

Chapter 19

A New Species of *Muramura* Pledge (Wynyardiidae: Marsupialia) from the Middle Tertiary of the Callabonna Basin, Northeastern South Australia

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ABSTRACT

Partial skeletons, including jaw fragments, collected by Richard H. Tedford and colleagues at Lake Pinpa in the Callabonna Basin of northeastern South Australia, represent a new species of the putative wynyardiid marsupial *Muramura*. The new species is slightly smaller and more gracile than its congener *M. williamsi* from the roughly contemporaneous Etadunna Formation of the Lake Eyre Basin.

INTRODUCTION

Vertebrate fossils were first noted in the area south of Lake Frome (fig. 19.1) by R.A. Callen in 1970. He brought these to the attention of R.H. Tedford who visited Adelaide the next year to organize an expedition into western Queensland. Tedford found the area so promising that he spent several weeks collecting there and had to return to Adelaide to reprovision before going on to Queensland. He subsequently returned to South Australia in 1973, and with a larger expedition, spent a month studying the geology and making a large collection of fossil mammals, birds, and reptiles (Tedford et al., 1977). By a happy combination of environmental factors, namely prolonged drought and strong winds, he found that the most productive site was the bed of the small salina, Lake Pinpa ("Pine Lake"; fig. 19.1; Tedford et al., 1977: figs. 1, 2), where the lowered water table allowed the dried surface to be blown away. (These conditions have not recurred since, and local heavy rains have raised the water table and washed several centimeters of fresh sand onto the lake bed.) The wind-scoured lake bottom revealed partial skeletons of animals that had apparently become mired in

the sticky clays of the Namba Formation (Callen and Tedford, 1976) during late Oligocene times (Woodburne et al., 1985, 1993). Among them were the specimens described in detail below and mentioned by Tedford et al. (1977).

METHODS AND ABBREVIATIONS

Specimens were measured using vernier calipers or an ocular microscope scale. Unlike my previous paper (Pledge, 1987), where the tooth homology system used was that of Archer (1978), the system used here follows the traditional one of Thomas (1888) as reinstated by Luckett (1993).

Abbreviations are as follows:

AMNH	American Museum of Natural History, New York
SAM	South Australian Museum, Adelaide
QMAM	field number for the joint AMNH–Queensland Museum–South Australian Museum expedition, 1973
NMV	Museum of Victoria, Melbourne
Wa	anterior width
Wp	posterior width
St	stylar cusp
ACu	astragalocuboid facet
AN	astragalonavicular facet

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AFi	astragalofibular facet
ATim	medial astragalotibial facet
ATil	lateral astragalotibial facet
CaCul	lateral calcaneocuboid facet
CaCum	medial calcaneocuboid facet
CLAJP	continuous lower ankle joint pattern (Szalay, 1994)
Mt	metatarsal

For dental abbreviations, see figure 19.2.

SYSTEMATIC PALEONTOLOGY

ORDER DIPROTODONTIA OWEN 1866

SUBORDER VOMBATIFORMES

WOODBURNE 1984

FAMILY WYNYARDIIDAE OSGOOD 1921

Muramura Pledge 1987

Muramura pinpensis new species

ETYMOLOGY: After the name of the type locality, Lake Pinpa, South Australia.

HOLOTYPE: SAM P36160 (QMAM 54 = AMNH 102219). Partial skeleton, comprising a badly crushed partial skull (both maxillae, left premaxilla, left auditory region), partial left and complete right dentaries, five ribs, distal part of right humerus, complete left ulna, incomplete left radius, left femur (crushed), left and right tibiae and fibulae (incomplete distally), incomplete left and right hind feet (figs. 19.3A, B, 19.4A, 19.5A).

HYPODIGM: SAM P36160, AMNH 102325 (QMAM 128), left and right partial dentaries, left and right partial pelvis (lacking pubes and part of ischia), left and right femora, tibiae, and fibulae, bones of left and right feet. AMNH 102398 (QMAM 267) damaged right maxilla with P3M1–4 (all molars worn or damaged). AMNH 102622 (QMAM 156) right maxilla with damaged P3M1, worn M2–4. SAM P36161 (= AMNH 102631, QMAM 178), left maxillary fragment with unworn M1–3. AMNH 102338 (QMAM 147), fragmentary left dentary with damaged p3m1–2, complete m3.

LOCALITY: AMNH site B, close to western shore, northern half of dry bed of Lake Pinpa (31°07'30" S, 140°12'50" E, G.R. 3180475, Curnamona 1:250,000 sheet, SH 54–12), figure 19.1.

STRATIGRAPHY AND AGE: Just below the

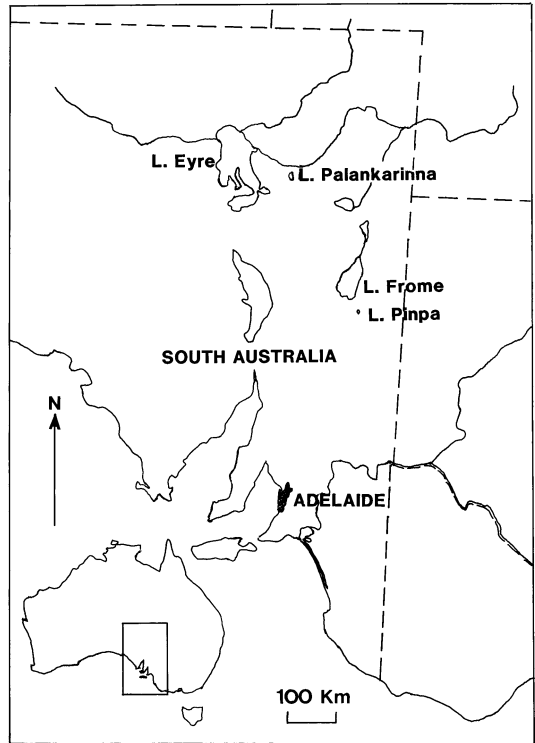


Fig. 19.1. Map showing the location of Lake Pinpa, one of several small, dry, deflation salinas to the south of the larger Lake Frome in north-eastern South Australia. See also Tedford et al. (1977: figs. 1, 2).

boundary (i.e., within the black palygorskite-rich lower unit) between upper and lower members of the Namba Formation (Callen and Tedford, 1976; Callen, 1977; Tedford et al., 1977), in gray clay believed to be Late Oligocene in age by biocorrelation with the lower part of the Etadunna Formation of the Lake Eyre Basin (Woodburne et al., 1985, 1987, 1993; Zone B—redefined Ditjimanka Local Fauna); *M. williamsi* comes from the top of the Etadunna Formation's Zone A—"Minkina Local Fauna" (Plane, 1986: 161). Zones A and (most probably) B approximately correlate with the Pinpa Local Fauna *sensu* Tedford et al. (1977).

DIAGNOSIS

Species of *Muramura* differing from *M. williamsi* in having narrower and generally shorter upper molars, upper premolars, and

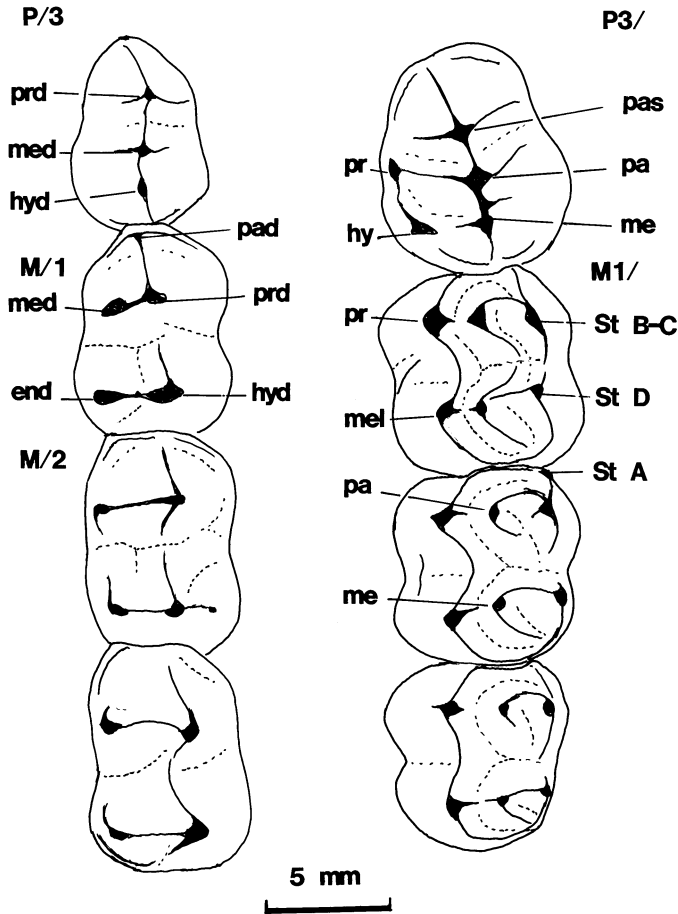


Fig. 19.2. Camera lucida drawings of lower and upper cheek teeth of *Muramura pinpensis* new species, identifying features mentioned in text; right lower teeth SAM P36160, upper left premolar (P3/) SAM P36160, left upper molars SAM P36161. Abbreviations: end, endoconid; hy, hypocone; hyd, hypoconid; me, metacone; med, metaconid; mel, metaconule; pa, paracone; pad, paraconid; pas, parastyle; pr, protocone; prd, protoconid; St A, stylar cusp A; St B–C, joined stylar cusps B and C; St D, stylar cusp D.

lower premolars; lower molars not consistent (tables 19.1, 19.2).

P3 differs in a more angular occlusal outline, more distinct cusps, small but prominent hypocone, reduced midlength constriction, and broader, less angular separation between parastyle and paracone.

M1 is narrower, lacks distinct cuspule at buccal end of precingulum, has weaker development of protoloph and metaloph, buccally more open transverse valley, strong postcingulum and post-St D crista.

M4 differs in having narrower posterior

moiety, no cuspule at buccal end of precingulum.

p3 is narrower with less waisted occlusal outline, rounded depressions between moieties, cruciform protoconid, and hypoconid present.

m1 has narrower protolophid, protoconid more medial, preprotocristid more medial, no premetacristid, weaker cristid oblique not crossing transverse valley, and deep narrow fissure on posterior side of hypolophid forming strong linguad posthypocristid.

Differs from *Namilamadeta* spp. (Rich and

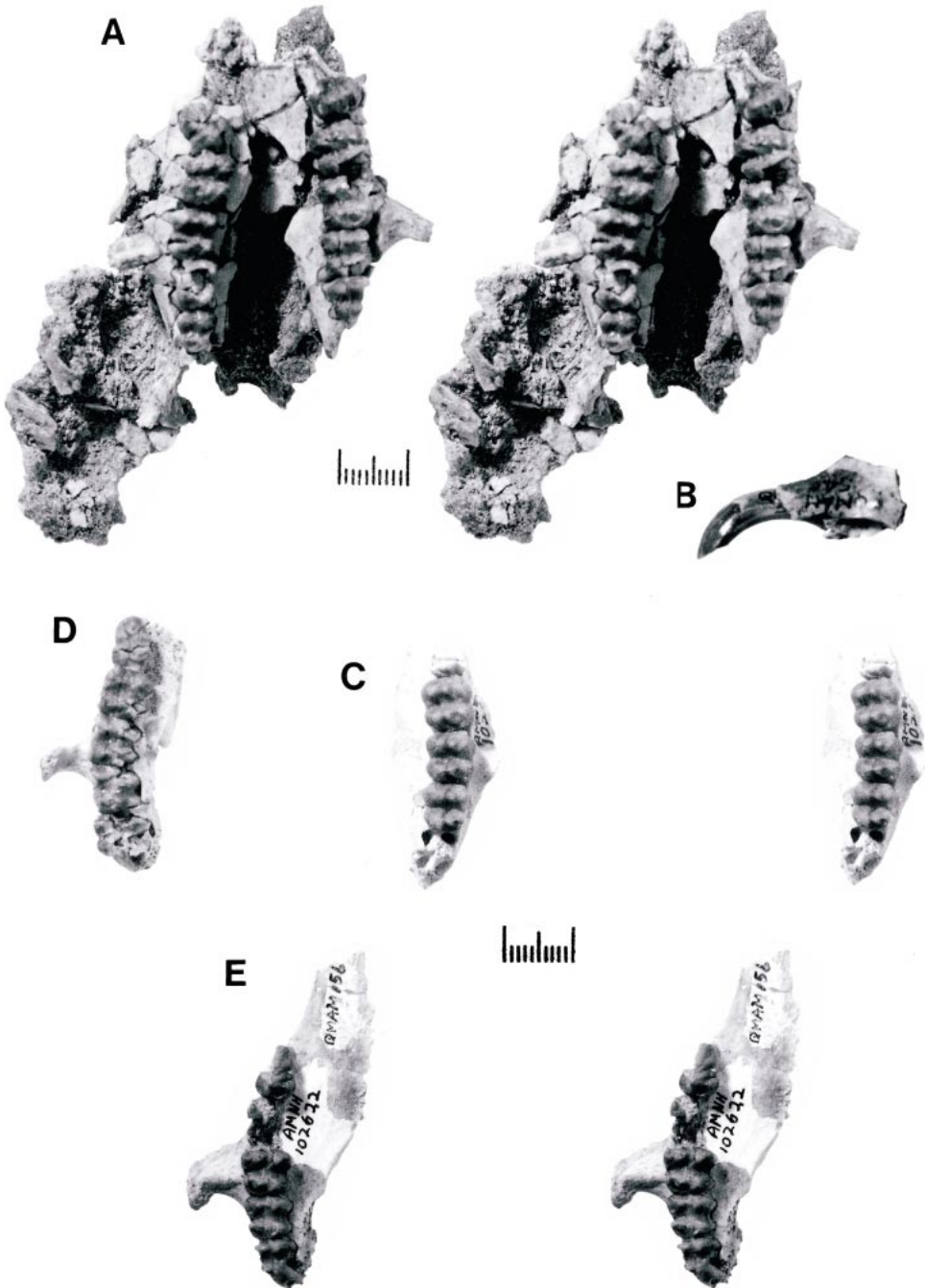


Fig. 19.3. *Muramura pinpensis* upper dentition. **A**, Holotype SAM P36160, crushed skull, palatal view (stereopair). **B**, Holotype SAM P36160, left premaxilla, lateral view. **C**, Paratype SAM P36161, left maxillary fragment, occlusal view (stereopair). **D**, Paratype AMNH 102398, right maxillary fragment, occlusal view. **E**, AMNH 102622, right maxillary fragment, occlusal view (stereopair). Scale: 1 cm.

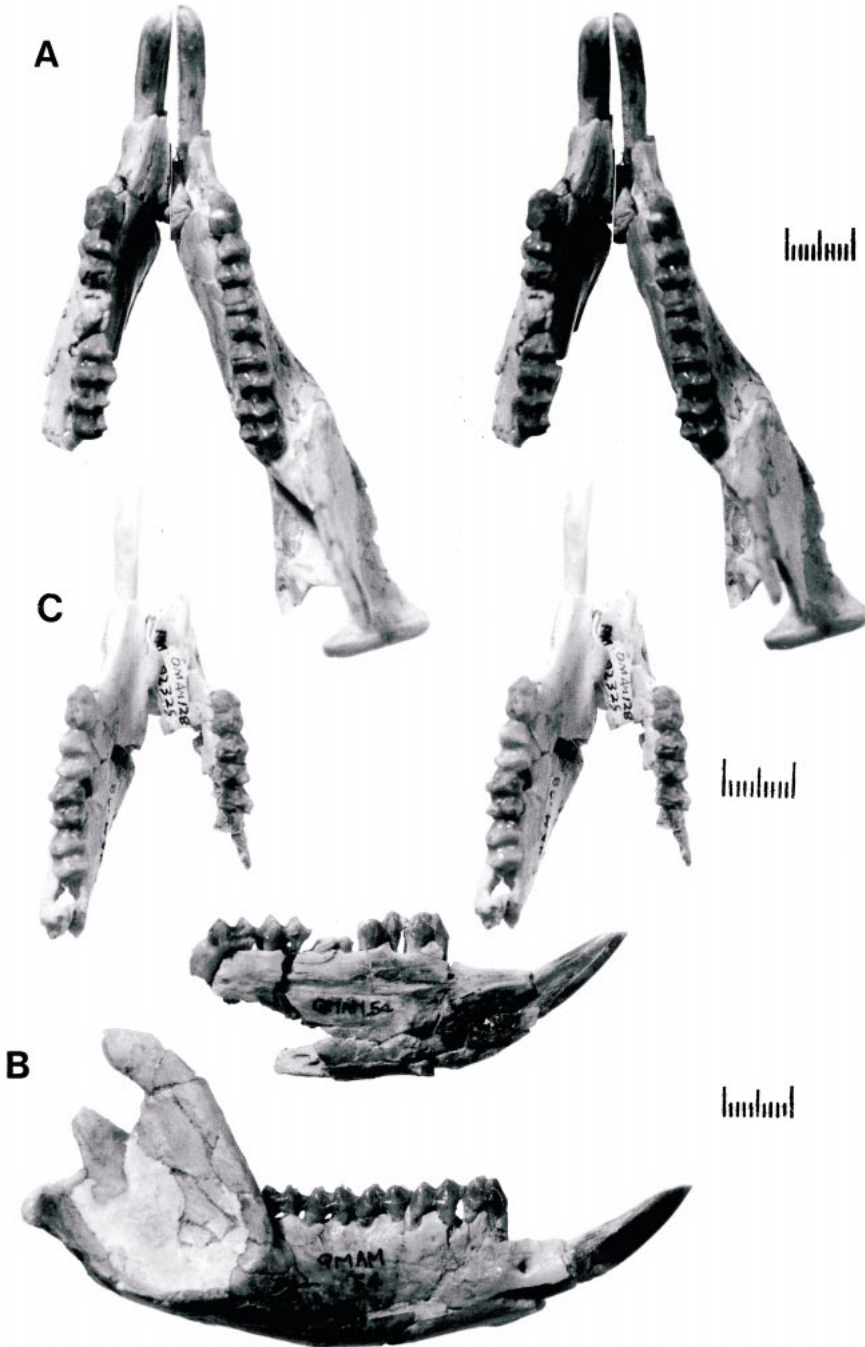


Fig. 19.4. *Muramura pinpensis* lower dentition. **A**, Holotype SAM P36160, left and right dentaries, occlusal view (stereopair). **B**, Holotype SAM P36160, left and right dentaries, in right profile. **C**, Paratype AMNH 102326, left and right dentaries, occlusal view (stereopair). Scale: 1 cm.

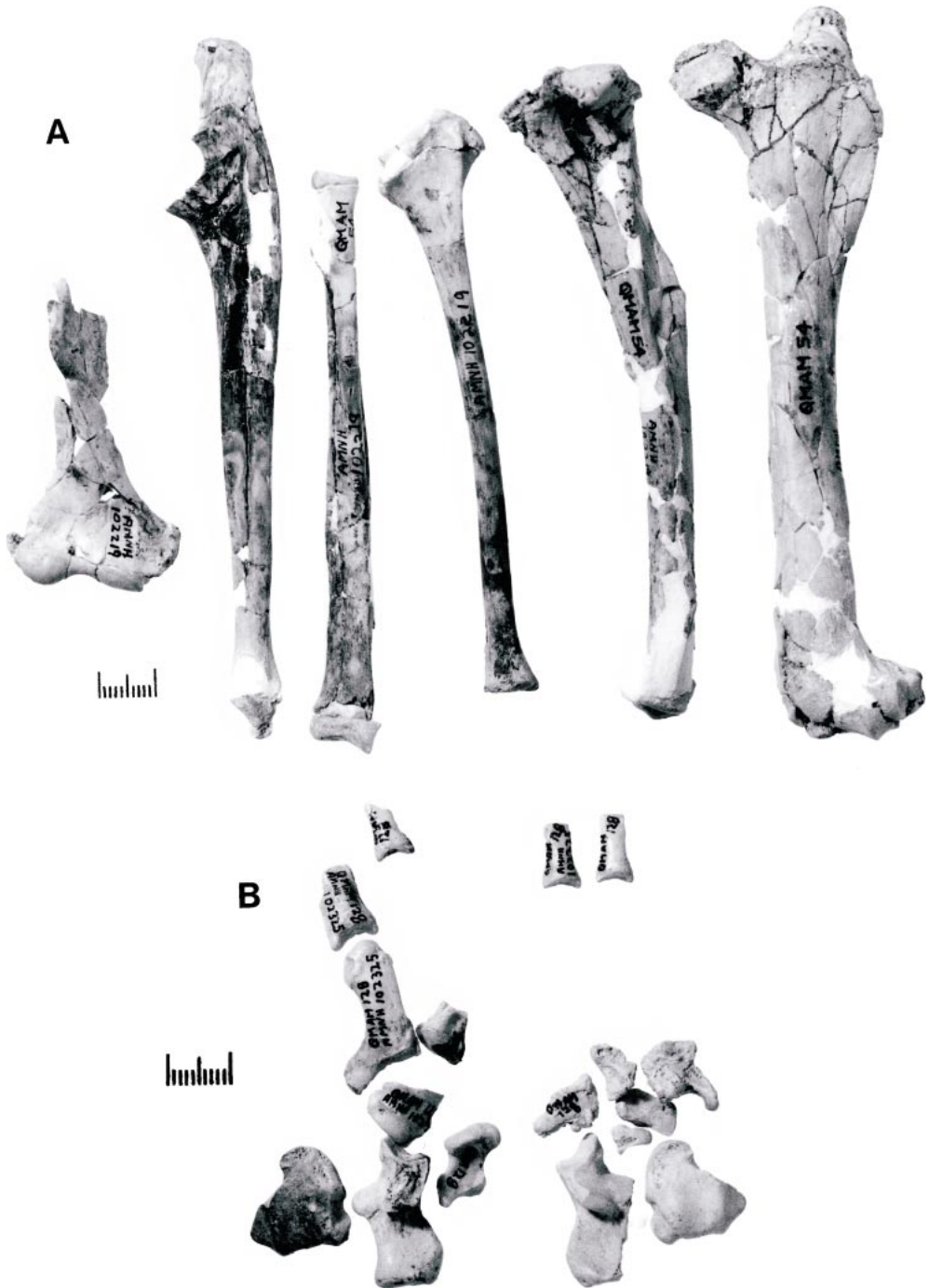


Fig. 19.5. *Muramura pinpensis* postcranial elements. **A**, Holotype SAM P36160, leg bones: partial right humerus, left ulna and left radius, right femur (posterior aspect), tibia (lateral), and fibula (medial). **B**, AMNH 102325: left and right pedal bones. Scale: 1 cm.

TABLE 19.1

Upper Cheek Tooth Dimensions of *Muramura williamsi* (P24524, P24525) and *M. pinpensis*, New Species, Including Referred Lake Yanda Specimen

Symbols and abbreviations: L, length; AW, anterior width; PW, posterior width; *, holotype, teeth heavily worn and with interdermal abrasion; #, holotype, teeth badly fractured; *l*, left; *r*, right; e, estimated.

	P3			M1			M2			M3			M4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
SAM P24525* <i>l</i>	8.7	5.8	6.5	7.1	7.9	7.8	6.8	7.9	—	7.0	—	6.7	6.4	6.3	5.8
SAM P24525* <i>r</i>	8.2	5.7	7.0	7.0	8.0	7.0	6.9	8.1	7.6	6.8	6.9	—	6.6	6.3	5.6
SAM P24524 <i>r</i>	8.8	6.3	7.1	8.0	8.4	8.1	7.5	8.0	7.5	7.5	7.3	6.6	7.0	6.4	5.2
SAM P36160# <i>l</i>	8.0	5.3	6.1	—	8.3	7.9	8.1	—	7.5	—	7.2	—	6.4	6.1	4.2
SAM P36160# <i>r</i>	8.6e	5.5	6.6e	8.0	8.0	7.6	7.7	8.3	—	7.4e	—	5.7	6.6	5.9e	4.3
SAM P36161 <i>l</i>	—	—	—	7.2	7.1	6.9	7.3	7.2	6.4	6.7	6.3	5.3	—	—	—
AMNH 102398 <i>r</i>	8.0	5.3	5.9	7.4	7.1	—	7.5	—	—	7.2	—	—	6.5	—	—
AMNH 102622 <i>r</i>	8.2	—	6.2	—	—	—	6.6	7.0	6.2	6.5	5.8	5.1	5.3	—	3.5
NMV 171630 ^a	—	—	—	—	—	—	—	—	—	7.4	5.4	6.0	—	—	—

^a Lake Yanda specimen.

Archer, 1979) in smaller overall tooth size, shorter simpler premolars with main cusps closer together and smaller hypocone, upper molars relatively shorter and broader with prominent paracones and metacones, and stylar cusps on all (Pledge, 1987).

DESCRIPTION

The following is a composite description, based on all known specimens, with individual variations noted where appropriate.

MAXILLA

The incomplete maxillae show that the masseteric process is fairly robust and possibly larger than in *M. williamsi*, and that the

cheek tooth row is slightly curved, unlike *M. williamsi*, and with third premolar everted.

UPPER DENTITION (fig. 19.3A–E)

SAM P36160 is so badly crushed and distorted that postpalatal fragments cannot be certainly associated even though they are fixed relative to each other, and the premolars are rotated so that RP3 diverges from the tooth line at nearly 50° and LP3 is almost at right angles. No attempt has been made to restore the skull.

UPPER INCISORS: Only a left I1 of SAM P36160 is preserved (fig. 19.3B). Although quite worn, the tooth is still open-rooted. It tapers slightly in both directions from the

TABLE 19.2

Lower Cheek Tooth Dimensions of *Muramura williamsi* (P24524, P24525) and *M. pinpensis*, New Species

Symbols and abbreviations: L, length; AW, anterior width; PW, posterior width; *, holotype, teeth heavily worn and with interdermal abrasion; #, holotype, teeth badly fractured; *l*, left; *r*, right.

	p3			m1			m2			m3			m4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
SAM P24525* <i>l</i>	6.3	4.3	5.1	6.9	5.1	5.3	7.4	5.4	5.3	6.4	5.5	5.2	7.5	5.4	5.2
SAM P24525* <i>r</i>	6.7	4.3	4.9	7.6	5.1	5.6	6.9	5.5	—	6.5	5.4	5.3	7.9	5.3	5.4
SAM P24524 <i>r</i>	6.9	4.5	5.2	8.0	5.6	6.0	7.5	5.8	5.9	7.6	5.8	5.7	7.8	5.5	5.3
SAM P36160 <i>l</i>	7.0	3.9	4.5	8.0	5.3	5.3	—	—	—	7.3	—	5.6	7.6	—	—
SAM P36160 <i>r</i>	6.7	3.7	4.6	7.8	5.1	5.6	7.6	—	—	7.6	—	5.5	7.9	5.3	5.5
AMNH 102325 <i>l</i>	6.5	4.0	4.5	7.2	4.6	5.2	7.8	5.2	5.1	7.3	5.3	5.2	—	—	—
AMNH 102325 <i>r</i>	6.6	3.8	4.6	7.6	4.9	5.0	—	5.5	—	—	—	—	—	—	—
AMNH 102330 <i>l</i>	—	4.3	5.0	7.9	—	—	7.5	5.6	—	7.9	5.7	5.3	—	—	—

base of the enamel, although the anterior taper is difficult to discern over such a short distance. On the outer curve (radius about 12.5 mm) of the tooth, the enamel extends about 9 mm and the root another 18 mm. Depth at the enamel base is 5 mm, width 4.5 mm. The dorsal (anterior) enamel margin is transverse, slightly anterior medially. There is a sharp angle at the dorsolateral quarter and the enamel margin curves sharply forward to follow the ventrolateral edge of the tooth. Medially the enamel forms a narrow (1 mm) band along the dorsal edge. Occlusal wear truncates the incisor at about 40° to the radius of curvature, but leaves a slight posterior crest as the surface is slightly concave in profile. Interdental appression bevels the tip medially.

This specimen seems to be slightly smaller than that of *Muramura williamsi*, although the latter is more worn and presumably from an older individual.

UPPER CANINE: The upper canine is not preserved for this species.

UPPER PREMOLAR: The only complete P3 (AMNH 102398) is very worn to the extent that the enamel is breached in a caries-like fashion on the lingual face of the longitudinal crest.

P3 is similar to that of *M. williamsi*, but smaller, relatively narrower, more angular and with cusps/cuspules more accentuated. It is relatively shorter than in *Namilamadeta snideri*. The anterior moiety is narrower than in both *M. williamsi* and *Namilamadeta*. The longitudinal crest with its three cusps is about on the midline, but tooth wear shifts it buccally and, in AMNH 102398, the cutting edge is closer to one-third the width from the buccal face. The P3s of SAM P36160 are badly fractured and expanded, with some chips missing. They are, however, less worn and display the cusps better than AMNH 102398.

The parastyle (Stirton, 1967) is about one-third the distance from the anterior edge, and the metacone almost the same distance behind that, with the paracone between them, slightly closer to the metacone than to the parastyle. The parastyle is separated from the paracone by wide deep grooves on both buccal and lingual faces of the crest; these grooves extend almost vertically to the base

of the tooth, and the cusps themselves are accentuated by sharp ridges that do the same. The separation between paracone and metacone is more muted, with a pair of shallower grooves only near the apex of the crest.

The parastyle is a four-sided pyramidal cusp, with two opposite edges forming part of the longitudinal ridge. It is reduced in size compared to the metacone, which is a round, flatter, cusp. The anterior crest curves slightly lingual. The anterior, buccal, and lingual crests of the parastyle may all end in a slight basal eminence or thickening. The lingual crest of the paracone also ends in a thickening where it meets the beginning of the short lingual cingulum—this is the only sign of a protocone in the sense that Stirton (1967) has used it. By contrast, the lingual crest from the metacone ends in a prominent, though small, hypocone, developed on the lingual cingulum. This is much more prominent than that shown in *M. williamsi*, though possibly not as much as in *Namilamadeta snideri*. The lingual cingulum extends from the hypocone posteriorly to the posterior extension of the longitudinal crest, as does a fine buccal cingulum coming from the buccal paracrista. There are apparently two roots.

The P3 differs from *M. williamsi* in: small size, relatively narrower, more angular and narrower anterior moiety, less marked constriction between anterior and posterior moieties, broader and less angular separation between parastyle and paracone, weaker development of the anterior half of the lingual cingulum, more obvious cusps, larger and rounder metacone, larger hypocone, longitudinal crest closer to midline.

The P3 differs from *Namilamadeta snideri* in: smaller size, shorter length, relatively narrow width anteriorly, greater separation of paracone and metacone, longitudinal crest more buccally situated, protocone less obvious, hypocone less obvious, weaker development of postbuccal cingulum.

UPPER MOLARS

M1: This is preserved in SAM P36160 (right and left, damaged), SAM P36161 (left, almost unworn), and AMNH 102398 (left, heavily worn and damaged). Although the last offers the best comparison (in terms of

TABLE 19.3

Distance (mm, measured using ocular micrometer at focus of apices) of Molar-Loph Cusps from Buccal Edge of Teeth of Paratype *Muramura pinpensis* (SAM P36161)

Abbreviations: pr, protocone; mel, metaconule; pa, paracone; me, metacone; St C, stylar cusp C; St D, stylar cusp D.

	Buccal edge	Cusp 1 (pr/mel)	Cusp 2 (pa/me)	Cusp 3 (St C/St D)	Lingual edge
M1 protoloph	0	0.8	2.9	5.0	7.4
M1 metaloph	0	0.8	3.2	4.5	7.2
M2 protoloph	0	1.0	2.9	4.7	7.2
M2 metaloph	0	0.5	2.7	4.2	6.6
M3 protoloph	0	0.7	2.5	4.5	6.3
M3 metaloph	0	0.6	2.3	3.8	5.6

degree of wear) with *M. williamsi*, the description following depends on SAM P36161.

M1 is the largest of the molar series. It is functionally bilophodont, but in the unworn state is selenobunodont, somewhat in the form of *Ilaria illumidens* (SAM P24927 = QMAM 181; Tedford and Woodburne, 1987; see also Tedford et al., 1977). There are six almost equal cusps in two transverse rows, with the two lingual pairs each linked by crests in a dilambdadont fashion. These cusps are, buccally from the innermost cusp: protocone, paracone, and stylar cusps B + C in the anterior row, metaconule (not the hypocone of placental molars, *vide* Tedford and Woodburne, 1987), metacone, and stylar cusp D (St D) on the posterior row. The protocone and metaconule are both about one-fifth the width of the tooth from the lingual edge. The paracone is about on the midline whereas the metacone is noticeably lingual of the line. The main stylar cusps are about one-fifth the width from the buccal edge of the tooth. Spacing of cusps relative to tooth width (measuring apices in millimeters from the buccal side) is indicated in table 19.3. Cusps are about the same height; the metacone is slightly more massive than the protocone, and stylar cusps B + C and D are slightly longer than the others because of their positions on the ectoloph. The proto-

cone is possibly the narrowest cusp in occlusal aspect.

From the buccal side of the apex of the protocone, the preprotocrista descends slightly buccally to a precingulum, about one-third the width of the tooth. The buccal end of the precingulum is marked by the small stylar cusp A. The postprotocrista descends posterobuccally and merges with the premetaconulecrista in the transverse valley. The postmetaconulecrista descends posterobuccally to join the postcingulum.

The crest between the protocone and paracone is deeply notched by a crevice extending from the precingulum that opens into the transverse valley. From the paracone, a crest descends anterobuccally, then curves and rises posterobuccally to the apex of St B as part of the protoloph. A postparacrista descends posterobuccally and fades out towards the floor of the transverse valley. From St B, a precrista extends longitudinally to St A then turns slightly lingual to join the precingulum. A buccally convex postcrista continues from St B up through St C, then descends into the transverse valley to join the precrista from St D.

The metacone mimics the paracone in being separated from the metaconule by a deep crevice, being joined to the St D by an anteriorly convex metaloph, and having a posterobuccally directed postmetacrista. The latter, however, joins the postcingulum at a slight eminence, just lingual of where the postcingulum bends and rises as the postcrista from St D.

A low-set posterolingual crest from the protocone constricts the lingual end of the transverse valley. The valley itself is divided into two almost equal parts by the entoloph joining the protocone and metaconule.

The M1 of SAM P36161 differs from *M. williamsi* in: smaller size, buccally more open transverse valley, presence of the posterolingual protocrista, absence of distinct cusplule at buccal end of precingulum separate from stylar crest, stronger development of postcingulum and postcrista from St D, weaker development of protoloph and metaloph.

AMNH 102398 differs from *M. williamsi* in: smaller size, more open transverse valley buccally, absence of cusplule at buccal end of

precingulum separate from stylar crest, stronger development of postcingulum and postcrista from St D.

Pinpa specimens differ from *Namilamadena snideri* (Rich and Archer, 1979; NMV P48993) in: smaller size, less separated stylar cusps B and C. Protocone, paracone and St B transversely aligned rather than forming a right angle, paracone closer to protocone, metacone closer to metaconule than St D rather than the reverse, protoloph and metaloph less developed, greater selenodonty, and stronger crests, particularly postmetacrista.

M2: AMNH 102622 is complete but heavily worn. Description is based on SAM P36161. M2 is similar to M1, differing in the following ways: narrower posteriorly (i.e., width of metaloph), preprotocrista arises from apex of cusp and joins precingulum at a greater angle, protoloph from paracone to St B straighter, postparacrista shorter and more buccally directed towards St C, postmetacrista shorter and does not meet postcingulum, lack of basal postprotocrista. Cusp spacings as in table 19.3.

M3 (SAM P36161) differs from M2 in smaller size; buccal protoloph more developed, straighter, more direct from paracone to apex of St B–C; St B and St C not separable; postprotocrista shorter, straighter; metaloph more developed; postmetacrista extends to St E; metacone equidistant between metacone and St D.

M4: This tooth is best preserved and least worn in SAM P36160. The anterobuccal corner is missing on the right side, but partially present on the left. This corner is also missing from the worn AMNH 102622, whose molars are more complete. The following is based on both specimens.

M4 differs from M3 in the following ways: smaller; metaloph relatively much narrower; paracone weakly developed and close to St B–C. Protoloph and metaloph well developed; metacone slightly closer to metaconule than St D; postmetacrista very weakly developed; postcingulum arcs smoothly from metaconule to St D.

This tooth differs from that of *M. williamsi* in smaller size, relatively narrower posterior moiety, relatively narrower lophs, absence of cuspule distinct from stylar crest at buccal end of precingulum.

Referred specimen NMV P171630 (from Lake Yanda, 31°00'40" S, 140°18'48" E, Callabonna Basin) is a left M3 in a maxillary fragment, with alveoli for M4. This specimen is from a slightly older individual than SAM P36161, to judge from the degree of tooth progression relative to the zygomatic arch. It is slightly larger than SAM P36161, but within the range of the Lake Pinpa sample.

Morphologically, this tooth is more similar to M2 of SAM P36161 in proportions and development of crests, particularly the postparacrista and postmetacrista. However, the lophs are better developed with shallower notches between protocone and paracone, metaconule and metacone; St C is much more distinct and the postcrista from it curves lingually into the transverse valley; there is a relatively sharp anterolingual ridge from the protocone not seen in SAM P36161.

On balance, this specimen represents a population that is slightly apomorphic with respect to the Pinpa sample, and plesiomorphic with respect to *Muramura williamsi*.

DENTARY

There are five dentaries, representing three individuals. SAM P36160 has a well-preserved right dentary and a fractured left, and the teeth are slightly worn. AMNH 102325 has incomplete dentaries and rather worn teeth. AMNH 102338 is a single left dentary, badly fractured; its teeth are least worn but only m3 is complete. The holotype of *M. williamsi* is much more worn than its paratype, whereas the Pinpa specimens of *M. pinpensis* are all less worn.

The best-preserved dentary of *M. pinpensis* is the right jaw of the holotype, SAM P36160, although the ascending ramus has been reconstructed. It is slightly shorter, smaller, and more lightly built than that of *M. williamsi*, but has a shorter tooth row. The diastema is shorter (12 mm vs. 17 mm), and the anterior mental foramen is more ventrally (5 mm below the alveolar margin) and more posteriorly placed (3–4 mm ahead of P3) than in *M. williamsi* (3 and 5 mm, respectively), and the incisor is less procumbent.

Most notable is the relative position of the articular condyle. This is only slightly (4–5 mm) above the occlusal plane of the molars,

compared with >20 mm in *M. williamsi*, and the mandibular notch is shallow, obtuse, and on the same level, compared with being deep and below the condyle. The posterior masticatory eminence is also less pronounced in *M. pinpensis*.

M. pinpensis differs in like manner from new species of *Namilamadeta* from Riversleigh in northwestern Queensland.

LOWER DENTITION (fig. 19.4)

i1: In the holotype (SAM P24525) of *M. williamsi* (Pledge, 1987) this tooth is extremely worn. The paratype i1 (SAM P24524, excavated since the initial description), is still heavily worn but can be used for comparison with the Lake Pinpa specimens. It is a relatively large tooth, elliptical in cross section (diameters 8.0×4.6 mm), slightly flatter medially. The outer (lower) edge is curved with a radius of approximately 45 mm, whereas the upper edge of the root is almost straight, even slightly concave. The crown is so worn that enamel is now found only on the buccal side of the tip and for a few millimeters along the truncated edge of the tooth. None is seen on the medial face. The occlusal surface is flat in the posterior half and slightly convex anteriorly. The diastema is about 18 mm in length.

The i1 of *M. pinpensis* is preserved in SAM P36160 (left and right) and AMNH 102325 (left); of these, the last is most worn, but still retains most of its enamel. Diastemas measure 12, 10, and 17 mm, respectively.

The crown has an outside curvature radius of about 45 mm whereas the upper edge is virtually straight except at the tip, where it is worn in a convex bevel. The enamel extends over the outer surface up to and for about 1 mm over a dorso-buccal longitudinal crest that almost parallels (converging slightly towards the tip) the outer curve of the tooth. This crest dies out about 1 mm above the gingival base of the enamel. On the medial side of the tooth, the enamel extends up from the outer curve as a longitudinal strip about 2 mm wide, which gradually tapers and ends at the gingival line. There is a small trapezoidal interdental appression facet on the medial surface of the enamel at the tip of the tooth. Depth of tooth at base of enamel is 6.8

mm and transverse thickness 4.0 mm in SAM P36160, 6.0 mm and 4.0 mm in AMNH 102325. These teeth therefore exhibit some variation.

p3: The Pinpa specimens are noticeably smaller than *M. williamsi* (although this is not obvious from the measurements). *M. williamsi* has a more waisted occlusal outline, with distinct buccal notch between moieties. *M. pinpensis* has a rounded depression between moieties. Cruciform protoconid has sharp cristids descending lingually, anteriorly and buccally, and back to the metaconid. Metaconid gives rise to equal cristids lingually and buccally. Smaller hypoconid, slight tendency to be cruciform in AMNH 102338. AMNH 102338 is least worn but most damaged, preserves strong postcingulum (stronger than the others) into which the long cristid runs.

m1: None of the Pinpa specimens is perfectly preserved, but none is as worn as in *M. williamsi*. They are either damaged (AMNH 102338, SAM P36160 left and right, AMNH 102325 right) or show irregular wear (AMNH 102325 left). Protolophid noticeably narrower than hypolophid (more than in *M. williamsi*). Protoconid more medial than in *M. williamsi*, closer to neomorph cuspid. (See discussion in Tedford and Woodburne, 1987.) Preprotocristid more medial, longer and straighter.

Protoconid least worn (highest) cusp on protolophid. Low cristid from metaconid to buccal end of precingulid seen in *M. williamsi* is absent in Pinpa specimens. Cristid obliqua stronger (and less worn) in *M. williamsi*, crosses transverse valley, whereas there is a deep narrow defile in Pinpa specimens (SAM P36160 right). Deep, narrow fissure on posterior side of hypolophid formed by lingually directed posthypocristid (SAM P36160 right, AMNH 102325 right and left, AMNH 102338 left)—not seen in *M. williamsi*.

m2: (absent from SAM P36160 left, complete but worn in AMNH 102325 left, damaged or incomplete in AMNH 102338 left, SAM P36160 right, AMNH 102325 right). Protolophid as wide as hypolophid. Precingulum wider than in m1, most anterior point at cuspule end of preprotocristid approximately on midline of tooth. Cristid obliqua

confluent with postprotocristid as a continuous midlink. Posthypocristid prominent, even on worn AMNH 102325 left, unlike *M. williamsi*.

m3: (AMNH 102338 left unworn, AMNH 102325 left worn with breached protoconid and hypoconid, SAM P36160 left and right both worn and damaged).

Cusps of about equal height—protoconid slightly higher and more worn. Lophids of equal width, about equal to precingulum. Preprotocristid well defined, meets precingulum at midline of tooth, with small cusplule, bounded medially by groove. Precingulum descends buccally past the midline and rapidly diminishes about 1.5 mm from the buccal face. Protolophid deeply notched at midline, protoconid midway between this and buccal face, metaconid at lingual end of protolophid. Protoconid relatively bulbous, more than hypoconid; lingual half of lophid narrow, with slight thickening just lingual of midline.

Sharp postprotocristid slopes lingually to meet cristid obliqua at midline of tooth. Buccal half of transverse valley narrower but rounder than lingual half. Posthypocristid leaves hypolophid crest close to midline, just buccal of deep median notch, and descends to short postcingulum below entoconid, forming a deep pocket. Entoconid (or highest point) about halfway between midline of tooth and lingual face. Lingual face relatively flat, defined by premetacristid that joins precingulum, postmetacristid, and pre-entocristid. The latter two do not join across the transverse valley. The posterior side of the tooth extends slightly posterobuccally, just buccal of the midline. Unworn enamel is not smooth but shows slight tuberculation.

m4: Only present in SAM P36160—left slightly damaged, right almost complete, both worn to breach cusps, but still not as much as in *M. williamsi*.

Precingulum more rounded than in *M. williamsi*, preprotocristid closer to midline. Postprotocristid (and midlink) more distinct, cristid obliqua sharper. Posthypocristid much more distinct, extends past midline to meet postcingulum and form two deep pockets, the larger below the buccal half of the hypolophid and the other below the hypoconid. Only a faint trace of the buccal pocket is seen

in *M. williamsi*, in part because of the high degree of wear on the posterior face of the hypolophid.

POSTCRANIAL ELEMENTS (figs. 19.5, 19.6)

Muramura williamsi is known from two almost complete, well-preserved skeletons, and detailed descriptions are in preparation by the author. By contrast, only partial skeletons from two individuals of *M. pinpensis* are preserved. They comprise five ribs, a partial humerus, an ulna, a radius, two incomplete pelves, three femora, four tibiae, four fibulae, and four incomplete feet. It is therefore possible to compare a number of elements that will help further to differentiate the two species.

Generally, the bones are noticeably smaller and more gracile than those of *M. williamsi*. Table 19.4 compares lengths and ratios of the limb bones of *M. pinpensis* and *M. williamsi*. Although few bones or ratios are comparable, it can be seen that in *M. pinpensis* the forelimb is relatively shorter, and the femur relatively longer than in *M. williamsi*. Other notable differences are considered below.

HUMERUS: Only the damaged distal end of the holotype humerus is preserved. It is slightly smaller than that of *M. williamsi*, but shows an actually larger and more elongate entepicondylar foramen, with a more angular medial epicondyle. The distal end of the deltoid crest is bladelike rather than thickened and combined with the supinator crest.

ULNA: The ulna differs from that of *M. williamsi* in being almost straight, more slender and noticeably shorter in the shaft, the olecranon process being as long but narrower and not deflexed downwards, the trochlear notch and coronoid process being narrower, and the radial notch less clearly defined.

RADIUS: The radius differs in being more curved, noticeably shorter, and more rapidly expanded distally.

FEMUR: All femora of *M. pinpensis* have been damaged at their extremities, and consequently comparison with *M. williamsi*, also damaged, is restricted. The femur is almost as long as that of *M. williamsi*, but differs in the head being even rounder, the greater trochanter narrower in the anterior–posterior di-

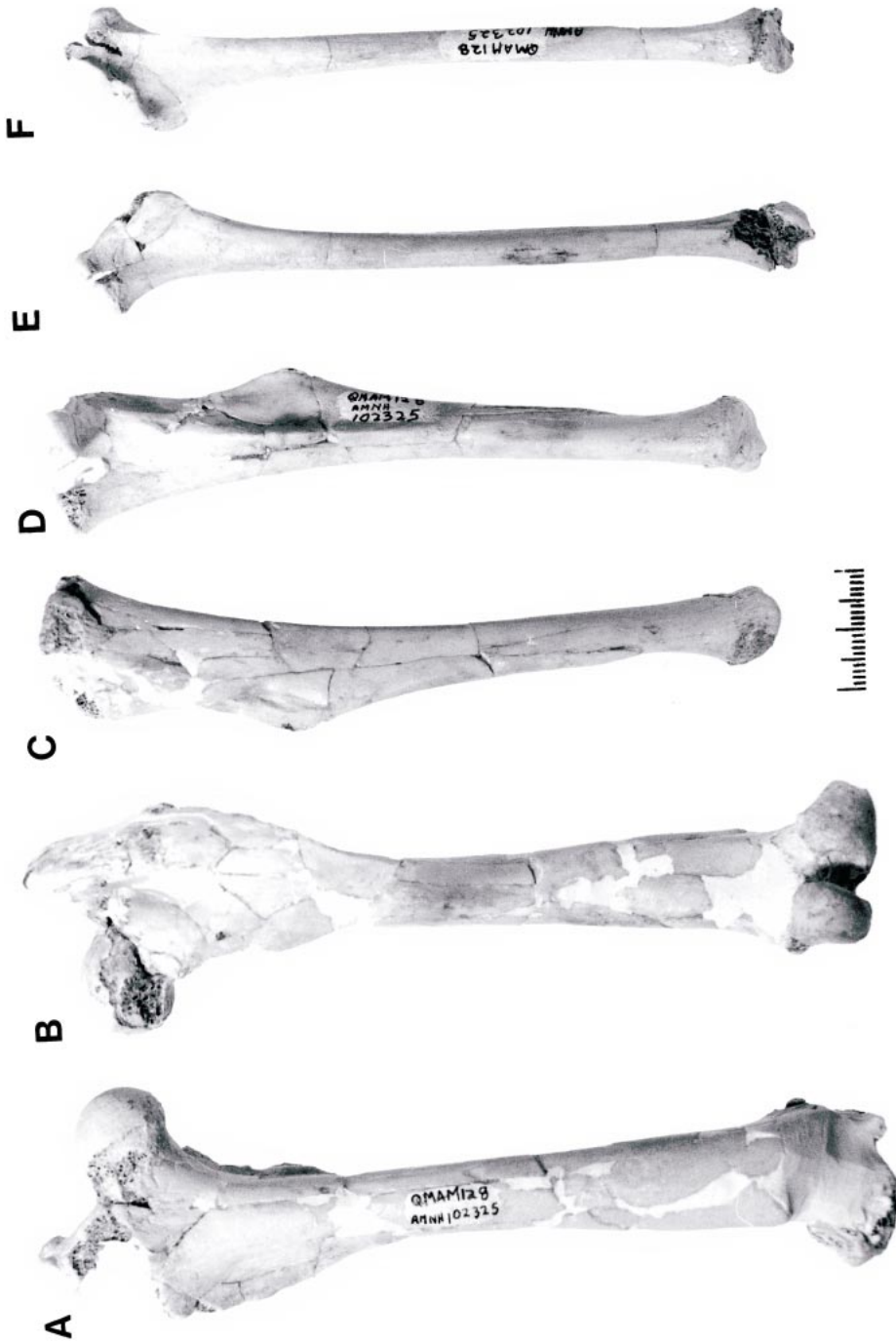


Fig. 19.6. *Muramura pinpensis* postcranial elements. Right hind leg bones, AMNH 102325: **A**, Tibia (medial aspect). **B**, Tibia (lateral). **C**, Fibula (medial). **D**, Fibula (lateral). **E**, Femur (anterior aspect). **F**, Femur (posterior). Scale: 2 cm.

TABLE 19.4

Comparison of Lengths (mm) and Various Ratios of Limb Bones of
M. pinpensis (SAM P36160, AMNH 102325) and *M. williamsi* (SAM P24524, P24525)

Abbreviations: Hum, humerus; l, left; r, right.

Specimen	Hum	Ulna	Radius	Femur	Tibia	Fibula	Hum/ femur	Hum/ radius	Hum/ ulna	Femur/ tibia	Femur/ fibula	Radius/ femur	Radius/ tibia
SAM P36160 <i>l,r</i>		131	108	133	119	107				1.12	1.24	0.81	0.91
AMNH 102325 <i>l</i>				145	127					1.14			
AMNH 102325 <i>r</i>				147	127	128				1.16	1.15		
SAM P24524 <i>l,r</i>	112	146	129	151	148		0.74	0.87	0.77	1.02		0.85	0.87
SAM P24525 <i>l</i>	100		130	148	140	138	0.68	0.77		1.06	1.07	0.88	0.93
SAM P24525 <i>r</i>	103	158	133	149	140	139	0.69	0.77	0.65	1.06	1.07	0.89	0.95

rection, and the notch between the greater trochanter and the head being deeper and more angular.

TIBIA: The tibia of *M. pinpensis* differs in being shorter and having a more prominent, angular tuberosity.

FIBULA: The fibula differs in having the shaft straighter and more uniform, a more distinct neck with expansion to the head more abrupt, and the two articular surfaces for the femur and tibia approximately equal.

PES: Associated foot bones are known from two individuals, SAM P36160 and AMNH 102325 (fig. 19.5B), to compare with the articulated feet of *M. williamsi*. There are small differences that can be seen in the calcaneum, the astragalus, and the cuboid that do not seem to be size or age related. The calcaneum of *M. pinpensis* is generally a more gracile bone, more slender and flaring distally in the tuber, with finer points, the CaCum facet (see Szalay, 1994, for fuller discussion) slightly larger than the CaCul, and lacking the distinct angular notch in the face lateral to the CaCul. The astragalus differs in having sharper boundaries between the facets on the dorsal side, ATil relatively larger, AFi flatter, ATim flatter and more rectangular rather than triangular; on the plantar side, the astragalar medial plantar tuberosity is rounder—not rather square and flat—and does not extend as far posteriorly, the orientation of the CLAJP is less transverse, and the depression between CLAJP and AN is shallower and rounder. Notable in the cuboid of *M. pinpensis* is that the articulation for metatarsal V is distinctly smaller than that for Mt IV, the angle between CaCu and ACu

is less acute, and the lateral plantar tuberosity is more rectangular.

CONCLUSION

Muramura williamsi, known from two more or less complete skeletons, was a well-proportioned small dog-sized animal with a head-body length of about 65 cm (preliminary estimate). The new species described here appears to have been somewhat smaller and more lightly built, with relatively shorter lower legs. This implies that it was less cursorial (Hildebrand, 1988) than *M. williamsi*. The feet of *Muramura* are morphologically similar to those of the burrowing wombats (Pledge, 1987) though not as specialized, and *M. pinpensis*, with its shorter lower limbs, might have been more adapted to a burrowing lifestyle than its congener. The sharp tibial and fibular facet boundaries on the astragalus suggest a tighter ankle structure with less flexibility, which may support this interpretation, although evidence of a slighter MtV could suggest otherwise.

Dentally, there are few obvious, non-size-related differences between *M. pinpensis* and *M. williamsi*, and most others involve proportional differences between comparable teeth. This might indicate that both species had similar diets, but for the observation that there is a major difference in the relative height of the articular condyle of the mandible above the molar occlusal plane, indicating a significant difference in jaw mechanics and hence biting strength (Hildebrand, 1988). *Muramura pinpensis*, with its lower condyle, would have had less “bite”,

and hence probably was restricted to softer vegetation. It is therefore apparent that, although the two species might have been nearly contemporaneous, their different morphologies indicate slightly different ecological guilds and separate lineages.

REFERENCES

- Archer, M. 1978. The nature of the molar-pre-molar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of Queensland Museum* 19(2): 157–164.
- Callen, R.A. 1977. Late Cainozoic environments of part of northeastern South Australia. *Journal of the Geological Society of Australia* 24(3): 151–169.
- Callen, R.A., and R.H. Tedford. 1976. New late Cainozoic rock units and depositional environments, Lake Frome area, South Australia. *Transactions of the Royal Society of South Australia* 108(3): 125–168.
- Hildebrand, M. 1988. *Analysis of vertebrate structure*, 3rd ed.; xvi, 701 pp. New York: John Wiley and Sons.
- Lockett, P. 1993. An ontogenetic assessment in dental homologies in the therian mammals. *In* F. Szalay, M. Novacek, and M. McKenna (editors), *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*: 182–204. New York: Springer-Verlag.
- Plane, M.D. 1986. Lake Palankarinna—ground observations. *In* R.T. Wells and R.A. Callen (editors), *The Lake Eyre Basin—Cainozoic sediments, fossil vertebrates and plants, landforms, silcretes and climatic implications*: 160–164. Sydney: Australasian Sedimentologists Group Field Guide Series No. 4, Geological Society of Australia.
- Pledge, N.S. 1987. *Muramura williamsi*, a new genus and species of ?wynyardiid (Marsupialia: Vombatoidae) from the middle Miocene Etadunna Formation of South Australia. *In* M. Archer (editor), *Possums and opossums: studies in evolution*: 393–400. Sydney: Surrey Beatty and Sons, and the Royal Zoological Society of New South Wales.
- Rich, T.H.V., and M. Archer. 1979. *Namilamadeta snideri*, a new diprotodontan (Marsupialia, Vombatoidae) from the medial Miocene of South Australia. *Alcheringa* 3: 197–298.
- Stirton, R.A. 1967. The Diprotodontidae from the Ngapakaldi Fauna, South Australia. *Bulletin Australian Bureau of Mineralogical Resources* 85: 1–44.
- Szalay, F.S. 1994. *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge: Cambridge University Press, xii, 481 pp.
- Tedford, R.H., M. Archer, A. Bartholomai, M. Plane, N.S. Pledge, T. Rich, P. Rich, and R.T. Wells. 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *Bureau of Mineralogical Resources, Journal of Australian Geology and Geophysics* 2: 53–57.
- Tedford, R.H., and M.O. Woodburne. 1987. The Ilariidae, a new family of vombatiform marsupials from Miocene strata of South Australia and an evaluation of the homology of molar cusps. *In* M. Archer (editor), *Possums and opossums: studies in evolution*: 401–418. Sydney: Surrey Beatty and Sons, and the Royal Zoological Society of New South Wales.
- Thomas, O. 1888. *Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History)*, London: British Museum, i–xiii, 1–401 pp.
- Woodburne, M.O., R.H. Tedford, M. Archer, W.D. Turnbull, M.D. Plane, and E.L. Lundelius. 1985. *Biochronology of the continental mammal record of Australia and New Guinea*. South Australia Department of Mines and Energy, Special Publication 5: 347–365.
- Woodburne, M.O., R.H. Tedford, and M. Archer. 1987. New Miocene ringtail possums (Marsupialia: Pseudocheiridae) from South Australia. *In* M. Archer (editor), *Possums and opossums: studies in evolution*: 639–679. Sydney: Surrey Beatty and Sons, and the Royal Zoological Society of New South Wales.
- Woodburne, M.O., B.J. MacFadden, J.A. Case, M.S. Springer, N.S. Pledge, J.D. Power, J.M. Woodburne, and K.B. Springer. 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. *Journal of Vertebrate Paleontology* 13(4): 483–515.