151 | R | 22·8 | 14·7 | 15·8 | 13·6 | 9·4 | 11·2 | 8·6 |
| UCMP 67119 | L | 22·0 | 17·2*a* | 16·9 | .... | .... | .... | .... |
| UCMP 67296 | L | 25·0 | 15·8 | 17·3 | .... | .... | .... | .... |
| UCMP 67460 | L | 25·0 | 17·4*a* | 17·0 | .... | .... | .... | .... |
| UCMP 69098 | L | 23·9 | 16·1 | 16·8*a* | .... | .... | .... | .... |
| UCMP 69099 | R | 24·3 | 15·0 | 15·3 | .... | .... | .... | .... |
| | L | 23·7 | 14·5 | 15·1 | .... | .... | .... | .... |
| UCMP 69103 | L | 23·3 | .... | .... | .... | .... | .... | .... |
| UCMP 69970 | R | 27·2 | 17·8 | 17·5 | .... | .... | .... | .... |
| Range, $M_1$ | | 20·1–<br>27·2 | 14·4–<br>17·8 | 14·7–<br>17·5 | 13·6 | 9·4 | 11·2 | 8·6 |
| $M_2$ | | | | | | | | |
| UCMP 69105 | R | 25·5 | 17·8*a* | .... | .... | .... | .... | .... |
| UCMP 69104 | R | 26·1 | 19·1 | 19·0 | .... | .... | .... | .... |
| UCMP 67151 | R | 26·8 | 19·0 | 19·3 | 13·7 | 12·3 | 13·2 | 11·3 |
| UCMP 67439 | L | 28·4 | .... | .... | .... | .... | .... | .... |
| UCMP 67119 | L | 27·3 | 20·2 | 19·8 | .... | .... | .... | .... |
| UCMP 67296 | R | 31·5*a* | 22·4 | 22·4*a* | .... | .... | .... | .... |
| | L | 30·4*a* | 19·8*a* | 20·7*a* | .... | .... | .... | .... |
| UCMP 67460 | L | 30·0 | 21·1 | 20·6 | .... | .... | .... | .... |
| UCMP 69098 | R | 27·2 | .... | 21·7 | .... | .... | .... | .... |
| | L | 28·2 | 18·3 | 20·8 | .... | .... | .... | .... |
| UCMP 69099 | R | 26·9 | 18·5 | 18·0 | .... | .... | .... | .... |
| | L | 26·1 | 18·0 | 18·2 | .... | .... | .... | .... |
| UCMP 69103 | L | 27·3 | 19·8 | 18·3 | .... | .... | .... | .... |
| UCMP 69966 | R | .... | .... | 19·4 | .... | .... | .... | .... |
| UCMP 69969 | L | 29·1 | .... | 20·0 | .... | .... | .... | .... |
| UCMP 69970 | R | 30·0 | 20·7 | 20·5 | .... | .... | .... | .... |
| Range, $M_2$ | | 25·5–<br>31·5*a* | 17·8*a*–<br>22·4 | 18·0–<br>21·7 | 13·7 | 12·3 | 13·2 | 11·3 |
| $M_3$ | | | | | | | | |
| UCMP 69105 | R | 30·0 | .... | .... | .... | .... | .... | .... |
| UCMP 69104 | R | 31·5 | 24·3 | 22·7 | .... | .... | .... | .... |
| UCMP 67439 | L | 31·3 | .... | 22·2 | .... | .... | .... | .... |
| UCMP 67119 | L | 30·2 | 27·7 | 22·2 | .... | .... | .... | .... |
| UCMP 69120 | L | 31·4 | .... | 22·5*a* | .... | .... | .... | .... |
| UCMP 69965 | R | 33·3*a* | 24·7 | 23·8 | .... | .... | .... | .... |
| | L | 32·8*a* | 23·8*a* | 24·1 | .... | .... | .... | .... |
| UCMP 67296 | R | 34·5 | 23·8 | .... | .... | .... | .... | .... |
| UCMP 67460 | L | 34·6 | 25·1 | 24·3 | .... | .... | .... | .... |
| UCMP 69098 | R | 31·8 | 24·7 | 23·2 | .... | .... | .... | .... |
| | L | 32·7 | 24·8 | 24·0 | .... | .... | .... | .... |
| UCMP 69099 | R | 29·9 | 22·3 | 21·0 | 12·6 | 13·2 | 12·9 | 11·5 |
| | L | 31·3 | 21·8 | 20·8 | 13·4 | 13·3 | 13·7 | 10·7 |
| UCMP 69103 | L | 31·2 | 23·7 | 22·7 | .... | .... | .... | .... |
| UCMP 69966 | R | 32·5 | 22·5 | 21·7 | .... | .... | .... | .... |
| UCMP 69969 | L | .... | 24·3 | 23·9 | .... | .... | .... | .... |
| Range, $M_3$ | | 29·9–<br>34·6 | 21·8–<br>27·7 | 21·0–<br>24·3 | 12·6–<br>13·4 | 13·2–<br>13·3 | 12·9–<br>13·7 | 10·7–<br>11·5 |

*a* = approximate. *m* = moderately worn.

Table 19: Measurements on lower molars of *Plaisodon centralis*—continued

| | Side | Length | Width of protolophid | Width of hypolophid | Height, unworn protoconid | Height, unworn hypoconid | Height, unworn metaconid | Height, unworn entoconid |
|---|---|---|---|---|---|---|---|---|
| $M_4$ | | | | | | | | |
| UCMP 69104 | R | 31·3*a* | 23·6 | 23·3 | 12·3*m* | .... | 12·3*m* | 9·9*m* |
| UCMP 67439 | L | .... | .... | 22·8 | .... | .... | .... | .... |
| UCMP 67119 | L | 31·9 | 23·7 | 21·8 | .... | .... | .... | .... |
| UCMP 69120 | L | 31·3 | .... | .... | .... | .... | .... | .... |
| UCMP 69965 | R | 34·4 | 24·0 | 23·1 | .... | .... | .... | .... |
| | L | 36·5 | 24·0 | 22·9 | .... | .... | .... | .... |
| UCMP 67296 | R | 34·9 | .... | 24·0 | .... | .... | .... | .... |
| | L | 36·0 | .... | .... | .... | .... | .... | .... |
| UCMP 67460 | R | 36·9 | 27·1 | .... | .... | .... | .... | .... |
| | L | 37·6 | .... | .... | .... | .... | .... | .... |
| UCMP 69098 | R | 34·9 | .... | .... | .... | .... | .... | .... |
| | L | 35·2 | 26·1 | 23·0 | 12·2*m* | 10·3*m* | 15·7*m* | 11·4*m* |
| UCMP 69103 | L | 33·1 | 24·4 | 23·2 | .... | .... | .... | .... |
| UCMP 69100 | L | 36·6 | 25·4 | 24·0 | .... | .... | .... | .... |
| UCMP 69966 | R | 33·9 | 24·3 | 21·4 | .... | .... | .... | .... |
| UCMP 69969 | L | 25·8 | 26·1 | 24·3 | .... | .... | .... | .... |
| UCMP 69970 | R | 36·3 | 25·5 | .... | .... | .... | .... | .... |
| Range, $M_4$ | | 25·8–<br>37·6 | 23·6–<br>27·1 | 21·4–<br>24·0 | 12·2*m*–<br>12·3*m* | 10·3*m*<br>.... | 12·3*m*–<br>15·7*m* | 9·9*m*–<br>11·4*m* |

*a* = approximate. *m* = moderately worn.

The anterior cingulum is found only lingual to the point where the paralophid crest from the protoconid joins the anterior end of the tooth. The labial cingulum is small. It occurs only at the labial mouth of the transverse valley. The posterior cingulum connects the posterior base of the hypoconid to that of the entoconid. The deepest part of the cingulum occurs in a slight swelling at the midline. The lingual cingulum is only slightly indicated. In lingual view the floor of the transverse valley is V-shaped. The axes of the lophids slant posterodorsally.

$M_2$ is constructed like $M_1$ except that the crest from the protoconid to the anterior end of the tooth is shorter and less well developed. The paralophid crest is not as great as in $M_1$. The metalophid is distinctly developed. It is stronger than in $M_1$. The anterior cingulum is more massive than in *Kolopsis* and extends across the anterior end of the tooth. The protolophid and hypolophid are about equally wide.

In $M_3$ and $M_4$ the protolophid becomes progressively wider relative to the hypolophid, but except for being larger these teeth do not differ materially from $M_2$.

### *Mandible*

The lower jaw (Table 20) of *Plaisiodon centralis* is larger than that of *Kolopsis torus*, but of generally similar proportions. The horizontal ramus decreases in depth from $M_3$ to $P_3$. The lower border curves upward below $M_1$ and $M_2$, before turning downward again, to the symphysis (Fig. 8a). The symphyseal region tapers anteriorly to the alveolus of the incisor. The mental foramen is below and usually in front of the first root of $P_3$. In UCMP 67443, the foramen is found at the tip of the anterior root of $P_3$.

The digastric process is rarely, and then only slightly, developed. The ventral edge of the angular portion of the jaw is usually smoothly rounded, curving gently upward behind the posterior tip of the angle. In some specimens (as the left half of

Table 20: Measurements on lower jaws of *Plaisiodon centralis*

| | | Length, symphysis | Length, dorsal edge incisor alveolus to rear, $M_4$ | Length, dorsal edge incisor alveolus to postalveolar process | Length, dorsal edge incisor alveolus to mandibular canal | Length, dorsal edge incisor alveolus to rear, condyle | Length, $P_3$–$M_4$ | Length, $P_3$ to postalveolar process | Length, $P_3$ to mandibular canal | Length, $P_3$ to rear, condyle | Length, rear of symphysis to digastric process | Length, anterior root $P_3$ to rear, mental foramen | Depth, dorsal edge jaw at $P_3$ to bottom, mental foramen | Depth, horizontal ramus below anterior root, $M_1$ | Depth, horizontal ramus below middle of $M_3$ | Length, rear of condyle to anterior edge ascending ramus | Length, postalveolar process to rear $M_4$ | Length, mandibular canal to postalveolar process | Anteroposterior width condyle across main axis of ascending ramus | Transverse width condyle | Width jaw, at rear of $M_3$ | Length, diastem, $I_1$–$P_3$ | Stage of maturity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UCMP 69105 | R | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | +2·8 | .... | 71·6 | 66·4 | .... | .... | .... | .... | .... | .... | 53·9 | 4 |
| UCMP 69104 | R | 83·8*a* | 174·9 | 190·2 | 216·9 | .... | 135·3 | 149·1 | 128·0 | .... | 86·1*a* | +3·9 | 15·7 | 49·5 | 50·0 | .... | 12·4 | 29·9 | .... | .... | 39·5 | 39·5 | 3 |
| UCMP 67443 | R | 100·5 | .... | .... | .... | .... | 135·4*a* | 154·5*a* | 177·6*a* | 232·7*a* | .... | —5·5 | 25·7 | 55·1 | 54·3 | 103·6 | 17·4 | 22·8 | 16·6*a* | .... | 37·9 | 47·2*a* | 4 |
| UCMP 69119 | L | .... | 179·8*a* | 195·4*a* | 233·5*a* | 134·1 | 152·8 | 152·8 | 186·7*a* | 231·2*a* | 86·1*a* | +2·2 | 25·3 | 55·9 | 54·7 | 110·9 | 14·3 | 39·8 | .... | .... | 40·5 | .... | 4 |
| UCMP 69120 | L | .... | .... | .... | .... | .... | .... | .... | .... | .... | 111·4 | .... | .... | .... | 62·7 | .... | .... | .... | .... | .... | 40·3 | .... | 4 |
| UCMP 69965 | R | 118·2 | 196·7 | 231·5 | 257·4 | .... | .... | .... | .... | .... | 114·6 | .... | .... | .... | 65·3 | .... | 31·5 | 25·2 | .... | .... | 43·7 | .... | 4 |
| | L | 118·2 | 206·3*a* | 234·4*a* | 267·9*a* | .... | .... | .... | .... | .... | .... | .... | .... | .... | 67·6 | .... | 27·8 | 31·5 | .... | .... | 44·6 | .... | 4 |
| UCMP 67296 | R | 146·1*a* | 199·9 | 234·5 | 265·4*a* | 295·0 | 145·7 | 171·9 | 205·0*a* | 246·8 | .... | —12·6 | 27·9*a* | 62·4 | 66·7 | 113·8 | 30·6 | 24·7*a* | 22·1 | 76·9 | 47·1 | 49·8 | 4 |
| | L | 146·1*a* | 202·1 | 233·5 | 254·3*a* | 297·9 | 148·1 | 180·0 | 202·0*a* | 247·0 | .... | .... | .... | 67·4*a* | 66·7 | 121·3 | 28·8 | 22·0*a* | 20·3*a* | 89·5 | 45·5 | 48·4 | 4 |
| UCMP 67460 | R | 114·1 | .... | .... | .... | .... | 148·8*a* | 180·1 | .... | .... | .... | +0·8 | 33·7 | 73·2 | 71·3 | .... | 33·1*a* | .... | .... | .... | .... | .... | 4 |
| | L | 114·1 | .... | .... | .... | .... | 146·9 | .... | .... | .... | .... | +3·7 | .... | 74·6 | .... | .... | .... | .... | .... | .... | 47·5*a* | .... | 4 |
| UCMP 69091 | R | 118·4 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 42·9 | .... | 4 |
| | L | 118·4 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 69·6*a* | 69·2*a* | .... | .... | .... | .... | .... | 42·6 | .... | 4 |
| UCMP 69098 | R | .... | .... | .... | .... | .... | 142·3 | 163·2 | 185·5 | 226·6 | .... | +3·2*a* | .... | .... | 70·1 | 112·8 | 16·5 | 27·6 | 23·5 | .... | 41·0 | .... | 4 |
| | L | .... | .... | .... | .... | .... | 142·7 | 162·5 | 187·4 | 222·7 | .... | +2·7 | .... | .... | 65·5 | 106·3 | 20·7 | 27·8 | 23·5 | .... | 42·7 | .... | 4 |
| UCMP 69103 | L | .... | .... | .... | .... | .... | 135·9 | .... | 176·5 | 213·0 | .... | .... | .... | .... | 58·5 | 107·7 | .... | 39·5 | 20·0 | 61·2*a* | 38·2 | .... | 4 |
| UCMP 69969 | L | 137·3 | 221·2 | 255·9 | 289·5 | .... | .... | .... | .... | .... | 148·9 | +2·5 | 31·3 | 67·8 | 69·5 | .... | 44·5 | 35·4 | .... | .... | 40·0*a* | 67·5 | 4 |
| Range | | 83·8*a*–146·1*a* | 174·9–206·3*a* | 190·2–234·5 | 216·9–267·9*a* | 134·1–297·9 | 135·3–152·8 | 149·1–180·1 | 128·0–205·0*a* | 213·0–247·01 | 86·1*a*–48·9 | —12·6 to +3·9 | 15·7–33·7 | 49·5–74·6 | 50·0–71·3 | 103·6–121·3 | 12·4–44·5 | 22·0*a*–39·5 | 16·6*a*–23·5 | 61·2*a*–89·5 | 37·9–47·5*a* | 47·2*a*–67·5 | |

*a* = approximate

UCMP 69098) a shallow concavity behind the digastric process corresponds to the lateral expression of the postdigastric sulcus. The ascending ramus rises more vertically than in *Kolopsis,* and anterior edge of the ramus rises past the body of the hypolophid of $M_4$ in mature specimens rather than behind it. The ascending ramus is nearly complete in UCMP 67443 and 69105. The tip of the coronoid process is not preserved and it is not certain that it would have curved posteriorly to overhang the condyle.

The masseteric fossa as seen in UCMP 67296 is broad and relatively shallow. The posterior masseteric eminence is not as sharply pointed as in *Kolopsis.* The position of the eminence, below the condyle and on a horizontal line drawn across the tips of the teeth, is similar to that in *Kolopsis.* The outline of the masseteric fossa is similar to that of *Kolopsis* except that its dorsal tip is below the level of the mandibular notch and the condyle. A small foramen is present in some specimens at the anteroventral end of the fossa. The mandibular notch is relatively sharper, less broadly open, than in *Kolopsis.*

In dorsal view each ramus converges toward the symphysis at an angle of about 10° as measured along the inside of the rami. The ridge between $P_3$ and the rear of the incisor alveolus turns inward anterior to $P_3$, but does not then flare outward as much as in *Kolopsis.* Between the two ridges the symphysis is broadly U-shaped transversely. The symphysis seems to be relatively narrower than in *Kolopsis.* The genial crest is absent in *Plaisiodon,* and the two genial pits are broader, shallower and farther forward than in *Kolopsis,* being found on the ventral rather than lower posterior surface of the symphysis.

The condyle is in a similar position to that of *Kolopsis,* but its dorsal articular surface is not as flat. In dorsal view, the articular surface of *Kolopsis* is sinuous, whereas that of *Plaisiodon* is somewhat straighter transversely. In *Kolopsis* the longitudinal axis of the ascending ramus is vertical and the articular surface of the condyle in posterior view is transversely horizontal. In *Plaisiodon,* the longitudinal axis of the ascending ramus slants dorsomedially. Consequently, the transverse articular surface of the condyle slants ventromedially.

The rami increase in width posteriorly, their greatest thickness being measured across $M_4$ as in *Kolopsis.* The postalveolar shelf and process are less distinctly developed than in *Kolopsis,* this area of the jaw generally indicated as a lingual swelling between $M_4$ and the mandibular foramen.

In the lingual view, the ventral lingual edge of the pterygoid fossa (Fig. 8b) forms a strong broad ridge. It fades out into the ventral border of the jaw at the anterior end of the pterygoid fossa, which is separate from and just posterior to the shallower digastric fossa, which tapers to fade out below the anterior end of $M_3$.

In ventral view, the ventral border of the jaw is not so concave lingually anterior to the pterygoid fossa as in *Kolopsis.* Consequently, the ventral border does not bow medially below $M_4$, and the digastric process is less well developed. The posterior surface of the angular process is relatively flat in an anterolateral direction, but the posteromedial tip of the angular process seems to extend to a point on a line with the longitudinal axis of the tooth row. In *Kolopsis* the tip of the angular process would lie lateral to the posterior extension of the longitudinal axis of the dentition.

The suprapterygoid ridge between the postalveolar shelf and the dorsal edge of the mandibular canal of *Kolopsis* is not present in *Plaisiodon.* The mandibular canal in *Plaisiodon* is not bounded by a dorsal and ventral crest, and the small spur of bone just anterodorsal to the foramen in *Kolopsis* is not present in *Plaisiodon.* The criteria by which mandibles of *Kolopsis torus* were segregated into growth stages also apply to those of *Plaisiodon centralis.* As indicated in Table 20, only mandibles of stages 3 and 4 were measured. The extreme variation in adult jaw size noted in *Pyramios alcootense* has not been observed in *K. torus* or *P. centralis.*

### *Remarks*

*Plaisiodon centralis* is larger than *K. torus.* As indicated by the general similarity of their upper and lower premolars, the strong paralophid crest on $M_1$ and the absence of enamel on the medial face of the lower incisor, these two genera are more closely related to each other than either is to *Pyramios alcootense.* A near structural ancestor for *Plaisiodon centralis* can be found in *Neohelos tirarensis* Stirton, 1967, of the Kutjamarpu fauna of South Australia The salient features which demonstrate this relationship are the presence of a hypocone on $P^3$, a single parametacone on $P^3$; a broadly triangular $I^3$ lacking a strong cleft in its labial surface and the absence of a distinct cusp in the position of the metastyle on $M^1$. On the other hand, its large size, the well developed anterior and posterior cingula on the upper molars, the absence of a longitudinal postparaconal crest on $M^1$, and the presence of a distinct metalophid on the lower molars of *Plaisiodon centralis* point to the separation of the two forms.

*Kolopsis torus* differs from *P. centralis* in the separation of the paracone and metacone on $P^3$, and the strong separation of a metastyle on $M^1$, but is less advanced and closer to *Neohelos tirarensis* in the broadly U-shaped immaculate transverse valleys of the lower molars and the vertical orientation of the lophids of the lower molars. *K. torus* otherwise differs from *N. tirarensis* in being larger and having an upper third incisor with an almost heart-shaped occlusal outline. *K. torus* is closer to the main evolutionary pathway within the lineage leading to *Zygomaturus trilobus* Owen, while *Plaisiodon centralis* is a terminal member of a sidebranch, the ultimate ancestor of which is currently unknown (Stirton, Woodburne, & Plane, this vol., p. 149 ff.).

## REFERENCE

NEWSOME, A. E., and ROCHOW, K. A., 1964—Vertebrate fossils from Tertiary sediments in Central Australia. *Aust. J. Sci.* 26, 11, 352.

Page 104 is blank.

# TWO NEW DIPROTODONTIDS FROM THE PLIOCENE OTIBANDA FORMATION, NEW GUINEA

by

M. D. PLANE

## CONTENTS

Page

Genus *Nototherium* Owen, 1845
    *Nototherium watutense* Anderson, 1937 .... 107
Genus *Kolopsis* Woodburne, 1967
    *Kolopsis rotundus* sp.nov. .... 111
Genus *Kolopsoides* nov. .... 118
    *Kolopsoides cultridens* gen.nov. et sp.nov. .... 119

REFERENCES .... 128

## SUMMARY

Three diprotodontids are found in the Otibanda Formation. Of these only one has been previously named. This animal is the largest, and as far as can be told from the present collections, the least numerous. It was named *Nototherium watutense* in 1937 by Charles Anderson and is known only from lower posterior molar teeth and one possible upper molar fragment. The lower molars are distinctive enough for some comparisons to be made with the diprotodontids from the Australian Alcoota and Palankarinna faunas. The second largest animal is not well represented either, but its upper dentition, particularly the premolar, bears striking resemblance to *Kolopsis torus* from the Alcoota fauna and shows similarities to a new species from the Palankarinna fauna. The smallest and by far the best represented species in our collections is most distinct and specialized in its upper premolar. It may be also related to the Alcoota species *Kolopsis torus*, but no late Pliocene or Pleistocene diprotodontids seem comparable.

## ACKNOWLEDGMENTS

This research was sponsored by the Bureau of Mineral Resources and the Museum of Paleontology, University of California, Berkeley. The author is particularly indebted to Dr John W. Evans, Director of the Australian Museum, Sydney, to Mr Harold O. Fletcher, Assistant Director, and to Jack T. Woods, Esq., Director of the Queensland Museum, Brisbane, for permission to describe and figure specimens from their collections. The excellent line drawings in the report are the work of Mr Owen J. Poe and Mrs Augusta Lucas.

My sojourn in Berkeley was made possible by the United States National Science Foundation Grant GB–1990. The research was partly financed by NSF Grant G–15957 and I make grateful acknowledgement of these grants, and of a grant-in-aid from the Commonwealth Public Service Board.

Page 106 is blank.

## Family DIPROTODONTIDAE

### Genus NOTOTHERIUM Owen, 1845

### NOTOTHERIUM WATUTENSE Anderson, 1937

*Type:* A.M. F36311, F36312; left and right posterior mandibular fragments. The left contains the posterior lingual corner of $M_4$, the anterior root of $M_4$ in the alveolus, the posterior root of $M_3$ in the alveolus, and the anterior alveolus of $M_3$ with no root in place. Both Anderson (1937) and Stirton (pers. comm.) have noted that although the specimens have different numbers they are probably from the same individual.

*Referred specimens:* A.M. F41443, F41444; same individual, left and right posterior mandibular fragments; right with $M_4$, $M_3$, and posterior moiety of $M_2$; left with $M_4$, posterior moiety $M_3$. GSQ F2760: posterior portion of left mandible with $M_4$, and posterior moiety $M_3$. UCMP 68740: anterior half of ? $M^3$.

*Type locality:* The locality was described (Anderson, 1937, p. 73) as 'on Roaring or Wiganda Creek, a tributary of the Watut River . . . the result of the construction of water races connected with sluicing operations . . .' N. H. Fisher revisited the locality in 1939 when further construction was underway. From a photograph that he took, I have been able to relocate the locality fairly accurately. It may be found on the Nauti 1 mile Sheet, Morobe District, New Guinea, and lies 4·5 miles south-west of the Gold and Power Company residence at Slate Creek on a water race, which formerly drew water from a tributary of Wiganda Creek, just downstream from the present site of Kaumunga village. The locality is 0·8 miles due north of the Otibanda triangulation beacon. No attitudes were obtainable on the coarse brown sandstone or blue-grey mudstone, but the general orientation of strata in this vicinity is strikes between 125° and 145° with south-westerly dips 7° - 15°.

*Age:* Middle Pliocene (7·6–5·7 million years before present).

*Specific diagnosis:* Smaller than other species of *Nototherium*; short, relatively massive mandible; posterior surface of deep symphyseal region rising steeply anterodorsally from below midpoint of $M_2$ to just below posterior moiety of $M_1$; symphysis not shallow, elongate and nearly flat as in other Nototheriinae; mandible proportionally and actually shallower relative to molar crown height than other species of *Nototherium*; digastric process (farther forward) than in *N. mitchelli* mandibular foramen low, at level of tooth row; molars with broadly V-shaped instead of tightly V-shaped transverse valley.

### *Description and Comparison*

*Mandible:* The digastric process is present but is broken off in the type and AM F41444. It exists in slightly broken condition in AM F41443 and GSQ F2760. A pronounced digastric sulcus is best seen in F41443 and a well developed digastric fossa is present in all three mandibles. The angular surface is slightly concave in its ventral outline. The anterior edge of the ascending ramus rises opposite the posterior moiety of $M_4$ in all the specimens. A postalveolar shelf behind $M_4$ is triangular, with the distance from the posterior cingulum of $M_4$ to the postalveolar process 28·0 in the type and 26·0 in F2760. It is broken off in the other specimens.

The postalveolar process, which is pointed, is lingual from the opening of the postdental canal which can be seen only in the type. This canal is 5·0 in diameter and 45·0 posterior to, and on a level with, the crown of $M_4$. On F41443 and F41444 the postdental canal can be seen, but its natural point of emergence has been broken away. It cannot be observed in F2760, but in the type and in F41443 and F41444 this canal runs labial to the tooth row. The depth of the mandible below $M_4$ is 57·0 in the type, 59·8 in F41443, 59·5 in F41444, and 67·0 in F2760. The width of the mandible below $M_4$ is 45·0 in the type, 41·0 in F41443, 40·6 in F41444, and 49·9 in F2760. In F41443 and F2760 the lingual border of the horizontal ramus swings in medially opposite $M_2$ to form the symphysis.

All the molars are long for their breadth with the median valleys broadly open. The anterior and posterior moieties are approximately equal in length. The posterior moiety of $M_4$ is lingually offset more than the posterior moieties in $M_2$ and $M_3$. There is no reduction in the breadth of the posterior moiety in either $M_3$ or $M_4$. A broad, low rounded metalophid on the anterior surface of the hypolophid extends from the hypoconid to a position in the median valley just labial to the midline of the tooth. Its development is almost exclusively from the hypolophid; there is only the slightest suggestion of ridge-like development on the posterior surface of the protolophid. The short paralophid from the protoconid on the lingual side of the tooth maintains an anteroposterior direction as opposed to a more anterolingual direction of the metalophid. Both protolophid and hypolophid are slightly crescentic. The posterior cingula are prominent and wide on $M_4$ and $M_3$, but in $M_2$ this structure is almost completely lost because of appression against $M_3$. The posterior cingulum on $M_4$ arises posterolabial to the entoconid. The cingulum continues around on to the labial side of the tooth, where it rises slightly to connect with a narrow ridge which descends from the hypoconid. The cingulum is deflected downward opposite the median valley and continues around on to the front of the tooth, where it forms the anterior cingulum. The labial cingulum rises again below the protoconid, to which it is connected by a narrow ridge in the same way that it is connected to the hypoconid. These narrow ridges and the extent of the posterior and labial cingula are most distinctive and can be best seen in F41443 and F41444 They are also evident on F2760. The anterior cingulum, a much narrower shelf than the posterior cingulum, ends directly below the metaconid. Neither a lingual cingulum nor a shelf-like structure across the median valley on either the lingual or the labial sides is developed.

All specimens, including the type, have undergone some wear on the $M_4$. What remains of the hypolophid in the type indicates that it is the oldest individual in the sample, while wear on the hypolophid of F2760 suggests that it is probably the youngest. In moderate stages of wear the low broadly rounded metalophid and the short paralophid appear as anterior spurs (Fig. 1) on the hypolophid and protolophid.

*Comparisons:* Anderson compared the type with *Nototherium victoriae*, *N. mitchelli*, *Euowenia grata*, '*Zygomaturus*' DeVis, and *N. tasmanicum*. He noted that this was the smallest diprotodontid yet described, being comparable in size only with *Euowenia grata*. He felt that as the genus *Euowenia* was typified by having

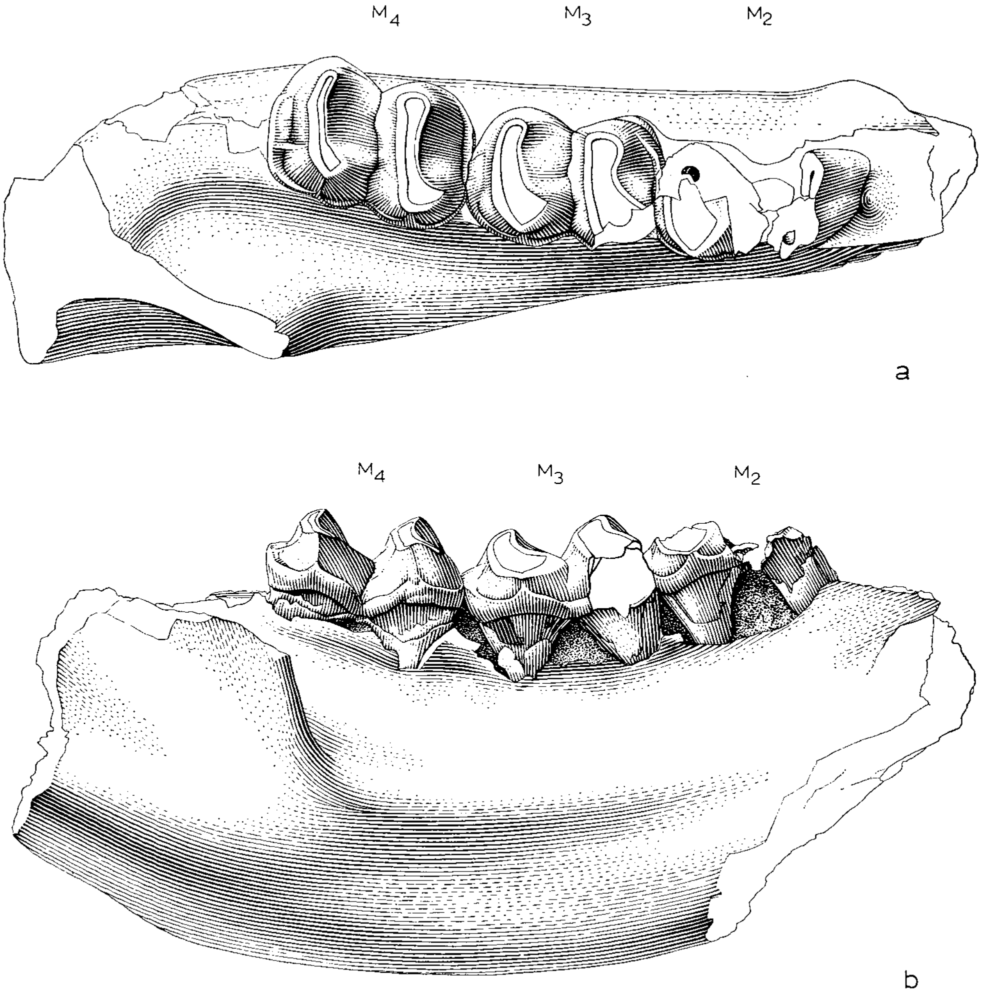


**Fig. 1.—*Nototherium watutense* Anderson, fragments of right mandible with M$_2$ to M$_4$, AM F41443; a, occlusal view; b. labial view x $\frac{3}{4}$.**

only two upper incisors, he would classify the Watut form as *Nototherium* (sensu lato) pending more discoveries. I have compared the specimens now referred to this species with *Nototherium inerme*, with the type of *Nototherium mitchelli*, with *Meniscolophus mawsoni*, and with *Pyramios alcootense*. Plate VIII in Owen (1845) was the basis for my comparisons with *N. inerme*.

A cast of the remaining parts of M$_3$ and M$_4$ in the type of *N. mitchelli* Owen, 1845, and Owen's (1877) figure, formed the basis for my comparisons of *Nototherium watutense* with *N. mitchelli*.

In *Nototherium inerme* the ventral border of the mandible is far more strongly curved anteroposteriorly than in *N. watutense*. The ventrolingual border of the mandible is ridged in *N. inerme* but broadly rounded in *N. watutense*. The posterior dorsal symphyseal surface is more steeply inclined in *N. inerme* than in *N. waiutense*.

The mandible of the type of *Nototherium mitchelli* is proportionally and actually deeper than that in *Nototherium watutense.* The digastric process in *N. mitchelli* is farther back than its equivalent in *N. watutense* and is not as sharply pointed. The digastric sulcus is not well defined. The postalveolar shelf is long and the postalveolar process is rounded. The mandibular foramen is higher on the ascending ramus than it is in *N. watutense.* From what little enamel remains on the molars of the type it is clear that the median valley was sharp and narrow. This contrasts with *N. watutense.*

For my comparisons with the species *Pyramios alcootense* I have had available the entire collection from the Alcoota quarries, but I used in particular the mandible UCMP 69571. The digastric process is broken in many of the specimens of *Pyramios,* but the process is weakly developed, as is the digastric sulcus. In both cases they are less developed than in *Nototherium watutense.* Another similarity is the position of the ascending ramus opposite the posterior moiety of $M_4$. The postalveolar shelf in *Pyramios* is not well developed, nor is the postalveolar process pointed. The process is rather rounded and nebulous but is, as in *Nototherium watutense,* lingual to the opening of the postdental canal. The mandibular foramen is on the level of the tooth row. *Pyramios* contrasts strongly with *N. watutense* in the morphology of the posterior part of the horizontal ramus. It is both deeper (64·0 below $M_4$) and narrower (41·3 below $M_4$). The molars in *Pyramios* are long for their breadth, particularly $M_3$ and $M_4$. The median valley is broadly V-shaped and $M_4$ is the only tooth with its posterior moiety lingually offset. The posterior moiety is not reduced in breadth. The metalophids are broad swellings rather than crests and the paralophids are weakly developed. The posterior cingulum is strong and continues around on to the labial side of the tooth as in *N. watutense,* but is not as well developed. The anterior cingulum is very weak and there is no lingual cingulum. The lophids are slightly crescentic and the spurs, also seen in *N. watutense,* develop with wear on the hypolophid and protolophid. Many of these features closely parallel those observed in *N. watutense*; however, in almost every case they are not as well marked.

Stirton (1955) has compared Anderson's type with *Meniscolophus mawsoni.* He noted the similarity in digastric process and sulcus and the differences in the dentition. These differences are the higher crowns, somewhat larger size of the teeth, the more tightly closed median valley, and the less complete anterior and posterior cingula. Similarities in the dentition which can be observed are: the length to breadth ratio, the development of a labial cingulum which connects via ridges to the hypoconid and the protoconid and which deflects downward opposite the median valley, the non-reduction of the posterior moiety of $M_4$, and the development of characteristic wear spurs on the lophs.

The short, massive lower jaw with its steeply rising ascending ramus, and steep, short, deep symphysis are the main reasons for retaining the taxonomic designation of Anderson. The similarities with *Pyramios alcootense* chiefly involve the molars: the broadly V-shaped transverse valleys, and the labial cingula rising as crests up the labial ends of the lophids. The former feature is suggestive of a general stage of advancement similar to that of *Pyramios alcootense,* but the latter character is of no significance in showing close relationships, for it occurs in only one of the specimens of *P. alcootense*, and furthermore is found in *Meniscolophus mawsoni* and, to judge from Owen's illustrations, the mandible of *Nototherium inerme*.

The digastric process and postdigastrc sulcus are only faintly developed in *P. alcootense*, but strongly developed in *N. watutense*. The fact that the ascending ramus rises past the posterior moiety of $M_4$ is of doubtful value, as this occurs in many other diprotodontids. The lingual position of the postalveolar process and shelf relative to the mandibular canal is the common situation in diprotodontids, so it is to be expected that *N. watutense* and *P. alcootense* should be similar in this respect.

### Genus KOLOPSIS Woodburne, 1967

### KOLOPSIS ROTUNDUS* sp.nov.

*Type:* QM F3858; left maxilla fragment with $M^3$, $M^4$ and the posterior root of $M^2$ in place; right $M^4$; right $P^3$; and posterior two thirds of the root of the left median upper incisor.

*Referred Specimens:* AM F38574; left maxilla fragment with portion of zygomatic process and $M^2$ and $M^3$ in place. AM F41443 and F41444; left and right mandibular fragments with right posterior two thirds of $I_1$, $M_2$, $M_3$ and $M_4$, and left posterior root of $I_1$, $P_3$, $M_1$, $M_2$ and $M_3$. These mandibular fragments have different numbers but are part of the same individual. BMR F20228; right mandibular fragment with $M_1$ and $M_2$ erupted and $M_3$ still partially in the alveolus. The posterior root of $P_3$ is in place and fragments of $M_4$ are in the alveolus. UCMP 68741; right $P_3$. UCMP 68706; right $P_3$.

*Type locality:* An alluvial gold mining property known as Niba Gold north-north-west of Bulolo township. This locality is downstream from the junction of the Bulolo and Watut Rivers. The Otibanda Formation is exposed in disused workings and at this locality is composed of light-coloured arkosic sandstone and tuff. The beds strike 38° and dip north-west at 21°.

Bulowat 1 mile Sheet, Morobe District, New Guinea. 7·2 miles north-north-west of the Bulolo Post Office. UCMP V6271.

*Age:* Middle Pliocene (7·6–5·7 million years before present).

*Specific diagnosis:* Upper incisor not as transversely compressed as *Kolopsis torus* Woodburne, 1967; $P^3$ of similar size to that in *K. torus*; length 19·6, width across paracone and protocone 15·6, width across hypocone and metacone 15·5, paracone and metacone 6·2 apart, paracone and metacone separated by shallow, wide, lingual and labial grooves; crest from metacone to posterior end of tooth short and steeply inclined; posterior cingulum with high contact to end of postmetaconal crest; paracone and metacone more rotund than in *K. torus*; parastyle separated from paracone by much narrower transverse cleft than in *K. torus*; parastyle nearly conical; no anterolingual emargination of basal outline between parastyle and protocone; crest connecting paracone and protocone high; slight posterolabial expansion of protocone but not enough to form a small depression on lingual side of paraconal-metaconal crest; labial cingulum not continuous past base of paracone; no mesostyle.

---

**Rotundus*, in reference to the rotund nature of the upper premolar.

Upper molars slightly longer and wider than in *K. torus*; anterior cingulum without anterior sloping, shelf-like protection; postparaconal crest stronger on posterior molars ($M^{3-4}$) than in *K. torus*.

Mandible more robust than in *K. torus*; horizontal ramus shallower and wider than *K. torus*; posterior edge of symphysis opposite median valley of $M_2$; genial crest absent; genial pits not well developed; digastric process and postdigastric sulcus stronger than in *K. torus*.

Lower incisor strongly curved with ovate cross-section; root widely open posterior, crown probably not inflected relative to root; enamel only on ventral half of lateral surface; enamel still in alveolus when $M_4$ in wear.

Lower premolar larger and more robust than in *K. torus*; main anteroposterior crest curved; sectorial crest terminates lingual to paralophid on $M_1$: both anterolingual and posterolingual crest strong and smoothly rounded; anterolingual crest not sharp as in *K. torus*; posterolingual basin shallower and more rounded than in *K. torus*; no prominent labial swelling above posterior root.

Lower molars have transverse valleys which are widely V-shaped; $M_1$ without cingulum on anterolabial corner, and no depression on surface in that area; anterior cingulum on lingual side of paralophid crest almost vestigial and closely appressed against anterior surface; anterior cingulum suppressed or absent on $M_{2-4}$; axes of lophids slant posterodorsally. All cheek teeth are higher crowned than in *K. torus*.

*Description and Comparison*

*Maxilla.* The maxillary fragment includes a partial zygomatic process. The process is broken, but the indications are that it was not large and that it did not inflect downward below the tooth row. When viewed from the front the process is at approximately 90° to the labial side of the tooth row. The process is bluntly pointed with the tip broken away.

*Upper Incisor.* The posterior two thirds of the root of a left $I^1$ is preserved in the type. This fragment (Fig. 2) is poorly preserved, but demonstrates that the tooth was strongly downcurved with a dorsal curvature approximately on an arc with radius 51·0. The ventral curvature is more gentle than the dorsal. The mesial surface of the incisor is neither flat nor straight, unlike *Kolopsoides cultridens*. It curves ventrolaterally.

*Upper Premolar.* Only one upper premolar is known. The tooth is five-cusped with a protocone, paracone, metacone, hypocone, and parastyle, and is distinct from the other small species of diprotodontid in this fauna. $P^3$ is 19·9 long and 15·9 wide. The metacone and paracone are joined to form a shearing ridge from which the parastyle is separated by a narrow transverse crevice. The hypocone is smaller than the protocone which is connected to the base of the paracone. The paracone was the highest cusp before wear began. All five cusps are bluntly cuspate. Cingula connect the base of the parastyle to the anterior base of the protocone, the posterior base of the protocone to the anterior base of the hypocone, and the base of the hypocone to the posterior base of the metacone. These cingula are on the lingual and posterior edge of the crown. A labial cingulum is developed from the posterior labial base of the metacone around to the slight commissure which separates the metacone from the paracone. At this point it turns upward and terminates in the commissure. There is another small ridge at the posterior base of the paracone anterior to the commissure between the metacone and paracone. There is no strong emargination at the base of the enamel between the anterior and posterior roots. The tooth has only two roots. The posterior root is the larger and curves around the back of the tooth to support the posterior half of the paracone, metacone, hypocone, and protocone. The anterior root supports the parastyle and the anterior half of the paracone.

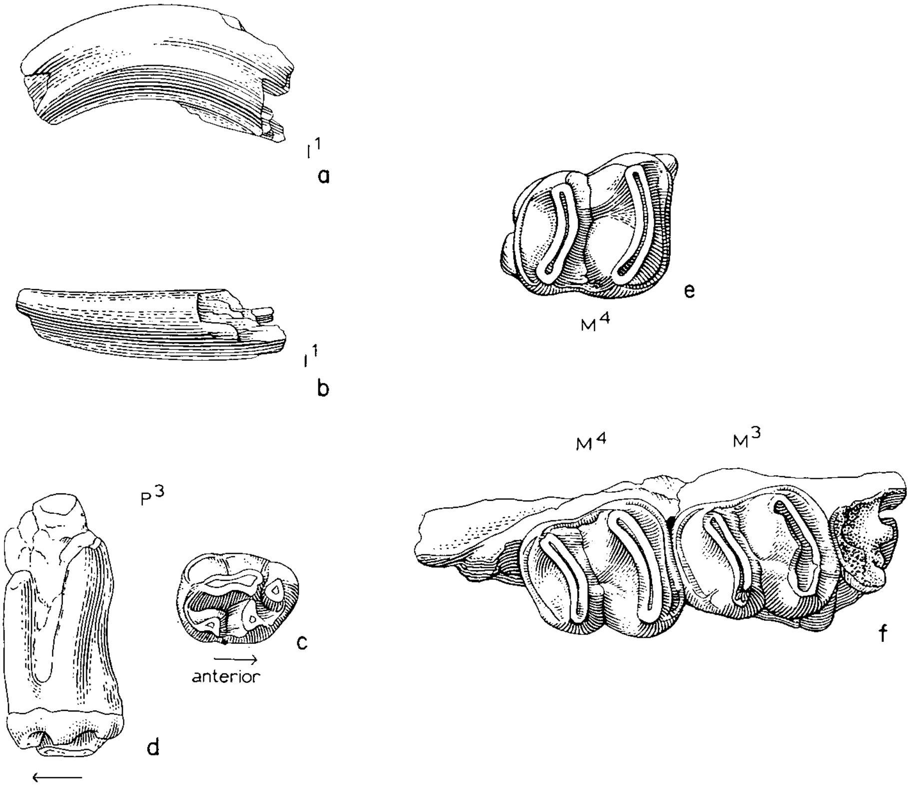


**Fig. 2.—*Kolopsis rotundus* sp.nov., type. a, upper median incisor, labial view; b, upper right median incisor, dorsal view; c, upper right premolar, lingual view; d, upper right premolar, occlusal view; e, upper right $M^4$, occlusal view; f, upper left $M^{3-4}$, occlusal view x $\frac{3}{4}$.**

*Upper molars.* There is no $M^1$ in our collection. The $M^2$ is a rather square, transversely bilophate tooth 20·8 long and approximately (the labial side of the tooth is broken) 19·1 wide on the specimen AM F38574. The protoloph is slightly wider than the metaloph. A parastyle and a metastyle are developed low down on the anterior and posterior cingula. The styles, neither of which is connected to the cusp above it, mark the lingual termination of the anterior and posterior cingula. The anterior cingulum is well developed, but terminates on the lingual side of the tooth below the protocone, to which it is connected by a slender ridge. A similar ridge descends from the protocone to join a well developed lingual cingulum. This cingulum is anterior to the labial end of the median valley. The posterior cingulum descends as a well marked ridge from the hypocone, but is narrow across the posterior part of the tooth, where it is appressed to $M^3$. It broadens to the rounded metastyle at its lingual termination. The transverse valley is U-shaped, but its base is a tight V. The postparaconal ridge is incipiently developed from the protoloph and metaloph, on the labial side of the tooth.

*$M^3$*. The two third molars in our collection show considerable diversity. In the type the parastyle is well developed but does not—as it does in AM F38754—form the labial termination of the anterior cingulum. The type has a strong broadly rounded postparaconal ridge developed from both the protoloph and the metaloph. The postparaconal ridge in F38754 is represented by a small, rounded swelling from the metaloph. The relative length and width of the two teeth are comparable, but the posterior moiety in the type is 3·0 narrower than the anterior moiety, while in AM F38754 I estimate the difference would be in the order of 1·0. In F38754 the posterior cingulum is very weak but the metastyle is well developed. In the type the posterior cingulum is strong but the metastyle is not well developed.

*$M^4$*. The fourth upper molars in the type are very similar to the third molar. The anterior cingulum is a little narrower, the parastyle is somewhat less strong and there is no metastyle. The protoloph is markedly wider than the metaloph which is much more strongly curved. The swellings in the median valley are not so well developed as those in $M^3$, but join to form a small obstruction to the otherwise open median valley.

*Mandible*. The digastric process is well marked and is rounded rather than pointed on AM F44470. It is broken on the juvenile BMR F20228. The digastric sulcus, posterior to the process, is shallow and smoothly rounded. A distinct digastric fossa can be seen in both F44470 and F20228. The pterygoid fossa, as seen in F44470, is deep, with a thick horizontal shelf marking its ventral termination. The anterior edge of the ascending ramus is opposite the anterior moiety of $M_4$. The postalveolar shelf is square (approximately 16 x 16) and the postalveolar process is pointed. The depth and width of the mandible below $M_2$ are 45·0 and 26·5, below $M_3$ are 44·2 and 31·6, and below $M_4$ are 42·3 and 39·1. The posterior end of the symphysis is opposite the anterior moiety of $M_2$ The mental foramen is below the anterior root of $P_3$.

*Lower incisors*. The posterior portions of both lower incisors are in place in the mandible AM F44471. The left ramus is broken off and obscured by the mandible, but the right tooth is observable as the mandible is broken along the symphyseal. region The incisor is ovate in cross-section and has a widely open root. What remains of the tooth is approximately 65·5 long, and I estimate its greatest depth to be approximately 20·0. The open end of the root is opposite the posterior moiety of $M_1$. Enamel is confined to the ventral surface, the lower half of the labial surface, and the ventral eighth of the mesial surface. As the enamel is still inside the alveolus on this mature individual and the root is widely open, it seems likely that the root of the incisor continued growing for a considerable time in this genus. The incisors are close together and probably converged to a sharp point at their median edge.

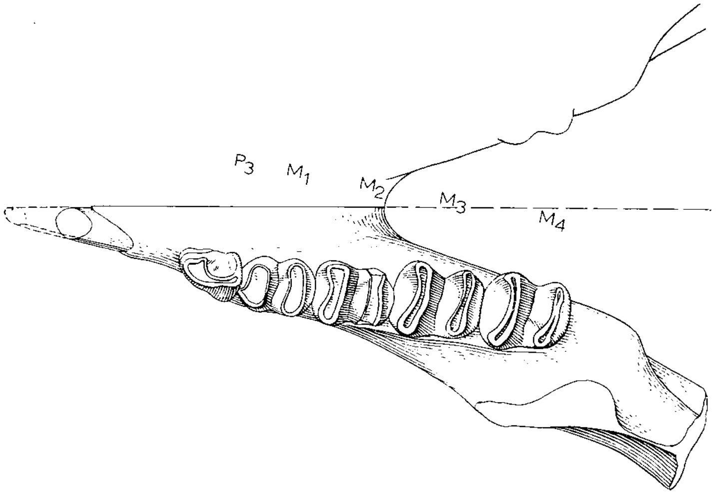


**Fig. 3.**—*Kolopsis rotundus* **sp.nov., composite from portions of left and right mandibles of one individual, occlusal view. AM. F44470 and F44471. x ½.**

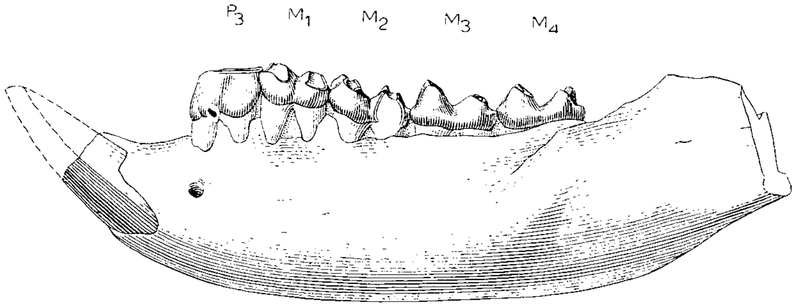


**Fig. 4.**—*Kolopsis rotundus* **sp.nov., composite from portions of left and right mandibles of one individual, labial view. A.M. F44470 and F44471. x ½.**

$P_3$. The premolar is well preserved in F44471, but UCMP 68706 has much of the enamel broken away from the ventral part of the crown. In F44471 the tooth is long for its width. In occlusal view it is seen to be triangular with a deep and wide lingual valley. There was evidently a high anteromedian cuspid and a low posterolabial cuspid, which were connected by an anterolingually curved crest. A second crest is prominently developed from the posterolingual end of the main crest. This is slightly curved and declines lingually. The tooth is much higher crowned than the molars posterior to it and the ventral border of the enamel is anteriorly downcurved. The depth of enamel on the anterior root is greater than that on the posterior root. There is a well marked emargination at the ventral border of the enamel on the labial side between the roots. The posterior moiety of the tooth has a bulbous profile.

*Lower Molars.* There are some minor differences in the lower molars from $M_1$ to $M_4$. As measured across the lophids the anterior moiety is slightly wider than the posterior moiety, except on $M_1$. All the lower molars are bilophate. The lophids are slightly crescentic and are directed posteriorly. $M_1$ is the only tooth with a well marked paralophid remnant. This is connected to the lingual side of the protolophid and makes a short ridge which appresses against the back of $P_3$. $M_1$ and $M_2$ have very weak anterior cingula and there are no anterior cingula on $M_3$ or $M_4$. A narrow posterior median cingulum is found on all the molars. On $M_3$ and $M_4$ there is a faint suggestion of a metalophid extending down into the median valley from the lingual side of the hypoconid. The median valleys are U-shaped and the axes of the lophids are directed posterodorsally. There are no labial or lingual cingula, but in the juvenile F20228 there are small cuspids at the labial and lingual ends of the median valley. Parastylid development is variable. They are small on $M_1$ and $M_2$ in F44471 and again small on $M_2$ of F20228. They are not present in $M_3$ or $M_4$. The height of the entoconid on the unworn $M_3$ of F20228 is 14·2.

Table 1: Length measurements on lower tooth rows in AM F44470 and F44471

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| $P_3$–$M_4$ | 103·9*a* | $M_1$–$M_4$ | 87·0*a* | $M_2$–$M_4$ | 68·2 | $M_3$–$M_4$ | 46·0 | length × width | |
| $P_3$–$M_3$ | 0·9 | $M_1$–$M_3$ | 64·0 | $M_2$–$M_3$ | 44·1 | length × width | | $M_4$ | 23·0 × 20·0 |
| $P_3$–$M_2$ | 58·2 | $M_1$–$M_2$ | 41·4 | length × width | | $M_3$ | 22·4 × 19·2 | | |
| $P_3$–$M_1$ | 36·2 | length x width | | $M_2$ | 21·9 × 16·9 | | | | |
| length x width | | $M_1$ | 19·8 × 14·7 | | | | | | |
| $P_3$ | 18·2 × 12·8 | | | | | | | | |

*a* = approximate.

**Fig. 5.—Skull of juvenile *Kolopsis rotundus* in coarse conglomeratic sediments. Koranga tail-race, Wau Basin.**

*Comparison*. This species of *Kolopsis* is most closely related to *Kolopsis torus*, the genotypic species, from the Alcoota fauna. It is comparable to *Zygomaturus keanei*, Stirton, 1967, from the Palankarinna fauna and *Z. gilli* Stirton, 1967, from Beaumaris, Victoria. For my comparisons with the species *Kolopsis torus* I had available the entire collection from the Alcoota quarries, but I referred most particularly to the type skull, CPC 6747, and the mandible UCMP 68925. All the specimens of the new species of *Zygomaturus* were also available to me. No comparisons can be made between the fragmentary incisor root of the type specimen and other species. The upper premolar of the type of *Kolopsis rotundus* strikingly resembles that of *K. torus*. They are the same width, but *K. rotundus* is 1·4 longer than *K. torus*. The position of the cusps is identical, but *K. rotundus* has better developed cingula. In *K. torus* an emargination in the cingulum connects the base of the protocone to the base of the parastyle; this cingulum is straight in *K. rotundus*. The premolar of *K. rotundus* is about 5·0 shorter than *Z. keanei* and 3·0 shorter than Stirton's (1957) restoration of the Beaumaris specimen. A vertical labial groove between the paracone and metacone is equally well developed in *K. rotundus*, *K. torus*, and *Zygomaturus keanei*. This groove is deeper in *Z. gilli*. The parastyle in *K. rotundus* and in *K. torus* is almost vertical; whereas in *Z. keanei* the parastyle has a distinct backward sweep. The paracone and protocone in *K. torus* and *K. robustus* are approximately equal in height. In *Z. keanei* the parastyle is higher and the hypocone is the lowest and smallest cusp. The hypocone in *K. rotundus* and *K. torus* is subequal with the protocone. The separation of protocone and hypocone is well marked by a wide valley in *K. rotundus* and *K. torus*, but is separated by a shallow commissure in *Z. keanei*. In *K. rotundus* and *K. torus* both the hypocone and the metacone are farther posterior than the corresponding cusp in *Z. keanei*. The roots of *K. rotundus* and *K. torus* are close together, in contrast to those in *Z. keanei*, which are widely divergent.

The $M^2$, $M^3$, and $M^4$ in *K. rotundus* are longer and wider than their equivalents in *K. torus*, shorter and narrower than their equivalents in *Z. keanei*, and slightly shorter than but approximately equal in width to their equivalents in Z. *gilli*. The metaloph is better developed in *K. rotundus* than in *K. torus* or *Z. gilli*. Metastyles and parastyles are present and equally developed in both species of *Kolopsis*. The parastyle and metastyle in *Z. gilli* are of similar size and shape to those in *Kolopsis*. None of the four species has a metastyle developed on $M^4$. All have well developed cingula at the lingual end of the median valley. A labial cingulum is developed only in *Z. keanei*.

The mandibles of *Z. keanei*, *K. torus*, and *K. rotundus* are all very different in size. Both species of *Kolopsis* are considerably smaller than *Z. keanei*, and *K. rotundus* is a little larger and far more robust than *K. torus*. The posterior edge of the symphysis is opposite the anterior moiety of $M_1$ in *Kolopsis torus*, opposite the posterior moiety of $M_2$ in *K. rotundus* and opposite the anterior moiety of $M_2$ in *Z. keanei*. Both species of *Kolopsis* have a digastric process; it is better developed in *K. rotundus* than in *K. torus* as are the digastric sulcus and digastric fossa. The digastric fossa is particularly well developed in *Z. keanei* and it is confluent with the pterygoid fossa. The postalveolar shelf is square in both species of *Kolopsis* but is triangular in *Z. keanei*. The lingual edge of the postalveolar shelf is strongly curved in toward the base of the ascending ramus in *Z. keanei*. The postalveolar process is present in all three species, being sharply pointed in *K. torus*, bluntly pointed in *K. rotundus*, and rounded in *Z. keanei*. The posterior portion of the ascending ramus below $M_3$ and $M_4$ is higher in *K. torus* than in *K. rotundus*, but *K. rotundus* is much wider and generally heavier. The construction of this portion of the horizontal ramus in *Z. keanei* is like the corresponding portion in *K. rotundus*.

The lower incisors of *K. rotundus* are very different from those of *K. torus*. Only the posterior two thirds of the incisor is known in *K. rotundus*, but this displays no indication of having an inflected tip. It is strongly curved and has a wide open root. In *Kolopsis torus* this tooth has an ovate cross-section, a fairly open root, and a rather short enamel cap. The tooth is not strongly curved and is much smaller than its equivalent in *K. rotundus*. In *Z. keanei* the root remains open but is compressed laterally. The teeth in the sample are not strongly curved, but they are ovate in cross-section posterior to the enamel cap, which is not inflected.

The lower premolars in *K. rotundus* and *K. torus* can be contrasted. *K. torus* is smaller than *K. rotundus*. In *K. torus* the anteroposterior ridge is straight and is directly in line with the paralophid on $M_1$. In *K. rotundus* this ridge is curved and its posterior end lies just lingual to the paralophid. A cingulum descends anterolabially from the posterior cuspid in both species; it is poorly developed in *K. torus*, but well developed and bluntly rounded in *K. rotundus*. A crest descends posterolingually from the anterior cuspid in both species. It is sharp and well defined in *K. torus* and rather more rounded in *K. rotundus*. The posterolingual basin which is situated between these crests is angular in *K. torus* but more rounded and not so deep in *K. rotundus*. In *Z. keanei* this basin is shallower than in either of the species of *Kolopsis* and the posterolingual crest is straight rather than anterolingually curved as in *Kolopsis*. Both species of *Kolopsis* have higher crowns than does *Z. keanei*. The posterior moiety of this tooth is far more bulbous on the labial side in the species of *Kolopsis* than it is in *Z. keanei*.

The lower molars in *K. rotundus* are larger than those in *K. torus*. They are similar in morphology: $M_1$ is the only tooth on which the paralophid is prominently developed. Anterior cingula are not well developed on any of the molars, but the posterior cingula are prominent on all molars. There is no development of lingual or labial cingula on either species. The median valleys are broadly open and very straight transversely. The suggestions of metalophids on the last two molars do not cross the median valley. The curvature of the lophids is slight.

## Genus KOLOPSOIDES* nov.

*Genotypic species*. *Kolopsoides cultridens* sp.nov.

*Generic diagnosis*. Narial opening much smaller than in *Kolopsis torus* or *K. rotundus*; parastyle connected to paracone by strong longitudinal crest; parastyle large; anteroposterior shearing crest elongate; hypocone larger than protocone; base of metacone bulbous and posterior to large emargination at base of crown between anterolabial and posterolabial roots; three discrete roots. Upper molars

---

*κωλωπσωιδες, after the general similarity of the teeth to those of *Kolopsis*.

similar in size and morphology to those in *K. torus*; postparaconal ridges less developed than in *K. rotundus* but with better developed postmetaconal ridges. Lower incisor smaller than in *K. rotundus*; root almost closed in mature specimens; crown and root vertical, ovate in cross-section, and enamel tip not inflected; ventral border more strongly curved than in *K. torus.* Lower premolar larger than *K. torus* but smaller than *K. rotundus*; posterolingual crest not strongly developed; posterolingual basin more restricted than in *K. rotundus*; posterior cuspid equal in size to anterior cuspid. Lower molars similar to *K. torus* and *K. rotundus*; metalophids on $M_{3-4}$ better developed than in *K. rotundus* or *K. torus*; posterior moieties on $M_{3-4}$ more lingually offset than in *K. torus* or *K. rotundus*; floor of transverse median valley rises more steeply to metalophid than in *K. torus* or *K. rotundus.*

The diagnostic characters of the genus are those of the genotypic species until other species have been described.

### KOLOPSOIDES CULTRIDENS* gen.nov. et sp.nov.

*Type:* UCMP 67601, mandibles complete with left and right dentitions except for left $I_1$ which is missing but has been restored. Ascending rami broken off just above tooth row. Inflected angles broken. Left upper dentition $I^1$, $P^3$, $M^{1-2}$, $M^4$. Right premaxillary fragment and upper $I^1$, and $P^3$.

*Referred specimens:* AM F37670, F37669; GSQ F2761; and UCMP numbers: $I^1$: 63624, 68711, 68712, 68713, 68714, 68717, 68718, 68719, 68721, 68724, 68725, 68736. $P^3$: 67604, 67605, 67606, 67613, 67614. $M^1$: 67603, 67607, 68737. $M^2$: 67602, 67612, 67615. $M^3$: 67608, 67609, 67616, 67617, 67618, 67619, 67620, 68705, 68707, 68735. $M^4$: 67611, 68701, 68731. $I_1$: 68715, 68716, 68720, 68722, 68723, 68726. $P_3$: 68733, 68734. $M_1$: 68710. $M_2$: 68727, 68729, 68703. $M_3$: 68702, 68704, 68709. $M_4$: 68736.

*Type locality:* UCMP V5564 at the 'Sunshine' alluvial gold sluicing workings in the type section of the Otibanda Formation.

*Age:* Middle Pliocene (7·6–6·1 million years before present).

*Description and Comparison*

*Upper Incisors.* Both median upper incisors are present in the type. They are badly shattered and incomplete (Fig. 6), but demonstrate many of the features noted in the better preserved specimens. The left tooth is the more complete. All the upper incisor teeth in this genus are strongly downcurved with the dorsal curvature approximately on an arc with a radius of 33·0. The posterior curvature is not as strong as the anterior. The two juvenile teeth, UCMP 68713, 68725, fall closer to an arc with a radius of 24·4. There is a marked occlusion facet on the tip of both teeth in the type, but it is best seen on UCMP 68721, 68712, and 68718. The shape of the facet is very like that in *Z. keanei* Stirton from the Palankarinna fauna. Enamel is confined to the anterior two-fifths of the tooth in mature specimens, but in juveniles and young individuals three quarters of the tooth may be enamel-covered. The enamel is smooth, has no distinct posterior border, and disappears basally beneath cement. A marked mesial groove parallels the posterior border of the tooth from

---

**cultridens*, in reference to the shearing nature of the upper premolar.

the root to the tip. This groove is somewhat variable, but in most specimens is best developed near the root termination and is still clear on many specimens at the tip Neither of the juvenile specimens has the groove which may be developed in later life. The groove is apparent in the type. The dentine of the root also has faint anteroposterior grooves. Growth of the incisor root probably continued well into maturity, as even in the oldest individuals, UCMP 68724, 68711, and 68717 the root is not closed. In cross-section the incisor is seen to be D-shaped with a flat mesial surface.

*Upper Premolar.* The type has both right and left upper premolars. These are in an early stage of wear and are well preserved. Five other upper premolars have been assigned to this genus. Of these, UCMP 67606, 67613, and 67614 are complete teeth in a good state of preservation. UCMP 67604 and 67605 are identifiable fragments.

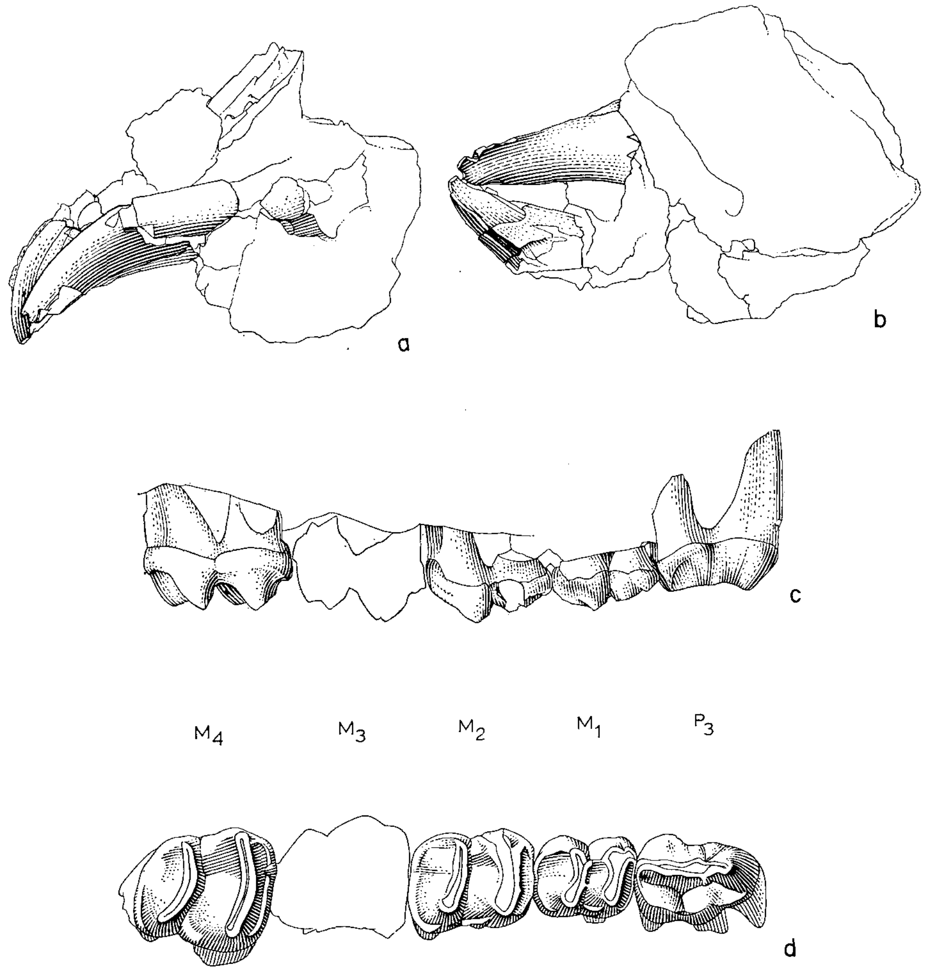


**Fig. 6.**—*Kolopsoides cultridens* **gen.nov. sp.nov., type a, upper median incisors, labial view; b, upper median incisors, occlusal view; c, upper cheek teeth $P^3$, $M^{1-2}$, $M^4$, labial view; d, upper cheek teeth $P^3$, $M^{1-2}$, $M^4$, occlusal view. UCMP 67601.**

Measurements on P$^3$

|  | Length | Width across hypocone and metacone |
|---|---|---|
| Right— |  |  |
| UCMP 67601 .... .... .... | 20·6 | 16·8 |
| UCMP 67613 .... .... .... | 18·9 | 14·3 |
| UCMP 67614 .... .... .... | 20·7 | 14·3 |
| Left— |  |  |
| UCMP 67601 .... .... .... | 22·9 | 16·4 |
| UCMP 67606 .... .... .... | 21·3 | 14·2 |

This tooth is basically five-cusped with the metacone, paracone, and parastyle forming a long, shearing ectoloph. Two faint emarginations on the labial side of the crest of the ectoloph delimit the lateral outline of these cusps. The hypocone is equal to, or larger than, the protocone. The tooth is long for its breadth and with one exception, UCMP 67613, is actually and relatively longer than the corresponding tooth in *Kolopsis rotundus*. It is 2·0 to 3·0 shorter than the restoration of the Beaumaris specimen (Stirton, 1957, p. 125) and 2·0 to 3·0 narrower. The tooth is lower-crowned than its equivalent in *Plaisiodon centralis*. The parastyle, paracone, and metacone are all higher than the protocone or hypocone. The metacone is the highest cusp in the unworn specimen UCMP 67606 and this cusp is probably the highest in all cases. However, wear also seems to be greater on this cusp, and in worn specimens the parastyle is the highest cusp. The protocone and hypocone are bluntly cuspate and are isolated from the ectoloph by a longitudinal valley, which is discontinuous because of the crest connecting the protocone with the paracone. This crest is variable, being strong in 67614 and almost non-existent in 67613. A cingulum which connects the protocone to the parastyle is developed in all the premolars. On it a small cusp may be developed, which is highly variable, being present on the left P$^3$ of the type and in 67614 but absent on the right premolar of the type and in 67613 and 67604. Weakly developed cingula connect the protocone to the hypocone, and the hypocone to the base of the metacone across the posterior margin of the tooth. There are no cingula on the labial side of the tooth. The tooth has three roots, and is unique among the diprotodontids in this respect. The posterior root is the largest. It is transversely flattened and supports the entire posterior moiety of the tooth. The anterior root is triangular and supports the parastyle, anterolingual cingulum, and part of the paracone. There is a labial emargination between these roots at the base of the crown (Fig. 6c), a feature not found in other diprotodontids. The third, the smallest and shortest root, supports only the protocone.

*Upper Molars.* M$^1$ is slightly longer than wide. It has a small, but well marked parastyle and a less well developed metastyle high on the metacone. The postparaconal ridge is variably developed and, where present (in the type), is seen to be a rounded swelling from both the protoloph and metaloph. The parastyle is distinct and is anterior to the protocone but in line with, and at the labial termination of, the anterior cingulum. A postparaconal ridge blocks the labial end of the median valley by connecting from the base of the paracone to the base of the metaloph. The posterior cingulum is continuous from the base of the hypocone across the back of the tooth and up to the base of the metacone, where it terminates as a metastyle. The labial outline of the tooth is strongly emarginated between the anterior and posterior roots opposite the median valley. No labial cingulum is developed. The protoloph is transversely slightly narrower than the metaloph and both are concave posteriorly. The anterior cingulum is continuous from the parastyle to the anterolingual base of the protocone. Two styles form a lingual cingulum across the median valley. They are discrete with a narrow opening between them. Neither is connected to the anterior or posterior cingulum. They originate from the posterior base of the protocone and the anterior base of the hypocone; the latter is the smaller.

$M^2$ is longer than wide by 2·0 to 3·0. The parastyle is less prominent than on $M^1$ and the degree of its connexion to the base of the paracone is variable. The style is distinct and anterior to the paracone. As on $M^1$ it marks the labial termination of the anterior cingulum. A second small style is developed on this cingulum in a median position. The postparaconal ridge is variable: it is well developed on the type but is faint on 67615. A metastyle is present but is less developed than in $M^1$. The posterior cingulum is well developed on the type and continues around on to the lingual side of the tooth. It makes a connexion with the hypocone by a narrow, lingual, vertical ridge which in turn is connected to the styles across the openings in the median valley. Two styles are present at the lingual opening of the transverse valley. As in $M^1$ the anterior is again the larger. The protoloph is transversely equal to or wider than the metaloph, and this may serve to distinguisih it from $M^1$.

The posterior molars $M^3$ and $M^4$ taper posteriorly with the metaloph becoming narrower relative to the protoloph. The metaloph also becomes increasingly lingually offset and more strongly curved. The parastyle persists as a very small cusp on the labial moiety of the anterior cingulum. A median style is also present on this cingulum. The parastyle is not always at the labial termination of the cingulum and this can be contrasted with its extreme labial position in $M^1$ and $M^2$. A postmetaconal ridge is well developed but the distinct metastyle seen in the anterior molars is no longer present. The styles developed on the lingual side of the median valley are still present, but are reduced, and the anterior one is still larger than the posterior. In the two molars, 67609 and 67617, the posterior cingulum continues around on to the lingual side of the tooth to connect with the styles at the opening of the median valley. There is no labial cingulum, but there is still a well marked emargination between the anterior and posterior moieties of the teeth.

The only skull parts which can be referred to this genus are UCMP 67601, a fragment of the right premaxilla of the type with the posterior portion of the root of the median incisor in place, and UCMP 67612 and 68737, right and left maxilla fragments with molars in place. Both these maxillae have fragmentary zygomatic processes. They are incomplete but sufficient remains to determine that they were fairly long (at least 15·0 below the tooth row), laterally ovate (15·0 x 25·0), and slender.

*Mandible.* The digastric process is present but broken off in the type. It is however present in UCMP 68736 and can be seen to be roundly pointed. The digastric fossa is well defined in both the type and UCMP 68736. The angular surface is slightly concave ventrally. The pterygoid fossa, as seen in UCMP 68736,

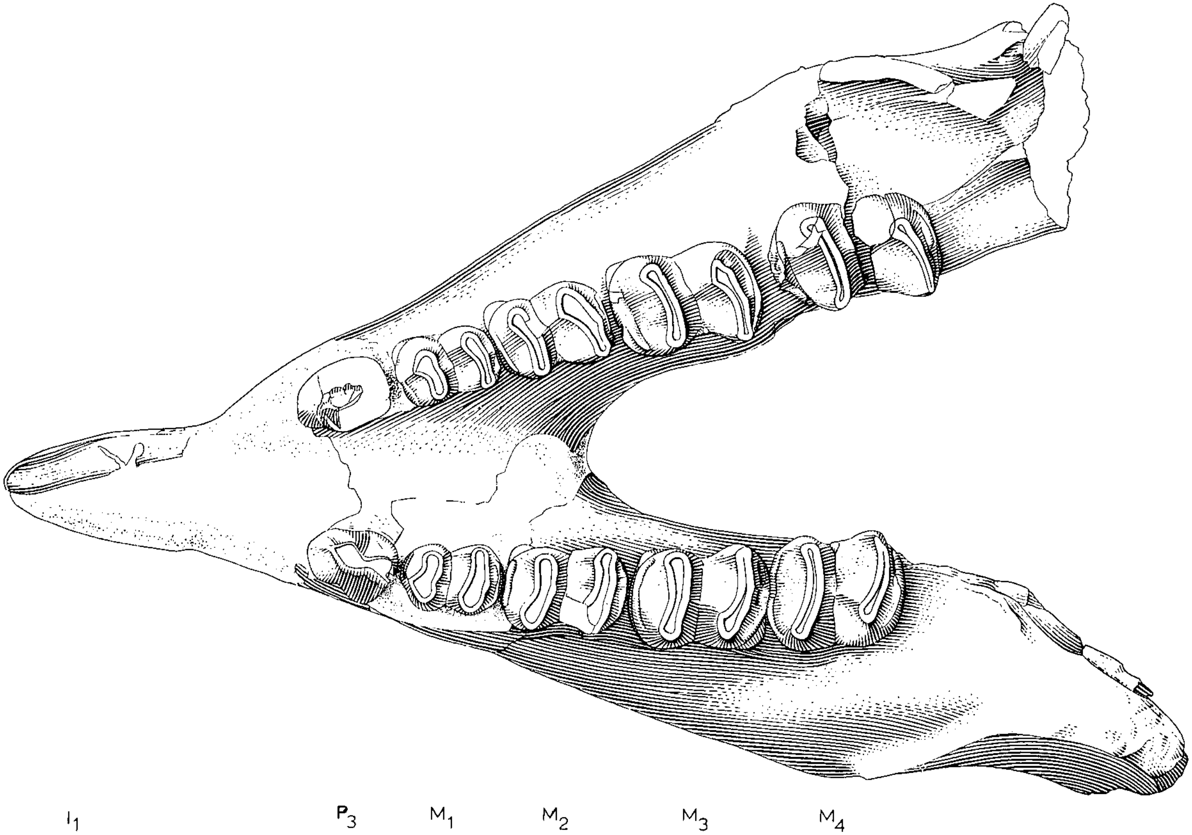


**Fig. 7.—*Kolopsoides cultridens* gen.nov. et sp.nov., type, mandible. UCMP 67601. x ¾.**

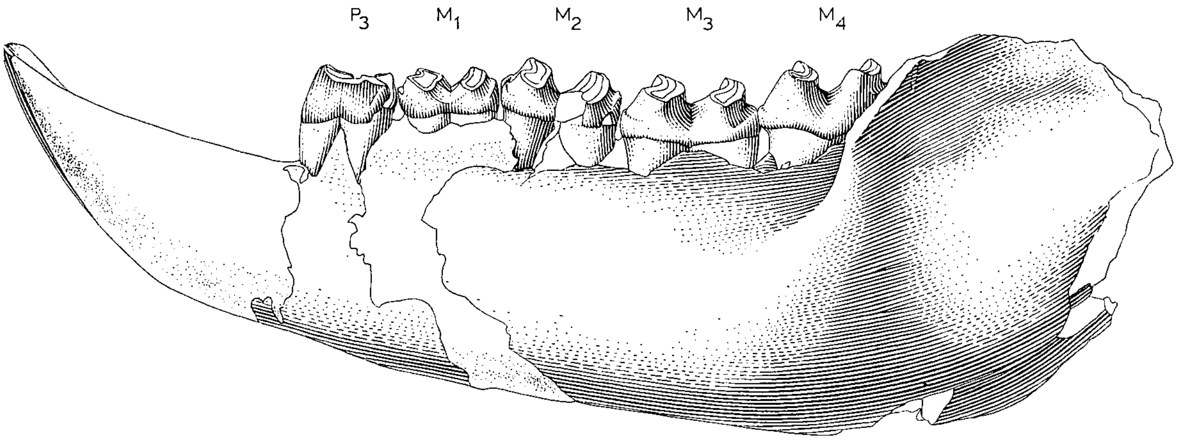


Fig. 8.—*Kolopsoides cultridens* gen.nov. et sp.nov., type, mandible, labial view. UCMP 67601. x ¾.

is deep. The anterior edge of the ascending ramus is opposite the posterior moiety of $M_4$. The postalveolar shelf behind the $M_4$ is square rather than triangular and the postalveolar process was probably not present but this area is broken in both mandibles. The mandibular foramen is on a level with the tooth row and 42·8 behind the posterior cingulum of $M_4$ in UCMP 68736. This cingulum is approximately 2·8 in diameter and runs labial to the tooth row. The depth of the mandible below $M_4$ is 48·7 on the left ramus of the type, 46·5 on the right ramus of the type 41·7 on the left ramus of UCMP 68736, and 55·5 on GSQ 2761. The width of the mandible below $M_4$ is 36·7 on the left ramus of the type, approximately 41·0 (distorted and broken) on the right ramus of the type, 27·6 on the left ramus of UCMP 68735, and approximately 43·2 on GSQ 2761. The symphysis terminates posteriorly opposite the posterior moiety of $M_2$ in both the type and UCMP 68736.

*Lower Incisor*. Only the right lower incisor remains in the type, but seven other lower incisors are known. They range in age from juvenile (UCMP 68726) to old individuals (UCMP 68720) with a fair spread of intermediate ages. The tooth is vertically compressed, being reniform in its posterior cross-section and slightly curved longitudinally. The ventral curve of all the teeth in the sample falls on an arc with a radius of approximately 76·0. The dorsal border of the tooth is much less concave and has a slight convexity just posterior to a dorsal projection of the posterior enamel termination. The tooth is deepest (16·5) at this point, which in mature specimens is approximately the middle of the tooth. The width at this point averages 10·0. The tooth tapers anteriorly and posteriorly from this median bulge. Whether the taper is more abrupt anteriorly or posteriorly depends on the stage of growth of the animal. In young individuals the tooth tapers rapidly anteriorly, whereas posteriorly the tooth remains open and tapering is not abrupt. In older animals with the occlusal surface near the ' median bulge ' the tooth remains fairly deep anteriorly but, as the root closes, it tapers rapidly posteriorly. The orientation of the tooth remains vertical throughout its length, with no inflection of the occlusal surface. A strong groove is developed on the mesial surface of the tooth and it is this groove that gives the posterior part of the tooth its reniform cross-section. In the older individuals the groove seems to have shifted posteriorly and can only be seen on the posterior third of the tooth. The enamel cap is confined to the ventrolabial surface of the tooth. In the juvenile specimen the enamel covers approximately 90 percent of the tooth and in the young individual approximately 50 percent. In the older animals the enamel cap is about 25 percent of the total length of the tooth.

$P_3$ has a triangular crown with a rather narrow base and long sides. The apex is anterior. High anterior and posterior median cuspids are connected by a longitudinal ridge. From the amount of wear in UCMP 68734, it is judged that the anterior cuspid was a little higher than the posterior one. At the base of the enamel there is a labial emargination between the anterior and posterior roots. The posterior moiety is notably more bulbous in outline than the anterior moiety. This emargination continues dorsally on to the crown of the tooth but does not form a particularly noticeable depression. There is no labial cingulum. Faint ridges originating at the crests of the anterior and posterior cuspids descend posteroventrally and anteroventrally but fade rapidly. The shear and wear on the tooth is along the labial side of the anteroposterior crest. The tooth has two long triangular roots, both of which curve posteriorly at their extremities. The anterior root is the longer.

The anterior and posterior moieties of $M_1$ are composed of lingual and labial cuspids connected by transverse lophids. The median valley is well defined and unobstructed. It is U-shaped in labial view. The protoconid is connected to the anterior cingulum by a strong paralophid remnant. The connexion of the cingulum to this lophid may mark the labial termination of the cingulum, but in the type, where the cingulum is weakly developed on the labial side of the lophid, this feature is not observable. The anterior cingulum is restricted to the anterior surface of the tooth, as is the posterior cingulum to the posterior surface. There is only a suggestion of labial or lingual cingula. The protolophid is narrower than the hypolophid and both are directed slightly posterolingually. The metaloph is very weakly developed from the anterior face of the hypolophid. It commences just below the hypoconid as a slight swelling and is directed anteroposteriorly. The posterion cingulum commences about a third of the way in from the labial edge of the tooth at the base of the hypoconid. It may be connected to the base of the hypoconid by a weak stylid. A small stylid is also developed on this cingulum at the midline, and labial to this the cingulum becomes less distinct and finally fades away below the entoconid.

Table 2: Length measurements on the type of *Kolopsoides cultridens*, UCMP 67601

| | $P_3$ | $M_1$ | $M_2$ | $M_3$ | $M_4$ |
|---|---|---|---|---|---|
| | | Right | | | |
| Length .... .... .... | 16·8 | 16·6 | 19·9 | 24·8 | 28·8*a* |
| Width .... .... .... | 12·4 | 12·8 | 16·0 | 20·4 | 23·4 |
| | | Left | | | |
| Length .... .... .... | 15·5 | 16·0 | 21·4 | 22·1 | 23·9 |
| Width .... .... .... | 11·9 | 13·1 | 16·5 | 19·6 | 20·6 |

Table 3: Length measurements on left tooth row of UCMP 67601

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $P_3$-$M_4$ | 105·3 | $M_1$-$M_4$ | 88·5 | $M_2$-$M_4$ | 69·7 | $M_3$-$M_4$ | 47·1 |
| $P_3$-$M_3$ | 80·4 | $M_1$-$M_3$ | 64·4 | $M_2$-$M_3$ | 45·9 | | |
| $P_3$-$M_2$ | 55·8 | $M_1$-$M_2$ | 39·8 | | | | |
| $P_3$-$M_1$ | 34·1 | | | | | | |

The length of all teeth taken at midline. *a* = approximate.

$M_2$ is transversely bilophate, like $M_1$. The protoconid is connected to the anterior cingulum as in $M_1$, but the link is not as strongly developed, although it is still clearly present. This tooth has a metalophid which starts at a point lingual to the hypoconid and descends anterolingually to the midpoint in the transverse valley. Its strength and direction can be contrasted with those in $M_1$. The anterior cingulum is well developed across the anterior basal portion of the tooth lingual to the protostyle. A labial cingulum is variously developed but is never prominent and does not block the labial end of the median valley. The posterior cingulum is as in $M_1$, but the swelling is strongly developed lingual to the midline. A lingual cingulum is weakly developed. The base of the transverse valley is broadly U-shaped in lingual view and the lophs slant posterodorsally as in $M_1$.

$M_3$ is like $M_2$ in every feature except the weakening of the paralophid. $M_4$ is again like $M_3$, except that it is the only tooth in which the hypolophid is narrower than the protolophid. In the last two molars the hypolophid is more strongly displaced in a lingual direction.

*Comparison.* *K. cultridens* is similar to the species of *Kolopsis* from the Alcoota and Awe faunas, and is also like *Z. gilli* in several features. It appears to be more distantly related to the other known diprotodontids. For my comparisons with the genus *Kolopsis* I used the skull of the type species, mandible UCMP 68925, lower incisor UCMP 68960, the type of the species *Kolopsis rotundus*, and the mandibles AM F44470 and F44471. For comparisons with the Beaumaris specimens I used casts and the illustrations in Stirton (1957).

The upper incisors are similar to those in the type of *Kolopsis torus*, but these teeth are poorly represented in this genus and no detailed comparisons are possible. The upper premolar of *Kolopsoides cultridens* is a most distinct tooth. It is 3·0 longer than *K. rotundus*, 3·5 longer than *K. torus*, and 0·8 longer than Stirton's (1957) restoration of the Beaumaris specimen. It is about 1·2 wider than either of the species of *Kolopsis* and 2·0 narrower than Stirton's restoration of the Beaumaris specimen. The basic five cusps are still present but the parastyle, paracone, and metacone form an elongate ectoloph. This contrasts with *Zygomaturus keanei*, the species of *Kolopsis*, and *Z. gilli*, in all of which the parastyle is a discrete cusp. The cingulum connexions in *Kolopsoides cultridens* are not as well developed as in *K. rotundus*. The development of a subsidiary cusp on the anterolingual cingulum between the parastyle and protocone is not found in other species. Five of the six specimens known have a hypocone which is considerably larger than the protocone. In both species of *Kolopsis* and in *Z. keanei* the hypocone is smaller. On the labial side of the tooth there is a very strong emargination in the enamel of the crown, between the roots. The base of the metacone is rounded and full (Fig. 6). This is contrasted with the metacone in both *K. torus* and *K. rotundus*, where the metacone is smaller than the paracone and there is no strong emargination between the anterior and posterior roots. *Kolopsoides cultridens* is the only known diprotodontid to have three roots on its upper premolar. The upper molars of *K. cultridens* are smaller than those in *K. rotundus* and about the same size as those in *K. torus*. The teeth are very much like those in *K. torus*. They contrast with *K. rotundus* in having less well developed metalophs and a far better developed postmetaconal ridge in the posterior molars.

*K. cultridens* contrasts strongly with *K. torus* in the area of the narial opening. The opening is over twice as high in *K. torus* and in *K. cultridens* appears to have been circular rather than ovate as in *K. torus*.

The mandible of *K. cultridens* is similar in size to *K. rotundus*. It has a long symphysis which terminates opposite the median valley of $M_2$. This contrasts with

*K. torus*. The mandible of the type is more rounded and heavier than either species of *Kolopsis*.

The incisors are much smaller than those known from *K. rotundus*. They are not as deep, shorter, smaller in cross-section, and less strongly upcurved. Root closure appears to have been well advanced by the time $M_4$ was in wear, and this contrast with *K. torus* is very strong. In *Kolopsoides cultridens* the tooth is vertical throughout and there is no inflection of the enamel cap at the occlusal surface as there is in *K. torus*.

The lower premolar is larger than its equivalent in *K. torus* but smaller than the same tooth in *K. rotundus*. It is distinct from these species in having no well developed lingual crest. The posterolingual basin is also poorly developed and the posterolabial bulge is not as evident as it was in *K. torus* or *K. rotundus*. The lower molars are generally similar to those in *Kolopsis* but differ from *K. torus* and *K. rotundus* in having the metalophids well developed on $M_3$ and $M_4$, as well as in $M_1$ and $M_2$. The posterior moieties on $M_3$ and $M_4$ are more lingually offset than their equivalents in *K. torus* and *K. rotundus*. The floors of the median valley rise more steeply at the midline, to the base of the metalophid and hypolophid, in *K. cultridens*, than they do in *K. torus* or *K. rotundus*.

## REFERENCES

ANDERSON, C., 1937—Palaeontological notes No. IV, fossil marsupials from New Guinea. *Rec. Aust. Mus.*, 20(-2), 73–76, 1 fig., 1 plate.

OWEN; R., 1845—Description and illustrated catalogue of the fossil organic remains of the Mammalia and Aves contained in the Museum of the College of Surgeons of England. *London, Richard and John E. Taylor.*

OWEN, R., 1877—Researches on the fossil mammals of Australia with a notice of the extinct marsupials of England. *London.* Vol. I, 522 pp., 36 figs, 1 plate.

STIRTON, R. A., 1955—Late Tertiary marsupials from South Australia. *Rec. S. Aust. Mus.*, 11, 247-268, 11 figs.

STIRTON, R. A., 1957—Tertiary marsupials from Victoria, Australia. *Mem. Nat. Mus. Vic.*, 21, 121–134, 6 figs.

STIRTON, R. A., 1967—New species of *Zygomaturus* and additional observations on *Meniscolophus*, Pliocene Palankarinna Fauna, South Australia. *This vol.*, 129–147.

# NEW SPECIES OF *ZYGOMATURUS* AND ADDITIONAL OBSERVATIONS ON *MENISCOLOPHUS*, PLIOCENE PALANKARINNA FAUNA, SOUTH AUSTRALIA

by

R. A. STIRTON

## CONTENTS

| | Page |
|---|---|
| INTRODUCTION | 131 |
| Fossil Localities | 131 |
| Acknowledgments | 132 |
| *NOTOTHERIUM* AND *ZYGOMATURUS* | 133 |
| Genus *Zygomaturus* Owen, 1859 | 134 |
| *Zygomaturus gilli* sp.nov. | 135 |
| *Zygomaturus keanei* sp.nov. | 136 |
| *Zygomaturus* sp. | 144 |
| Genus *Meniscolophus* Stirton, 1955 | 145 |
| REFERENCES | 147 |

## SUMMARY

A new species of the marsupial genus *Zygomaturus*, family Diprotodontidae, is described, and further comments are made on the genus *Meniscolophus*. These are from the Pliocene Mampuwordu Sands at Lake Palankarinna. The *Zygomaturus* species, although clearly related to *Zygomaturus trilobus* of the late Pleistocene, is not as advanced. Another species of *Zygomaturus* from the Sandringham Sands of Victoria is also described. The relationships and systematics of the genera *Nototherium* and *Zygomaturus* are discussed; both genera are recognized.

Page 130 is blank.

# INTRODUCTION

The remains of diprotodontids have been collected from three localities in the Mampuwordu Sands, where they are exposed in the escarpment off the north-western shore of Lake Palankarinna. The Woodard Quarry was recorded by Stirton (1955), the Lawson-Daily Quarry in Stirton, Tedford, & Miller (1961), and the Keane Quarry by Stirton (1963).

Refined age determination of the Palankarinna fauna is still questionable. Previously we thought it might be early or possibly middle Pliocene, i.e., equivalent to the Clarendonian or Hemphillian mammalian Ages in North America; now however it would seem to be late Pliocene as based on a comparison of the stage in evolution of a diprotodontid in the Awe fauna of New Guinea, where potassium-argon dates are available. This, however, is not conclusive because less advanced species may have prevailed in the equatorial latitudes of New Guinea.

The genus *Meniscolophus* Stirton was described in 1955 and some specimens of another diprotodontid, also from the Woodard Quarry, were discussed and illustrated at that time. The meagre representation of the second form necessitated postponement of a formal designation of its genus and species until the premolars were found. Subsequent material from all three quarries now makes it possible to clarify its relationships.

## FOSSIL LOCALITIES

Lake Palankarinna is about 18 miles west and slightly south of the Etadunna station, and approximately 8 miles south of Cooper Creek in the Tirari Desert, which is between the eastern shore of Lake Eyre and the Birdsville Track, South Australia. The escarpment west of the lake can be seen from the Cannuwalkaninna Dune. The escarpment retains its relief because of a thick resistant gypsiferous caprock that has formed in the Tirari Formation, but may occur in the overlying Katipiri Sands where they have channelled into the Tirari rocks. Gullies have dissected the escarpment and in places have cut back a hundred yards or more. These gullies develop into wide washes where they emerge between escarpment ridges. It has been at, or near, the prominences at the ends of the ridges that we have located the Mampuwordu Sands, but not all the sites have produced fossils.

All three fossil localities are off the north-west shore of the lake in the grid coordinate 657433, grid zone 5, of the Marree Sheet, South Australia 1:506, 880; Australian Army H.Q., Cartographic Co., 1942.

*Woodard Locality*, V5367. About three-fourths of a mile south-west of the north-west corner of the lake, in an area where the escarpment prominences are at their lowest relief. The fossils were collected in a lenticular stream deposit remnant of about 3 feet* in maximum thickness. The bed is truncated by the Tirari Formation and soon pinches out into the low ridge. Below, the channel sands cut into the Etadunna green arenaceous claystone. The sands are ferruginous, grey or greyish green, contain clay-balls, and are unconsolidated. At the base there are small

---

* Previously we thought the bed was much thicker at this site, because we believed the overlying Tirari was part of the same formation.

pebbles of duricrust, limestone, and quartz. Most of the specimens are well preserved, but the bones and jaws evidently were broken and somewhat weathered before they were partly encased in sand that was cemented by gypsum. The quarry was depleted in 1954.

*Keane Locality*, V6265. This is on the north side of the first prominence to the north-east of the Woodard Quarry. Basally there is a thin greenish claystone and a clay-ball unit, overlain by a thin yellow cross-bedded sand; above this the fossiliferous unit is a friable compact white sand which is from 2 to 6 feet thick. The channel cuts into the underlying Etadunna and is truncated by the Tirari above. The bones and teeth are partly crushed and not as well preserved as those in the other quarries. Consequently they are difficult to collect when partly surrounded by gypsum.

*Lawson-Daily* Locality*, V5769. The quarry is near the top of the fifth prominence to the north and slightly east of the Keane Quarry. This is near the north end of the escarpment. It can also be located by a nearly isolated prominence we have called Mammelon Hill, which is across a rather wide wash almost directly to the east. In contrast to the 14 feet of Mampuwordu Sands in Mammelon Hill, the bed in the Lawson-Daily Quarry ranges from a few inches to about 2 feet in thickness. The section includes a greenish claystone, clay-balls, and some sand mixed with pebbles at the base, where gypsum has invaded as horizontal sheets and in a honeycomb pattern vertically. There are mostly fine-grained sands above. The quarry sands pinch-out in the ridge to the west of the quarry. As at the other sites the Mampuwordu cuts into the Etadunna below and is covered by the Tirari above. The Lawson-Daily locality is probably a marginal depression to a deeper channel, as indicated by the thickness of the sands in Mammelon Hill. Sands were probably deposited in the depression mostly after the peak of high waters; then as the waters receded to the main channel the muddy water remaining in the depression cleared as silt settled to the bottom to form the mudstone. The greenish grey mudstone was evidently derived from reworked Etadunna sediments and the greyish colour effect from fine-grained quartz sand from another source. Most of the bones and mandibles are complete or nearly so, and evidently have not been transported very far; for the most part they are well preserved, although partly, or entirely, enclosed in gypsum which is difficult to remove.

## ACKNOWLEDGMENTS

For the sending to Berkeley of generic plastotypes and for the privilege of studying their collections, grateful acknowledgement is given to Jack T. Woods and Alan Bartholomai of the Queensland Museum, Harold O. Fletcher of the Australian Museum, and J. A. Sutcliffe of the British Museum (Natural History).

The illustrations were done by Owen J. Poe.

This research was made possible by United States National Science Foundation grants G5632 and G15957. It is part of a cooperative project with the South Australian Museum.

---

* The Lawson and Daily Quarries were first found on opposite sides of the same prominence, but later found to be parts of the same quarry.

## *NOTOTHERIUM* AND *ZYGOMATURUS*

A discussion of the systematics and classification of the Pleistocene diprotodontids *Nototherium* Owen, 1845, and *Zygomaturus* Owen, 1859, is included here to clarify their standing and to help in interpreting the relationships of the late Tertiary genera.

Although Owen (1859a) formally established the nomen *Zygomaturus trilobus* he believed that the type was not generically separable from *Nototherium.* Consequently most of the literature on these animals in the later part of the nineteenth century used the nomen *Nototherium.* Lydekker (1887) followed Flower (1884) in recognizing only one species, and used the nomen *N. mitchelli.* Owen had previously suspected (1859b, p. 185) that the differences between the specimens might be due to sexual dimorphism. The genotypic species is *Nototherium mitchelli** but unfortunately nearly all the enamel and much of the dentine is missing from the crowns of $M_3$ and $M_4$ in the type specimen.

Nevertheless enough enamel remains on the labial side of the posterior surface of the protolophid in $M_3$ to show that the transverse median valley was deep and narrow as in illustrations of *N. inerme.* This is in marked contrast to the wide U-shaped valleys in *Zygomaturus trilobus* Owen, the type specimen of which is a moderately well preserved skull with most of the teeth complete. The obliquity of the crescentic lophids in *N. inerme* is not clearly demonstrable in the shattered crowns in the type of *N. mitchelli.* It appears, however, that the labial end of the hypolophid did not curve as abruptly anteriorly and somewhat lingually to block the transverse valley as in *Euowenia.* Among the other features shared by *N. inerme* and *N. mitchelli* are the high position of the mandibular foramen on the ascending ramus, and the relatively short horizontal ramus. Owen further states that the $P_3$ of *Nototherium* has one root. I have not seen this tooth, although a single alveolus is shown in a mandible of the Hughes collection which Owen called *N. mitchelli* (1859b, pl. IX, fig. 2). However, specimen F.5058 in the Australian Museum collection can be assigned to *Nototherium* and has the remains of two roots in the $P_3$ alveoli. An illustration of upper cheeckteeth, evidently referable to *Nototherium*, is in Owen, 1872, plate IX, figure 5, and 1877, plate XLIII, figure 5.

The nomen *Zygomaturus trilobus* was introduced in reference to an excellent cranium by W. S. MacLeay in an article ' Report on Donations to the Australian Museum during August, 1857.' This was published in the *Sydney Morning Herald* newspaper. It apparently was not the intention of MacLeay to propose a binomial in the technical sense (see quotation of letter to Owen, 1872, p. 43 and 1877, p. 251) as set forth in Section III, Article 8 of the International Code of Zoological Nomenclature. In fact MacLeay stated that the article was ' principally intended to please the donor, and to induce him to send us more specimens '. The nomen *Z. trilobus* MacLeay, 1857, therefore is invalid; however Owen (1859a) quoted MacLeay's description in the Quarterly Journal of the Geological Society, London, again using the nomen *Z. trilobus* (see Simpson, 1945, p. 47). The valid nomen then is *Zygomaturus trilobus* Owen, 1859.

---

* We are grateful for the assistance of W. D. L. Ride and J. A. Mahoney who determined the correct genotypic species of *Nototherium.*

Owen (1859b; 1872; 1877) illustrated and again described the *Zygomaturus* cranium and identified it as *Nototherium mitchelli.* In this classification he was followed by Flower (1884) and Lydekker (1887; 1889). This generic identity was emphatically denied by DeVis (1888; 1895) and in these discussions he used the nomen *Zygomaturus trilobus* MacLeay. At last in 1907 DeVis, not realizing that Owen had already established the nomen, directed attention to its invalidity in MacLeay's newspaper article and then proposed the generic nomen *Simoprosopus*, with a generic diagnosis. Possibly a typesetter's mistake in DeVis' paper resulted in the binomial appearing as *Simoprosobus trilobus.*

Perhaps the most diagnostic character of *Zygomaturus* has been the bulbous five-cusped $P^3$, but no specimen with direct association of upper and lower dentitions has been found. This made comparison with the lower teeth of *Nototherium* questionable. Fortunately in the Keane Quarry, $P^3$, the upper molars, and both lower jaws with all of the cheekteeth were found as parts of an individual animal.

In summary the genera can be contrasted in: the very different size and shape of the upper premolar; the shape of the median valley in upper and lower molars; the relative and actual length of the horizontal ramus; and the orientation of the symphysis, steep and short in *Nototherium* and relatively flat and long in *Zygomaturus.*

## Genus ZYGOMATURUS Owen, 1859

*Genotypic Species. Zygomaturus trilobus* Owen, 1859.

*Revised Generic Diagnosis.* Three upper incisors. $I^1$ with enamel crown not extending into alveolus. $P^3$ large, bulbous, quinquetubercular. Upper molars with wide V-shaped transverse median valleys; short and wide postparaconal ridge does not cross crease of median valley or extend to apex of paracone; small parastyles, mesostyles, and metastyles usually present on upper molars, but no metastyle on $M^4$. Symphyseal region and lower incisors nearly horizontal. Lower incisor with enamel crown only slightly upturned and not extending into alveolus. $P_3$ nearly triangular; posterolabial crest extending to posterior end of tooth; without posterior cingulum; with two roots. Lower molars with crescentic lophids transverse in direction; the transverse median valley widely U-shaped, accentuated by posteriorly directed depression on anterior surface of hypolophid and lingual to metalophid ridge.

### *Beaumaris Diprotodontid from Victoria*

Our knowledge of the family Diprotodontidae has increased considerably since a preliminary description of a $P^3$ and part of a maxillary tooth row from Beaumaris, Victoria, appeared in Stirton (1957). The genus and species of these specimens can now be determined with some confidence. Because they appear to be intermediate between *Kolopsis* and *Zygomaturus* their generic assignment might be questionable but this relationship if borne out by future discoveries makes them all the more important in the phylogenetic paper presented in this series. The diagnosis then will precede that of the Palankarinna species.

## ZYGOMATURUS GILLI[*] sp.nov.

*Holotype.* Left $P^3$ with parastyle and part of lingual side of tooth abraded. MUGD reg. 2020.

*Referred Specimen.* Posterior moiety of $M^2$, $M^3$ and $M^4$ complete in part of right maxilla. NMV P15909.

*Specific Diagnosis.* Much smaller than in Palankarinna species. Length of $P^3$ 23·2; width across paracone and protocone 17·4; paracone and metacone about 17·0 apart, demarcated by deep, narrow, labial and lingual grooves; crest from metacone to posterior end of tooth steeply inclined; posterior cingulum with high contact to end of postmetaconal crest; paracone and metacone more bulbously expanded than in *Kolopsis rotundus*; parastyle not adequately preserved for diagnosis, but appears to have been closer to paracone than in *Kolopsis torus*; crest connecting protocone and paracone higher than in *K. rotundus*; posterolabial expansion of protocone forms moderately broad contact with anterolingual base of metacone and partly closes a small depression on lingual side of paraconal-metaconal crest; hypocone considerably reduced relative to size of protocone; labial cingulum not continuous past base of paracone; with mesostyle.

*Upper molars.* Anterior cingulum with anterior sloping, shelf-like projection; posterior moiety of $M^4$ relatively narrower, as compared with anterior moiety, than in *K. torus* or *K. rotundus*; no mesostyles on $M^3$ and $M^4$.

**Fig. 1.—A.** *Zygomaturus gilli*, **sp.nov. Holotype, abraded left $P^3$, partly restored, occlusal view, natural size, MUGD 2020.**
**B.** *Zygomaturus keanei*, **UCMP 70122, natural size. Left upper premolar.**

*Type locality.* Nodule bed of calcareous nodules, ferruginous nodules, and vertebrate remains in matrix of coarse clear-quartz sand; from base of Black Rock member of Sandringham Sands Formation. Sea cliffs of Port Phillip Bay, on axis of anticline near Beaumaris boatsheds opposite Bondley Street, Beaumaris, Victoria.

*Fauna.* Beaumaris.

*Stage.* Cheltenhamian.

*Age.* Considered as late Miocene or early Pliocene by invertebrate palaeontologists and stratigraphers, but used here and elsewhere in these papers as early Pliocene.

---

[*] Named for Edmund Gill, Assistant Director, National Museum of Victoria, Melbourne.

## PALANKARINNA DIPROTODONTIDS

### ZYGOMATURUS KEANEI* sp.nov.

*Holotype.* Mandible with both rami fused at symphysis; base of left incisor, $P_3$ to $M_4$ all fractured; right incisor missing, $P_3$ to $M_4$ present, anterior end of $P_3$ missing, $M_1$ partly broken; posterior parts of rami complete except coronoids, specimen somewhat distorted. Both upper incisors; part of left maxilla with $P^3$ to $M^4$ ($P^3$ and $M^1$ separated from maxilla in quarry); right $P^3$ partly restored; right $M^2$; right $M^4$. SAM P13844.

*Paratypes.* Left $P^3$, UCMP 66326; right $M^1$, UCMP 70121; right $M^2$, 70120; left $I^3$, UCMP 44622; left $I^3$, UCMP 45409.

*Referred Specimens.* Woodard Quarry: part of left maxilla with $M^1$ to $M^3$, UCMP 44398 (Stirton, 1955, p. 263, fig. 6); left $P^3$, UCMP 70122; left $M^1$, UCMP 44400 (Stirton, 1955, p. 265, fig. 11); right $M^1$, UCMP 45356; part of left $M^1$, UCMP 45355; right $M^4$, UCMP 45353; left $M^4$, UCMP 45354; fragmentary left $M^2$, UCMP 44623; fragment upper molar, UCMP 45357; three well-worn lower incisors, UCMP 44619, 44620 and 44621; anterior end of lower incisor, UCMP 45409; $P_3$ and $M_1$, UCMP 70123; part of left mandible with $M_2$ to $M_4$, most of symphysis, and part of alveoli for incisors, UCMP 44390 (Stirton, 1955, pp. 264–265, fig. 10; the 44397 number in the legend should read 44390); part of left mandible with much of angular fossa and $M_4$, UCMP 44401 (Stirton, 1955, p. 264).

*Specific Diagnosis.* $P^3$ smaller than in *Zygomaturus trilobus*, much larger than *Zygomaturus gilli*; average length across paracone and protocone about 25·5; height of paracone estimated at 17·2; hypocone separated from protocone by shallow commissure; cingula subdued, valleys between cusps relatively and actually shallower than in *Z. trilobus*; crevice between paracone and parastyle narrow; hypocone farther posterior from apex of metacone than in *Z. trilobus.*

Upper and lower molars with cingula not as prominent, crease in bottom of transverse medial valley not as clear cut, valley appears to be not as widely open and lophs and lophids relatively and actually lower than in *Z. trilobus*; transverse valleys of lower molars U-shaped.

$P_3$ slightly larger but possibly lower crowned than in *Z. trilobus*, approximately 16·8 (see '*N. mitchelli*, Owen,' 1877, text p. 280, pl. XL, for comparison, which is *Z. trilobus*).

*Fauna.* Palankarinna.

*Age.* Late Pliocene.

### *Description*

*Upper incisors.* Two medial upper incisors have been associated with the holotype. The one of the right side is complete and well preserved; the left is fractured with parts slightly displaced. The tooth is strongly curved with a measurement of 140·2 around the anterior curvature. The radius of the arc is about 37·5. The tip is worn off almost to a point anteriorly; on the posterior surface wear is greatest on the lateral side in the holotype; but the total length was probably no more than

---

* Named for Mr Vincent P. Keane, Adelaide, who furnished heavy equipment for the excavations in the Tirari Desert.

5·0 longer than the above figure. Across the curvature it measures 105·0. Enamel is confined to the anterior and lateral surfaces of the terminal two-fifths of the tooth, and it is convex transversely. The enamel surface is smooth. Basally it is overlapped by about 1·5 of what appears to be cement. The anteroposterior measurement across the base of the crown is 28·0, and transversely it is 19·4. The root has a wide shallow groove on the mesial side; it is convex laterally, although there is a pronounced groove near the posterior edge of the mesial surface with a ridge and a much smaller groove anterior to the ridge. The greatest anteroposterior dimension of the root is 31·7 and this decreases to about 29·0 at the open base, where it is partly broken away. The transverse measurement gradually diminishes to 7·2 at the basal opening. The dentine of the root has faint parallel grooves anteroposteriorly.

The enamel surface is complete in the upper incisor of a young specimen, UCMP 44622, from the Woodard Quarry. The tip is barely worn on its posterior surface and the edge is 8·5 wide and essentially chisel-shaped. The terminal third is more abruptly curved downward than the posterior two-thirds. The widely ovate open root was about 11·0 behind the edge of the enamel.

A left median incisor UCMP 70125 of a very old animal was found in the Lawson-Daily Quarry. All the enamel is worn away, so only a rounded knob of dentine caps the root. The root, however, is well preserved. This specimen is larger than the incisors of the holotype. The anteroposterior measurement at the lower edge of the worn surface is 33·8, and transversely it is 24·8. The wide shallow groove of the mesial surface is deeper and consequently more accentuated than in the holotype. The lateral surface is conspicuously different with a rounded ridge, about 10·0 high, 8·0 behind the anterior edge. This ridge diminishes from a width of 15·5 near the worn surface to about 5·5 at the base. Behind the ridge a wide depressed surface extends across to the posterior edge. The greatest anteroposterior dimension of the root is 37·2 and at the closely compressed but still open base it is about 33·8. The parallel grooves of the dentine surface are much more pronounced than in the holotype. The features in this specimen evidently are to be expected in the old animals. There is evidence, then, of an increase in size of the middle and posterior parts of these teeth with open roots, as the animals become older.

*Upper premolar.* Right and left upper premolars have been identified as belonging to the holotype. These are well worn and the one of the right side has been partly restored. An isolated left $P^3$ UCMP 66326 also came from the Keane Quarry and another UCMP 70122 from the Woodard Quarry.

Table 1: Measurements of $P^3$

|  | Length | Width across protocone and paracone | Width across hypocone and back of metacone |
|---|---|---|---|
| Right: |  |  |  |
| SAM P13844 | 25·3 | 21·0 | 19·0*a* |
| Left: |  |  |  |
| SAM P13844 | 25·2 | 19·6 | 19·0 |
| UCMP 66326 | 25·2 | 21·2 | 19·5 |
| UCMP 70122 | 26·3 | 21·2 | 19·2*a* |

*a* = approximate.

This tooth is about 2·0 to 3·0 shorter than in *Z. trilobus* Owen (Bingara specimens), about 2·0 longer than in *Z. gilli* (Stirton, 1957, p. 125), and about 5·0 longer than *Kolopsis rotundus* from the Awe fauna of New Guinea. There are similar differences in the width of the tooth.

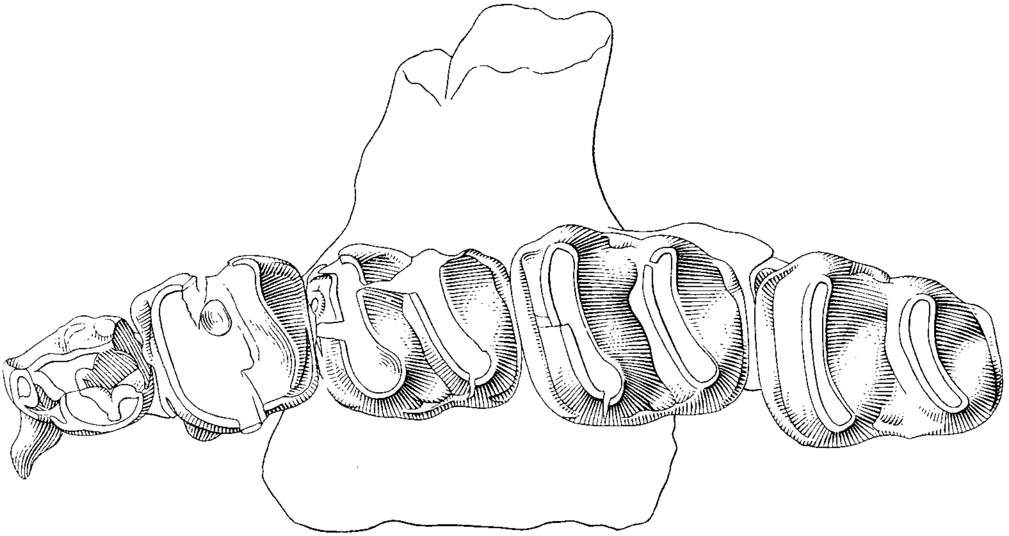


**Fig. 2.—*Zygomaturus keanei*, sp.nov. Part of holotype, SAM P13844, natural size. Part of left maxilla with well worn $P^3$ to $M^1$, $M^2$ to $M^4$, occlusal view.**

The five-cusped arrangement of parastyle, paracone, metacone, protocone, and hypocone is clear. The paracone is the highest and is separated from the metacone, second in height, by a short but constricted crest. Opposite this constriction the vertical labial groove and depression behind the paracone is about as deep as in the Awe species (there is, however, only the groove and not a somewhat widened depression in *K. rotundus*), but shallower than in the Beaumaris specimen, and on the whole not as pronounced as in *Z. trilobus*, and in three of the four specimens a small stylar cusp is developed at its base. The labial outline is convex anteroposteriorly. The parastyle slants somewhat back toward the paracone; therefore the crevice between the cusps is neither as deep nor as wide as in *Z. trilobus*. The parastyle is higher than the protocone and the hypocone is the lowest cusp. The hypocone is separated from the protocone by a shallow commissure as compared with the deeper crevice in *Z. trilobus* and the wider and deeper valley in *K. rotundus*. The hypocone is farther posterior in position than the metacone. The valleys anterolabial and posterolabial to the protocone are shallower than in *Z. trilobus*. The lingual cingulum descends onto the parastyle, the protocone and the hypocone. Because of appression against $M^1$, the posterior cingulum is mostly obliterated. Labially a cingulum is partly developed except in UCMP 70122. The lingual outline is strongly convex opposite the protocone and hypocone. The two roots are widely divergent.

*Upper molars.* The differences in the upper molars from $M^1$ to $M^4$ are seen in their size, width of anterior moiety as compared with posterior moiety, and prominence of the parastyles and metastyles, although the metastyles are not developed in some specimens. The molars in bulk size from largest to smallest are $M^3$, $M^4$, $M^2$ and $M^1$.

In all the upper molars the lophs are slightly crescentic and slightly more transverse in direction than in *Meniscolophus.* The protoloph appears to be nearly transverse and the metaloph is slightly oblique. A wide short ridge extends from the posterior base of the paracone back to the crease in the middle of the transverse median valley. It is here called the postparaconal ridge. The crease is not as sharp as in *Z. trilobus.* The valley is widely V-shaped and this is accentuated by a wide, anteriorly directed, depression on the posterior surface of the protoloph and lingual to the postparaconal ridge mentioned above. The cingula are well developed on all sides of the teeth but discontinuous opposite the protoloph and the metaloph on both the lingual and labial sides. The cingula in *Z. keanei,* however, are less prominent than in *Z. trilobus.* Although the size of the stylar cusps varies considerably they usually diminish in size from $M^1$ to $M^4$; there is no trace of the metastyle in $M^4$ of the specimens available. The height of the hypocone in UCMP 44400 is about 12·8 and the paracone in the holotype is 17·0. Otherwise the teeth are too much worn for reasonable estimations of height. On the whole the upper molars of *Z. keanei* show a closer resemblance to *Z. trilobus* than to the Beaumaris specimen or to *Kolopsis.*

*Mandible.* Both horizontal rami, including the fused symphysis, and all but the coronoid and condyles in the posterior part of the jaw are preserved. The symphyseal region displays a horizontal outline of its ventral border, and it is steeply inclined posterodorsally at the midline. Consequently the incisors are procumbent and the symphyseal sulcus between the diastemal crests is less convex anteroposteriorly at the midline than in *Meniscolophus.* The dorsal and ventral midline is not grooved. The subalveolaris fossae are well impressed into the bone on each side of the 8·0 long spina mentalis, but there is no torsus transversus. The alveolar border behind the incisor is broken away but an approximate length of the incisor to $P_3$ diastema is 53·0. The mental foramen is round, 5·5 in diameter, and about 28·0 below the anterior end of $P_3$. Length of the symphysis is about 106·5; its posterior end is below the anterior moiety of $M_2$.

The lower border of the mandible is convex, especially from a point below the anterior end of $M_3$ back to the angle. The digastric process and the digastric sulcus are not as prominent as in *Meniscolophus.* Although these features are prominent in the holotype they are subdued in UCMP 44401; therefore that area evidently is somewhat variable. The pterygoid fossa and the digastric fossa appear to be confluent, but the anterior end of the pterygoid fossa shows a greater deepening of the surface than the posterior end of the digastric fossa. The holotype is too much crushed to show a true depth of the pterygoid fossa and the area is not preserved in UCMP 44401. The digastric fossa fades out anteriorly below $M_2$. The postalveolar shelf is 19·5 long anteroposteriorly; from the inner end of $M_4$ it curves rather abruptly posterolabially toward the base of the ascending ramus. The anterior border of the ascending ramus is nearly vertical, and opposite the posterior moiety of $M_4$. The masseteric fossa measures about 100·0 between its anterior edge on the ascending ramus and the masseteric eminence below the condyle. The convex posterior surface between the angular process and masseteric eminence is about 93·0. The mandibular foramen is 55·0 behind and on a level with the base of the crown of $M_4$.

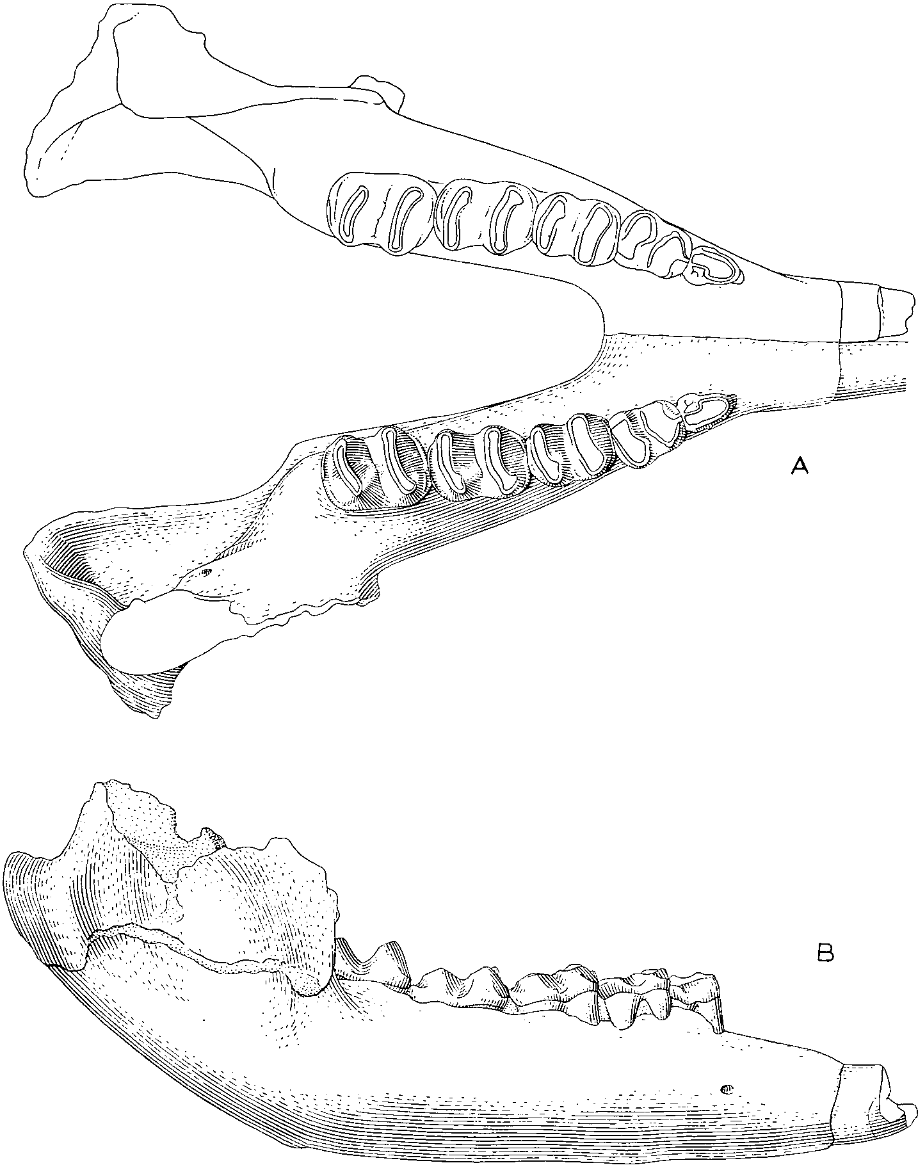


Fig. 3.—*Zygomaturus keanei*, sp.nov. Part of holotype, mandible, SAM P13844. A, dorsal view; B, labial view. x $\frac{1}{3}$.

Table 2: Measurements of Upper Molars, *Zygomaturus keanei*

| | KEANE QUARRY | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $M^1$ | | | $M^2$ | | | $M^3$ | | | $M^4$ | | |
| | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. |
| SAM P13844 | 28·5 | 27·0 | 27·1 | 34·5 | 30·5 | ? | 39·3 | 35·5 | 30·9 | 41·4 | 33·7 | 28·2 |
| SAM P13844 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 41·0 | 34·0 | 28·9 |
| UCMP 70121 | 31·0 | 27·2 | 27·1 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 70120 | .... | .... | .... | 33·9 | 29·3 | 27·4 | .... | .... | .... | .... | .... | .... |
| | | | | WOODWARD QUARRY | | | | | | | | |
| UCMP 44400 | 28·8 | 25·5 | 25·4 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 44398 | 33·0 | 28·0 | 28·0 | 39·3 | 33·6 | 31·2 | 43·4 | 36·4 | 32·3 | .... | .... | .... |
| UCMP 45256 | 32·9*a* | 27·5 | 28·9 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 44623 | .... | .... | .... | 37·3 | ? | 32·0 | .... | .... | .... | .... | .... | .... |
| UCMP 45353 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 42·8 | 35·7 | 32·5*a* |
| UCMP 45354 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 38·6 | 33·2*a* | 26·4 |
| | | | | *Zygomaturus* sp.<br>LAWSON-DAILY QUARRY | | | | | | | | |
| UCMP 70126 | .... | .... | .... | 30·0 | 26·8 | 26·2 | 34·3 | 29·4 | 26·6 | 33·7 | 27·8 | 22·1 |
| | | | | *Zygomaturus gilli*<br>BEAUMARIS, VICTORIA | | | | | | | | |
| NMV 15909 | .... | .... | .... | ? | ? | 20·7 | 27·7 | 25·7 | 21·8 | 27·0 | 23·5 | 18·8 |

NOTE.—The length of $M^1$, $M^2$ and $M^3$ were measured from the parastyle to the metastyle; a midline length was taken for $M^4$; *a* = approximate; ant. m. is anterior moiety, post. m. is posterior moiety. Measurements for the two numbers of SAM P13844 is from the right and left sides.

Table 3: Measurements of Lower Molars, *Zygomaturus keanei*

KEANE QUARRY

| | $M_1$ | | | $M_2$ | | | $M_3$ | | | $M_4$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. | length | width ant. m. | width post. m. |
| SAM P13844 | 29·2*a* | 20·0 | ? | 34·0 | 26·0 | 25·9 | 40·2 | 28·3 | 28·2 | 43·3 | 31·4 | 28·2 |
| WOODARD QUARRY | | | | | | | | | | | | |
| UCMP 70123 | 29·6 | 20·5*a* | 22·2 | .... | .... | .... | .... | .... | .... | .... | .... | .... |
| UCMP 44390 | .... | .... | .... | 37·7 | 29·0*a* | 28·3 | 42·8 | 32·4 | 29·7*a* | 43·3 | 32·7 | 29·3 |
| UCMP 44401 | .... | .... | .... | .... | .... | .... | .... | .... | .... | 43·7 | 32·2 | 29·3 |

The lengths of all lower molars taken at midline; *a* = approximate; ant. m. is anterior moiety; post. m. is posterior moiety.

Measurements: length of mandible from angular process to edge of incisor alveolus in SAM P13844 is 352·0; depth of ramus below M$_2$ and M$_4$ in SAM P13844 is 65·0 and 68·0, in UCMP 44399 is 76·0 and 77·0; depth of ramus below M$_4$ in UCMP 44401 is 89·0; width of ramus below M$_3$ in SAM P13844, in UCMP 44399 and 44401 is 45·0, 54·0 and 48·0.

*Lower incisors.* The lower incisor in the left ramus of the holotype is broken off apparently at the edge of the alveolus above, but more remains below where part of the enamel is preserved. The three well worn incisors, UCMP 44619, 44620 and 44621, with the roots preserved, belonged to adult animals; 44619 and 44620 are larger than 44621 and the latter is about equivalent to the holotype. In fact 44619 and 44620 probably belonged to one animal.

The lower border is curved in a radial arc of about 132·0. Most of the enamel crown is worn away but there is a length of 42·0 in 44619 and 44620 and 34·0 in 44621; the widths are about 22·3 and 19·0. The widths are somewhat deceptive because of the overlapping cement. Occlusion occurred on the posterior surface. The lower border of the enamel is broadly rounded. The length of the root is about 91·5 in all three; however the open end, dorsoventrally, is 36·7 in 44619 and 44620 and 28·8 in 44621. The mesial side of the root is broadly concave and the lateral side is convex, but with a longitudinal narrow groove in 44621. *Z. keanei* differs from the one specimen of *Z. trilobus* available in that the root is deeper dorsoventrally at the base of the enamel, but this is probably variable.

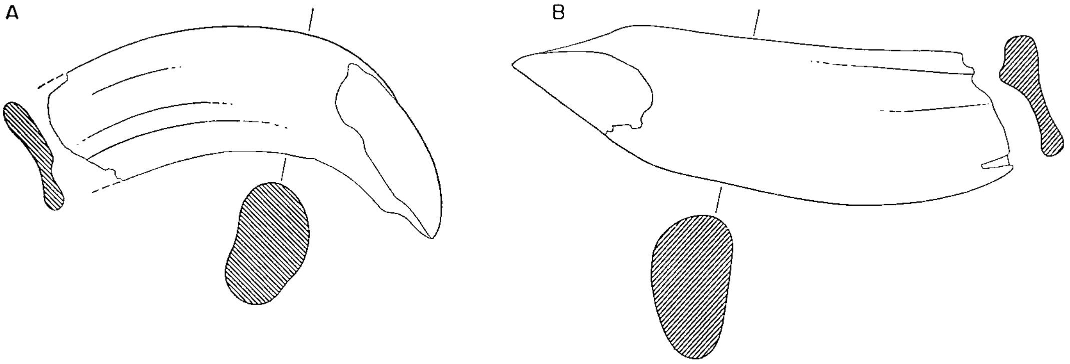


**Fig. 4.—*Zygomaturus keanei*, sp.nov. A, part of holotype, right I$^3$, lateral view, SAM P13844. B, lateral view of lower incisor, UCMP 44619. x ½.**

*Lower premolars.* P$_3$. The best preserved lower premolar is UCMP 70123. In the holotype the tooth is much more worn. There is a high anteromedian main cuspid and a small posterolabial cuspid, which are connected by a crest. The crest of the anterior surface from the base of the enamel assumes a greater angle in sloping back to the apex of the main cuspid than in *Z. trilobus* BMNH 43952 (see Owen, 1877, pl. XL), and a spur off the posterolingual corner of the main cuspid appears to be more strongly developed than in the Pleistocene species. The posterior crest, which is directed lingually from the posterolabial cuspid, is abraded because of appression against $M_1$ in UCMP 70123 but it appears to have been no more prominent than in *Z. trilobus* and much less so than in *Kolopsis rotundus.* It did not curve anteriorly at the lingual end.

The posterolingual valley between the main cuspid and the posterior crest is shallower and its surface is not as steeply declined lingually as in *Kolopsis rotundus.* This feature cannot be adequately compared with *Z. trilobus* from Owen's illustration. A labial cingulum extends from the base of the main cuspid back to the base of the posterolabial cuspid, but the depression above it is not as conspicuous as it appears in Owen's illustration of *Z. trilobus.* Furthermore in neither *Z. keanei* nor *Z. trilobus* is the enamel surface extended as far down, nor is that lower area as bulbous as in *Kolopsis rotundus.* UCMP 70123 is longer, 20·8, and wider across the base of the talonid, 15·7, but apparently was lower crowned than in *Z. trilobus* BMNH 43952. The tooth has two roots. The anterior root is larger and longer, 37·8, than the posterior, 25·7; both are curved posteriorly. It may be noted that a $P_3$ of *Zygomaturus* from the Mammoth Caves and in the Western Australian Museum not only has a much different outline, as viewed from above, from BMNH 43952, but its anteroposterior length is about 3·3 shorter and the talonid is higher in relation to the main cuspid.

*Lower molars.* There is very little difference in lower molars from $M^1$ to $M_4$ except the progressive increase in size. As measured across the lophids the anterior moiety is slightly wider than the posterior moiety, except on $M_1$.

All the lophids of the lower molars are slightly crescentic and transverse in direction. A wide but not sharply defined ridge extends from the anterolabial corner of the hypoconid down to the crease in the middle of the transverse median valley. This structure is considered as homologous with the metalophid. As in the upper molars, the crease in the bottom of the transverse median valley is not as sharp as in *Z. trilobus.* The valley is U-shaped; its anteroposterior width is particularly accentuated by a posterior directed depression on the anterior surface of the hypolophid and lingual to the metalophid ridge that descends into the valley from the hypoconid. The valley is also U-shaped labial to that ridge. The anterior and posterior cingula are not as prominent as in *Z. trilobus*, but better developed than in *Kolopsis rotundus.* There are no labial and lingual cingula, except a faint development across the mouths of the transverse valleys. Parastylids are small on $M_1$ and $M_2$, but otherwise stylid cusps are not present. The height of the protoconid in the holotype is about 20·0. All the lower teeth available are too much worn for accurate measurements on heights of crown, or to determine if the crests of the lophids in little worn or unworn teeth curve as much posteriorly as in *Z. trilobus.*

### ZYGOMATURUS sp.

$M^2$ to $M^4$, attached to part of a palate (UCMP 70126) that came from the Lawson-Daily Quarry, are much smaller (see Table 2) and appear to be otherwise significantly different from *Zygomaturus keanei.* Since the sample is small, and premolars are lacking, its naming as a new species cannot be justified; it is possible—though unlikely—that the specimen is a small individual of *Z. keanei.* On the whole its size is intermediate between *Z. keanei* and *Z. gilli* from the Sandringham Sands, Beaumaris, Victoria, NMV 15909 (Stirton, 1957, p. 126).

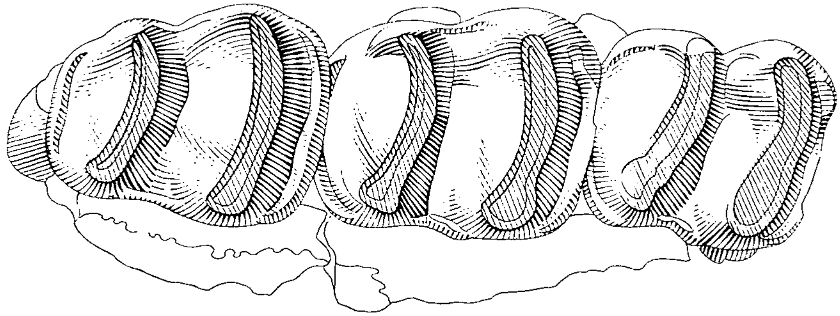


Fig. 5.—*Zygomaturus* sp. Right M² to M⁴, occlusal view, UCMP 70126. Natural size.

The lophs are much as they are in *Z. keanei*, but even more like those in *Kolopsis rotundus* Plane, 1967, from New Guinea, and in *Z. gilli* NMV 15909. The ridge from the base of the paracone in the transverse median valley is greatly subdued as in *K. rotundus* and in *Z. gilli*, and the depression of the posterior surfaces of the protolophs and metalophs appears to extend farther forward, and sweep from side to side of the lophs. Consequently the valleys are almost U-shaped. There is no mesostyle, and the parastyles and metastyles are more reduced. The protocone on M⁴ is about 13·5 in height.

At first it was thought the assemblage from the Lawson-Daily Quarry might represent an older fauna, because the site also yielded a rather small *Meniscolophus* M⁴. On the other hand the large incisor UCMP 70125 described under *Z. keanei* likewise was discovered in the quarry. Furthermore, preliminary comparisons of the macropodid specimens from the Woodard and Lawson-Daily Quarries reveal no significant differences.

## Genus MENISCOLOPHUS Stirton, 1955

*Genotypic species. Meniscolophus mawsoni* Stirton, 1955

In the light of our present knowledge it seems advisable to revise the diagnosis of the genus so that it can be compared with the other genera included in this series of papers. As in most cases where the genera of a family are not adequately known some of the characters listed, or combinations of them, may eventually not prove diagnostic.

*Revised generic diagnosis.* Upper incisor, P³, M¹, and M⁴ not known. Upper molars with narrow, sharply V-shaped transverse median valleys; slight postparaconal and postprotoconal expansions on posterior surface of protoloph of M² and M³, no ridge or expansion from anterior surface of metaloph; no stylar cusps on M¹ or M²; anterior cingulum directed more downward than in *Zygomaturus*; cingula across mouths of transverse median valley more prominent than *Zygomaturus*, *Euryzygoma*, or *Euowenia*, or in the upper molars referred to *Nototherium*.

$I_1$ moderately upturned; enamel on anterior and labial surfaces, labial surface nearly flat, anterior surface convex; occlusion on posterolingual surface of apex; anterior end worn off; mesial and lateral grooves faintly indicated beyond alveolus.

$P_3$ very much like the one in *Euryzygoma*; triangular but posterior and labial outlines convex; no hypoconid or talonid; cingulum continuous posteriorly from position on labial side of central cuspid around to posterolingual base of that cuspid; slight ridge descends from cuspid to posterior cingulum.

Lower molars with lophids nearly transverse; transverse median valley narrow and sharply V-shaped; prominent metalophid descends from anterolingual corner of hypoconid to block valley near midline of tooth; labial cingulum more extensive than in *Zygomaturus*, less extensive and less prominent than in *Euryzygoma*; posterior cingulum sharply elevated from both sides at midline of tooth.

*Referred specimens.* Two rather large third incisors, $I^3$, from the Keane Quarry are referred to *M. mawsoni*. One, UCMP 70131, is well worn and the end of the root is missing, but the other, UCMP 70124, is moderately worn and otherwise complete.

The occlusal outline is triangular with the base of the triangle anterior. The appression facet for $I^2$ is 7·8 wide. The greatest transverse width near the base of the crown is 16·5, and anteroposteriorly it measures 17·8. The enamel-covered crown curves inward and the labial surface 31·5 in length. That surface is marked by one faint and two well defined vertical grooves. On the lingual side the enamel is about 18·5 in length, and that surface too is irregular anteroposteriorly. The posterior end is widely rounded, 11·3 wide at the base of the enamel, but this tapers in on both sides until it reaches the occlusal surface. The root is rounded but with a groove down the anterior surface and a rather sharp ridge on the lingual side. On the lingual side the length of the root above the enamel is 44·2, but above the enamel on the labial side it is only 37·8. The end of the root is round and open with a thin edge, its diameter there being about 11·0.

An unworn right $M^4$ of *Meniscolophus* from the Lawson-Daily Quarry is smaller than any of the known specimens that have been found. Nevertheless it is probably a small individual of *M. mawsoni*. Unfortunately a $M^4$ of the larger animal was not found, and therefore a direct comparison cannot be made. This tooth is 3·2 shorter anteroposteriorly than $M^3$ in the holotype and the anterior moiety is 3·1 narrower than the posterior moiety of $M^2$ in the holotype, SAM P13647, of *M. mawsoni*.

The protoloph and metaloph are crescentic, especially the metaloph. The direction of the protoloph is slightly oblique, but the metaloph is nearly transverse. A postprotoconal ridge extends from the apex of the protocone about halfway up toward the crease in the transverse median valley. There is no postparaconal expansion as in $M^2$ of the holotype, or basal ridge as seen in *Zygomaturus*. The transverse valley is sharply V-shaped, and more elevated in the midline area than in *Zygomaturus*. A depression on the posterior surface of the protoloph is apparently better developed than on $M^2$ of the holotype, but this comparison may be more apparent than real because of the stage of wear in the holotype. In any event the depression is not extended as much anteriorly as in *Zygomaturus*. The posterior surface of the metaloph is apparently more depressed than on the protoloph, but this is largely due to the greater prominence of a posthypoconal ridge and the presence of a postmetaconal ridge. In this feature *Meniscolophus* finds its closest similarity in *Euryzygoma*. As in the other molars of the holotype the anterior cingulum is directed more downward than in *Zygomaturus*. The cingula across the lingual and labial mouths of the transverse median valley are more prominent than in *Zygomaturus*, *Euryzygoma*, or *Euowenia*, or the upper molars referred to in *Nototherium*. There is a posterior cingulum.

*Measurements:* length 34·1; width of anterior moiety 25·7; width of posterior moiety 21·2; heights of protocone 18·5, paracone 21·0, hypocone 17·6, and metacone 17·3.

Part of a $M^1$, or $M^2$, UCMP 60883, and the posterior moiety of a $M_2$, UCMP 57196, are also from the Lawson-Daily Quarry. The widths of their posterior moieties are 28·0 and 22·8. As in the lower molars of the holotype, the posterior cingulum is sharply elevated from both sides at the midline of the tooth.

## REFERENCES

DEVIS, C. W., 1888—Note on the genera *Zygomaturus* and *Nototherium*. *Proc. Roy. Soc. Qld*, 5, 111-116.

DEVIS, C. W., 1891—In confirmation of the genus *Owenia*, so-called. *Proc. Linn. Soc. N.S.W.*, 6, 159-165, 1 pl.

DEVIS, C. W., 1895—On the mandible of *Zygomaturus*. *Proc. Roy. Soc. Qld*, 11, 1-11.

DEVIS, C. W., 1907—Fossils from the Gulf Watershed. Occasional notes. *Ann. Qld Mus.*, 7, 1-7.

FLOWER, W. H., 1884—Catalogue of the specimens illustrating the osteology and dentition of vertebrated animals, recent and extinct, contained in the Museum of the Royal College of Surgeons of England. Part II, Class Mammalia other than man. *London*, 779.

LONGMAN, H. A., 1921—A new genus of fossil marsupials. *Mem. Qld Mus.*, 7(2), 65-80, 1 fig., 4 pls.

LYDEKKER, R., 1887—Catalogue of fossil mammals in the British Museum (Natural History), V. 345 pp., 55 figs.

LYDEKKER, R., 1889—*Nototherium* and *Zygomaturus*. *Ann. Mag. nat. Hist.*, 149-152.

MACLEAY, W. S., 1857—Report on donations to the Australian Museum during August, 1857. *Sydney Morning Herald, Sydney*.

OWEN, R., 1845—Report on the extinct mammals of Australia, with descriptions of certain fossils indicative of the former existence in that continent of large marsupials representative of the order Pachydermata. *Rep. Brit. Assoc. Adv. Sci., New York*, 1844. *London*, 223-240.

OWEN, R., 1859a—On some outline-drawings and photographs of the skull of *Zygomaturus trilobus* MacLeay (*Nototherium*, Owen?). *Quart. J. geol. Soc. Lond.*, 15, 168-175.

OWEN, R., 1859b—On a collection of Australian fossils in the Museum of the Natural History Society at Worcester with descriptions of the lower jaw and teeth of the *Nototherium inerme* and *Nototherium Mitchelli*, Owen; demonstrating the identity of the latter species with the *Zygomaturus* of MacLeay. *Quart. J. geol. Soc. Lond.*, 15, 176-186, 2 pls.

OWEN, R., 1872—On the fossil mammals of Australia. Part V. Genus *Nototherium*. *Phil. Trans.*, 162, 41-82, 1 fig., 9 pls.

OWEN, R., 1877—Researches on the fossil remains of the extinct mammals of Australia with a notice of the extinct marsupials of England. *London*. Vol. I, 522 pp., 36 figs, 1 pl.; vol. II, 131 pls.

PLANE, M. D., 1967—Two new diprotodontids from the Pliocene Otibanda formation, New Guinea. *This vol.*, 105-128.

SIMPSON, G. G., 1945—The principles of classification and a classification of the mammals. *Bull. Amer. Mus. nat. Hist.*, 85, 350 pp.

STIRTON, R. A., 1955—Late Tertiary marsupials from South Australia. *Rec. S. Aust. Mus.*, 11, 247-268, 11 figs.

STIRTON, R. A., 1957—Tertiary marsupials from Victoria. *Mem. nat. Mus. Vic.*, 121-134, 6 figs.

STIRTON, R. A., 1963—Fossil marsupials and drifting sands. *Aust. nat. Hist.* 14(6), 180-184, 3 figs.

STIRTON, R. A., TEDFORD, R. H., and MILLER, A. H., 1961—Cenozoic stratigraphy and vertebrate palaeontology of the Tirari Desert, South Australia. *Rec. S. Aust. Mus.*, 14, 19-61, 4 figs.

# A PHYLOGENY OF THE TERTIARY DIPROTODONTIDAE AND ITS SIGNIFICANCE IN CORRELATION

by

R. A. Stirton, M. O. Woodburne, and M. D. Plane

## CONTENTS

| | Page |
|---|---|
| INTRODUCTION | 151 |
| NGAPAKALDI GENERA | 153 |
| KUTJAMARPU GENUS | 154 |
| ALCOOTA GENERA | 154 |
| BEAUMARIS SPECIES | 155 |
| AWE GENERA | 155 |
| PALANKARINNA GENERA | 157 |
| SEQUENCE OF FAUNAS | 158 |
| REFERENCES | 160 |

## SUMMARY

A phylogeny of the Diprotodontidae with genera from the late Oligocene or early Miocene to the Pleistocene is presented. This includes seven Tertiary genera not represented in the Pleistocene. The subfamilies Palorchestinae, Nototheriinae, Zygomaturinae, and Diprotodontinae are diagnosed. Both the Nototheriinae and Zygomaturinae are shown as intercalary lineages, although some genera in the Zygomaturinae are arranged into a near ancestor-descendant lineage. The ancestry of the Diprotodontinae is not known. The most diagnostic characters of the genera and subfamilies are found in the upper premolar, but other useful features occur in the other teeth, the cranium and mandible. It appears that the rate of evolution was not appreciably different from that in placental mammals with a similar habitus.

## INTRODUCTION

A phylogeny is an author's interpretation of the evolution and relationships of a group of organisms through time. The interpretation of the phylogeny of any given group may change over a period of years, occasionally because authors' ideas differ on the evaluation of the previously existing evidence, but more often because the old evidence is reconsidered in the light of new information. No single worker has, or is likely to have, all the phylogenetic evidence on any group of organisms; therefore *the* phylogeny is probably not attainable.

Evidence from genetics, stratigraphy, dispersal and distribution, as well as morphology, is or may be utilized in the construction of a phylogenetic tree. Precision in Epoch and Age determinations is desirable in well controlled phylogenetic interpretation, but this is not possible in the known sequence of Australasian continental faunas. Nevertheless the succession of middle to late Cainozoic rock units and faunas which occurs in the Tirari Desert of South Australia (Stirton, Tedford, & Miller, 1961) provides a measure of stratigraphic stability for evaluating the temporal position of other faunal assemblages. Regardless of the effect which new information may have on the placement of the Lyellian Epoch boundaries relative to the continental faunas of Australia, the faunal succession as presented here is internally consistent. If, however, the age of the Etadunna Formation, containing the Ngapakaldi fauna, is Miocene as suggested by Ludbrook (1963), the rate of evolution of the Diprotodontidae would exceed that of other large brachydont herbivores of comparable habitus (e.g., rhinoceroses, tapirs, groundsloths). Diprotodontids are of relatively large size, seem to have been moderately abundant, and their remains are easily recognizable. It is hoped that this phylogeny of the Diprotodontidae will be useful when studies on continental stratigraphy are extended to other areas in Australasia.

The phylogeny presented here is controlled by stratigraphy on the one hand and the apparent evolutionary trends on the other. Evolutionary trend, used here in the sense of Huxley (1876) and Le Gros Clark (1958), is based on *intercalary types* in contrast to ancestor-descendant lineages based on *linear types*. The genera and species in the Awe fauna of New Guinea, with potassium-argon dates for the beds in which they occur, must still be used in the intercalary sense until closely related diprotodontids of the same, or nearly the same, age are found in Australia. As pointed out later in this paper, *Kolopsis rotundus* Plane, 1967, represents a genus previously common in the Miocene in the middle latitudes of Australia, which lingered on into the Pliocene in the equatorial latitudes of New Guinea.

During the course of this study it was found that the Tertiary diprotodontids can be grouped into four major lineages, two of which are composed of intercalary types while members of a third seem to be more nearly aligned in an ancestor-descendant relationship. Because the known genera of diprotodontids have, up to now, mostly been limited to the Pleistocene, the subfamily names have been derived from familiar Pleistocene genera. Although this paper is primarily concerned with Tertiary members of the subfamilies it has been necessary to include some remarks on various Pleistocene genera in order that they may be linked to their Tertiary ancestors.

The four subfamilies of the Diprotodontidae which are recognized in this study are the Palorchestinae Tate, (1948), the Nototheriinae Lydekker (1887), new rank, the Zygomaturinae, new subfamily, and the Diprotodontinae Gill (1872), new rank. The greatest diversity of genera occurs in the Nototheriinae and the Zygomaturinae. As in the diagnoses of other taxonomic groups, not all the characters listed completely separate every genus within a subfamily from all other members of the family. Each subfamily lineage extends across a wide span of time and contains different genera. Therefore, each point given in a subfamily diagnosis may not apply equally to all members of the lineage. Nevertheless it is felt that the genera as listed in the subfamilies are related more closely to each other than any of them are to genera assigned to other subfamilies.

### Subfamily Palorchestinae Tate, 1948

*Revised Diagnosis.* $P^3$ small and medium sized; simple; triangular outline; transversely bicusped; with parametacone (metacone slightly separated in *P. azeal*); crest continuous from parametacone to anterior end of tooth; protocone isolated or nearly so; parastyle faintly indicated in some specimens. $P_3$ with one cuspid; low transverse talonid crest except in *Ngapakaldia.* Molars with strong midlink in Pleistocene genera, incipient in Pliocene forms, not present in *Ngapakaldia*; narrow V-shaped transverse median valleys (except in *Ngapakaldia*). Palate wide and not constricted between diastemal crests. Large epitympanic fenestra in superficies meatus area posterior to glenoid fossa. Very small postglenoid process. See Woods (1958) for a discussion on the relationships of *Palorchestes.*

Genera: *Ngapakaldia* Stirton, 1966a; *Pitikantia* Stirton, 1966a; *Palorchestes* Owen, 1873.

### Subfamily Nototheriinae, new rank

*Diagnosis.* $P^3$ small and medium sized; simple; triangular outline; bicuspid; paracone and metacone not separate; crest continuous from parametacone to anterior end of tooth; protocone connected to paracone (except in *Pyramios*); no parastyle. $P_3$ with one cuspid; posterior cingulum. Molars without midlinks; narrow V-shaped transverse median valleys. Palate narrow and constricted between diastemal crests (except possibly in *Euowenia*). No epitympanic fenestra in superficies meatus area posterior to glenoid fossa. Large postglenoid process.

Genera: *Pyramios* Woodburne, 1967; *Meniscolophus* Stirton, 1955; *Euryzygoma* Longman, 1921 (syn. *Diarcodon* Stephenson, 1963); *Euowenia* De Vis, 1891; *Nototherium* Owen, 1845.

### Subfamily Zygomaturinae, new subfamily

*Diagnosis.* $P^3$ large; complex; bulbous outline; quinquetubercular (except in *Neohelos* and *Plaisiodon*); paracone and metacone separate but on same crest (except in *Plaisiodon* and *Neohelos*); protocone isolated or connected to paracone with wear; strong isolated parastyle (but connected to paracone by high crest in *Kolopsoides*). $P_3$ with one cuspid (two arranged anteroposteriorly in *Kolopsoides*); no posterior cingulum. Molars without midlinks; wide V-shaped or U-shaped transverse median valleys. Palate narrow and constricted between diastemal crests. No epitympanic fenestra in superficies meatus area posterior to glenoid fossa. Large postglenoid process.

Genera: *Neohelos* Stirton, 1967b; *Plaisiodon* Woodburne, 1967; *Kolopsis* Woodburne, 1967; *Kolopsoides* Plane, 1967; *Zygomaturus* Owen, 1859 (syn. *Simoprosopus* De Vis, 1907).

### Subfamily Diprotodontinae, new rank

*Diagnosis.* $P^3$ small; complex; ' horse-hoof ' pattern, lophodont; quadritubercular; paracone and metacone distinct; protocone connected to metacone; no hypocone; small parastyle. $P_3$ bilophodont, usually connecting with wear lingually forming ' horse-hoof ' pattern; reduced paralophid; with posterior cingulum. Molars without midlinks; narrow deep transverse median valleys with cement. Palate as deep groove between diastemal crests. No epitympanic fenestra in superficies meatus area posterior to glenoid fossa. Large postglenoid process.

Genus: *Diprotodon* Owen, 1838.

## NGAPAKALDI GENERA

The oldest known diprotodontids are in the Ngapakaldi fauna, which we believe is late Oligocene or possibly early Miocene in age. There are two genera, *Ngapakaldia* and *Pitikantia*. The two species of *Ngapakaldia* are *N. tedfordi* Stirton, 1967a, and *N. bonythoni* Stirton, 1967a. The numerous specimens clearly show that the Diprotodontidae were well advanced in their evolution at that time. The molars are bilophodont and there is no direct evidence of their derivation from animals with tribosphenic patterns. It is interesting to note the presence of alveoli for vestigial canines in *Ngapakaldia*, a character that is retained in some living macropodids, but not known in post-Ngapakaldi diprotodontids. Perhaps the best evidence that the nearest familial relationships of the Diprotodontidae are with the Vombatidae is seen in the ventral mesial expansion of the squamosal excluding the alisphenoid from the auditory region.

The assignment of these genera to the subfamily Palorchestinae does not necessarily indicate that the palorchestines are the basic stock from which all later diprotodontids arose, although this might be demonstrated by future discoveries. The presence of two genera in the fauna and their advanced stage of evolution shows that there must have been considerable diversity in the family at that time.

The more generalized nature of *Ngapakaldia*, in contrast with the later diprotodontids, is seen immediately in the rather normal profile of the cranium, the absence of a digastric process and digastric sulcus in the mandible, and in alveoli for vestigial upper canines. The greatly reduced postglenoid process, large epitympanic fenestration in the superficies meatus area, great expansion of the epitympanic sinus, and width of the palate between the diastemal crests are in keeping with the classification of *Ngapakaldia* in the Palorchestinae. The absence of any trace of midlinks in the molars, the lanceolate lower incisors with narrow roots, and the simple construction of the premolars, however, is our evidence for not placing the genus in the direct ancestry of the later palorchestines.

Unfortunately the cranium of *Pitikantia* is not known. Nevertheless, the teeth in the type species reveal characters that support our belief that it is much nearer, if not in, an ancestral position to *Palorchestes*. Similarity is seen in the incipient midlink on $M_1$, the spatulate incisor with vertically deep narrow roots, and the tendency toward developing a talonid on $P_3$.

## KUTJAMARPU GENUS

The genus *Neohelos* Stirton, represented by five isolated teeth in the Kutjamarpu fauna, is the oldest and most primitive diprotodontid in the subfamily Zygomaturinae. We believe it is approximately middle Miocene in age. Insofar as can be determined now, neither of the Ngapakaldi genera is its ancestor, although the zygomaturine lineage probably extends back into the Oligocene.

*Neohelos tirarensis* Stirton, 1967b, was evidently slightly larger than *Ngapakaldia bonythoni*. Furthermore the dental characters are much more like those of the other zygomaturines than those of *Ngapakaldia*. $P^3$ is well advanced in evolution toward a quinquetubercular arrangement of cusps: the parametacone is not separated into two cusps; but the hypocone is well developed and there can be little doubt that a parastyle was present. Other zygomaturine features are seen in the nearly square outline of $M^1$ and $M^2$, and the widely V-shaped transverse median valleys of the upper molars. In $M_4$ the valley is U-shaped as in *Kolopsis torus*. These characters, then, exclude *Neohelos* from the other subfamilies.

## ALCOOTA GENERA

It is obvious that the Alcoota fauna is younger than the Kutjamarpu and certainly older than the Palankarinna. It also appears to be older than the Awe fauna from New Guinea, but how much older is difficult to determine. The most likely age assignment falls somewhere near the late Miocene and early Pliocene.

The Alcoota genera show that considerable phyletic diversification had taken place by middle Tertiary time. Three subfamilies, the Nototheriinae, Zygomaturinae, and Palorchestinae, are represented in the fauna. *Pyramios alcootense* Woodburne, 1967a, a large animal, is the oldest known member of the Nototheriinae. Its size and other characters show that it is well advanced in that lineage. Basicranial characters indicate a basic relationship with the Zygomaturinae and not the Palorchestinae. The divergence of the Nototheriinae and Zygomaturinae from a common ancestry must have been at least as early as Ngapakaldi time. The divergence of their common ancestor from the Palorchestinae evidently was even earlier.

Distinctive nototherine characters in *Pyramios*, which are in marked contrast to those in *Neohelos*, are seen in $P^3$, which is triangular in outline, bicusped, has a single parametacone, no parastyle (or at least faintly indicated), and no hypocone. Another interesting feature is the dorsal profile of the cranium, which is only slightly depressed anterior to the orbits. This is essentially the profile that will probably be seen in all, or nearly all, of the early diprotodontids.

The Alcoota zygomaturines are *Plaisiodon centralis* Woodburne, 1967a, and *Kolopsis torus* Woodburne, 1967a. *P. centralis* is about the same size as *Pyramios alcootense*. It retains the quadritubercular pattern of $P^3$ seen in *Neohelos* as well as a broadly triangular, posteriorly elongate $I^3$ which lacks a strong vertical cleft in its labial surface. *P. centralis* and *N. tirarensis* also lack a metastyle on $M^1$. As demonstrated by its larger size, high trenchant parametacone on $P^3$, strong anterior and posterior cingula of the upper molars, absence of a longitudinal postparaconal crest on $M^1$, and the presence of a distinct metalophid in the lower molars, *Plaisiodon* is considerably removed from *Neohelos.* From the available evidence it appears that the two genera are only broadly related within the subfamily and probably had a common ancestry prior to Kutjamarpu time. *Plaisiodon centralis* may represent an early branch of the Zygomaturinae which became extinct in the late Miocene or early Pliocene. It has not been found in the later faunas.

*Kolopsis torus* is smaller than *Pyramios* or *Plaisiodon,* and its teeth are higher crowned and larger than in *Neohelos.* Although possibly more closely related to *Neohelos* than is *Plaisiodon, Kolopsis* has attained a quinquetubercular arrangement of the cusps on $P^3$ by the separation of the paracone and metacone. The shape and other features in the cheekteeth in *Neohelos* and *Kolopsis* are more alike, however, than the teeth in either genus are like those in *Plaisiodon.* It is possible that the separation of the paracone and metacone took place somewhere between Kutjamarpu and Alcoota time, if indeed *Neohelos* and *Kolopsis* are in an ancestor-descendant lineage. The cranium in *Kolopsis torus* has essentially the same profile as in *Plaisiodon* and *Pyramios.*

Preparation of the palorchestine material from the Alcoota fauna has not been fully completed at this time. It will be described in a publication by Woodburne which will deal with the Alcoota fauna as a whole (Woodburne, 1967b).

## BEAUMARIS SPECIES

*Zygomaturus gilli* Stirton, 1967c, is the only diprotodontid we have in direct association with a marine invertebrate fauna. The specimens were described and illustrated by Stirton (1957), but the genus and species were not named. Singleton (1941) assigned a late Miocene age to the invertebrates, and this was followed by Gill (1950) and Glaessner (1951). Crespin (oral communication), however, believes that it is early Pliocene; and this seems to be internally consistent with the evidence adduced in this paper. If the age of *Z. gilli* is indeed late Miocene, there can be little doubt that the Alcoota is a much earlier Miocene fauna. *Z. gilli* is phyletically related to *Kolopsis torus* of the Alcoota fauna. Although the Beaumaris species is classified as belonging to the genus *Zygomaturus* it retains some *Kolopsis* features. It is the most primitive species of *Zygomaturus* now known. If, as the evidence now indicates, *K. torus* is ancestral to *Z. gilli* then *Kolopsis rotundus* from New Guinea is structurally intermediate in some of its characters between the two Australian species. The Awe fauna, however, is probably younger than the Beaumaris fauna (see further discussion under the Awe genera).

## AWE GENERA

Although there are potassium-argon dates of 5·7 m.y. and 7·6 m.y. for different levels in the Otibanda Formation in New Guinea, it is still not possible to correlate the Awe fauna precisely with the Pliocene faunas of Australia in which diprotodontids have been found. The use of stage of evolution for correlation may be misleading in reference to the Awe diprotodontids. In the Northern Hemisphere there are examples of mammalian groups which survived in lower latitudes after having become extinct in the middle latitudes where they were formerly distributed. The somewhat anomalous geochronological position of *Kolopsis rotundus,* which maintains certain primitive features in relation to members of the subfamily occurring in somewhat older Australian faunas, may indicate that a similar phenomenon has occurred in the Australasian region.

The advanced condition of the Awe species, *K. rotundus,* compared to the Alcoota species, *K. torus,* can be demonstrated in the following features of the $P^3$ of the New Guinea form: the greater height of crown, the more widely separated paracone and metacone, the more robust nature of the five major cusps, the shorter and steeper postmetaconal crest, the steeper labial surfaces, and the more labial position of the apices of the paracone and metacone.

On the other hand, a comparison of *K. rotundus* from the middle Pliocene with *Z. gilli,* which most probably comes from the early Pliocene, reveals that although it occurs later in time, the New Guinea species is more primitive than *Z. gilli* from the Sandringham Sands. Characters in the upper third premolars which reveal this relationship include: posterolingual base of the protocone in *K. rotundus* not expanded to contact the anterolabial base of the metacone as in *Z. gilli,* small depression between the protocone and paracone not developed in *K. rotundus,* shallower labial vertical groove between the paracone and metacone than in *Z. gilli,* size of the hypocone in *K. rotundus* larger relative to that of protocone than in *Z. gilli.*

*Kolopsis torus* differs from *Z. gilli,* not only in the above characters which separate *K. torus* from *K. rotundus,* but also in those characters in which *Z. gilli* differs from *K. rotundus.* In other characters, however, such as the absence of a well developed cingulum labial to the molar parastyles and the lack of a premetaconal crest on the metaloph of the upper molars, *K. torus* is more directly aligned with *Z. gilli* than is *K. rotundus.* Nevertheless, *K. torus* is more primitive than either *K. rotundus* or *Z. gilli.* If the age of *Z. gilli* is early Pliocene, then that of *K. torus* must be no later than early Pliocene and is probably late Miocene.

*Kolopsoides cultridens* represents another side branch of the Zygomaturinae. It appears to be more closely related to *Kolopsis* than to *Plaisiodon.* This is demonstrated in the separation of the paracone and metacone on $P^3$, the nearly square outline of $M^1$, and the shape of $P_3$, which is relatively short and wide. It could have evolved from a diprotodontid like *Neohelos tirarensis* of the Kutjamarpu fauna. Some of the most conspicuous characters of *Kolopsoides* which distinguish it from *Kolopsis* are its elongate, three-rooted $P^3$, which has a widely emarginated labial outline, a large parastyle that is aligned with, and connected to, the paraconal-metaconal crest and a hypocone which is larger than the protocone, $P_3$ with the two major cuspids aligned anteroposteriorly, and the retention of metalophid-like structures in the lower molars. No other species of *Kolopsoides* are known, but they may be discovered eventually in the Miocene or early Pliocene deposits in Australia.

*Nototherium watutense* Anderson, 1937, is not sufficiently known to offer the evidence we should like. It has been assigned to the genus *Nototherium* because it appears to be more closely related to the late Pleistocene species of *Nototherium* than to *Pyramios alcootense* of the Alcoota fauna. The short rather massive horizontal ramus, the posterior end of the symphysis below $M_2$, the steep inclination of the posterior symphyseal surface, and the reduced midlink-like structures seem to relate it to *Nototherium* rather than *Meniscolophus.* Discovery of the premolars and incisors will help clarify its relationships.

## PALANKARINNA GENERA

The Palankarinna fauna can still not be correlated closely. It appears, however that *Zygomaturus keanei* is more closely related to the late Pleistocene *Z. trilobus* than it is to *Z. gilli* of the Beaumaris fauna. This would tend to support a late Pliocene age for the Palankarinna. It might be argued that the Palankarinna is early Pleistocene, but it must be remembered that the Mampuwordu Sands in which the fauna occurs is overlain by the Tirari Formation, and that formation in turn is dissected by the Katipiri Sands (see Stirton, Tedford, & Miller, 1961). The Kanunka fauna in the lower part of the Katipiri Sands is clearly older than the late Pleistocene Malkuni fauna in the upper part of the Katipiri.

The protemnodont in the Kanunka is also more primitive than those in the late Pleistocene. This, together with the apparent absence of any indication of *Diprotodon optatum*, resulted in Stirton, Tedford, & Miller (1961) considering the Kanunka fauna as early Pleistocene. The stratigraphic position of these faunas, then, has led us to believe that the age of the Palankarinna fauna is not younger than late Pliocene.

*Meniscolophus mawsoni* is clearly referable to the subfamily Nototheriinae as defined in this paper. Only the one species is known. Unfortunately $I^1$, $I^2$ and $P^3$ have not been found. *Meniscolophus* may have been derived from *Pyramios*, but certain characters in *Pyramios* such as the deep narrow horizontal ramus, the broadly spatulate lower incisors with enamel covering the dorsomesial surface, and the weakly developed metalophid-like structures in the lower molars, suggest that the relationship between these genera is of an intercalary nature.

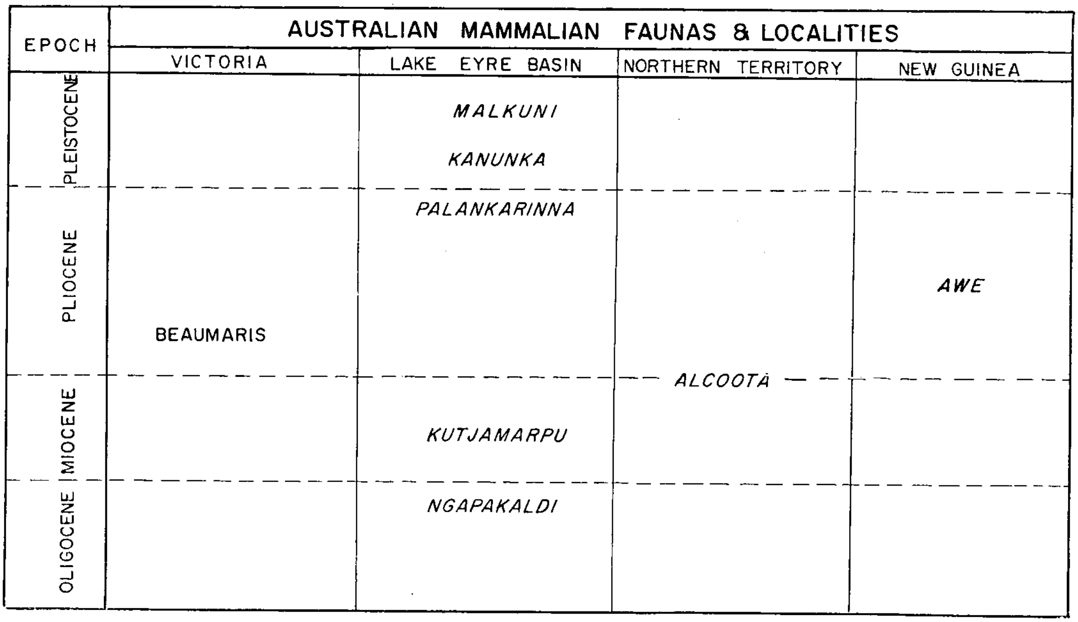
It is even less certain that *Meniscolophus* is in a directly ancestral position with respect to the Pleistocene genera *Nototherium* and *Euryzygoma.* An evaluation of the relative position of these genera is made more difficult because the lower incisor and $P_3$ of *Nototherium* and $P^3$ of *Meniscolophus mawsoni* are not known. Nevertheless the metalophid-like structure, especially in $M_3$ and $M_4$, originates at the labial end of the hypolophid in both *Nototherium* and *Euryzygoma*, not lingual to the labial end as in *Meniscolophus.* A rather wide triangular $P_3$ with its prominent posterior cingulum is found in both *Euryzygoma* and *Meniscolophus.* Features which distinguish *Euryzygoma* from *Meniscolophus* are the long lower incisor with enamel on the ventral and mesial surfaces extending far back into the alveolus near the open end of the tooth, its rather square cross-section, its procumbency; the higher crowned lower molars, the oblique orientation of their lophids and the prominent mesostylids on $M_1$ and $M_2$.

*Euowenia* appears to be less closely related to *Meniscolophus.* This is interpreted from its massively rooted, nearly vertically directed lower incisor, small rather elongate $P_3$, and the high midlink-like structure which completely blocks the transverse median valley in the lower molars.

*Diprotodon* is even more remotely related as revealed in the subfamily diagnosis. We suspect it is closer to the Nototheriinae than to the Zygomaturinae. However, its ancestors are not known and we cannot confirm this supposition on the basis of the available evidence.

## SEQUENCE OF FAUNAS

The temporal relations of the faunas which have yielded the diprotodontids discussed in this series of reports, shown in Figure 1, is the result of a combination of several lines of evidence.



| EPOCH | AUSTRALIAN MAMMALIAN FAUNAS & LOCALITIES | | | |
|---|---|---|---|---|
| | VICTORIA | LAKE EYRE BASIN | NORTHERN TERRITORY | NEW GUINEA |
| PLEISTOCENE | | *MALKUNI*<br>*KANUNKA* | | |
| PLIOCENE | BEAUMARIS | *PALANKARINNA* | *ALCOOTA* | *AWE* |
| MIOCENE | | *KUTJAMARPU* | | |
| OLIGOCENE | | *NGAPAKALDI* | | |

**Fig. 1.—Chronological succession of the faunas which have yielded the diprotodontid remains discussed in this series of reports.**

The physical relations of the formations which contain the various faunal assemblages in South Australia (Stirton, Tedford, & Miller, 1961) have provided a stable lithostratigraphic base upon which local biostratigraphic interpretations have been made. Thus, the Etadunna Formation (Ngapakaldi fauna) is unconformably overlain by the Mampuwordu Sands (Palankarinna fauna), which is succeeded by the unfossiliferous Tirari Formation. The Tirari is cut by the Katipiri Sands (Kanunka and Malkuni faunas).

The Ngapakaldi fauna is clearly older than the Palankarinna; the Palankarinna is older than the Kanunka and Malkuni faunas. Although superpositional relationships of the Kanunka and Malkuni faunas cannot be demonstrated on lithologic grounds, the animals of the Kanunka represent an earlier stage of evolution. The Kanunka fauna has been interpreted (Stirton et al., 1961) as being older than the Malkuni.

A fifth fauna in the South Australian sequence, the Kutjamarpu, is older than the Palankarinna on the basis of the stage of evolution of its mammals. Unfortunately this cannot be corroborated on lithostratigraphic grounds because the sediments of the Wipajiri Formation (Stirton, Tedford, & Woodburne, 1966) do not occur in association with the Mampuwordu Sands, both rock units being localized in occurrence. On the other hand the younger age of the Kutjamarpu fauna relative to the Ngapakaldi can be demonstrated by both lithological and biological criteria. Not only is the Kutjamarpu fauna more advanced than the Ngapakaldi, but the Wipajiri Formation is channelled into the Etadunna.

The occurrence of the meagre fauna at Beaumaris, Victoria, in marine rocks which contain megafossils of the Cheltenhamian Stage is a second cornerstone in this succession of Tertiary vertebrate faunas. As indicated above, the age assignments based on the marine fossils range from late Miocene to early Pliocene. Regardless of the precise Lyellian age of the megafossils, the stage of evolution of the associated diprotodontid material is later than that of the Kutjamarpu fauna and older than that of the Palankarinna fauna. The significance of *Zygomaturus gilli* from the Beaumaris fauna, relative to *Kolopsis rotundus* of the New Guinea Awe fauna, with its middle Pliocene radiometric date, has been discussed above. In this particular instance it is fortunate that the relative ages of the Beaumaris and Awe faunas could be established by other criteria than mammalian stage of evolution.

The non-diprotodontid elements of the Alcoota fauna from the Northern Territory, to be reported on at a later date, are more primitive than known Pliocene and later relatives. This is at least broadly consistent with the possible late Miocene age indicated for the Alcoota assemblage by the pre-Beaumaris stage of evolution of *Kolopsis torus.*

Therefore while diprotodontid evolution has been a prime source of information for the construction of Figure 1, the faunal succession portrayed therein has been supported and clarified by evidence from other mammalian groups, invertebrate biostratigraphy, lithostratigraphy, and radiometric geochronometry. The phylogeny of the Diprotodontidae presented in Figure 2 should provide a useful tool for dating middle and late Tertiary continental faunas in Australasia. It is expected that the practical value of this phylogeny will be increased as it is further refined on the basis of additional information.

## REFERENCES

CLARK, W. E. LE GROS, 1958—Bones of contention. The Huxley Memorial Lecture. *J. Roy. anthropol. Inst.*, 88, 2 figs.

DE VIS, C. W., 1891—In confirmation of the genus *Owenia*, so-called. *Proc. Linn. Soc. N.S.W.*, 159–165, 1 pl.

DE VIS, C. W., 1907—Fossils from the Gulf Watershed. Occasional notes. *Ann. Qld Mus.*, 7, 1–7.

GILL, E. D., 1957—The stratigraphical occurrence and palaeoecology of some Australian Tertiary marsupials. *Mem. nat. Mus. Vic.*, 21, 135–203, 18 figs, 4 pls.

GILL, T., 1872—Arrangement of the families of mammals with analytical tables. *Smithson. misc. Coll.*, 11.

GLAESSNER, M. F., 1951—Three foraminifera zones in the Tertiary of Australia. *Geol. Mag.*, 88, 273–283.

HUXLEY, T. H., 1876—Lectures on evolution. *New York* (Reprinted in the Thinker's Library, 1931, 96 pp.). *Not seen.*

Longman, H. A., 1921—A new genus of fossil marsupials. *Mem. Qld Mus.*, 7(2), 65–80, 1 fig., 4 pls.

Ludbrook, N. H., 1963—Part II. Subsurface Stratigraphy, *in* Johns, R. K., and Ludbrook, N. H., 1963. Investigations of Lake Eyre. *S. Aust. Dep. Min. Rep. Invest.*, 24, 1–104, 17 figs.

Lydekker, R., 1887—Catalogue of fossil mammals in the British Museum (Natural History). Part V. 345 pp., 55 figs.

Owen, R., 1838—Fossil remains from the Wellington Valley, Australia, *in* Mitchell's three expeditions into the interior of eastern Australia. 2nd ed. *London, Boone*, 359–363, 3 pls.

Owen, R., 1845—On the extinct mammals of Australia. *Rept. Brit. Assoc. Adv. Sci.*, for 1844, 14, 223–240.

Owen, R., 1859—On some outline-drawings and photographs of the skull of the *Zygomaturus trilobus* MacLeay (*Nototherium* Owen?). *Proc. geol. Soc. Lond.*, 15, 168–176, 1 pl.

Owen, R., 1873—On the fossil mammals of Australia. Part IX. Family Macropodidae. Genera *Macropus*, *Pachysiagon*, *Leptosiagon*, *Procoptodon*, and *Palorchestes*. *Proc. Roy. Soc.*, 21, 386–387.

Plane, M. D., 1967—Two new diprotodontids from the Pliocene Otibanda Formation, New Guinea. *This Vol.*, 105–125.

Stephenson, N. G., 1963—Growth gradients among fossil monotremes and marsupials. *Palaeontology*, 6(4), 615–624, 1 pl.

Singleton, F. A., 1941—The Tertiary geology of Australia. *Proc. Roy. Soc. Vic.*, 53, 125 pp., 15 figs, 3 pls.

Stirton, R. A., 1955—Late Tertiary marsupials from South Australia. *Rec. S. Aust. Mus.*, 11(3), 247–268, 11 figs.

Stirton, R. A., 1957—Tertiary marsupials from Victoria, Australia. *Mem. nat. Mus. Vic.*, 21, 121–134, 6 figs.

Stirton, R. A., 1967a—The Diprotodontidae from the Ngapakaldi fauna, South Australia. *This Vol.*, 1–44.

Stirton, R. A., 1967b—A diprotodontid from the Miocene Kutjamarpu fauna, South Australia. *This Vol.*, 45–51.

Stirton, R. A., 1967c—A new species of *Zygomaturus* and additional observations on *Meniscolophus*, Pliocene Palankarinna fauna, South Australia. *This Vol.*, 129–147.

Stirton, R. A., Tedford, R. H., and Woodburne, M. O., 1966—A new formation and fauna from the Tirari Desert, South Australia. *Rec. S. Aust. Mus.*

Tate, G. H. R., 1948—Results of the Archbold expeditions. No. 59. Studies on the anatomy and phylogeny of the Macropodidae (Marsupialia). *Bull. Amer. Mus. nat. Hist.*, 91, 237–351, 3 figs.

Woodburne, M. O., 1967—Three new diprotodontids from the Tertiary of the Northern Territory, Australia. *This Vol.*, 53–103.

Woodburne, M. O., 1967b—The Alcoota fauna. *Bur. Min. Resour. Aust. Bull.* 87.

Woods, J. T., 1958—The extinct marsupial genus *Palorchestes*. *Mem. Qld Mus.*, 13(4), 177–193, 5 figs.

ALEX. B. DAVIES, Government Printer, Western Australia

843/3/66—1350

# A PHYLOGENY OF THE DIPROTODONTIDAE

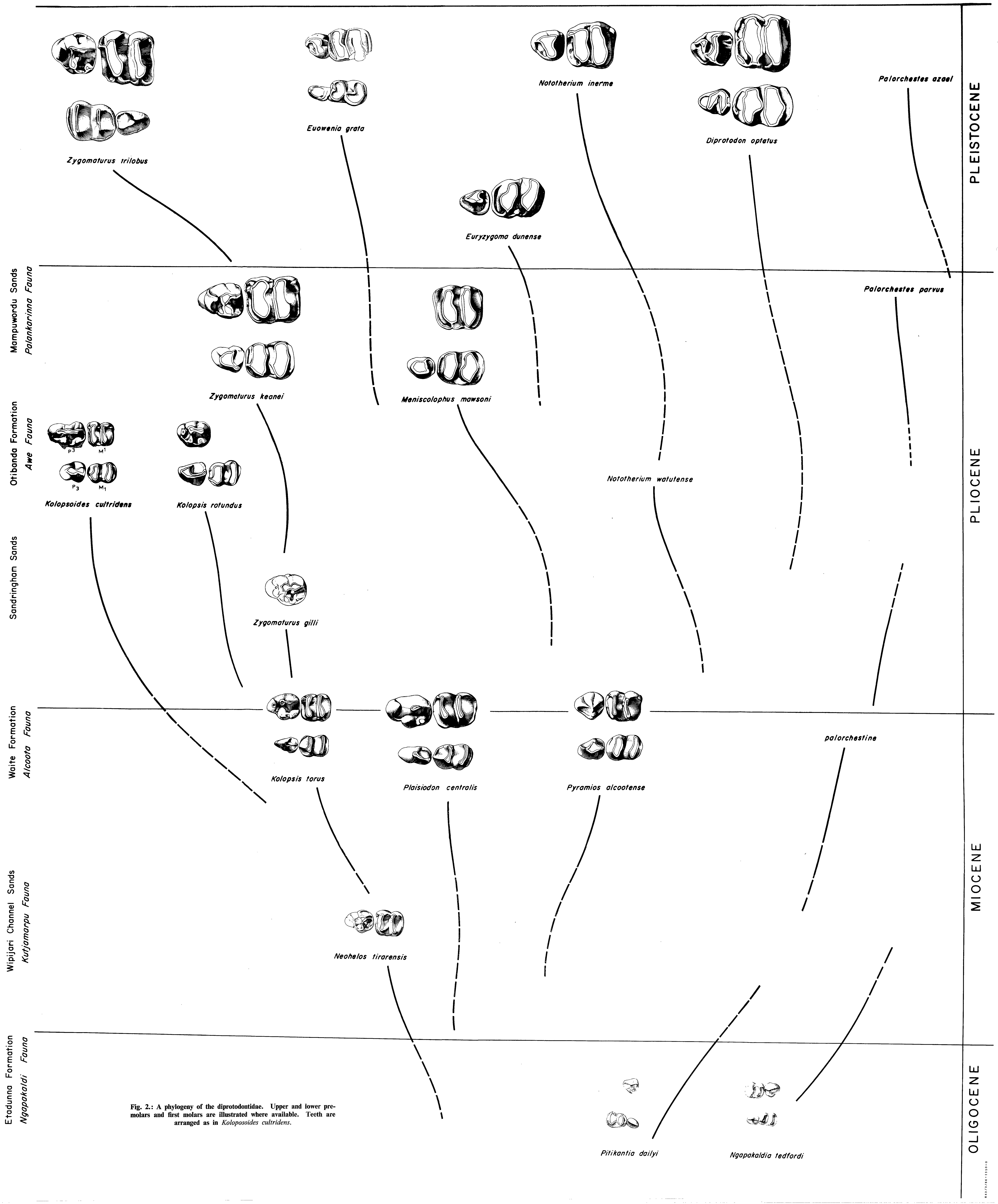


**Fig. 2.: A phylogeny of the diprotodontidae. Upper and lower premolars and first molars are illustrated where available. Teeth are arranged as in *Koloposoides cultridens*.**