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THE RIVERSLEIGH WYNYARDIIDS

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At least 18 different localities, mostly on D-Site Plateau, at Riversleigh have yielded wynyardiid material. Most of the 121 specimens examined are isolated teeth or small fragments of jaw. One almost perfect skull, an imperfect skull lacking basicranium, another crushed flat before burial, two partial skulls, 14 maxillae and 11 dentaries are recorded. These were studied metrically and morphologically and resolve into three distinct species described here: the more gracile *Namilamadeta albivenator* sp. nov. mainly from White Hunter site, *N. superior* sp. nov. from Upper Site, and the aberrant *N. crassirostrum* sp. nov. from other sites. Two isolated premolars from another site indicate a fourth taxon. Although dentally similar, the species are distinguishable from each other and from *N. snideri* of the Tarkarooloo Basin of South Australia, which provides, by correlation with the Lake Eyre Basin, the only independent age dating for this part of the extensive Riversleigh deposits. ❐
Riversleigh, mid-Tertiary, Marsupialia, Diprotodonta, Wynyardiidae, Namilamadeta.

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Wynyardiidae was established (Osgood, 1921) for a unique specimen found in the middle of the 19th Century, near the Tasmanian coastal town of Wynyard. It was a partial skeleton, including a damaged skull and mandible, buried in marine sediments of the Fossil Bluff Sandstone. First described in 1900 (Spencer, 1901), *Wynyardia bassiana* was for many years the oldest known Australian marsupial, although its age and affinities were often disputed (e.g. Gill, 1957; Ride, 1964). The age has been resolved as Longfordian, i.e. Early Miocene (e.g. Ludbrook, 1967, 1973; Quilty, 1966). Unfortunately, there were no teeth which would have facilitated assessment of relationship with other marsupials, and attention focussed on the basicranial region (e.g. Ride 1964, Aplin 1987).

This monopoly as the oldest Australian marsupial held until 1953, when Stirton (1954) discovered Tertiary mammals in the Lake Eyre Basin of northern South Australia. The recognised age of the oldest of these is considered to be late Oligocene (Woodburne et al., 1993), as Stirton had believed (Stirton et al., 1961), following a period where it was considered to be Mid-Miocene (e.g. Woodburne et al., 1985). In 1971, Tedford, examining similar sediments (Namba Formation; Callen & Tedford, 1976) near Lake Frome, 300km to the southeast of Stirton's sites, found mammal fossils correlative with those of the Etadunna Formation of the Lake Eyre Basin. In 1973, Tedford discovered two partial skeletons and some jaws of a rather unusual diprotodontan marsupial (Tedford et al., 1977). Pledge (2003) later described them as *Muramura pinpensis*. Features on some postcranial bones suggested to Tedford a relationship with *Wynyardia*, and a tooth was figured as '?Wynyardiidae QMAM 178'. This allowed Rich & Archer (1979) to refer their new species *Namilamadeta snideri* to the ?Wynyardiidae.

Discovery in 1983 of two complete skeletons of *Muramura williamsi* (Pledge, 1987), which have similar dentition to Tedford's material and to *Namilamadeta*, permitted comparison of the basicranial region (Aplin, 1987) and certain limb bones of *Wynyardia* with the new material (work in progress). This has strengthened the wynyardiid affinities of *Namilamadeta*.

The first specimens referable to *Namilamadeta* from the extensive Riversleigh limestone deposits (Archer et al., 1989, 1991, 1995, 1997) were recovered in 1986. Since then, about 120 specimens from 19 different localities have been obtained, and are the subject of this study.

MATERIALS AND METHODS

Specimens are housed at the University of New South Wales, School of Biological Sciences, Vertebrate Palaeontology Laboratory, prefix 'AR', or the Queensland Museum Palaeontological collections, prefix 'QMF'. SAMP refers to specimens in the palaeontological collections of the South Australian Museum, and NMVP to those held by Museum Victoria.

Specimens were measured with vernier calipers or by a calibrated ocular scale in a Nikon SMZ-10 stereoscopic microscope. Measurements were subjected to graphical bivariate analysis on a locality-by-locality basis to ascertain uniformity of samples, and relationships between localities. Computer tomography X-ray scans were performed by Mr Ross Harper, Lyell McEwin Hospital, Elizabeth, South Australia, on two skulls of different *Namilamadeta* species, on a foam pad in a Toshiba Aquilion multislice spiral CT scanner using 0.5mm slice thickness, and reconstructed on both bone and soft tissue algorithms at 0.3mm slice spacing. Images were produced for each algorithm. All images were transferred in DICOM format to a high-end workstation running Voxar 3-D software. High resolution, multiplanar and 3-dimensional images were created, and captured as greyscale 2-D and colour-rendered 3-D sequences in both single image and movie format. Resultant images allowed both linear and volumetric measurement of various structures, including air-filled or matrix-filled cavities (R. Harper, pers. comm.).

Schematic morphology and terminology are given in Fig. 1. Although Archer's (1978) tooth homology system for marsupials is more pragmatic and practical (i.e. the first molariform tooth should be called the first molar), and was used in Pledge (1987), Australian authors have recently adopted, with varying degrees of reservation, Luckett's (1993) version of Flower's (1867) tooth notation, with Archer's M1 becoming dP3. This scheme is followed here in the interests of conformity.

Because of uncertainties of their relative ages, specimens from each Riversleigh locality were treated as a locality population sample for comparison with the other localities, and with the type specimen from Lake Tarkarooloo, South Australia. Paucity of comparable material often meant sample size was very small, and frequently only one specimen, with the result that any statistical treatment was pointless. However, some localities yielded numerous good jaw specimens so that samples of like teeth were of useable size. The collection included three fairly complete skulls (one crushed, another lacking the basicranium), two partial skulls, eight complete maxillae and eight dentaries (lacking only incisors in all but one, which is complete). These are all from Site D Plateau (Archer et al., 1991) and mostly from four sites; Wayne's Wok, Camel Sputum, White Hunter and Mike's Menagerie; except for one specimen from the 'Mesa' (Roo Site), of uncertain stratigraphic provenance.

Because the fossil localities are essentially isolated lenticular deposits, it has been difficult to arrange sites in relative stratigraphic order. Archer et al. (1989) separated sites into three 'systems', a practice criticised by Megirian (1992, 1994). Creaser (1997) examined individual geologies in an attempt to fit them into a sequence, but there seems to be contradiction between other authors when organising sites according to taxonomic and biostratigraphic characters. A recent summary, based upon the occurrences and relationships of fossil macropodoids, was given by Cooke (1997).

Riversleigh fossil faunas are very rich in the Australian context, and have been considered to represent a sub-tropical 'rainforest' environment (Archer et al., 1991), although unlike anything extant today. This is supported by Cooke's (1997) assessment based on the dental adaptations of the diverse and widespread macropodoid species. Megirian's (1992) interpretation, based on geological evidence, is for relatively dry, even semi-arid, conditions across a range of different depositional environments, with any rainforest being riparian along perennial streams, separated by mesic habitats. In the modern tropical situation, marsupial diversity is high, yet in any particular guild, related species can be differentiated readily by size or (tooth) morphology or both, as well as preferred environment. It is therefore assumed, for parsimony, that each site contains only one species, since tooth-size measurements form fairly discrete clusters (except possibly in the case of Dirk's Towers) and on inspection this appears to be the case. Initial collecting separated the several Tower sites, which were later amalgamated. However, it seems here that Towers sites may represent different time periods in a shifting depositional environment, or a mixed fauna of species from two or more different habitats. The ages of these sites are uncertain for some authors (e.g. Cooke, 1997), being indicated as either System A or B.

There is little or no indication in the teeth themselves for any sexual dimorphism, although it should be expected if modern kangaroos are any guide (Bartholomai, 1971) (however, data in Crowcroft (1967) for *Lasiorhinus latifrons* is equivocal with respect to dentition), but there is a suggestion of dimorphism in the robustness of one or two dentaries which are noticeably larger

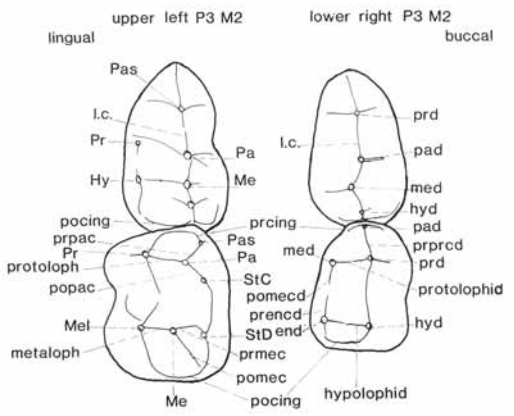


FIG. 1. Schematic diagram of upper and lower premolars and molars (M^1) to show morphology and terminology.

than others in their samples and therefore possibly represent 'alpha-males' (e.g. QMF 12461 from Camel Sputum).

Initially, only isolated teeth and jaw fragments were available. Each cheek-tooth was measured for three parameters; length, anterior width and posterior width (see Appendix 1). In an effort to discriminate between localities (= populations), various graphical treatments were given to these data. By trial and error, individual bivariate scatter diagrams of length vs posterior width of upper and lower premolars (P^3, P_3) and molars (M^1, M_1) gave an indication that certain localities could be grouped together whilst others were distinct. These separations were confirmed by plots of premolar length vs M1 length for associated teeth in jaws. Sample sizes for associated teeth were noticeably reduced when P3 and M1 were both required, but each locality sample separated distinctly from all other localities (Fig. 2). By associating isolated teeth on the basis of preservation, degree of wear and handedness, sample sizes were slightly enlarged for White Hunter and Camel Sputum upper teeth. This slightly enlarged their respective fields to the extent that the Camel Sputum sample could be extended to overlap with the diffuse Wayne's Wok sample. The Wayne's Wok site is rather extensive (tens of metres) compared with others. Similarly, the White Hunter sample could be affiliated meristically with Dirk's Towers 6, which has no lower jaw representatives. (The Dirk's Towers collections, initially numbered and treated separately, were also spread over several metres, and could represent a moving depocentre if the faunal content can be shown to vary from one number to another.)

Plotting length vs width, length vs length/ posterior width (e.g. Fig. 3), premolar length vs molar length, and P3 vs M1 length/ posterior width ratios produced similar separations.

Six or seven complete or partial skulls were recovered from several localities showing two distinct morphotypes, based on the morphology of the snout (with a hint of gradation between localities at one extreme), which partly coincide with the separations based on dental criteria.

The teeth from various wynyardiid localities can be grouped or subgrouped on P3 and M1 meristic grounds:

1.White Hunter, Quantum Leap, Upper Site: 1a. Dirk's Towers 6;1b. LSO Site
2. Camel Sputum, Neville's Garden, Dirk's Towers 5: 2a. Wayne's Wok; 2b. Mikes Menagerie; 2c. Hiatus Site, Roo Site(no premolar-molar association preserved)

The skulls group as follows:

1. (tapering snout, plesiomorphic) Upper Site, White Hunter, *N. snideri*
2. (bulbous snout, apomorphic)
2a. Wayne's Wok
2b. Camel Sputum (slightly less apomorphic)

The *Namilamadeta snideri* tooth hypodigm overlaps the dimensions fields of the Dirk's Towers 6 and Camel Sputum samples. However, morphological differences can be found to separate the South Australian species from them. The Upper Site skull also stands alone, as does the LSO dentary. The remaining sites; Outasite, Judy's Jumping Joint, RSO, Sticky Beak, and Dirk's Towers 4, have not provided appropriate material for this analysis.

For the premolar and first molar teeth only, the White Hunter complex is distinct in most tooth measurements from the Camel Sputum complex which is closer to the type species *Namilamadeta snideri*. The latter, however, does not display the inflated rostrum of the larger group. The Camel Sputum complex could be considered to be in a cline with Wayne's Wok and Mike's Menagerie at the upper extreme; and if P^3 only is considered, then Outasite is even farther to the extreme and could represent a fifth group. At the same time, it must be said that the White Hunter sample of M^1 falls within the field of the *Namilamadeta snideri* type series, for which there is some variation e.g. length 8.9-9.6, posterior width 7.4-8.2, n = 3 (cf.

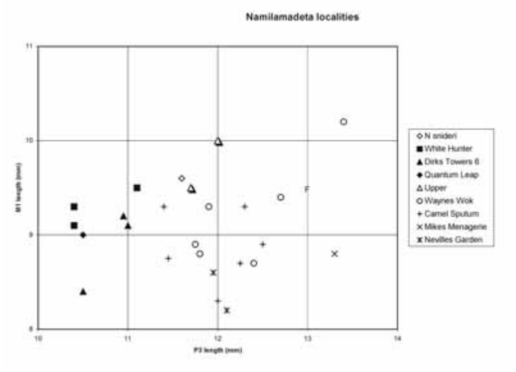


FIG. 2. Bivariate scatter diagram of lengths of upper premolars (P^3) vs associated upper molars (M^1) of *Namilamadeta* spp. from different Riversleigh sites, and for *N. snideri*.

White Hunter length 9.1-9.55, posterior width 7.3-8.2, n = 4. See Appendix 1). The fields of P^3 overlap: *N. snideri* length 11-11.3, n = 2; width 7.05-7.15, n = 2; cf. White Hunter length 10.4-11.3, n = 4; width 6.5-7.3, n = 4.

Combining the above groupings gives us the following breakdown in which several sites cannot be allocated for lack of characters:

1.small teeth, tapering snout: White Hunter, (Quantum Leap, Dirk's Towers 6, LSO Site)
2.large teeth, tapering snout: Upper Site
3.large teeth, bulbous snout: Camel Sputum
4.large teeth, very bulbous snout: Wayne's Wok
5.very large premolars: Outasite
6.unallocated, large teeth: Neville's Garden, Dirk's Towers 5, Mike's Menagerie, Hiatus, Roo Site.

The last have been referred to the combined group 3+4 on the basis of measurement similarities, and in some cases (Neville's Garden, Dirk's Towers 5, Judy's Jumping Joint) the orientation of the anterior mental foramen.

White Hunter sample (group 1) is considered here as a separate taxon, close to but different from the type species *N. snideri*. Apart from morphological differences, part of the rationale for this is geographic separation between the sites, uncertainty of contemporaneity, and the rather poor state of preservation (and hence inadequate description) of *N. snideri*. Upper Site (group 2) also represents a separate taxon, while the Camel Sputum and Wayne's Wok samples (groups 3 and 4) may be related at a subspecific level or as a third new species. The Outasite sample is considered too small to characterise a new species.

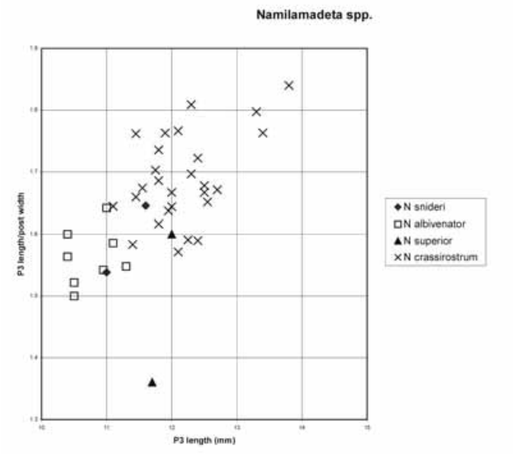


FIG. 3. Bivariate scatter diagram of upper premolar (P^3) lengths vs. the ratio of length:posterior width, according to perceived species. Compare with Fig 2.

In approximate descending stratigraphic order, the Riversleigh sites represented by species of *Namilamadeta* are (after Cooke, 1997; Creaser 1997): Judy's Jumping Joint; Neville's Garden, (Roo Site?); Upper; Dirk's Towers (part); Mike's Menagerie; Camel Sputum; Outasite, RSO; Wayne's Wok; Quantum Leap; Dirk's Towers (part); Sticky Beak; White Hunter; LSO(?); Hiatus.

The Wayne's Wok assemblage is considered to correlate (e.g. Cooke, 1997) with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation of the Lake Eyre Basin, while White Hunter equates with the Ngama local fauna, zone D of the Etadunna Formation at Lake Palankarinna (Myers & Archer, 1997; Woodburne et al., 1993).

SYSTEMATIC PALAEONTOLOGY

MARSUPIALIA (Illiger, 1811)
DIPROTODONTIA Owen, 1866
VOMBATIFORMES Woodburne, 1984
VOMBATOMORPHIA Aplin & Archer, 1987
Family WYNYARDIIDAE Osgood, 1921

Namilamadeta Rich & Archer, 1979

Namilamadeta albivenator sp. nov.
(Figs 5-7)

MATERIAL. HOLOTYPE. QMF23834 partial skull - right maxilla M^{34}; P^3 M^{12} (AR 16775); left and right

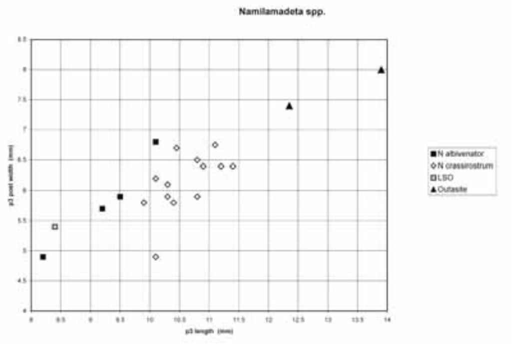


FIG. 4 Bivariate scatter diagram of lower premolar (P3) lengths vs posterior widths. Compare with Fig. 3.

premaxillae, left maxilla, fragmented palate and rostrum (AR 17188) (Fig. 5) from. White Hunter site, Hal's Hill, D Site Plateau (Archer et al., 1991), considered to be a lower assemblage in System B, Oligo-Miocene (Archer et al., 1989). This assemblage is also equated with the Ngama local fauna (latest Oligocene) of the Lake Eyre Basin (Myers & Archer, 1997; Woodburne et al., 1993).. PARATYPE. QMF 40278, right dentary with I_1 P_3 M_{14} (Fig. 6). REFERRED SPECIMENS. White Hunter: QMF 51337, left and right nasals, premaxillae (no teeth), left maxilla P^3 M^{12}, right maxilla fragment, P^3 (Fig. 7C, D); QMF 51338, left P^3; QMF 51339, left M^1; QMF 51340, dentary fragment with M_3; QMF 51341, juvenile left dentary with P_2 M_{13}; QMF 51342, juvenile right dentary (M_3 missing); QMF 51343, left dentary, all teeth; QMF 51344 right lower incisor; QMF 23499 right $M_{3?}$; QMF 30700, complete right dentary split longitudinally through the teeth. Dirk's Towers 6: QMF 13093, left maxilla; QMF 20035, a right maxilla; QMF 20037, right maxilla; QMF 23494, left premaxilla; QMF 30506, left dentary fragment with P_3M_1 (locality unspecified, but referred here because its size and morphology match topotypic material), QMF 36343, right M^4. Quantum Leap: QMF 24138, a left maxilla with P^3M^{13}. LSO: QMF 36348, right M^1; QMF 36349, right M^3; QMF 36350, left M^1; QMF 40251, a perfect right dentary.

ETYMOLOGY. *Albus* (Latin): white, *venator* (Latin) hunter; thus named for the locality.

DIAGNOSIS. Small, having relatively broad premolars combined with narrow molars. Skull lightly built with tapering snout.

DESCRIPTION. Holotype comprises the anterior part of the skull, lacking the cranium. QMF51337 preserves the anterior part of the rostrum, including the nasal passage. Nasals are long and slender, each with, on the inner surface, a hemicylindrical dorsolateral groove 34mm across that together form a distinct longitudinal canal along the roof of the nasal passage, which is circular in cross-section (excluding the canal), with a diameter of about 15mm at the posterior edge of the premaxilla. Narial opening retracted almost to the level of the front of the canine (missing), at which the premaxilla is narrowest; width of 11.5mm. Anterior mental foramen opens just ahead of the level of the P^3; directed backwards and slightly downwards. Lachrymal bone roughly semicircular on the face, with foramen near edge of the orbital rim.

Upper Incisors. LI^1 preserved; long, open-ended, curved tooth, slightly smaller than that of *N. snideri*. Slight tapering is discernible; apparent size difference may be a matter of age of the animal. Alveoli indicate incisors I^2 and I^3 of the same order of size as in *N. snideri*.

Canine. RC^1 small, smaller than I^3 judging from alveoli, and slightly smaller than that of *N. snideri*. Bilaterally compressed and bladed, and with a rounded apex in profile.

Upper Premolars. Relatively short (only slightly longer than M^1) and rectangular (i.e. of fairly uniform width) in occlusal view with a right-angled anterior point. Slight midway constriction labially. Longitudinal crest strongly developed and slightly labial of the midline; extending from the anterior-most point through a high parastyle at the first quarter mark, to an elongate parametacone at roughly the two-thirds mark, and on to the postcingulum. Lingual and labial crests extend equally and strongly from the parastyle, almost to the base of the enamel. A strong crest extends slightly anterolabially from the paracone which is slightly labial of the longitudinal crest, and another extends slightly posterolabially, thus making a broad labial buttress. A weak crest extends anterolingually to a small discrete protocone about midway along the lingual side of the tooth. (Protocone not developed in QMF51338.) A lingual crest from the metacone goes to the base of a strong hypocone. Postcingulum extends labially from the end of the longitudinal crest, to the base of the paracone buttress and more strongly lingually to the hypocone.

Upper Molars. M^1 is the characteristic tooth of the genus (and indeed family, *vide* Tedford et al., 1977), being distinguished by a well-developed anterobuccal preparacrista linking to a prominent stylar cusp B or parastyle (see Rich and Archer, 1979: 201). In *N. albivenator*, this tooth is smaller and narrower than in *N. snideri*. As with *N.*

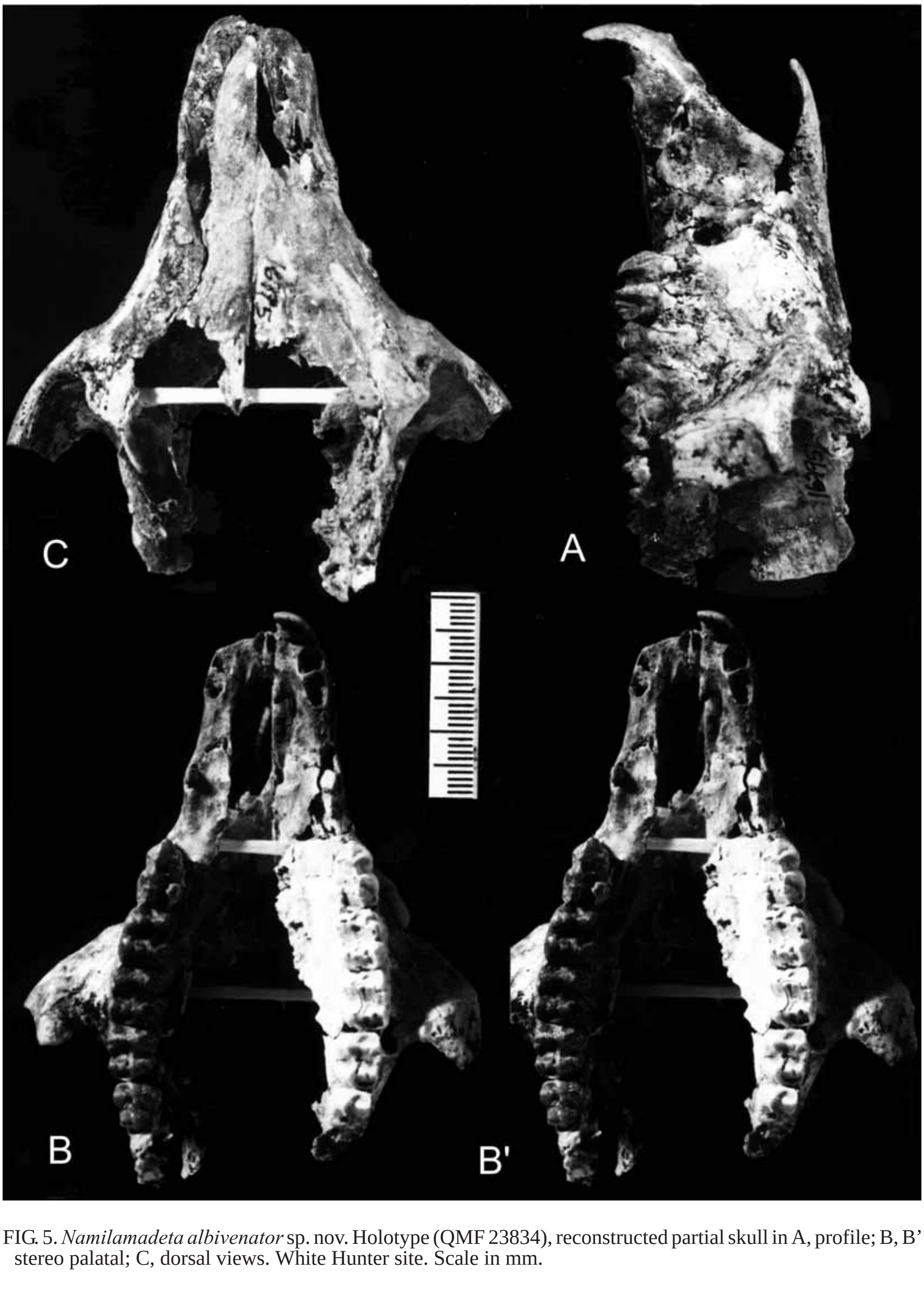


FIG. 5. *Namilamadeta albivenator* sp. nov. Holotype (QMF 23834), reconstructed partial skull in A, profile; B, B' stereo palatal; C, dorsal views. White Hunter site. Scale in mm.

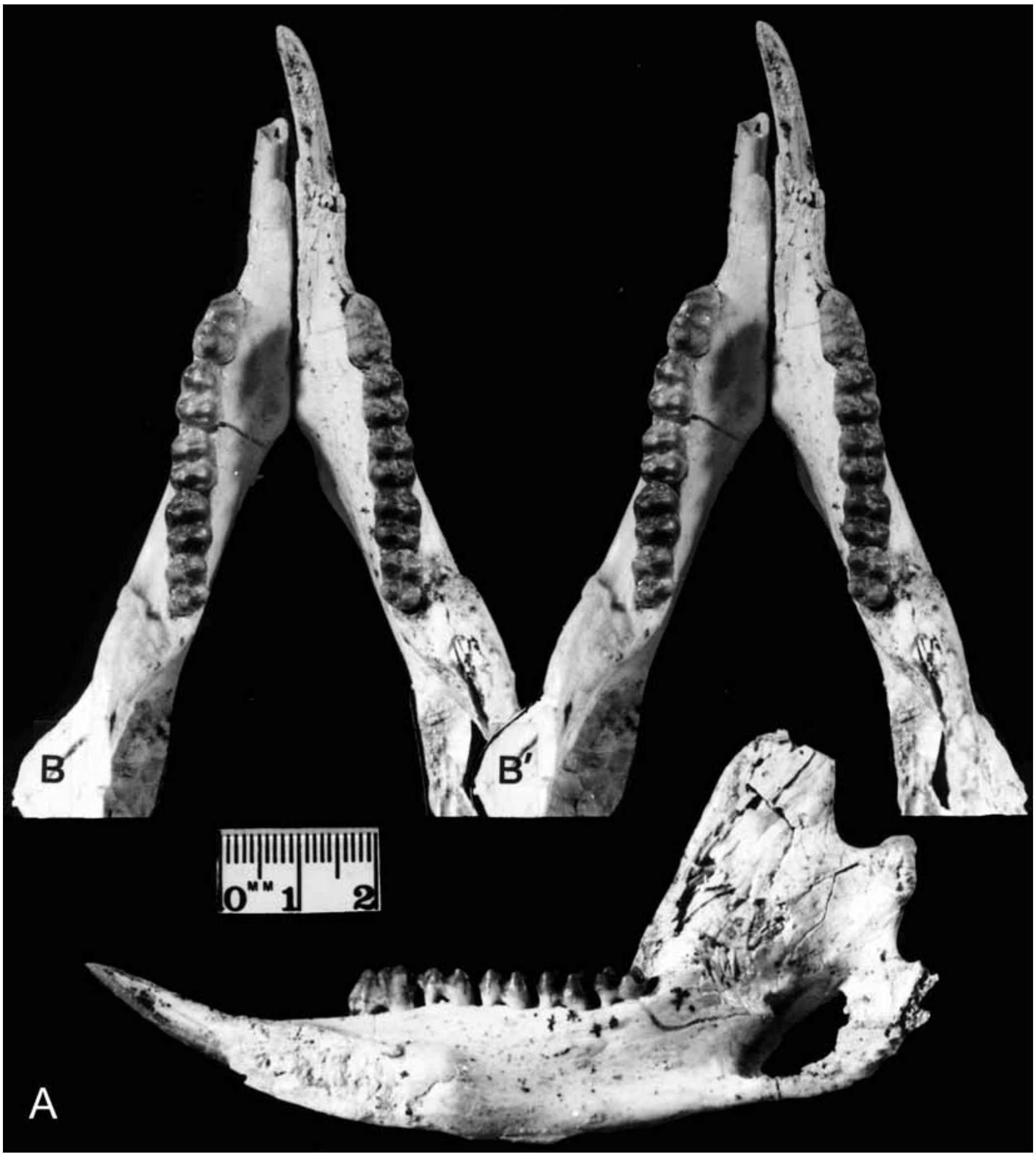


FIG. 6. *Namilamadeta albivenator* sp. nov. Paratype (QMF40278), dentary in A, medial & B, B' stereo occlusal views. White Hunter site.

superior the tooth is more quadrate, with the posterolingual corner being more angular. The postparacrista is deflected only slightly from the line of the protoloph, possibly a little more than in *N. snideri*, and is approximately at right angles to the preparacrista, slightly more than *N. snideri* and less than *N superior* (below). The parastyle is more like *N. snideri* (NMV 48993) than *N. superior* but the parastylar spur is not as marked.

M^2: The several examples of this tooth are better preserved and less worn than in the *N. snideri* series, but are similar to them in all respects except overall proportions and possibly the parastylar corner where the parastyle is

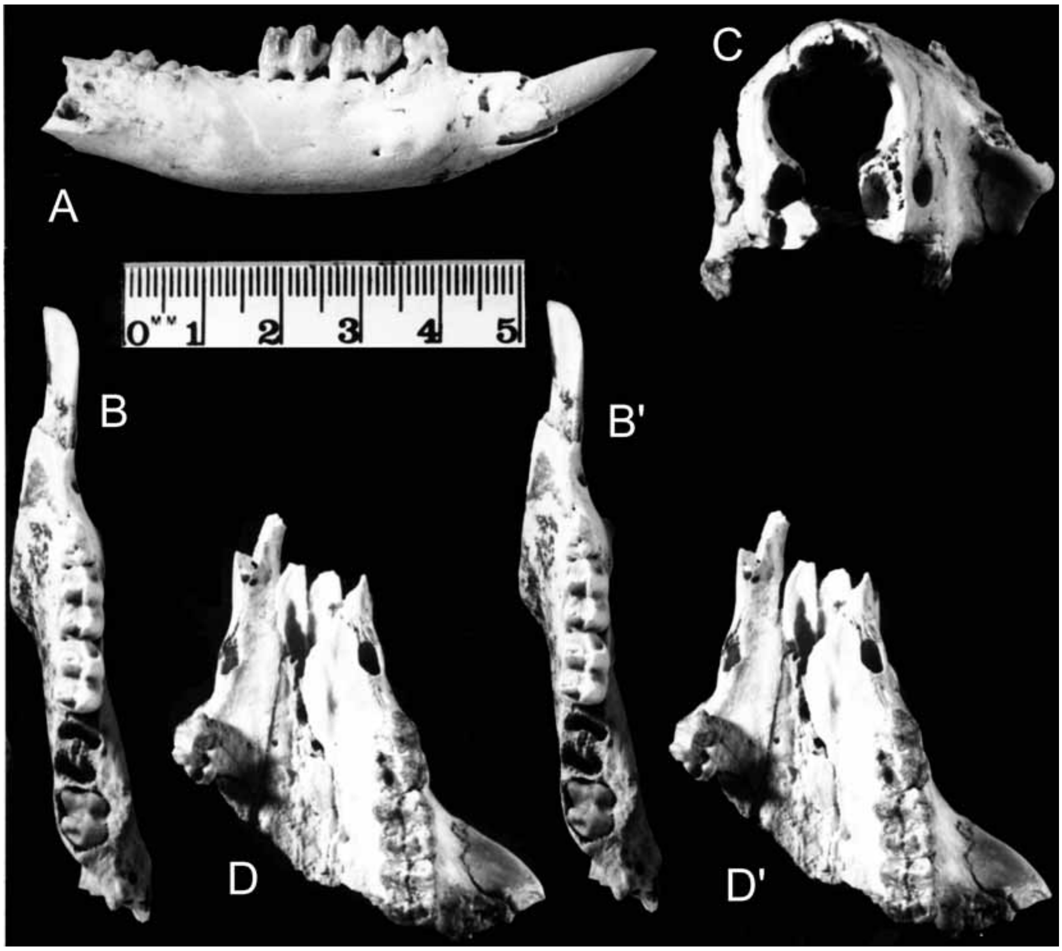


FIG. 7. *Namilamadeta albivenator* sp. nov. Referred specimens: juvenile dentary (QMF51342) in A, lateral; B, B' stereo occlusal view; snout (QMF51337) in C, anterior; D, D' stereo palatal views. White Hunter site.

slightly inside the line of the buccal face of the tooth. The precingulum of *N. albivenator* may be slightly wider transversely than *N. snideri* and the postcingulum narrower. Features of this tooth are better seen in *N. superior*.

M^3 in *N. snideri* damaged posterolingually and quite worn. Protoloph in *N. albivenator* shows only the slightest thickening in the position of the paracone, no more than in *N. superior* (QMF 51348). Stylar cusp B is reduced to insignificance at the end of the precingulum. Metacone considerably reduced, compared to M^2, more obvious than the paracone. Tooth effectively bilophodont.

M^4 is known only from the right side (fragment QMF23834) of the holotype. It is slightly narrower in the protoloph and hence less triangular than that of *N. snideri*. Anterior half of the tooth is similar to that of M^2 and M^3, but the posterior part is laterally compressed. Postmetaconulecrista is reduced compared with *N. superior* but more apparent than in *N. snideri*. The postcingulum is also poorly expressed compared with *N. snideri*.

Dentary. There are two young adult dentaries, which are probably a pair; Paratype QMF40278 (AR12793) (right) and QMF51343 (left), and two incomplete juvenile jaws; QMF51341 (left) and QMF51342 (right, Fig. 7A, B) of different ontogenetic ages. The adult jaws do not occlude neatly with either skull specimen.

TABLE 1. Cranial dimensions of *Namilamadeta* spp., *Muramura williamsi* and *Wynyardia bassiana* type specimens. * = second values from QMF 51337.

Cranial Dimension	*N. snideri*	*N. albivenator**	*N. superior*	*N. crassirostrum*	*M. williamsi*	*W. bassiana*
Total length			148	>128	140.4	>105
Zygomatic width	>>60	~76 (e)	85	>76	80	67
Max. height	>47		57	46	47.5	>35
Rostral length	~49	43	45	47	44	>20
Rostral width	>32	22.5; 33	39	37	32	~24
Rostral height	~41	29; 32	33	35	29	>18
P3 M4 length	44	41.5	44.5	43.6	35.9	
Width between P3	~22	19;21	26.3	22.9	19.8	
Width between M2	24	>22	27.8	23.1	20.0	
Width between M4		21	25.4	22.1	21.2	
Length before P3	30	30	36	32	34.5	
Length I3 C1	10.5	10.5	12.5	15.4	13.5	
Length C1 P3	8.9	7	8	3.5	9.0	
Palate length to palatal vacuity.	~52	~49	54.8	56	55	
Width suboccipital			58		61	
Width occiput			44	>42	~46	

Dentaries are slender and gracile, shallower than those of *N. crassirostrum* (e.g. QMF51363, Camel Sputum) with a shallower, less sharply bounded masseteric fossa. These differences could be due to sexual or developmental age differences. (The dentary from LSO site, QMF40251, is slightly, but not significantly, smaller overall.) Ventral edge not keeled as in QMF51363, although it has the same curved profile. The incisor follows and extends this gentle curvature.

Left and right rami not fused. The symphyseal surface is rough and extends to the posterior end of the premolar and there is a further bulge to the end of M_1 caused by the incisor root. Diastema is about 10mm long and the exposed incisor another 24mm dorsally (26mm ventrally). Anterior mental foramen opens about 4mm anterior of and below the premolar. Horizontal ramus is deepest below M_2, about 18mm. Buccinator groove absent on the lateral surface, only a slight depression below M_1. Ascending ramus has a broad base, nearly 39mm level with the toothline, tapers slightly. Anterior edge reclines at about 70° to the molar occlusal surface, and the coronoid process reaches a height of about 32mm above it. Articulating condyle about 17mm above the occlusal surface of the molars. Total dentary length is about 112mm, bone length 95mm, total height 57mm, and width normal to the symphyseal midline 37mm.

Lower Incisor. Five known: QMF40278, QMF51343 (tip broken off), QMF51342, QMF51344 (an isolated tooth in a fragment of dentary), and QMF40251.

Inscisors are deep and open-rooted, tapering gently towards the tip. Curved ventral profile and a straighter dorsal profile accentuated by occlusal wear to produce a chisel point (best seen on the juvenile QMF51342). Unless there is postmortem torsion due to, say, differential shrinkage between enamel and dentine, all teeth show a marked inward curvature of the tips across the midline of the jaw, to the extent that the dentaries could not have fused without greatly affecting the incisors. Little or no sign of interdental appression is seen on the medial surface of the teeth, indicating some degree of ligamental padding in the symphyseal region.

Enamel is restricted to the convex ventrolateral surface of the incisor and a strip nearly 2mm wide on the ventral edge of the median face. Dorso-laterally the enamel forms a raised edge above the dorsal surface. This is truncated anteriorly by the occlusal bevelled surface which is at, or just below, the occlusal surface of the molar teeth. In cross-section, the incisor is slightly more than a quarter circle.

Premolars. The deciduous premolar dP_2 is known from QMF51341 and QMF51342, and in both cases is underlain by P_3. Tooth is molariform, being elongate triangular with three distinct cusps: the relatively large (and tallest) anterior cusp (protoconid), a smaller more slender lingual cusp midway along the tooth (hypoconid) and a broader posterior cusp (hypoconulid). The three cusps approximate the relationships and spacing of the posterior cusps on P_3 (e.g. in QMF40278). The first and third cusps are on the midline of the tooth, and align with the preprotocristid and protoconid of M_1.

P_3. The permanent premolar is present but unerupted in both juvenile jaws. It has not been excavated from its crypt in QMF51342, but has been freed in the less ossified, younger QMF 51341, where the enamel crown of P_3 has barely started to form; only the four cusps are preserved. The P_3 is better exemplified in QMF40278, QMF 51343 and QMF40251.

This tooth is relatively short compared with *N. crassirostrum*, being only a little longer than M_1. It is slightly wider posteriorly, tapering gently forwards to the level of the anterior cuspid where both sides converge sharply towards the extremity of the median crest. The anterior cuspid (protoconid?) is on the midline at about the one-quarter point and supports symmetrical buccal and lingual crests. The largest cuspid is just behind the midpoint; being on the median, longitudinal crest, it is slightly bladed. There is a broad buccal buttress to this cuspid, the paraconid. The metaconid is displaced slightly lingually and is separated from the paraconid by a shallow dip in the median crest which returns to the midline and drops away to the small hypoconid. Descending on either side of the hypoconid are the buccal and lingual branches of a very weak postcingulum which curve forwards and disappear.

Lower Molars. M_1 is best seen, in its unworn state, in QMF51342. It is marginally the longest of the lower molars but its anterior width is less than that of the succeeding M_2 and $M_{3,}$ although its posterior width may equal or exceed that of M_2. Thus, the tooth has a slight anterior taper.

The tooth is bilophodont, with the lophids considerably narrower at their crests than at their bases, and with the protolophid narrower than the hypolophid. The hypolophid is transverse, normal to the tooth row and lingual face of the tooth. The protolophid is directed slightly posterolingually, so as to converge eventually with the hypolophid. Both lophids have a shallow notch about halfway across. The protoconid is about on the midline of the tooth, the hypoconid just buccal of it. Metaconid and entoconid are right at the lingual face of the tooth.

A longitudinal crest starts at the paraconid on the precingulum, at the anterior end of the midline, and continues unbroken through the protoconid and hypoconid before curving slightly lingual and joining the posterior cingulum. A shallow basin is defined buccally by the preprotocristid and the precingulum and a deeper one lingually. The latter renders the metaconid as a very slender cusp compared with the other cusps. There is no distinct premetacristid, but a weak postmetacristid joins a stronger pre-entocristid at the bottom of the transverse median valley. The postcingulum forms a small deep pocket on the posterior face of the tooth.

M_2 differs from M_1 in being slightly shorter and more rectangular and the protoconid and hypoconid more buccally placed. The precingulum is broader on the lingual side of the longitudinal crest, the lophids are transverse and parallel, there is a median bulge on the protolophid, and a bulge on the cristid obliqua near the bottom of the transverse valley. The metaconid is slightly stouter than in M_1.

In contrast to QMF 51342, M_2 of QMF 40278 shows a distinct postmetacristid-pre-entocristid.

M_1 and M_2 of QMF 51342 are noticeably longer than their equivalents in the more mature, adult QMF 40278. This may in part be by reduction of the latter by interdental appression, but the distance between protoconid and hypoconid is also greater in QMF 51342.

Looking now at the paratype QMF 40278, M_3 resembles M_2 except that the protolophid is slightly broader now than the hypolophid, and the postcingulum is straighter.

M_4 resembles M_3 except for being smaller, and its postcingulum forms a relatively large pocket behind the reduced hypolophid.

REMARKS. Differs from *N. snideri* in having smaller (shorter), narrower premolar P3 with small but distinct protocone. Differs from *N. superior* sp. nov. in having a cylindrical nasal passage, a larger I^1; smaller, more rectangular P^3 with a distinct separate lingual cusp (protocone) anterior of the enlarged separate hypocone;

smaller molars; M^2 without crest between paracone and parastyle. Differs from *N. crassirostrum* sp. nov. in having a tapering snout with narrower nasal passage, anterior mental foramen directed more longitudinally at about 10° to the axis of the skull rather than 50-60°; smaller more rectangular P^3, smaller molars. Lower premolars more tapered anteriorly, i.e. relatively broader posteriorly, and shorter; second and third cuspids more closely united, third cuspid less offset lingually; M_1 narrower anteriorly (paraconid closer to metaconid); dentary more gracile; shorter tooth row. Differs from Outasite taxon in having much smaller upper premolars.

Namilamadeta sp. cf. **N. albivenator**

REFERRED MATERIAL. LSO Site (Lee Sye's Outlook), northern D-Site Plateau. Low in the Verdon Creek Sequence, probably System A (Creaser 1997). QMF 40251, right dentary, QMF 36348 unerupted, damaged lM^1, QMF 36349 right maxilla fragment with M^3, QMF 36350 rM^1.

DESCRIPTION. *Upper Molars*. The few upper molars referred to this species are virtually indistinguishable from those of *N. albivenator*.

Dentary. The dentary is lightly built, less deep than that of *N. albivenator*, and thinner in the corpus of the ramus. Viewed from below, it is slightly convex buccally (*N. albivenator* is almost straight), and the angular shelf is wider. From behind, the notch between the angular process and the neck of the condyle is deeper, the neck is slimmer and the condyle transversely narrower and abruptly expanded from the ascending ramus. The ascending ramus has a steeper leading edge (67° vs 62° to the occlusal plane), is lower, shorter longitudinally, and the coronoid process is also shorter. The mandibular foramen opens into both the pterygoid and the masseteric fossae. The mental foramen opens level with the front edge of the premolar rather than 2–3mm ahead of it as in *N. albivenator*. The diastema is short (11mm vs 13mm) and the incisor is robust and less procumbent, being inclined at 40° vs 35°.

Lower Incisor. The incisor is quite a robust tooth: thicker (4.5mm vs 4.1mm), deeper and straighter than that of *N. albivenator*. Its occlusal facet is also more obtuse, in keeping with the steeper angle of the tooth.

Lower Premolar. The P_3 is one of the most distinctive features of this taxon. It is short with roughly parallel sides until level with the paraconid, when the buccal face abruptly turns across to the anterior point of the tooth. A sharp cristid rises from this point up to the apex of the paraconid, which is well separated from the protoconid, and continues longitudinally through the protoconid to a small cuspid on the posterior cingulum. About midway along this half of the cristid, the metaconid is a distinct cusp well separated on the lingual side of the ridge, with no obvious link to it.

REMARKS. Differs from *N. crassirostrum* in having a much slighter dentary with smaller teeth overall, shallower masseteric fossa, anterior mental foramen level with the beginning of P_3 rather than ahead of it, premolar shorter and less parallel-sided, its longitudinal crest more inturned anteriorly and metaconid displaced more lingually, first molar narrower anteriorly.

Differs from typical *N. albivenator* in having a more gracile dentary with steeper leading edge of the ascending ramus, narrower coronoid process, more abrupt articular condyle, deeper masseteric fossa, anterior mental foramen level with the beginning of P_3 rather than 23mm ahead of it, M_1 more rectangular with protolophid and hypolophid almost equal, much shorter P_3 with the metaconid markedly displaced lingually, shorter diastema, and a shorter, straighter and thicker lower incisor.

Namilamadeta superior sp. nov.
(Fig. 8)

MATERIAL. HOLOTYPE. QMF40276, a near complete skull, lacking only left and right I^3 and C^1, with right I^1, I^2 and M^2 damaged; from Upper Site, Godthelp Hill, eastern end of D Site Plateau (Archer et al., 1991), considered to be an upper assemblage in System B: early Miocene (Archer et al., 1989), and has been correlated with the Kutjamarpu local fauna of the Lake Eyre Basin (Godthelp et al., 1989).

ETYMOLOGY. *Superior* (Latin): upper, higher - referring to the type locality name and generally to the perceived higher stratigraphic position within System B.

DIAGNOSIS. Skull similar in size to that of *N. snideri* but slightly more gracile; masseteric processes up to 50% larger and broader, malar fossa deeper, infraorbital foramen smaller and directed more posteroventrally.

DESCRIPTION. *Skull.* To be described in detail elsewhere. Skull 148mm long parallel to the occlusal plane, and 85mm across zygomatic arches. Slender, but rather high and short tapered rostrum expands smoothly into a relatively broad `face' at the orbits. Nasal opening about 17mm high (excluding the dorsal channel), 14mm wide, widening to become more equidimensional

FIG. 8. *Namilamadeta superior* sp. nov. Holotype (QMF 20476), skull in A, lateral; B, B’ stereo palatal.

farther in. Nasals long and slender, expanding at the frontal suture to twice anterior width but not extending as far forward as in *Muramura williamsi* (Pledge, 1987), only to about halfway between the beginnings of I^1 and P^3, but farther than in *N. crassirostrum* (q.v.). In anterior view they are hemicylindrical, forming a small (~5mm diameter) channel on the dorsal side of the nasal passage. This feature is more strongly developed than in other species. Narial opening is retracted almost to the level of the P^3, at which point the premaxilla is a minimum 9mm wide. "Forehead' is only slightly 'dished' in the naso-frontal area, unlike the marked depression seen in profile in *N. crassirostrum*, see below.

Orbits directed anterodorsally and a little laterally. Lachrymal bone roughly semicircular, with a fairly large foramen well forwards on the dorsal surface, about 5mm anterior of the orbit. Jugal border of orbit thickened and accentuates the depression of the malar fossa ('masseteric fossa' of Pledge (1987)). Ventrally from this, the maxilla extends a solid masseteric process about 13mm, some 6mm below the occlusal plane of molars. Cheek-tooth rows noticeably convex buccally, unlike those of *Muramura* where they are straight and very slightly divergent posteriorly, and the congeneric *N. crassirostrum*, where they are also straight and parallel. Jugals fairly deep, with a simple interdigitation with the squamosals, and form an almost square cheek outline in dorsal view (i.e. the width is approximately equal to the length between the front of the orbit and the posterior root of the squamosal part of the cheek bone, about 79 x 75mm). The upper part of this squamosal wing curves medially. Frontals are unfortunately damaged, but the highest point of the skull is about at the frontal-parietal suture, where weak lateral crests converge before forming the more prominent sagittal crest. The lambdoidal crest overhangs the supraoccipital bone and its condyles. Strongly developed basioccipital process, larger and straighter than in *Muramura*, and similar to that in *Macropus*. Auditory region well preserved on the left side, less so on the right, and is similar to Aplin's description (1987) of *Wynyardia*. This supports assignment of *Namilamadeta* to the Wynyardiidae. Briefly, a squamosal tympanic wing (SQW) roofs the anterior tympanic cavity, there is no tympanic process of the squamosal (SQP), nor an epitympanic sinus of the squamosal (SQS), but there is an alisphenoid lamina on the tympanic process (details to be published elsewhere).

Upper Incisors. Only the first two are preserved in the skull. I^1 has an occlusal surface not much larger than I^2, which already shows considerable wear. It is noticeably smaller than I^1 of *N. snideri* and *N. albivenator,* but larger than in *N. crassirostrum*. However, I^1 is much 'higher' and seems to increase in diameter slightly as it emerges. It is apparently rootless, like the I^1 of wombats and of *Diprotodon*, but this may simply be a manifestation of its relative youth, since Rich and Archer (1979) found in *N. snideri* that the root itself had a slight taper suggesting eventual closure.

The relative size of I^1 with respect to I^2 and I^3 differs markedly from the situation in *N. snideri* and *N. albivenator* QMF23834, and in QMF-23494 from Dirk's Towers 6, the only other Riversleigh I^1 specimen, which closely resembles *N. snideri*.

I^2 is relatively low crowned, with the enamel fully exposed and the root just visible between it and the bone of the premaxilla. To judge from the alveoli, I^3 could be approximately the same size as I^2 and the canine. Both preserved incisors are heavily worn, in contrast to the cheek teeth, where the enamel is barely breached on the highest cusps of M^1.

Upper Premolars. P^3. The premolars of the skull are somewhat figure-of-eight shaped, with a noticeable midway constriction. The longitudinal crest is almost straight, extending from the rounded angular anterior extremity of the tooth, along the midline through the protocone and paracone, then a slight lingual dog-leg to the metacone and returning to a small cusp on the blunt posterior cingulum. There is a buccal rib transverse from the protocone, stronger than that going lingually. A lingual crest that meets the longitudinal crest midway between protocone and paracone forms the anterior border of a pocket created by the strong hypocone and the crest joining it to the metacone.

Upper Molars. In this species, M^1 is very similar to that of *N. snideri* in both size and morphology. The differences are (comparing with the least worn example of the latter, NMV P48993): 1) the tooth is more quadrate because the posterolingual corner is squarer and less rounded; 2) the postparacrista is directed more posteriorly, i.e. it is less aligned with the protoloph, thus being more symmetrical with the preparacrista and enclosing a more obtuse angle; 3) the parastyle is virtually on the precingulum, and not connected to it by a short but distinct curved crest; 4) the metacone is closer to stylar cusp D; 5) the precingulum almost equals the postcingulum instead of being three quarters the transverse width; 6) the parastylar ‘spur’ of Rich and Archer (1979) is reduced.

M^2. In *N. snideri* this tooth is, like the rest of the tooth row, considerably worn and shows no stylar cusp B nor the linking preparacrista (Rich & Archer, 1979). The type of *N. superior* does show such features, although muted by wear. There is a well-developed preparacrista going anterobuccally to a small but distinct parastyle at the buccal end of the precingulum; it is almost symmetrical with the postparacrista that links to stylar cusp C, which is almost as high as the paracone. Unlike the situation in M^1 where these crests enclose an obtuse angle, estimated c. 100-110°, in M^2 the angle is acute, c. 70-80°. There is no parastylar ‘spur’. In other respects M^2 is similar to M^1.

M^3. This tooth shows increasing lophodonty, unrelated to wear. In the skull, QMF 40276, the protoloph is defined by the protocone and stylar cusp C, with the paracone being a barely noticeable irregularity. Stylar cusp B is a minute enlargement at the buccal end of the precingulum and is unconnected to the paracone. Instead it is joined to stylar cusp C by a low crest. On the metaloph, the metacone is still distinct but greatly reduced.

M^4. This tooth is greatly compressed in the posterior moiety. Anteriorly it is similar to M^3, with only slight thickening on the protoloph at the site of the paracone. On the metaloph, the metacone and stylar cusp D have fused into a rather broad low cusp, separate from the metaconule, and a loph strictly does not exist.

Dentary. No dentary is known from Upper Site, nor any isolated lower teeth, to allow comparison with other sites.

REMARKS. Differs from (reconstructed) skull of *N. albivenator* in having a more pointed, tapering rostrum and higher profile, and laterally compressed nasal passage. Differs from skull of *N. crassirostrum* in lacking inflated rostrum caused by large sinuses within maxillae, and having laterally compressed nasal passage. I^1 about half the diameter of *N. snideri*, but canine possibly larger than in that species.

Upper premolars mostly longer and wider than *N. snideri,* with the hypocone not linked to the buccal crest (parametacone). Upper molars closely similar to *N. snideri*, noticeably shorter than premolar.

Upper premolars differ from *N. albivenator,* and many *N. crassirostrum* specimens, in being longer with an anterior taper, less rectangular and narrower in the anterior moiety, and in having no or only very small accessory cusp on the lingual cingulum anterior of the hypocone. They are slightly wider than most of those of *N. crassirostrum*, about the same length as those from Camel Sputum and Neville’s Garden sites, and shorter than most from Wayne’s Wok and Mike’s Menagerie. Upper molar M^1 differs from *N. albivenator* and *N. snideri* in having a crest between paracone and parastyle.

Namilamadeta crassirostrum sp. nov.
(Figs 9-11)

MATERIAL. HOLOTYPE. QMF31462, incomplete skull lacking the nasals, occiput, basicranium, and zygomatic arches (Fig. 9). Wayne’s Wok Site. PARATYPE. QMF51375, right dentary (Fig. 10). Wayne’s Wok site. REFERRED MATERIAL. Wayne’s Wok Site; QMF51345 left maxillary fragment, QMF51346 left maxilla, QMF51347 right maxillary fragment, QMF51348 juvenile right maxilla, (which possibly goes with) QMF51349 juvenile left maxilla, QMF51350 rP^3, QMF51351 left maxilla fragment P^3M^{12}, QMF31480 right premaxilla and maxilla, QMF30836 right dentary fragment, QMF51352 lM_2; numerous isolated teeth. Dirk’s Towers 4; QMF51353 rP^2, QMF51354 lP^3, QMF36342 lP^3, QMF51355 lM^2. Dirk’s Towers 5; QMF51356 rM^1, QMF24218 left dentary. Camel Sputum; QMF40279 a partial skull including full palate and left side of face back to frontal bone but no incisors, QMF51357 right maxilla fragment with P^{2-3}, QMF51358 rP^2, QMF51359 right maxilla fragment rM^{14}, QMF51360 rM^{24}, QMF20497 rM^{14}, QMF20498 rM^{23}, QMF20574 left maxilla, QMF30303 palate with premaxillae, QMF 30534 maxilla fragment, QMF 12461 right dentary, QMF 51361 dentary fragment rM_{24}, QMF 51362 left dentary, QMF 51363 left dentary; numerous isolated teeth. Mike’s Menagerie; QMF 51364 right maxillary fragment P^3M^{12}, QMF 51365 left dentary P_3M_{14}; numerous isolated teeth. Roo Site; QMF 51366 juvenile dentary; Sticky Beak; QMF 51367 left I_1. Judy’s Jumping Joint; QMF 51372 left P^3, QMF 51376 right P^3.

TYPE LOCALITY AND STRATIGRAPHIC POSITION. Wayne’s Wok site, Hal’s Hill, D Site Plateau (Archer et al., 1991). System B, 3-4 metres below Upper Site (Archer et al., 1989). The Wayne’s Wok faunal assemblage contains a number of species in common with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation, Lake Eyre Basin (e.g. Godthelp et al., 1989, Archer 1994, Cooke 1997).

ETYMOLOGY. Crassus (Latin): thick, rostrum: beak, snout - in reference to the bulbous snout shown in the skull.

DIAGNOSIS. Skull with inflated rostrum. Anterior of anterior mental foramina (AMF) parallel; lateral sides of premaxillae converge

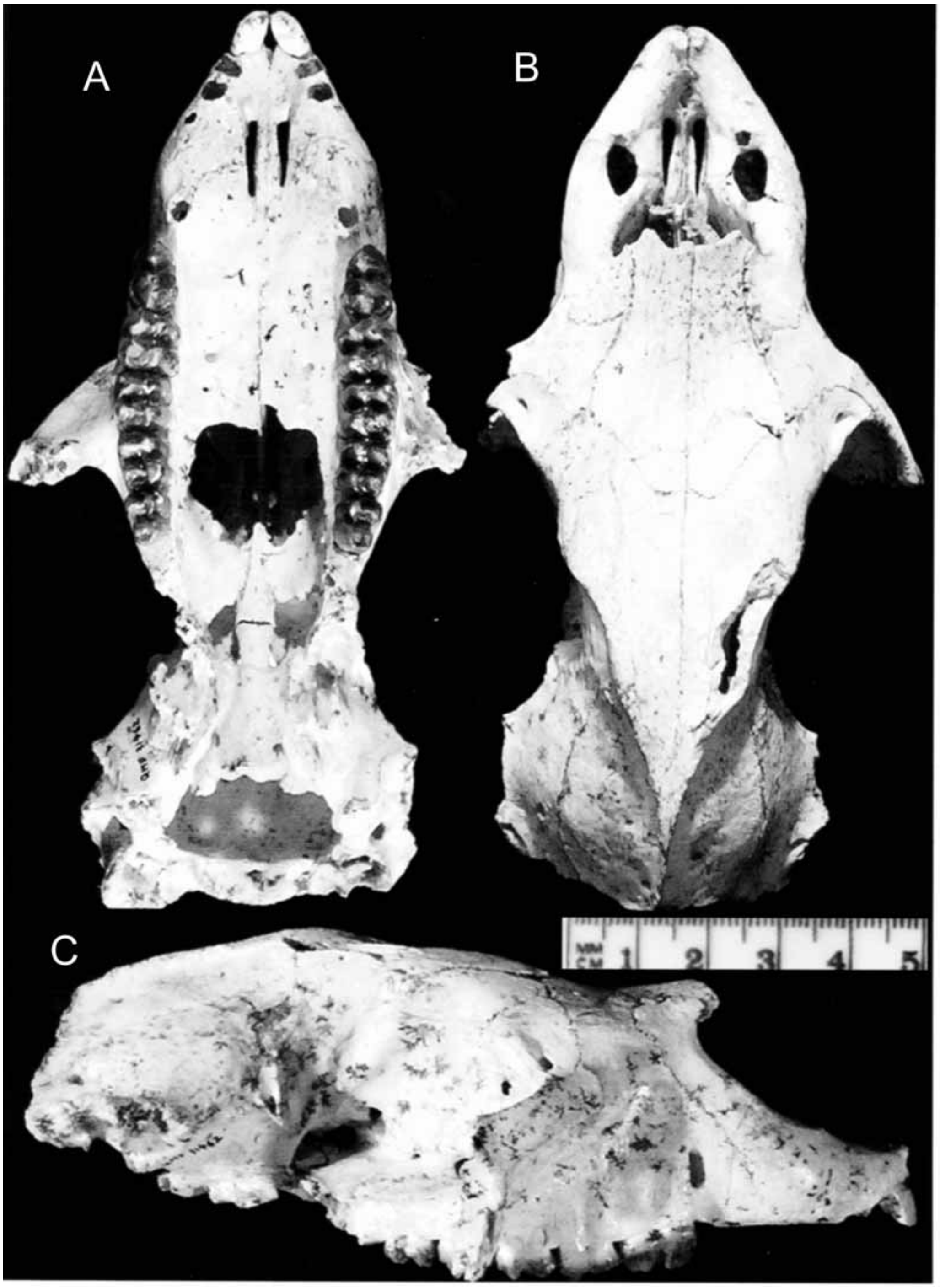


FIG. 9. *Namilamadeta crassirostrum* sp. nov. Holotype (QMF31462), incomplete skull in A, occlusal; B, dorsal; C, lateral views. Wayne's Wok site.

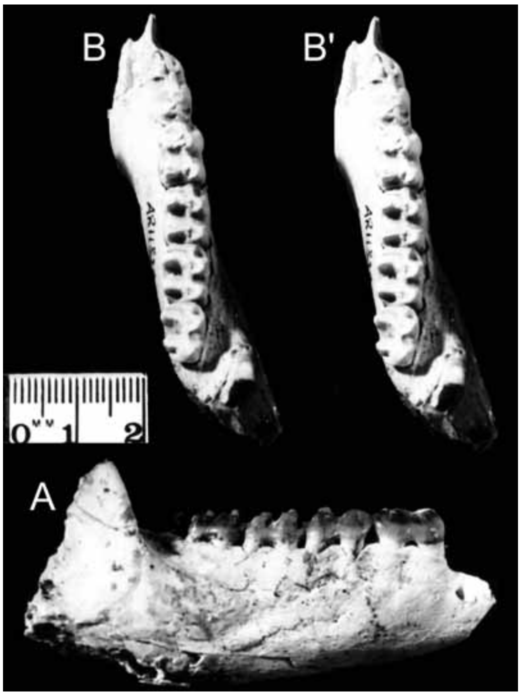


FIG. 10. *Namilamadeta crassirostrum* sp. nov. Paratype (QMF51375), dentary in A, lateral; B, B' stereo-occlusal views. Wayne's Wok site.

strongly at 60°. Lower border of naris greatly thickened by large sinus developed mainly in premaxilla and opening vertically upwards. Posterior border of naris almost level with AMF rather than canine. Nasals apparently short, extending only 1cm beyond P^3. AMF a near-vertical slot entering almost transversely (at about 60° to midline), rather than an ovate hole entering almost longitudinally. Canine closer to premolar. Cheek-tooth rows almost straight and parallel rather than convex buccally.

DESCRIPTION. *Skull*. Occiput, basicranium and zygomatic arches unavailable. About the same size as the skull of *N. superior* (Table 1), with a preserved length of 129mm (QMF31462), with inflated snout. Nasal opening almost circular (diameter 2.53cm) in anterior view, compared with a tall, narrow opening in *N. superior*. Rostrum parallel-sided in posterior half, the same width at the level of the premolars as at a point about midway along the premaxilla, at which point, it tapers sharply forwards to produce a V-shaped incisor arcade, instead of the elliptical ones in other *Namilamadeta*. This is the result of a pair of large inflated sinuses developed mainly in the premaxillae but extending back into the portion of the maxillae in front of the anterior mental foramina. Sinuses each have a large (up to 5mm diameter) ovate dorsal opening in what would otherwise have been the lower narial edge of the premaxilla; the openings have a smooth regular margin with no sign of the roughness associated with a pathological condition (C. Pardoe, pers. comm.). The feature is therefore considered real, especially as it is seen almost identically in all premaxillary specimens from the Wayne's Wok and Camel Sputum sites. (It appears slightly less developed in the Camel Sputum specimen; none of the other sites referred to this species have yielded premaxillae.)

Possibly associated with this feature is the slight posterior displacement and reorientation of the AMF, now directed, initially, inwards at about 60° to the midline (CT scans show the canal turns abruptly to the posterior, about 3mm inside the bone). This diagnostic character enables even small fragments of maxilla to be identified, e.g. QMF51372, a P^3 in a fragment showing the foramen and a trace of the sinus, from Judy's Jumping Joint. In addition, the naris is retracted as far as the premolar, instead of level with the canine in *N. superior*, *N. albivenator* and *N. snideri*. The nasal bone appears to be tilted slightly upwards at the front (giving a 'dished' appearance in profile), the tip being broken off just ahead of its suture with the premaxilla, and its maximum width (at the fronto-lachrimal junction) is less than in *N. superior*. The dorsal wing of the premaxilla is narrower and thicker than in the other species, and the dorsal wing of the maxilla is much narrower, but the malar fossa is slightly shallower. Masseteric process of jugal broken off, so it is not possible to compare it with the deep ones of *N. albivenator* and *N. superior*. So far as can be compared, the posterior part of the skull is similar to the other species.

Upper Incisors. Only first incisors are present in the holotype; and are smaller than in *N. superior*. Very worn second and third incisors occur in the Camel Sputum specimen QMF30303, but appear also to be smaller. From the alveoli, the incisor arcade of the holotype is V-shaped, as compared to being more U-shaped in *N. superior*.

Upper Canine. One damaged representative; small, alveoli vary from 3–4mm in diameter, about the same as in *N. superior*.

Upper Premolars. DP^2 is known from a tooth associated with an unerupted P^3 (QMF51357) and another (QMF51358) from Camel Sputum

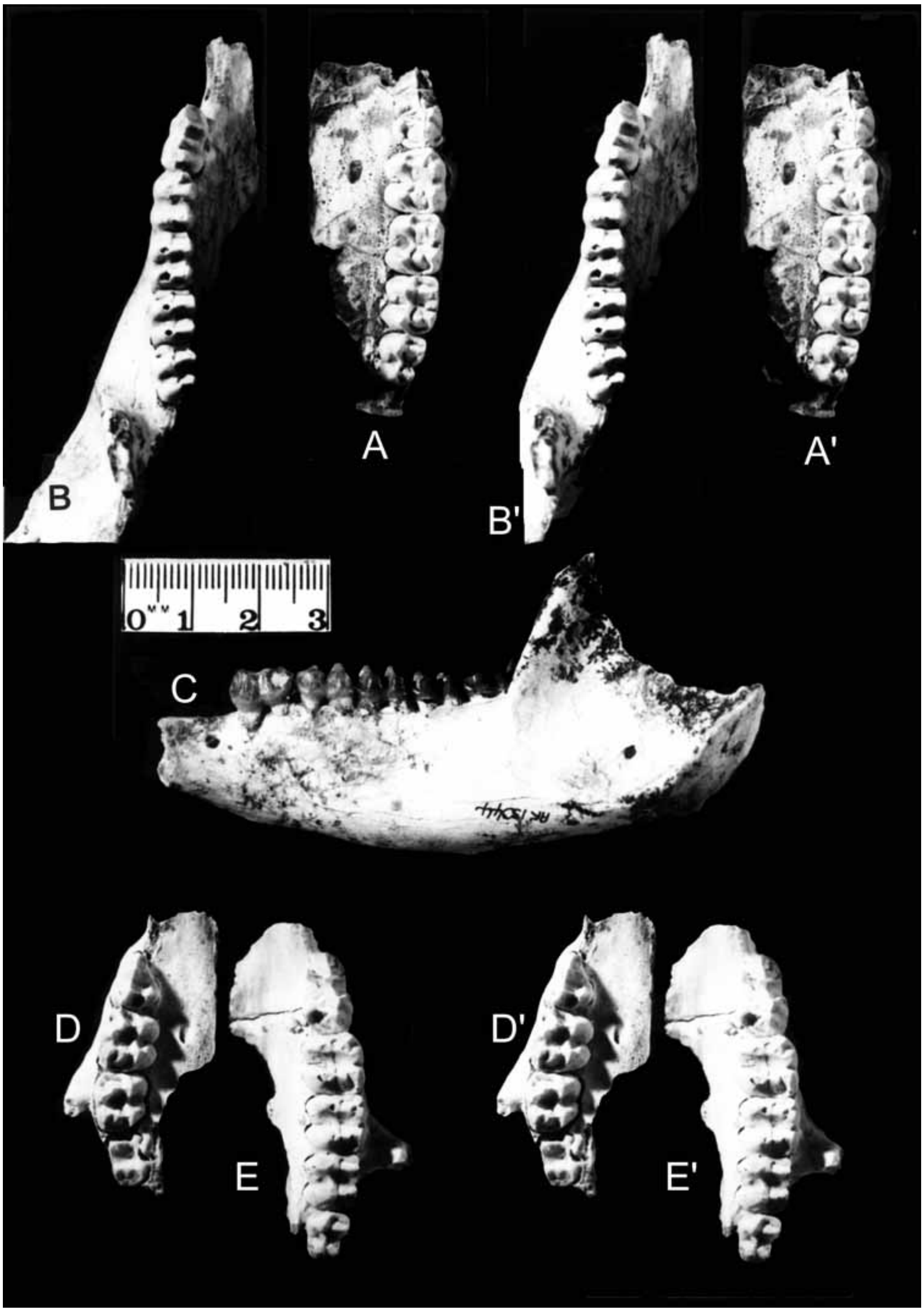


FIG. 11. *Namilamadeta crassirostrum* sp. nov. Referred specimens: A, A' left maxilla QMF 20574 (Camel Sputum site); B, B' left dentary QMF51363, (Camel Sputum site); C, QMF51363 in lateral view; D, D' juvenile right maxilla QMF51348 (Wayne's Wok site); E, E' adult left maxilla QMF51346 (Wayne's Wok site, all in stereo-occlusal view.

site and three, each associated with M^1 and M^2, from Wayne's Wok (QMF51347, QMF 51348 and QMF51349). Teeth are roughly equilateral-triangular, slightly longer than wide and blunt posteriorly. Buccal crest with a distinct protocone in the anterior moiety, about equally as high as the anterior-most of the two close cusps (paracone) on the posterior moiety. Hypocone distinct near the lingual corner, having only a slight link with the paracone. These teeth differ from a DP^2 (QMF51353) from Dirk's Towers 4, which is slightly smaller, has a more trenchant buccal crest and lacks a distinct metacone.

P^3. Two site-related morphs are apparent. Shorter ones (Camel Sputum and Neville's Garden) are wider posteriorly, taper more than the longer ones (Wayne's Wok), and have a small cingular cusp anterior of the hypocone. Two specimens from Wayne's Wok (QMF51350, QMF51351 probably the same individual) and one from Mike's Menagerie (QMF51364) have exceptionally long P^3s and are wider anteriorly relative to others of this species.

Upper Molars. Similar in size and form to those of *N. superior*. M^1 : In unworn examples from Wayne's Wok (QMF51347, 51348, 51349) M^1 has stylar cusp C more developed and stylar cusp B expanded buccally to form a distinct anterobuccal pocket on the outside of the preparacrista. These features are quickly obliterated with wear. Of the Camel Sputum specimens, QMF51359 is too worn for detailed comparison, but QMF20574, scarcely worn, shows slightly more resemblance (in disposition of pre- and post-paracristae) to *N. snideri*, although its degree of ornamentation and cusp development on P^3 is much stronger.

M^2. Second molar slightly shorter than first and about the same width. It differs in the reduction of stylar cusp B to a variably distinct cuspule at the junction of the preparacrista and precingulum, e.g. clear in QMF51346 and QMF51348 from Wayne's Wok but obscure in QMF20574 from Camel Sputum; this may indicate a subspecific difference between two localities. The paracone is quite distinct at about the outer third point on the protoloph and equal to stylar cusp C in size, while the metacone is midway between the metaconule and stylar cusp D. Thus, it is quite similar in form to the M^1, but quite different to the M^2 of *N. albivenator*.

M^3. Parastyle further reduced and paracone no longer distinguishable, although the metacone is still apparent. This resembles the M^2 of *N. albivenator*. The metacone of M^3 is slightly larger in *N. crassirostrum* from Camel Sputum (QMF20574) and the unworn QMF51348 from Wayne's Wok than that of *N. superior*.

M^4. The simplification process has continued in this tooth, with the posterior narrowing of the crown and reduction in size of the metacone.

Dentary. Relatively lightly built, fairly deep (more than in *N. albivenator*) slightly deeper posteriorly. Ventral margin slightly convex in profile, more so in QMF12461 from Camel Sputum, also noticeably deeper. In paratype QMF40277 and QMF12461 the ventral margin is rounded, but in QMF51363, (Camel Sputum), it bears a distinctly angular keel. In the paratype, the cheek-tooth row is 45.7mm long; depth of dentary at P_3M_1 is 20.6mm, at M_3M_4 is 22.3mm. Anterior mental foramen situated just in front of the premolar at about one-third depth. Dentaries are not fused; symphysis extends level with posterior end of premolar. The ascending ramus (QMF51363) rises steeply at some 70º to the occlusal surface. It is broad with a deep, sharply-bounded masseteric fossa, pierced externally by a small masseteric foramen. Internally is the larger opening of the mandibular foramen, farther back and just below the level of the teeth. A shallow buccinator groove extends diagonally on the outer face from just below the posterior root of the premolar to well below M_3. Post-alveolar shelf is short. The diastema anterior of the premolar is short, about 12mm in QMF51363. Incisive alveolus large, oval in cross-section, slightly narrower ventrally, and at this point the dentary is 6mm wide.

Lower Incisor. Two are known: QMF51366 with associated left P_2 and molars, from Roo Site, and a well-worn isolated left incisor QMF51367 from Sticky Beak Site. QMF51366 is barely worn at the tip, but is broken at the base, so its full length is unknown. Preserved enamel length is about 34mm. Tooth slightly curved, ventrally convex, and towards tip shows increasing curvature medially. Towards the base, the dorso-ventral diameter reaches 6.7mm, with a transverse diameter of 3.8mm. In cross-section the incisor is roughly elliptical, but with a dorso-medial bulge, with a concomitant shallow groove ventromedially just above the medial edge of enamel, and a sharp dorso-lateral edge of the lateral side of the enamel. Dorso-medial bulge is enamel-free. Enamel distribution extends down from the dorso-lateral edge, around and up about 1.5mm on the medial side of the tooth.

Lower Premolars. P_2 is known only from the Roo Site specimen QMF51366. It is elongate and triangular bearing three cuspids: an isolated protoconid with a straight crest extending to the anterior corner, an equally tall but more lingual hypoconid and a smaller posterobuccal hypoconulid joined to it by a crest. A weak postcingulum forms a shallow basin on the posterolingual side of the hypoconid.

P_3 generally almost parallel-sided, with a rather pointed anterior end and a blunt posterior (e.g. QM 40277 (WW), QMF51363 (CS), QMF51365 (MM)), but others show a little more taper (e.g. QMF51362, QMF12461 (CS)) being slightly wider posteriorly.

A longitudinal crest is almost central, interrupted at about the one-third point by the protoconid, from which buccal and lingual crests extend, and at the two-thirds point by the metaconid on the buccal side of midline giving rise to a slight buccal crest. Halfway between the metaconid and the posterior end of the tooth, and slightly lingual to the midline is the hypoconid with a lingual crest. Longitudinal crest continues to a small cusp on postcingulum, which extends equally on either side to form shallow basins on the flanks of the metaconid and hypoconid. On unworn teeth (QMF51362), the longitudinal crest therefore appears as a widely-open zigzag. Protoconid and metaconid are equally high, with the hypoconid slightly lower. There is a minute cusp at the halfway point, ahead of the metaconid, that scarcely interrupts the longitudinal crest, and the posterior-most cusp on the postcingulum is the lowest.

Lower Molars. M_1. Longest and, generally, the widest of the lower molars, although its anterior width is often less than that of the succeeding M_2 and M_3. Thus, it tapers noticeably forwards. In the unworn specimen from Roo Site (QMF51366), M_1 is bilophodont. Its protolophid is narrower than the hypolophid and bears cusps only at its buccal and lingual extremities. The protolophid is normal to the lingual face of the tooth, unlike the hypolophid which trends anterolingually, thus converging with it. Both lophids are notched about half-way across.

Protoconid and hypoconid are just buccal of the midline, and are highpoints on a longitudinal crest that starts at the paraconid (?) on the extremity of the precingulum, continues back along aligned pre- and postprotocristids and cristid obliqua, then curves lingually as the post-hypocristid, and merges into the postcingulum. The precingulum defines shallow basins on either side of the preprotocristid. There is no premetacristid, but a weak postmetacristid parallels the longitudinal crest and crosses the transverse valley to meet the entoconid about half-way up. A weaker postentocristid joins the postcingulum low down on the back of the tooth. With a little wear, the weaker crests are obliterated, as in QMF51375.

M_2-M_4. Posterior molars are essentially identical, with minor proportional changes, a possibly widening precingulum, and a narrower hypolophid on M_4. Development of the postcingular basin may vary. In the deep-jawed (Alpha-male?) QMF12461, the postcingulum forms a particularly well-defined and deep fossette, particularly on M_4, that is considerably deeper than on other specimens. One isolated tooth, QMF51352 from Wayne's Wok, presumably a left M_2, has the barest suggestion of a medial neomorphic cuspid on the protolophid, just lingual of the notch.

REMARKS. First upper molar smaller in lateral diameter than in other species except perhaps *N.* cf. *albivenator*, much smaller than in *N. snideri*. Upper premolars parallel, not converging anteriorly, more rectangular than in other species. Upper molars similar to those of *N. superior.* M^1 differs from both *N. albivenator* and *N. snideri* in having a crest between paracone and parastyle. Lower premolars differ from those of *N. albivenator* in being more rectangular, with anterior width only slightly less than posterior width, in being absolutely longer and larger relative to M_1, and in having second and third cuspids on the longitudinal crest separated, with third cuspid noticeably displaced lingually.

Namilamadeta sp. indet.

MATERIAL. QMF51368, lM^2; QMF51369, lP_3; QMF51370, lP_3; QMF51371, left dentary fragment with M_{2-4}. Outasite, Godthelp Hill. Low (basal?) in System B (Archer et al., 1989,1991; Cooke 1997; Creaser 1997).

DESCRIPTION. The small sample from this site makes it difficult to characterise the taxon with any certainty. However, several features are noteworthy if all the specimens are conspecific: a) the upper premolar P_3 of QMF51370 is longer and wider than in any other species or specimen (e.g. Fig. 4), M^2 is more equidimensional than in *N. albivenator*, but similar in size and proportion to *N. superior*, and the lower molars are similar in size to *N. crassirostrum*.

TABLE 2. Comparison of character states of some features of upper teeth of *Namilamadeta* spp., using *Muramura* as an outgroup.

Character	*Muramura*	*N. snideri*	*N. albivenator*	*N superior*	*N. crassirostrum*
I1 size	slightly broader than I2	large, approximately equal to N. albivenator	large, slightly smaller than N. snideri	little more than half breadth of N. snideri	small, converging
I2-3	slightly smaller than I1	small relative to I1	small relative to I1	moderately large relative to I1	slightly smaller than I1
P3 size	small, > length of M1	larger than M1 (~20% more)	slightly larger than M1 (~10%)	larger than M1 (20%)	larger than M1
protocone	very slight bump	no	small but distinct cusp	minute cusp	
hypocone	well developed	well developed	relatively large	relatively large	relatively large
shape	rectangular	rectangular - larger than N. albivenator	roughly rectangular	roughly triangular, broader posteriorly, constricted medially	roughly rectangular, about size of N. snideri
M1 shape	rectangular	roundly quadrate	quadrate	quadrate	quadrate
postero-lingual corner	rounded	round	sub-rounded	sub-angular	sub-rounded
angle between pre- & post paracristae	n.a.	<90°	approx 90°	>90°	>90º
parastyle	preparacrista crest curves lingually at end	crest curves lingually at end	like N. snideri	on cingulum, at junction with straight crest	like N. snideri
parastylar spur	insignificant	marked	less than N. snideri	insignificant	
M2 preparacrista	strong, goes to ectocrista	strong	absent	weak	strong
parastyle	at corner of tooth	at corner of tooth	slightly lingual of corner	at corner of tooth	lingual of corner
stylar cusp C	absent	indistinct	distinct	insignificant	distinct
paracone	strong, midway between Pr and StB	indistinct, closer to StB	indistinct	closer to StB	distinct, closer to StB
metacone	closer to metaconule	closer to StD	midway	~ midway	closer to StD
M3 paracone	strong, midway	not apparent	slight thickening	slight thickening	slight thickening
StB	distinct	weak	weak	distinct	indistinct
metacone	strong, midway	distinct, close to StD	distinct, midway	distinct, closer to StD	closer to StD
M4 shape	elongate, triangular	broad, triangular	rounded, triangular	triangular	tapering rectangular
postmetaconule-crista	moderate	insignificant	distinct	strong	Strong

DISCUSSION

Age. In South Australia, the vertebrate fossil-bearing beds of the Lake Eyre Basin are well-defined stratigraphically at and near Lake Palankarinna, the type locality of the Etadunna Formation and Ngapakaldi Fauna (Stirton et al., 1961, 1968), and superposition can be clearly demonstrated (Woodburne et al., 1993). Species correlation, both vertebrate and microfossil, between different basins, including marine sequences, has helped to establish the ages of the sediments. Stirton's early assessment of an Oligocene age for these formations and faunas (Stirton et al., 1961) was initially based on the stage of evolution he perceived in diprotodontoids (Stirton, Woodburne & Plane 1967), and palynological assessment (Balme, 1963; pp. 89-104 in Johns & Ludbrook, 1963), and current thinking has returned to this point of view (Woodburne et al., 1993) as a result of new information, which is admittedly still only tentative, with a Late Oligocene age (24-26 million years old) based on foraminifers, isotopic dating of sedimentary illite, and magnetostratigraphy (Woodburne et al., 1993).

In contrast, one of the problems of the numerous Riversleigh fossil assemblages is the uncertainty of their relative ages because of the type of sedimentary environment that has preserved them. Intercontinental correlation of bat species (Sigé, Hand & Archer, 1982) has helped define the age of some localities at least, and some taxa have allowed correlation with geological units of the Lake Eyre Basin. Tentative stratigraphies have been worked out (e.g. Archer et al., 1989, 1991, see Megirian 1994 for alternative) based primarily on faunal content of the different localities and perceived stage of evolution of various taxa within them (e.g. Cooke, 1997). Wayne's Wok assemblage is considered (e.g. Cooke, 1997) to correlate with the putative early Miocene Kutjamarpu local fauna of the Wipajiri Formation of the Lake Eyre Basin, while White Hunter equates with the Ngama local fauna, zone D of the Etadunna Formation at Lake Palankarinna (Myers & Archer, 1997, Woodburne et al., 1993).

Namilamadeta snideri is from the Namba Formation at Lake Tarkarooloo (Rich & Archer, 1979) in the Tarkarooloo Basin (Callen, 1977) some 300km SE of Lake Palankarinna. The Namba Formation is correlated on lithological and faunal grounds with the Etadunna Formation. Pledge (1986) suggested that the Tarkarooloo Local Fauna was slightly older than the Ngama Local Fauna (Zone D of Woodburne et al., 1993) at Lake Palankarinna. A single specimen (SAMP24648) from the Ngama Local Fauna closely resembles the posterior three-quarters of rM_4 of *N. crassirostrum,* e.g. QMF12461 from Camel Sputum, rather than the supposedly contemporaneous *N. albivenator*, from White Hunter.

Overall, *N. snideri* may be approximately the same age as *N. albivenator*. It appears to be older than *N. crassirostrum*, which seems to have had a longer time range. The relative position of *N. superior* is uncertain. The oldest of all seems to be the Hiatus material. A simple explanation may be to assume two more-or-less contemporaneous but ecologically mutually exclusive lines, with *N. snideri* giving rise to *N. albivenator* and then *N. superior*, while a *N. crassirostrum*-like form appeared in Ngama time and continued in north Queensland until mid-System B time.

Relationships. Comparison of character states of various features on upper teeth of *Namilamadeta* spp., using *Muramura* sp. as a demonstrably older outgroup (Table 2), gives no clear species polarity. While the species are distinct, they are too close in age to be separated by this method. (Only upper dentitions were considered here because lower teeth are unknown for *N. snideri*, which is critical for extra-regional correlations, and for *N. superior*.)

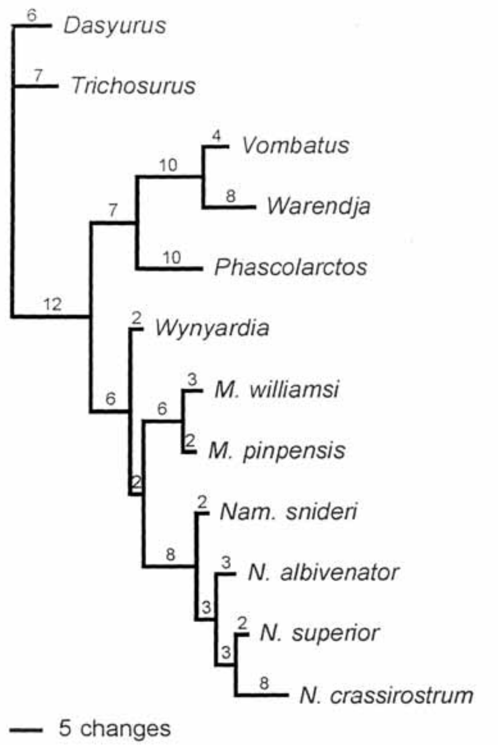


FIG. 12. Phylogram showing relationships of *Namilamadeta* spp. relative to *Muramura*, *Wynyardia*, *Phascolarctos*, *Warendja*, *Vombatus*, *Trichosurus*, and *Dasyurus*; from matrix, Table 4.

A broader cladistic analysis was attempted, using PAUP* 4.0b10 (Swofford, 2000), on 62 cranial and dental characters, and twelve taxa (Tables 3-4) with *Dasyurus* as the outgroup, but with little clear result except grouping the species of *Muramura* and *Namilamadeta* as two sister genera related to *Wynyardia* (Fig. 12). Koalas and wombats form a sister group to the wynyardiids. This tree (tree length 114) implies a closer relationship of these genera to koalas than wombats, and *Wynyardia* is a sister group to the Vombatiformes. This rather unexpected result may be because no postcranial characteristics could be used, due to the lack of recognised bones for *Namilamadeta*, and the lack of dental information for *Wynyardia*. The best consensus tree (tree length 62) for wynyardiids was that produced by analysis of eight taxa (*Trichosurus* as outgroup) and 22 informative characters, and is similar to that in Fig. 12.. The relationships implied are: *Wynyardia* ((*Muramura williamsi*,

TABLE 3. Score of character states of vombatiformes and outgroup marsupials

Charac	*Dasyu*	*Trich*	*Phasc*	*Vomb*	*Waren*	*Wyn.b*	*M.will*	*M.pin*	*N.snid*	*N.albi*	*N.sup*	*N.cras*
1	0	0	1	1	1	1	1	1	1	1	1	1
2	0	1	1	1	1	1	1	1	1	1	1	1
3	1.64	1.58	1.68	1.23	3.22	1.69	1.69				1.76	1.73
4	3.4	2.64	2.65	2.67	3.35	2.33	2.59				2.58	2.83
5	0.92	0.75	1.05	0.92	1.0	(0.55)	1.08		(1.32)	1.55	0.93	0.98
6	X	X	X	X	X	X	X	X	X	X	X	+
7	t	t	t	t	t	t	t	t	t	t	t	b
8	+	+	+	X	?	?	-?		?	+	+	+
9	x	X	X	X	X	X	X	X	X	X	X	+
10	long	long	long	long	long	long	long		long	long	long	trans
11	0	0	0	1	1		0		0	1		1
12	0	0	1	1	1		1	1	1	1		1
13	0	1	1	0	0	1	1	1	1	1	1	1
14	0	0	0	0	0	1	1	1	1	1	1	1
15	X	X	+	X	+	X	X		+	+	+	X
16	curv	curv	straight	curv	curv	curv	straight	?	?	curv	curv	straight
17	taper	taper	parallel	taper	taper	taper	parallel	?	?	taper	taper	?
18	0	0	1	1	0	0	0			0	0	0
19	0	1	1	1	1	1	1				1	1
20	0	0	1	1	1	0	?				0	
21	0	1	1	1	1	0	0				0	
22	1	1	0	0	1	1	1				1	
23	0	0	1	1	1		1					
24	0	0	1	1			0					
25	0	0	0	1	1		1	1	1	1	1	1
26	2.0	1.67	1.6	na	na		1.83		1.67	1.83		
27	0	0	0	1	1		0		0	0	0	0
28	0	0	1	1	1					0		0
29	str	str	str	str	str		str	curv	?curv	curv	curv	str
30	na	tri	triangul	tri	triang		rect	rect	rect	rect	rect	rect
31	-	1	1	0			1	1	1	1	1	1
32	0	0	1	0			0	0	1	1	1	1
33	1.6	1.25	1.2	1.27	1.3		1.29	1.25	1.76	1.57	1.6	1.76
34	0.67	0.8	0.875	0.74	0.75		1.1	1.18	1.2	1.1	1.2	1.41
35	0.625	0.72	0.97	0.625	0.77		0.84	0.88	0.82	0.89	0.85	0.87
36	-	0	1	1			0	1	0	1	1	1
37	-	-	0	1	1		1	1	1	1	1	1
38	0	1	1	0	0		0	0	0	0	0	0
39	0	-	0	0	0		1	1	1	1	1	1
40	0	1	0	1	1		0	0	0	0	0	0
41	0	0	1				0	0	0	1	0	1
42	0	1	0	1			0	0	0	0	0	0
43	na	0.92	1.11	1.0	0.92		1.03	1.03	0.97	1.04	1.01	1.0
44	na	1.35	1.08	1.2	1.21		1.23	1.16	1.51	1.33	1.33	1.38
45	0	0	1	1	1	0	1	1		1		1
46	70	70	75	75	57		70	70		60		65
47	0	0	0	1	1		0	0		0		0
48	20	20	30	15	18		30			25	(25)	25
49	deep	deep	m-shall	deep	shallow		med	med?		shall		deep

Charac	*Dasyu*	*Trich*	*Phasc*	*Vomb*	*Waren*	*Wyn.b*	*M.will*	*M.pin*	*N.snid*	*N.albi*	*N.sup*	*N.cras*
50	0	0	1	0	0		0	0		0		0
51	0	0	1	1	1		1			1		1
52	str	str	str	str	str		str	str		str		curv
53	1.86	1.51	1.5	1.25	1.71		1.15	1.37		1.73		1.67
54	0.83	0.96	0.83	0.625	0.72		0.83	0.88		1.16		1.08
55	0.86	0.97	0.77	0.8	0.61		0.95	0.87		0.95		0.92
56	0.52	0.65	0.69	0.625	0.69		0.77	0.74		0.71		0.69
57	0.78	0.98	1.00	1.0	1.00		1.23	1.10		1.00		1.06
58	0.73	0.92	1.00	1.0	0.93		1.04	1.04		1.04		1.00
59	0.25	0.28	0.26	0.25	0.26	0.19	0.31	?	?	?	0.30	0.37
60	na	0.66	0.56	0.78	1.0	?	0.73	0.44	?	?	0.52	0.51
61	3.78	3.95	3.75	3.5	4.7	?	3.9	?	?	?	3.17	2.9
62	0.59	0.75	0.59	0.27	0.67	?	0.56	0.59	0.55	0.53	0.58	0.73

M. pinpensis)(*Namilamadeta snideri* (*N. albivenator* (*N. superior*, *N. crassirostrum*))).

Morphology. Distinctive rostral morphology in *N. crassirostrum*, although different in detail, invites comparison with some macropodid species, e.g. *Sthenurus stirlingi* Wells & Tedford, 1995; *Sthenurus baileyi* Prideaux & Wells, 1998; *Congruus congruus* McNamara, 1994, and to a lesser extent, *Macropus rufus* and *M. antilopinus*, where the nasal expansion has been considered to be an adaptation for a hot, dry climate. In some *Macropus* spp., e.g. *M. robustus*, this has been interpreted as sexual dimorphism, particularly for an Alpha male (M. Archer, pers. comm.). It is felt that sexual dimorphism in this character can be ruled out because it appears to be site specific, the two never co-occur. The expanded nasal cavity of *N. crassirostrum* may therefore indicate drier conditions for this species. Similarly the primitive zygomaturine *Silvabestius johnnilandi* (Black & Archer, 1997) from VIP Site (coeval with Wayne's Wok; Creaser, 1997), which differs from its older congener *S. michaelbirti* (from Hiatus Site) in having a swollen rostrum.

These macropodids, however, show nothing similar or analogous to the sinus in *N. crassirostrum*. No osseous structure like this appears to occur in other marsupials, although it has been suggested that it may be equivalent to the nasovomerine organ, otherwise known as Jacobson's Organ. This is known in a variety of marsupials (Broom, 1896), but is enclosed in cartilage and opens ventrally into the oral cavity. In our situation, the sinus is blind except for a large ovate opening on the dorsal edge of the thickened premaxilla; there is no natural connection with the mouth directly or through the anterior palatal foramen. It is possible the fossa was lined with nasal mucosa, perhaps to concentrate scents or to moisten incoming air (P. Murray, pers. comm.). The feature appears to be unique: the only analogy might be the paired pits for the nasal diverticula in *Equus*, *Tapirus* and *Onohippidium* (Gregory, 1951: figs. 21.43B, 21.70A, B1); these, however, are outside the nasal cavity.

The other distinctive feature of the rostrum is the retracted premaxillary margin. While this is not as extreme as in tapirs or palorchestids (but note the similarity to the mid-Miocene *Propalorchestes novaculacephalus* Murray, 1986, as reconstructed in Fig. 3A of Murray, 1991), it suggests that *N. crassirostrum* possessed a mobile snout.

WYNYARDIID CHARACTER STATES

1. carnivorous/omnivorous (0), vs herbivorous (1)

2. teeth tritubercular (0): diprotodontan (1)

3. skull slender, length: width less than 1.7 (0)

4. skull low, length: height less than 2.6 (1)

5. rostral height: width just anterior to jugal root less than1.0 (0)

6. presence (1) or absence of large paired sinuses in upper surface of premaxillae (0)

7. snout tapering (0) or bulbous (1)

8. nasals projecting (1)

9. premaxilla edge retracted (1) to level of P3 or not (0)

10. infraorbital foramen in maxilla oriented longitudinally (0) or transversely (1)

11. infraorbital foramen close to premax/maxillar suture (1), i.e. expansion of premax at expense of maxilla

12. presence of malar fossa (or depression) (1)

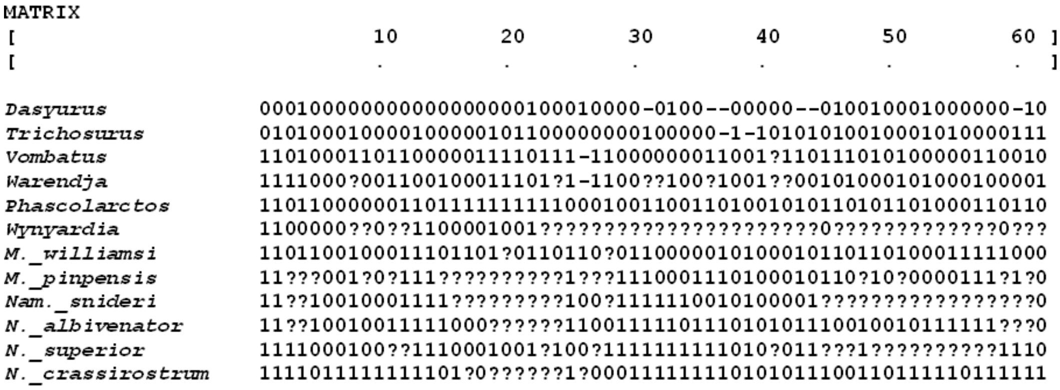
13. development of masseteric processes (1)

14. enlargement of masseteric processes (1)
15. great expansion of anterior interorbital area (1)
16. zygomatic arches angular, straight (1) or curved (0)
17. zygomatic arches parallel (1) or tapering forwards (0)
18. sagittal crest present (0)
19. auditory capsule roofed by alisphenoid (0) or squamosal (SQW) (1)
20. no squamosal process (SQP) (0)
21. no squamosal sinus (SQS) (0)
22. alisphenoid component to tympanic process (0)
23. tail long (0), short (1)
24. tail very short (1)
25. incisor I1 greatly enlarged (1)
26. incisor I1 diameter >1.7 times greater than I3 (1) or less (0)
27. upper canine present (0) or lost (1)
28. P2 present (0) or lost (1)
29. upper tooth-rows straight (0) or curved (1)
30. premolar P3 rather triangular, small, sectorial (0), rectangular, large (1)
31. P3 has longitudinal crest (1)
32. P3 has strong lingual crest for hypocone (1)
33. P3 length: width greater (1) or less (0) than 1.3
34. P3:M1 length greater (1) or less than 1.2 (0)
35. P3:M1 width greater (1) or less than 0.85 (0)
36. upper molars selenodont (1)
37. selenodonty reduced (1)
38. presence of stylar cusps on upper molars (0)
39. stylar cusps enlarged (1)
40. stylar shelf lost (1)
41. parastyle on M1 reduced (1)
42. primary cusps on upper molars labial (1) or midway on lophs (0)
43. M1 anterior width less than posterior width (0) or equal or greater (1)
44. M4 rectangular or triangular; metaloph slightly shorter (0) or much shorter than protoloph (1) (prl:mel<1.3>)
45. dentary shallow (0) or deep (1)
46. anterior border of ascending ramus more (1) or less than 65o (0)
47. coronoid process wide (0) or narrow(1)
48. articular condyle on (<25o) (0) or above molar occlusal plane (1)
49. masseteric fossa shallow (0) or deep (1)
50. angular process very reduced (1)
51. I2 present (0) or lost (1)
52. lower cheek tooth-row straight (0) or curved (1)
53. P3 length: width greater (1) or less than 1.5 (0)
54. P3:M1 length greater (1) or less than 1.0 (0)
55. P3:M1 width greater (1) or less than 0.9 (0)
56. M1 width: length more (1) or less than 0.7 (0)
57. length M1 : M2 more (1) or less (0) than 1.0
58. width M1 : M2 more (1) or less (0) than 1.0
59. rostral:total skull length less than 0.3 (0)
60. I3 P3 diastema: cheek-tooth row length more than 0.7 (0)
61. skull: cheek-tooth row length greater than 4 (0)
62. palatal width: cheek-tooth row length less than 0.6 (0) 0 plesiomorphic; 1 apomorphic

CONCLUSIONS

Metric and morphological examination of 121 specimens from 18 Riversleigh localities demonstrates at least three distinct taxa are

TABLE 4. Matrix of scores for PAUP 4.0b1 analysis



```
MATRIX
[                                 10        20        30        40        50        60 ]
[                                  .         .         .         .         .         . ]

Dasyurus           0001000000000000000001000100000-0100--00000--010010001000000-10
Trichosurus        01010001000010000010110000000010000 0-1-10101010010001010000111
Vombatus           1101000110110000011110111-11000000011001?11011101010000110010
Warendja           1111000?001100100011101?1-1100??100?1001??00101000101000100001
Phascolarctos      11011000000110111111111100010011001101001010110101101000110110
Wynyardia          1100000??0??1100001001??????????????????????0?????????????0???
M._williamsi       1101100100011101101?0110110?0110000010100010110110100011111000
M._pinpensis       11???001?0?111??????????1???1110001110100010110?10?0000111?1?0
Nam._snideri       11??10010001111?????????100?1111110010100001?????????????????0
N._albivenator     11??10010011111000??????11001111101110101011100100101111111???0
N._superior        1111000100??1110001001?100?1111111111010?011???1??????????1110
N._crassirostrum   1111011111111101?0??????1?000111111110101011100110111110111111
```

present. *N. albivenator,* primarily from White Hunter site, (plus DT6 and LSO), is noticeably smaller than the almost unique specimen *N. superior* from Upper Site and the *N. crassirostrum* complex from the remaining sites. While *N. snideri* is morphologically closer to *N. albivenator*, it seems closer in size to *N. superior*. Thus, no conclusion can be reached about their relative ages, although *N. snideri* seems on other evidence to be slightly older or about the same age as *N. albivenator*.

In general, the Riversleigh *Namilamadeta* spp. support a correlation of 'System B' sites with the upper part of the Etadunna Formation of the Lake Eyre Basin, and therefore a late Oligocene to earliest Miocene age. Physiological considerations of the skull morphology of *N. crassirostrum* suggest an adaptation to hotter/drier conditions during some period of the early Miocene. Structure of the auditory region in *N. superior* supports assignment to the Family Wynyardiidae, as originally suggested by Rich & Archer (1979).

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APPENDIX 1.

Measurements of considered teeth of *Namilamadeta* spp. All measurements in millimetres.

Namilamadeta snideri Rich & Archer 1979

Tom O's Quarry			
SAM P19951	holotype - partial palate and rostrum		
tooth	length	ant. width	post. width
rI1	6.2	4.5	
lI1	6.3	4.5	
lI2	>4.5	4.5	
lI3	4.5	3.3	
lC1	3.2	2.0	
rP3	11.0	5.7	7.15
lP3	11.6	5.95	7.05
lM1	9.6	8.2	8.5
lM2	9.2	8.5	8.3
lM3	8.6	7.8	7.1
lM4	7.2	6.5	4.3
NMV P8993			
rM1	8.55	7.3	7.3
NMV P8994			
rM1	9.6	7.95	8.2
rM2	9.1	8.0	7.7
rM3	8.7	7.1	6.5

Namilamadeta albivenator sp. nov.

White Hunter - Riversleigh			
AR 16775	(joins to QMF 23834, AR 17188) Holotype		
rP3	10.4	5.8	6.65
rM1	9.3	7.2	7.3
rM2	8.9	7.7	7.4
QMF 51337			
rP3		6.15	
lP3	11.1	6.2	7.0
lM1	9.5	7.6	7.7
lM2	8.7	7.55	7.3
AR 17188	(joins to AR 16775, QMF 23834) maxilla		
lI1	5.6	3.7	
rC1	2.5	2.0	
lP3	10.4	5.8	6.5
lM1	9.1	7.5	7.7
lM2	8.95	7.45	7.1
lM3	8.9	6.7	6.0
lM4		6.2	
QMF 51338	premaxilla		
lP3	11.3	6.3	7.3
QMF 51339			
lM1	9.55	7.9	8.2
QMF 23834	(joins to AR 16775, and AR 17188) maxilla		
rM3	8.3	6.95	5.7
rM4	7.2	5.8	4.4
QMF 51340	dentary fragment broken tooth		
rM3	~1	6.5	
QMF 51341	left juvenile dentary with P2, M1, and M2-3 in crypt		
lP2	6.3	2.9e	4.3
lM1	9.7	5.9	5.5
lM2	9.4e	5.8e	in crypt
lM3	in crypt		
QMF 40278	right dentary, almost perfect (paratype)		
rI1	6.5	4.2	>25
rP3	9.2	4.5	5.7
rM1	8.3	5.4	6.2
rM2	8.2	5.9	6.1
rM3	8.2	6.0	5.9
rM4	7.7	5.4	5.0
QMF 51342	r. dentary, juvenile, rM3 missing, rM4 unerupted		
rI1	>6.4		4.25
rP2	6.0	3.0	4.4
rM1	9.5	5.6	6.0
rM2	9.3	5.8	6.1
QMF 51343	dentary, fractured. I1 broken (pair to AR 12793?)		
lI1	>6.2		>4
lP3	9.5	4.8	5.9
lM1	8.5	5.6	6.2
lM2	8.2	6.0	6.2
lM3	8.2	5.9	5.8
lM4	7.7	5.3	4.8
QMF 51344	lower		
rI1	6.7	4.8	
QM F23499	lower		
rM3?	8.8	5.9	5.9 (cf. QMF 51342)
QM F30700	right dentary, split lengthwise through teeth		
rI1	5.7	3.75	
rP3	10.1	5.5	6.8
rM1	8.7	6.3	7.0
rM2	8.3	6.75	6.8
rM3	7.9	6.5	6.0
rM4	7.8	5.9	5.7
Dirk's Towers - DT6			
QMF 13093	left maxilla, dark preservation cf. QMF 23494		
lP3	10.5	5.7	7.0
lM1	8.4	8.0	7.5

lM2	8.7	7.8	7.3
lM3			6.2
lM4	6.8	5.8	4.3
QMF 20035	right maxilla, light preservation		
rP3	11.0	5.5	6.7
rM1	9.1	8.2	8.7
rM2	8.2	7.9	7.4
rM3	8.2	7.1	6.3
rM4	7.5	5.8	4.7
QMF 20037	(2 pieces) maxilla		
rP3	10.95	5.75	7.1
rM1	9.2	8.0	7.6
rM2	8.5	7.5	7.0
rM3	8.2	6.75	6.2
QMF 23494	left premaxilla, (cf. QMF 13093, also N. snideri)		
lI1	6.5	4.9	
lI2	3.3	4.1	
lI3	3.1	3.2	
QMF 36343			
rM4	6.5	6.1	5.2
QMF 30506	left dentary fragment (locality unspecified)		
lP3	8.2	4.3	4.9
lM1	9.0	5.0	5.3
Quantum Leap			
QMF 24138 -	left maxilla,P3-M3		
P3	10.5	5.9	6.9
M1	9.0	7.6	8.4
M2	8.5	7.9	7.8
M3	8.2	6.9	6.5
L.S.O.			
QMF 36348	upper		
rM1	>8.9		8.6
QMF 36349	right maxilla fragment		
rM3	7.9	6.4	5.8
QMF 36350			
lM1	8.8	7.9	7.8
QMF 40251	right dentary		
rI1	6.2	4.2	
rP3	8.4	5.0	5.4
rM1	9.0	5.0	5.3
rM2	8.9	5.6	5.3
rM3	8.3	5.9	5.4
rM4	7.8	5.3	4.9

N. superior sp. nov.

Upper Site			
AR15875	upper		
rM2	8.6	8.2	7.4
AR15876	upper		
lM3	8.3	7.75	7.3
AR16127	lower		
lMx (damag.)	8.75	~6.7	
AR12884	upper		
rM2?	8.8	7.7	7.5
QMF 40276	skull (holotype) N. superior		
lI1	4.9	3.9	
lI2	5.1	4.1	
I3 and C1	missing		
lP3	12.0	6.3	7.5
lM1	10.0	8.9	8.8
lM2	8.5	8.8	8.1
lM3	8.4	7.7	6.5
lM4	7.6	6.4	4.8
rI1 damaged			
rI2	4.9e	4.6e	damaged
rP3 split	11.7	~6.9	~8.6
rM1 split	9.5	~9.5	~8.8
rM2	8.5		8.0
rM3	8.5	7.7	6.3
rM4	7.8	6.4	4.8

N. crassirostrum sp. nov.

Waynes Wok			
QMF 51346	left maxilla		
lP3	12.4	6.25	7.8
lM1	8.7	8.8	9.0
lM2	8.75	8.6	8.1
lM3	8.65	7.8	7.15
lM4	(7.3)	(6.1)	(5.1)
QMF 51348	juvenile right maxilla		
rP2	8.7	(4.5)	6.7
rM1	9.0	8.4	8.4
rM2	8.9	7.8	7.3 partly erupted
rM3	unerupted		
QMF 51349	juvenile left maxilla		
lP2	8.45	(4.4)	6.5
lP3	11.9	5.5	6.75 (ex crypt)
lM1	9.3	8.5	8.4
lM2	8.7	7.8	7.9
QMF 51351	mature left maxilla fragment (cf. QMF 51350)		
lP3	13.4	6.8	7.6
lM1	10.2	9.3	9.2

lM2	9.0	8.95	8.4
QMF 51350	(cf. QMF 51351) upper		
rP3	13.8	6.7	7.5
QMF 51345	upper		
lP3	12.8e		
lM1	9.2	9.3e	8.9
lM2	8.9	8.7	8.4
lM3	8.4	7.6	7.05
QMF 51347	upper		
rP2	8.0	4.2	6.6
rM1	9.2	8.2	8.3
rM2	8.4	7.7e	(7.2) unerupted
AR 9820	isolated crowns, upper		
?lM2	>8.8	~8	7.4 damaged
?lM3	8.3	7.4	7.0
AR 12858	worn		
lM1	9.3	9.5	9.4
lM2	8.6	8.2	7.8
QMF 51375	mature worn right dentary (paratype)		
rP3	11.4	5.7	6.4
rM1	10.3	6.8	7.0
rM2	9.4	7.1	6.5
rM3	9.0	6.9	6.2
rM4	9.0	6.1	5.4
AR 9711	left dentary fragment		
P3	10.1	5.3	6.2
AR 10789	lower		
rP3	10.9	5.4	6.4
AR 10639	lower		
lP3	10.4	5.2	5.8
AR 10638	lower		
rP3	9.9	5.1	5.8
AR 10565	lower		
lM2	8.9	6.4	6.1
AR 11866	lower		
lP3	10.3	5.0	5.9
AR 12860	lower		
lM2?	9.7	6.7	7.1
QMF 51352	lower		
lM2	9.2	6.5	6.5
QMF 24507	lower		
lM1	9.9	6.2	6.9
QMF 30755	upper		
lM4	7.9	6.75	5.0
QMF 30756	upper		
rP3	12.1	6.2	7.7
QMF 30757	upper		
rM1	9.0	9.1	8.8
QMF 30758	upper		
rM1?	9.0	8.7	8.2

QMF 30759	upper		
rM4	7.6	6.5	5.3
QMF 30760	upper		
rM2	8.6	7.6	7.3
QMF 30762	lower		
rM1	9.3	5.9	6.1
QMF 30836	right dentary fragment		
rP3	>9.3		5.6
rM1	9.1	6.3	6.7
QMF 31462	imperfect skull swollen snout (holotype)		
rI1	4.4	3.6	
lI1	4.5	3.6	
rP3	11.8	6.1	7.0
lP3	11.75	6.1	6.9
rM1	8.8	8.4	8.5
lM1	8.9	8.6	8.7
rM2	8.6	7.6	7.6
lM2	8.7	7.8	7.8
rM3	8.2	7.1	6.6
lM3	8.3	7.0	6.4
rM4	7.3	6.1	5.0
lM4	7.0	6.25	5.15
QMF 31480	right premaxilla and maxilla		
rP3	12.7	6.45	7.6
rM1	9.4	8.8	8.7
Camel Sputum			
AR 8686	upper		
P3	11.45	5.9	6.9
M1	8.75	8.0	8.0
AR 10038	upper		
lM1? damaged	9.2	>8.0	~7.9e
lM2?	9.0	8.7	8.2
AR 11840	upper		
lM2	8.5	8.5	8.2
lM3	8.3	7.7	7.0
lM4 alveolus			
AR 12881	upper		
rP2	8.8		7.0
QMF 51357	upper		
rP2	8.5		7.0
rP3 unerupted	12.55	6.3	7.6
QMF 51358	upper		
rP2	8.4		7.8
QMF 51359	upper		
rM1	8.55	7.9	8.0
rM2	8.3	7.7	7.4
rM3	7.9	7.1	6.7
rM4	smashed		
QMF 51360	upper		
rM2	9.0e	9e	8.2

rM3	8.7	8.2	7.5
rM4	7.5	6.7	4.7
QMF 20497	upper		
rM1	9.7	9.1	9.2
rM2	8.9	8.6	8.6
rM3	8.6	7.9	6.9
rM4	7.7	6.6	4.9
QMF 20498	upper		
rM2	8.25	8.1	7.9
rM3	8.3	7.15	6.8
QMF 20574	maxilla		
lP3	11.4e	~6.2	7.2e
lM1	9.3	8.8	9.1
lM2	8.9	8.4	8.7
lM3	8.8	7.7	7.3
lM4	7.7	6.5	4.95
QMF 40279	partial skull left side damaged		
lP3	12.3	>5.4	6.8
rP3	12.0	6.0	7.3
lM1	9.3		
rM1	8.3	8.0	7.9
lM2	7.7	7.3	7.5
rM2	7.4	7.4	7.3
lM3	8.2	6.6	<7.1
rM3	8.0	6.7	6.4
lM4	7.7	<6.3	<4.8
rM4	7.8	6.1	4.2
QMF 30303	mature palate, with premaxillae		
lI2 very worn	3.9	4.1	
lI3 very worn	3.7	3.3	
lC1 damaged			
lP3	12.25	6.2	7.7
rP3	12.5	damaged	damaged
lM1	8.7	8.5	8.3
rM1	8.9	8.1	8.3
lM2	8.6	8.1	7.8
rM2	8.2	7.9	7.6
lM3	7.9	7.2	6.4
rM3	7.7	7.4	6.6
lM4	7.5	6.3	5.7
rM4	7.3	6.2	4.8
QMF 30534	right maxilla, fragment		
rM1?			8.1
rM2?	8.8	8.1	7.8
AR 12946	upper		
rP3	12.5	6.1	7.45
AR 13374	upper		
lP3	11.8	5.9	7.3
AR 16838	upper		
rP3	12.3	6.1	7.25

AR 10691	upper		
lM2	9.4	8.9	8.8
AR 10686	upper		
rM2	8.6	8.2	7.7
AR 16839	upper		
lM3?	8.8	7.9	6.9
QMF 23490	upper		
lM2	8.9	8.6	8.6
QMF 51361	right dentary fragment		
rM2	9.1	6.7	6.7
rM3	8.7	6.6	6.2
rM4	8.3	6.1	5.7
QMF 51362	left dentary, venter missing		
lP3	10.8	5.4	6.5
lM1	9.5	5.8	6.9
lM2	9.0	6.8	6.8
lM3	8.6	6.6	6.2
lM4	8.6	6.3	5.7
QMF 51363	left dentary, L 90.5mm, D at M2 23.3mm		
lP3	10.3	5.6	6.1
lM1	8.7	6.3	6.7
lM2	8.5	6.6	6.3
lM3	8.3	6.6	5.9
lM4	8.6	6.1	5.4
AR 13898	dentary fragment with split M1 unmeasurable		
AR 17073	lower		
rM4	8.1	6.4	5.1
QMF 12461	right dentary		
rP3	10.8	5.1	5.9
rM1	9.0	6.1	6.7
rM2	8.8	6.6	6.5
rM3	8.7	6.5	6.0
rM4	8.4	6.2	5.6
Mike's Menagerie			
QMF 51364	right maxilla		
rP3	13.3	6.75	7.4
rM1	8.8	8.4	8.5
rM2	8.2e	7.9	7.8
AR 12868	upper		
rP3 unerupted	11.45	5.1	6.5
AR 9744	abraded, eroded, unmeasurable		
AR 9745	upper		
lM2	8.7	8.3	9.0
AR 9762	upper		
rM3	8.6	8.05	7.6
AR 9913	upper		
rM3?	8.8	8.3	8.0
AR 12871	upper		
rM2?	8.9	8.3	8.5
QMF 51365	left dentary fragment		

lP3	11.2	5.7	6.4
lM1	10.0	>6.8	>6.9
lM2	9.2	>7.2	>6.8
lM3	8.8	7.1	6.4
lM4	8.7	6.3	5.6
AR 10703	fragment, right dentary alveoli for P3, M2 3		
rM1	8.9	6.1	6.6
AR 9742	lower		
lP3	10.1	4.5	4.9 unerupted
AR 9743	lower		
lM1	9.9	6.4	6.7
AR 9915	lower		
rM1	10.0	6.2	6.5
AR 12869	lower		
lM1	9.7	6.5	6.7
AR 12870	(fits AR10703)	lower	
rM2?	8.8	6.6	6.5
AR 16961	lower		
rM2? or 1	9.4	6.0	6.6
Dirk's Towers DT4			
QMF 51353	upper		
rP2	>7.9	(5.4)	>6.8 damaged
QMF 51354	upper		
lP3	11.8	5.7	6.8
QMF 51355	upper		
lM2	9.05	7.7	7.6
QMF 36342	(site unspecified) upper		
lP3	12.0	5.9	7.2
Dirk's Towers DT5			
QMF 51356	upper		
rM1	8.7	8.4	7.9
QMF 24218	left dentary, with P3 M4		
P3	10.45	5.6	6.7
M1	8.8	6.5	6.8
M2	8.7	6.7	6.5
M3	8.5	6.8	6.3
M4	>8.0	>6.1	>6.1
Sticky Beak			
QMF 51367			
lI1	6.5	3.8	
QMF 51373			
rP3	11.1	5.25	6.75
Roo Site			
QMF 51366	juvenile dentary remnants		
lI1	~11.7	3.8	
lP2	8.9		5.3
lP3 unerupted	incomplete		
lM1	9.4	5.8	6.7
lM2	8.6	6.5	5.9
lM3 incomplete	-	6.4	-

Unallocated:

cf. *N. crassirostrum*

Neville's Garden			
QMF 51374	upper		
rP3	11.55	5.8	6.9
QMF 23014	maxillae		
rP3	11.95	5.9	7.3
rM1	8.6	7.5	7.95
rM2	8.2	7.8	7.25
rM3	8.1	6.9	6.4
rM4	>6.4	5.6	4.5
QMF 23201	left maxilla fragment		
lP3	12.1	6.1	6.85
lM1	>8.2	>8.4	>8 crown missing
Outasite			
QMF 51368	upper		
lM2	8.1	8.0	7.8
QMF 51369	lower		
lP3	12.35	6.0	7.4
QMF 51370	lower		
lP3	13.9	6.6	8.0
QMF 51371	left dentary fragment		
LM2	9.4	7.2	6.8
lM3	8.8	6.9	6.3
lM4	8.5	6.5	5.4

cf. *N. crassirostrum*

Judy's Jumping Joint			
QMF 51372			
lP3	12.4	6.0	7.2
QMF 51376			
rP3	12.5	5.8	7.5
RSO			
AR 11109	lower		
rM2	9.1	5.9	6.0
J.H.			
QMF 30724			
lP3	>12.6	7.1	8.5

Isolated teeth

Bone Reef			
AR17590	lower		
rM2	9.0	6.1	6.1
rM3	8.8	6.2	5.6
rM4	8.2	5.8	5.25

cf. *N. crassirostrum* crushed skull lacking rostrum

Hiatus			
QMF 23216			
lM1	8.6	8.0	7.8
rM1			8.2
lM2	8.0	7.2	7.0
rM2	8.2	7.5	7.5
lM3	7.6	6.4	6.2
rM3	7.6	6.7	6.1
lM4	6.7	5.4	4.0
rM4	6.6	5.5	3.9

APPENDIX 2. Mean values for *Namilamadeta* spp. tooth dimensions, various localities.

Tooth	Length	Anterior Width	Posterior Width	N
Tom O's Quarry	*N. snideri*			
P^3	11.3	5.83	7.1	2
M^1	9.25	7.82	8	2
M^2	9.15	8.25	7.8	2
M^3	8.65	7.45	6.8	2
White Hunter	*N. albivenator*			
P^3	10.8	6.03	6.86	4
M^1	9.36	7.55	7.73	4
M^2	8.85	7.57	7.27	3
M^3	8.6	6.83	5.85	2
M^4	-7.2	6	-4.4	2(1)
P_3	9.35	4.65	5.8	2
M_1	8.77	5.53	6.13	3
M_2	8.56	5.9	6.13	3
M_3	8.4	5.93	5.87	3
M_4	7.7	5.35	4.9	2
Dirk's Towers DT6	*N. albivenator*			
P^3	10.82	5.65	6.93	3
M^1	8.9	8.07	7.93	3
M^2	8.47	7.73	7.23	3
M^3	8.2	6.93	-6.23	2(3)
M^4	7.15	5.8	4.5	2
Upper Site	*N. superior*			
P^3	11.85	6.6	8.15	2
M^1	9.75	9.2	8.8	2
M^2	8.6	-8.23	7.75	4(3)
M^3	8.4	7.72	6.7	3
M^4	7.7	6.4	4.8	2
Waynes Wok	*N. crassirostrum*			
P^3	-12.52	6.26	7.36	8(9)
M^1	9.16	8.8	8.71	12
M^2	8.73	8.07	7.74	11
M^3	8.37	7.38	6.84	5
M^4	7.42	6.34	5.11	5
P_3	10.33	-5.28	6.01	7(6)
M_1	9.65	6.05	6.68	4
M_2	9.3	6.68	6.55	4
M_3	9	6.9	6.2	1
M_4	9	6.1	5.4	1
Camel Sputum	*N. crassirostrum*			
P^3	12	6.08	7.28	6
M^1	9.1	8.36	8.44	5
M^2	8.77	8.47	8.23	10
M^3	8.49	7.66	7.01	7
M^4	7.63	6.6	4.85	3
P_3	10.63	5.37	6.17	3
M_1	9.07	6.07	6.77	3
M_2	8.73	6.67	6.57	4
M_3	8.57	6.57	6.07	4
M_4	8.4	6.22	5.5	5
Mike's Menagerie	cf. *N. crassirostrum*			
P_3	12.38	5.93	6.95	2
M_1	8.75	8.35	8.75	2
M_2	8.55	8.1	8.15	2
M_3	8.7	8.18	7.8	2
LSO	cf. *N. albivenator*			
M^1	8.85	-7.9	8.2	2(1)
P_3	8.4	5	5.4	1
M_1	9	5	5.3	1
M_2	8.9	5.6	5.3	1
M_3	8.3	5.9	5.4	1
M_4	7.8	5.3	4.9	1
Neville's Garden	*N.* sp.			
P^3	11.87	5.93	7.02	3
M^1	8.4	7.95	8	2
Outasite	*N.* sp.			
P^3	13.13	6.3	7.7	2
Judys Jumping Joint	cf. *N. crassirostrum*			
P^3	12.45	5.9	7.35	2
Hiatus (skull)	*N.* sp.			
M^1	8.6	8	-8	1(2)
M^2	8.1	7.35	7.25	2
M^3	7.6	6.55	6.15	2
M^4	6.65	5.45	3.95	2

APPENDIX 3 . Data for bivariate analyses of P3, M1

Specimen no.	Locality	lP3	wP3	lM1	aM1	pM1	P3 l/pw	M1 l/pw
SAMP19951	*N. snideri*	11	7.15				1.54	
SAMP19951	type	11.6	7.05	9.6	8.2	8.5	1.65	1.13
NMV8993				8.55	7.3	7.3		1.17
NMV8994				9.6	7.95	8.2		1.17
AR16775	White Hunter	10.4	6.65	9.3	7.2	7.3	1.56	1.27
QMF51337		11.1	7	9.5	7.6	7.7	1.59	1.23
AR17188		10.4	6.5	9.1	7.5	7.7	1.60	1.18
QMF51338		11.3	7.3				1.55	
QMF51339				9.55	7.9	8.2		1.16
QMF13093	Dirks Towers	10.5	7	8.4	8	7.5	1.50	1.12
QMF20035		11	6.7	9.1	8.2	8.7	1.64	1.05
QMF20037		10.95	7.1	9.2	8	7.6	1.54	1.21
QMF24138	Quantum Leap	10.5	6.9	9	7.6	8.4	1.52	1.07
QMF40276	Upper site	12	7.5	10	8.9	8.8	1.60	1.14
QMF40276*	type	11.7	8.6	9.5	9.5	8.8	1.36	1.08
QMF51346	Waynes Wok	12.4	7.8	8.7	8.8	9	1.59	0.97
QMF51348				9	8.4	8.4		1.07
QMF51349		11.9	6.75	9.3	8.5	8.4	1.76	1.11
QMF51351		13.4	7.6	10.2	9.3	9.2	1.76	1.11
QMF51350		13.8	7.5				1.84	
QMF51345				9.2	9.3	8.9		1.03
QMF51347				9.2	8.2	8.3		1.11
AR12858				9.3	9.5	9.4		0.99
QMF30756		12.1	7.7				1.57	
QMF30757				9	9.1	8.8		1.02
QMF30758				9	8.7	8.2		1.10
QMF31462r	type	11.8	7	8.8	8.4	8.5	1.69	1.04
QMF31462l		11.75	6.9	8.9	8.6	8.7	1.70	1.02
QMF31480		12.7	7.6	9.4	8.8	8.7	1.67	1.08
AR8686	Camel Sputum	11.45	6.9	8.75	8	8	1.66	1.09
QMF51357		12.55	7.6				1.65	
QMF51359				8.55	7.9	8		1.07
QMF20497				9.7	9.1	9.2		1.05
QMF20574		11.4	7.2	9.3	8.8	9.1	1.58	1.02
QMF40279l		12.3	6.8	9.3			1.81	
QMF40279r		12	7.3	8.3	8	7.9	1.64	1.05
QMF30303l		12.25	7.7	8.7	8.5	8.3	1.59	1.05
QMF30303r		12.5		8.9	8.1	8.3		1.07
AR12946		12.5	7.45				1.68	
AR13374		11.8	7.3				1.62	
AR16838		12.3	7.25				1.70	
QMF51364	Mikes Menagerie	13.3	7.4	8.8	8.4	8.5	1.80	1.04
AR12868		11.45	6.5				1.76	
QMF51354	DT	11.8	6.8				1.74	
QMF36342		12	7.2				1.67	
QMF51356				8.7	8.4	7.9		1.10
QMF51373		11.1	6.75				1.64	

Specimen no.	Locality	lP3	wP3	lM1	aM1	pM1	P3 l/pw	M1 l/pw
QMF36350	DT			8.8	7.9	7.8		1.13
QMF51374	Nev Garden	11.55	6.9				1.67	
QMF23014		11.95	7.3	8.6	7.5	7.95	1.64	1.08
QMF23201*		12.1	6.85	8.2	8.4	8	1.77	1.03
QMF51372	Judys JJ	12.4	7.2				1.72	
QMF51376		12.5	7.5				1.67	
QMF30724*	JH	>12.6	8.5					
QMF23216+ AR91	Hiatus			8.6	8	7.8		1.10
no.		lp3	pwp3	lm1	awm1	pwm1	p3 l/pw	m1 l/pw
QMF40278	paratype	9.2	5.7	8.3	5.4	6.3	1.61	1.32
QMF51342	White Hunter			9.5	5.6	6		
QMF51343		9.5	5.9	8.5	5.6	6.2	1.61	1.37
QMF30700		10.1	6.8	8.7	6.3	7	1.49	1.24
QMF30506	D6	8.2	4.9	9	5	5.3	1.67	1.70
QMF51375	paratype	11.4	6.4	10.3	6.8	7	1.78	1.47
AR9711	Waynes Wok	10.1	6.2				1.63	
AR10789		10.9	6.4				1.70	
AR10639		10.4	5.8				1.70	
AR10638		9.9	5.8				1.71	
AR11866		10.3	5.9				1.75	
QMF24507				9.9	6.2	6.9		1.43
QMF30762				9.3	5.9	6.1		1.52
QMF30836			5.6	9.1	6.3	6.7		1.36
QMF51362	Camel Sputum	10.8	6.5	9.5	5.8	6.9	1.66	1.38
QMF51363		10.3	6.1	8.7	6.3	6.7	1.69	1.30
QMF12461		10.8	5.9	9	6.1	6.7	1.83	1.34
QMF51365	Mikes Menagerie	11.2	6.4	10	6.8	6.9	1.75	1.45
AR10703				8.9	6.1	6.6		1.35
AR9742		10.1	4.9				2.06	
AR9743				9.9	6.4	6.7		1.48
AR9915				10	6.2	6.5		1.54
AR12869				9.7	6.5	6.7		1.45
QMF24218	D5	10.45	6.7	8.8	6.5	6.8	1.56	1.29
QMF51373	StickyBeak	11.1	6.75				1.64	
QMF51366	Roo			9.4	5.8	6.7		1.40
QMF40251	LSO	8.4	5.4	9	5	5.3	1.56	1.70
QMF40281	Outasite	12.35	7.4				1.67	
QMF40282		13.9	8				1.74	