

The Macropodidae (Marsupialia) of the early Pleistocene Nelson Bay Local Fauna, Victoria, Australia

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Abstract

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The Nelson Bay Local Fauna, near Portland, Victoria, is the most diverse early Pleistocene assemblage yet described in Australia. It is composed of a mix of typical Pleistocene taxa and relict forms from the wet forests of the Pliocene. The assemblage preserves a diverse macropodid fauna consisting of at least six genera and 11 species. A potentially new species of *Protomnodon* is also possibly shared with the early Pliocene Hamilton Local Fauna and late Pliocene Dog Rocks Local Fauna. Together, the types of species and the high macropodid diversity suggests a mosaic environment of wet and dry sclerophyll forest with some open grassy areas was present in the Nelson Bay area during the early Pleistocene.

Keywords

Early Pleistocene marsupials, Macropodinae, Nelson Bay Local Fauna, Australia, *Protomnodon*, Hamilton Local Fauna.

Introduction

The Macropodoidea (kangaroos and relatives) are one of the most conspicuous elements of the Australian fauna and are often also common in fossil faunas. At least six genera and at least 11 species of macropodid are present in the Nelson Bay Local Fauna (LF), a diverse early Pleistocene assemblage recovered from palaeosols exposed in sea cliffs at Nelson Bay, near Portland, Victoria (38° 36' S, 141° 35' E). Other aspects of the fauna have previously been described and discussed, including an ektopodontid *Darcus duggani* (Rich et al., 2006), a giant phascolarctid (Piper, 2005), a giant pseudocheirid *Pseudokoala cathysantamaria* (Archer et al., 1997; Piper, 2007), diprotodontids and palorchestids (Piper, 2006a; Price and Piper, 2009), dasyurids, *Thylacinus cynocephalus*, peramelids, thylacoleonids, vombatids, phalangerids, pseudocheirids, petaurids, *Zaglossus* and murids (Gerdtz and Archbold, 2003; Piper, 2007). In this paper, the macropodid fauna is described, with the exception of *Baringa nelsonensis* Flannery and Hann, 1984, the most abundant member of the Nelson Bay LF, which has been described in detail elsewhere (Flannery and Hann, 1984; Piper and Herrmann, 2006). Inferences about the palaeoecology are also briefly discussed. For details of the geology and age of the Nelson Bay Formation, see Boutakoff (1963), MacFadden et al. (1987), Rich et al. (2006) and Piper (2007).

Terminology and abbreviations

Classification within the Macropodidae follows Kear and Cooke (2001), dental morphological terminology follows Ride (1993) and Prideaux (2004), and dental enumeration follows

Lockett (1993) and Lockett and Woolley (1996). All specimens are registered in the Museum Victoria palaeontology collection (prefix NMV P). All measurements are in millimetres.

Systematic palaeontology

As many of the taxa present in the Nelson Bay LF are well-known Pleistocene or extant species, detailed descriptions are generally unnecessary, so only diagnostic features and variation are discussed. As there is considerable intraspecific variation within species of *Protomnodon*, and a revision of Pleistocene material is required, fuller descriptions are given of the *Protomnodon* specimens from Nelson Bay to aid future researchers in such a task. Measurements for all specimens are given in the online Supplementary Material.

Macropodidae Gray, 1821

Sthenurinae Glauert, 1926

Simosthenurini Prideaux, 2004

Simosthenurus* sp. cf. *S. occidentalis Glauert, 1910

Referred material. NMV P216045, anterior half right I3; NMV P216047, posterior fragment left I3; NMV P216048, left I3; NMV P218251, talonid right m1?; NMV P216042, worn right dp2; NMV P173664, proximal phalanx IV; NMV P216147, proximal phalanx IV. Note: NMV P173639, a left i1 identified by Hann (1983) as *Simosthenurus* sp. cf. *S. occidentalis* has been re-identified during this study as the very worn i1 of *Palorchestes pickeringi* Piper, 2006a.

Remarks. The molar, although poorly preserved, is clearly identifiable as a simosthenurine owing to the presence of numerous fine enamel crenulations, straight lophs, a divided cristid obliqua and being low crowned (figs. 1B–D) (Prideaux, 2004). Both the molar and premolar (fig. 1A) fall within the size range of the southeastern population of *S. occidentalis* and are also similar to this species in overall morphology, in particular the development of the molar enamel crenulations. However, Prideaux (2004) stated that the molars of *S. occidentalis* are inseparable from *S. eurykaphus*; therefore, they are only tentatively referred to *Simosthenurus* sp. cf. *S. occidentalis* pending the discovery of more complete material.

Although they cannot be positively identified, as no other sthenurines have so far been identified in the Nelson Bay LF, and their overall morphology is consistent with that of *S. occidentalis*, it is most parsimonious to refer the I3 (fig. 1E) and postcranial elements (figs. 1I–N) to the same species as the other dental elements until such alternative evidence arises.

Simosthenurus occidentalis is one of the most common and widespread species of sthenurine in the mid to late Pleistocene. A single tooth from the late Pliocene Dog Rocks LF, Victoria, is referred to *Simosthenurus* sp. cf. *S. occidentalis* (Prideaux, 2004). Like this specimen, the Nelson Bay material is evidence for the presence of an *occidentalis*-like simosthenurine prior to the mid Pleistocene.

Simosthenurini sp. indet.

Referred material. NMV P216899, left I1.

Remarks. A single small, slightly worn sthenurine I1 is present in the Nelson Bay assemblage (figs. 1F–H). It is narrow and rounded allaying it with the *Simosthenurini*, and is sub-triangular in cross-section as in ‘*Procoptodon*’ *gilli* and ‘*Simosthenurus*’ *browneorum* (Prideaux, 2004), but is much smaller than either (crown length ~ 9.3 mm, occlusal length 3.2 mm, occlusal width 3.5 mm). Because of its small size and triangular cross-section it is unlikely to belong to *Si. occidentalis* (which is robust and oval), suggesting a second species of simosthenurine is present in the Nelson Bay LF.

Macropodidae Gray, 1821

Macropodinae (Gray, 1821)

***Macropus (Macropus) cf. giganteus titan* Shaw, 1790**

Referred material. NMV P216235a, right I3; NMV P200668, right I3; NMV P216039, talonid left M; NMV P216038, talonid left M; NMV P216043, lingual half metaloph right M; NMV P218244, metaloph left M; NMV P200697, left dp2; NMV P173634, partial left dentary containing m1–4; NMV P215983, left m2 and m3; NMV P200664, talonid left m; NMV P200583, partial right femur shaft and distal epiphysis; NMV P215912, partial femur shaft; NMV P215913, partial left femur shaft; NMV P200569, partial left fifth metatarsal; NMV P216124, partial left fifth metatarsal; NMV P216167, distal manus phalanx; NMV P173673, caudal vertebra; NMV P200559, partial dorsal vertebra; NMV P200560, partial dorsal vertebra; NMV P200561, partial rib and vertebra centrum; NMV P200582, anterior caudal vertebra; NMV P216232, three dorsal vertebrae and two partial anterior caudal vertebrae; NMV P216233, partial sacrum.

Remarks. Only a few isolated dental and postcranial elements indicate the presence of a large grazing macropodid in the Nelson Bay assemblage (fig. 2). The partial left dentary figured and described in Hann (1983) (NMV P173634) is missing from the Museum Victoria collections and so could not be examined. The features of the lower molars are consistent with those contained within the missing partial dentary described by Hann (1983), and so are judged to belong to the same species. The molars are much larger than the extant *Macropus giganteus*, falling within the size range of the larger fossil *Macropus giganteus titan* from Lancefield, Lake Colongulac, Spring Creek (Minhamite) and Queensland (Flannery, 1981), and in the case of NMV P215983 are towards the high end of this range. The premolar and incisors fall within the size ranges of both extant and fossil specimens, as do two *Macropus* metatarsals. Therefore, overall it seems that the Nelson Bay specimens represent the larger *Macropus giganteus titan* typical of the Late Pleistocene, indicating that the increase in body size experienced by this species had already occurred by the early Pleistocene.

***Macropus (Notamacropus) spp.* Dawson and Flannery, 1985**

Referred material. NMV P173678, right I2; NMV P200669, left I2; NMV P215807, left I2; NMV P215808, left I2; NMV P215809, left I2; NMV P215814, I2; NMV P200643, worn left I3; NMV P215813, left I3; NMV P215815, worn right I3; NMV P216046, unerupted left I3; NMV P173656, right maxillary fragment containing partial dP3 and M1?; NMV P187189, left dP3?; NMV P215783, metaloph left dP3?; NMV P200626, worn left M1?; NMV P187185, left M3 or M4; NMV P216887, left M3 or M4; NMV P200675, trigonid left m2?; NMV P200606, trigonid left m3?; NMV P215821, left m3?; NMV P173655, right i1; NMV P216895, partial left i1.

Remarks. A few isolated and partial molars are tentatively referred to *Macropus (Notamacropus) spp.* on the basis of being high crowned; possessing strong midlinks; having a vertical hypolophid, which is not markedly rounded or convex posteriorly and lacks any ornamentation or a posterior cingulid; possessing a strong preparacrista; and lacking a forelink on upper molars (fig. 3) (Dawson and Flannery, 1985).

The lower molars differ from *Baringa nelsonensis* in being relatively broader, with a broader, shorter, more upturned anterior cingulum and stronger premetacristid (fig. 3A). They differ from *Thylogale billardieri* in being much larger and higher crowned, and possessing a broader, shorter more upturned anterior cingulum. They are most similar overall to *Macropus (Notamacropus) rufogriseus* in size and in the morphology of the anterior cingulum.

Two small, unworn i1s may be referable to *Macropus (Notamacropus)* as they are lanceolate in shape, long relative to depth, bear sharp dorsal and ventral enamel flanges and lack any thick ventrolingual enamel (fig. 3B) (Dawson and Flannery, 1985). They are closest in size to *Macropus (Notamacropus) parryi* (max. depth, 5.4 mm and 5.3 mm, respectively).

Two upper molars (NMV P187185, P216887) are similar in size and morphology to *Macropus (Notamacropus) eugenii*, but also show some similarities to *Petrogale* (fig. 3C). Four other smaller upper molar specimens (NMV P173656, P187189, P200626, P215783) all possibly represent anterior

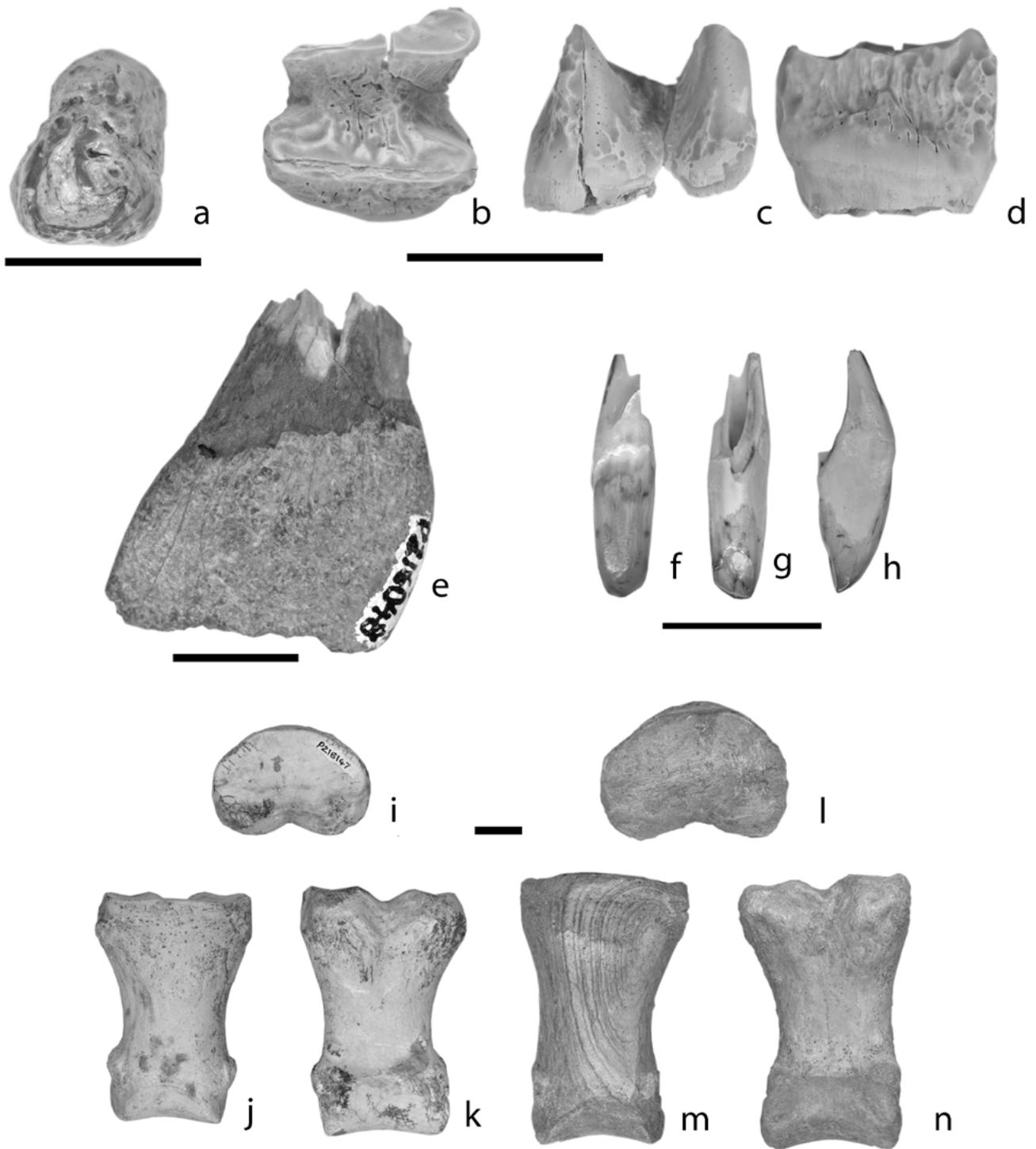


Figure 1. *Simosthenurus* sp. cf. *Si occidentalis*: a, NMV P216042, right dp2, occlusal view; b–d, NMV P218251, right m1?, occlusal, labial and posterior views; e, NMV P216048, left I3, labial view. *Simosthenurin* sp. indet.: f–h, NMV P216899, left I1, labial, lingual and posterior views. *Simosthenurus* sp. fourth proximal phalanges: i–k, NMV P216147, proximal, dorsal and plantar views; l–n, NMV P173664, proximal, dorsal and plantar views. Scale bars = 10 mm.

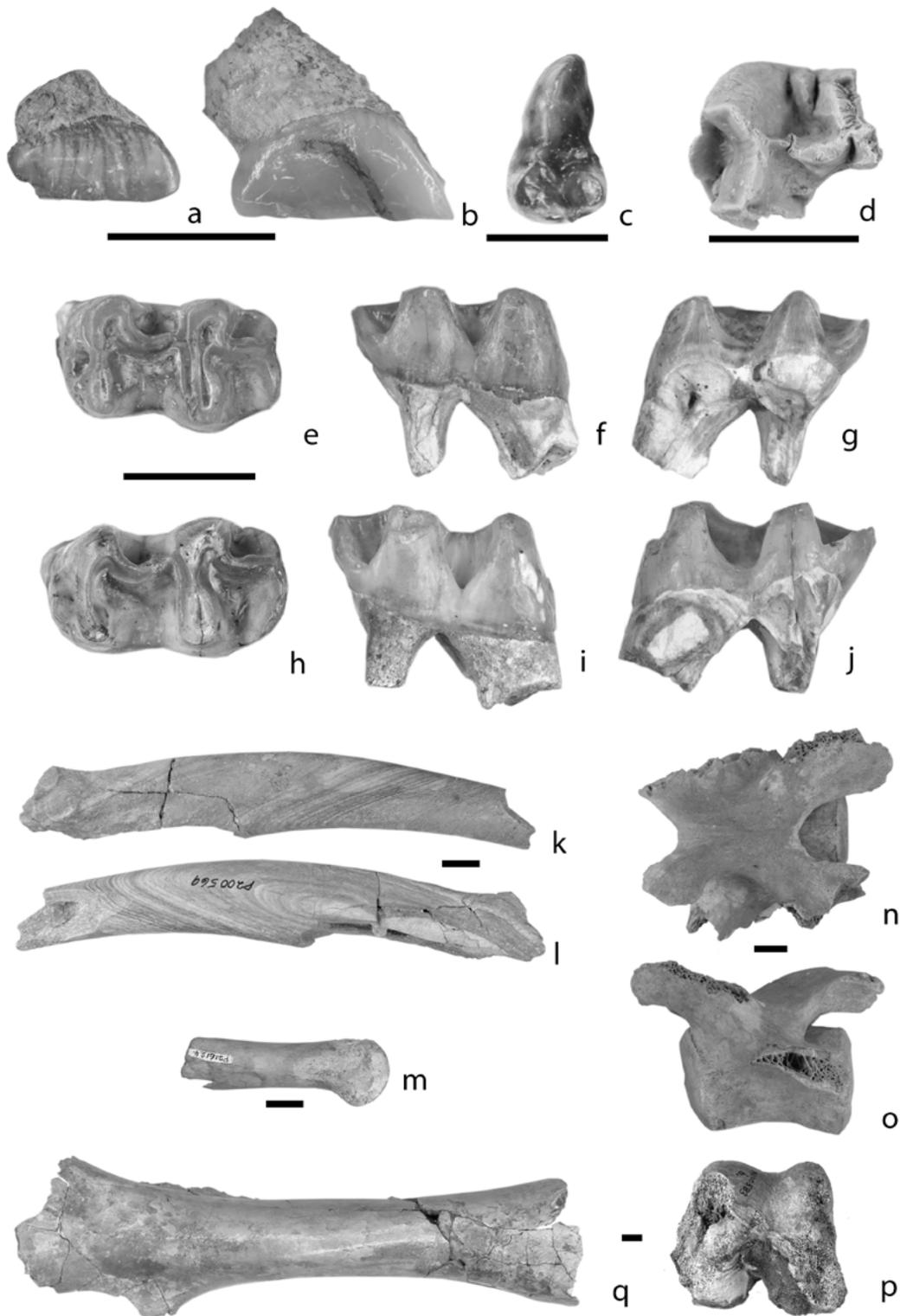


Figure 2. *Macropus (Macropus) giganteus titan*: a, NMV P2000668, right I3, labial view; b, NMV P216235a, right I3, labial view; c, NMV P200697, left dp2, occlusal view; d, NMV P216039, talonid left M, occlusal view; e–g, NMV P215983, left m2, occlusal, labial and lingual views; h–j, left m3, occlusal, labial and lingual views. k, l, NMV P200569, left fifth metatarsal, medial and lateral views; m, NMV P216124, partial left fifth metatarsal, lateral view; n, o, NMV P200582, caudal vertebra, dorsal and lateral views; p, q, NMV P200583, right femur shaft and distal epiphysis. Scale bars = 10 mm.

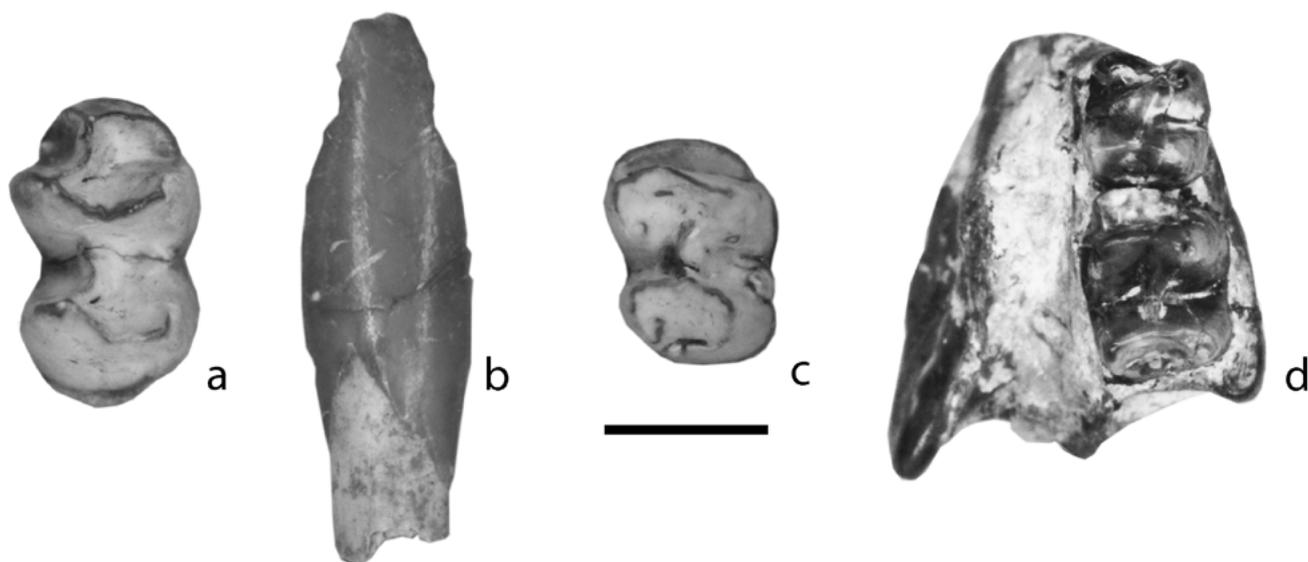


Figure 3. *Macropus (Notamacropus)* spp.: a, NMV P215821, left m3?, occlusal view; b, NMV P173655, right i1, labial view; c, NMV P187185, left M, occlusal view; d, NMV P173656, right dP3–M1?, occlusal view. Scale bar = 5 mm.

and deciduous molars from the same species (fig. 3D). They are smaller and relatively narrower, and have a much longer, narrower anterior cingulum than *Thylogale billardierii*, but are quite close in both size and morphology to *Macropus (Notamacropus) parryi*.

A few isolated upper incisors are also referable to this genus. They are similar in size and morphology to *Macropus (Notamacropus) rufogriseus* and *Macropus (Notamacropus) parma*.

Many of the features used here to identify these specimens as *Macropus* are also present in species of *Petrogale*, *Onychogalea* and *Prionotemnus*, and to add further difficulties there are no single characters that can be used to distinguish *Macropus* from other macropodines (Dawson and Flannery, 1985). At least two species are present in the Nelson Bay LF; however, owing to the fragmentary nature of the specimens, and a lack of association with premolars or incisors, identification to species level is extremely difficult and identification to generic level is questionable.

Thylogale sp. cf. *billardierii* (Desmarest, 1822)

Referred material. NMV P173658, right I1 and partial left I1; NMV P200485, left I1; NMV P200486, right I1; NMV P200487, right I1; NMV P207870, right I1; NMV P187178, left I2 and I3; NMV P200484, left I2; NMV P200483, left I3; NMV P200634, right I3; NMV P216260b, right I3; NMV P173573, left P3; NMV P200415, left P3; NMV P200417, left P3; NMV P200418, left P3; NMV P215784, left M1?; NMV P215779, right M2 and metaloph right M1?; NMV P215872, left M2?; NMV P216889, partial right M2?; NMV P215778, right M3; NMV P200439, right trigonid M3 or M4; NMV P216105, right M4 in maxilla fragment; NMV P215890, left anterior dentary fragment containing root of i1; NMV P215824, left i1; NMV P215906, root and posterior end of i1; NMV P165469e, left p3; NMV P215791, left p3; NMV P187860, right dp3; NMV P187861, left dp3; NMV

P187862, left dp3; NMV P215964, trigonid right dp3; NMV P215804, right m1–3 in dentary fragment; NMV P200699, left m1?; NMV P200427, hypolophid left m1; NMV P187205, hypolophid left m2; NMV P216884, right m2; NMV P173588, left m3; NMV P200425, hypolophid right m3; NMV P215801, right m3; NMV P215851, worn right m3; NMV P218243, hypolophid right m3; NMV P215860, trigonid left m3; NMV P200642, trigonid left m3 or m4?; NMV P215802, trigonid right m3 or m4; NMV P200426/P200423, left m4?

Remarks. The majority of the material consists of isolated complete and partial molars and upper incisors (fig. 4). The isolated molars are very similar in morphology to *Baringa nelsonensis*, but can be distinguished based on size, as they are smaller. The lower molars, p3s and upper incisors are virtually indistinguishable from the extant *Thylogale billardierii*, but are slightly smaller. A small, isolated slightly worn i1 is referred to *T. sp. cf. billardierii* as it is very similar in size and morphology to *T. billardierii*, being long and narrow, with narrow dorsal and ventral enamel flanges, a ventrolingual enamel band and a subhorizontal wear facet (length 22.1 mm, maximum depth 6.2 mm) (fig. 4A).

The P3 NMV P173573 is worn, so appears to be slightly shorter than the P3 of *T. billardierii*, but is very similar morphologically. It was previously identified as a dP2 of *Baringa nelsonensis* (Flannery and Hann, 1984; Piper and Herrmann, 2006). Some of the upper molars are virtually indistinguishable from those of *T. billardierii* (e.g. NMV P215779); others are more tentatively referred to *T. sp. cf. billardierii*.

Overall, these specimens clearly belong to *Thylogale* and are closest in morphology to extant *T. billardierii*, but are about 8% smaller. A small specimen of *T. billardierii* has been reported from Mt Hamilton, Victoria (Wakefield, 1963). *T. billardierii* formerly occupied SE South Australia and Victoria, but is now extinct on the mainland, and is restricted to Tasmania and the larger Bass Strait islands (Strahan, 1995).

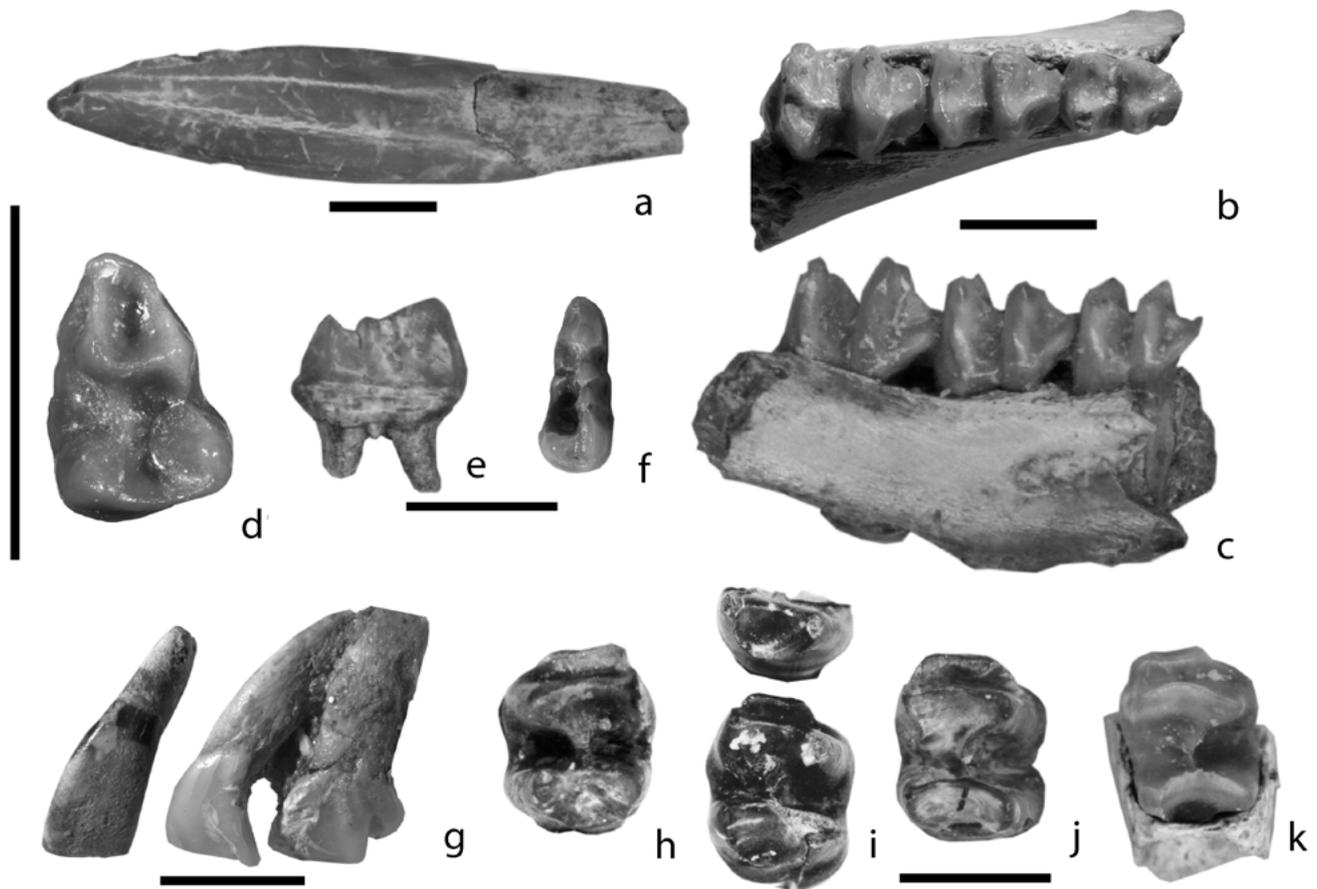


Figure 4. *Thylogale* sp. cf. *T. billardierii*: a, NMV P215824, left i1, labial view; b, c, NMV P215804, right partial dentary with m1–3, occlusal and labial views; d, NMV P187860, right dp3, occlusal view; e, NMV P215791, left p3, labial view; f, NMV P200415, left P3, occlusal view; g, NMV P200485, left I1, NMV P187178, left I2–3, labial view; h, NMV P215784, left M1?, occlusal view; i, NMV P215779, right M1–2, occlusal view; j, NMV P215778, right M3, occlusal view; k, NMV P216105, right M4, occlusal view. Scale bars = 5 mm (h–k all to same scale).

***Protomnodon* sp. cf. *brehus* (Owen, 1874)**

Referred material. NMV P201127, crushed left and right dentaries with i1, p3, m1–4; NMV P215985, left dentary fragment with m3–4; NMV P215991, trigonid right m; NMV P215994, tip of right i1; NMV P201153, tip of left i1; NMV P216001, right dp2; NMV P173647, left dp2; NMV P215995, right dp2.

Remarks. The specimens here referred to *Protomnodon* sp. cf. *brehus* Owen (1874) are very similar in size and morphology to *P. brehus* as described by Bartholomai (1973) from the eastern Darling Downs, Queensland (fig. 5). They conform to the revised generic definition of Dawson (2004) with the exception of the lower incisors, which show greater similarities to *Silvaroo bila* Dawson, 2004.

P. sp. cf. brehus is less common in the Nelson Bay LF than *P. roechus*. It is distinguished from *P. roechus* by the following characters, which are considered here to be enough to warrant the separation of the Nelson Bay material into two large species (see below): 1) the crest of dp2 is more markedly curved lingually at its posterior end; 2) p3 is slightly broader, has three to four well-defined vertical grooves and ridges, and is unconstricted at

the posterior one-third; 3) the lower molars are relatively broader; 4) the anterior cingulum is shorter and broader, extending across the entire anterior face of the protolophid; 5) a stronger premetacristid and an anterolingual fossette are present; 6) a well-developed horizontal posterior cingulid and postentocristid are present; 7) m4 is less constricted across the talonid basin.

The lower molars of *P. sp. cf. brehus* from Nelson Bay differ from *P. brehus* from other faunas in the size of the m3 and m4, which are both relatively shorter and narrower than most other specimens. The i1s are also smaller, shallower dorsoventrally but wider buccolingually, and are more lanceolate than the i1s of *P. anak*, *P. brehus* and *P. roechus*. In these features the incisors are more similar to smaller Pliocene *Protomnodon* species e.g. *P. snewini* (Bartholomai, 1978) and *P. otibandus* (Plane, 1967), but differ from them in the unusual vertical wear pattern and lack of a ventral enamel flange.

***Protomnodon roechus* Owen, 1874**

Referred material. NMV P215986, left P3, M1–4 in maxilla fragment, and associated premaxilla fragment with alveoli for I1–3;

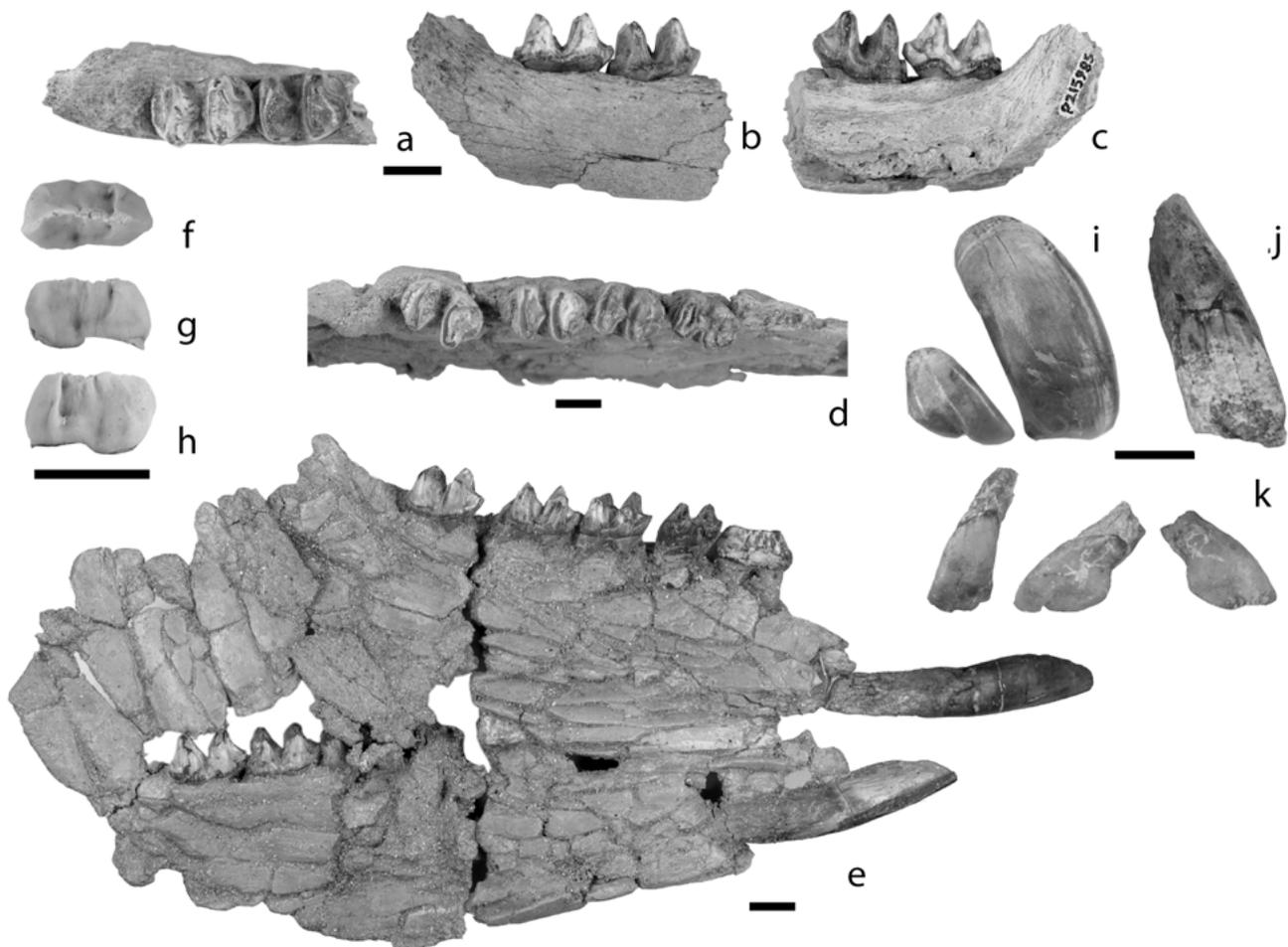


Figure 5. *Protetnodon* sp. cf. *P. brehus*: a–c, NMV P215985, left dentary fragment with m3–4, occlusal, lingual and labial views; d, e, NMV P201127, crushed dentaries, right p3, m1–4, occlusal view, and right and left il, p3, m1–4, labial and lingual views, respectively; f–h, NMV P173647, left dp2, occlusal, lingual and labial views. *Protetnodon* sp. upper incisors: i, NMV P173663, right I1, I3, labial view; j, NMV P215990, right I1, labial view; k, NMV P173688, left I2–3, right I3, labial view. Scale bars = 10 mm.

NMV P173645, right dP2; NMV P173643, left P3; NMV P173644, right P3; NMV P173628*, left P3; NMV P215999, anterior half left P3; NMV P173682, posterior half right P3; NMV P173687, incomplete right P3; NMV P200648/P200657, right M1 and P3 fragment; NMV P173685/P200654*, left M2; NMV P200649/P200653*, left M3; NMV P173681, right M3; NMV P216003, right M3; NMV P173686, left M4 and associated right anterior cingulum of M4; NMV P173683, right i1; NMV P215988, worn left i1; NMV P216041, left i1 tip; NMV P165457, partial right dentary containing p3, m1–4; NMV P173640, dentary fragment containing right p3, m1–2, and associated partial i1 and m3; NMV P173641, associated right p3, dp3, m1, m2; NMV P173642, dentary fragments containing p3, m1–2, m4 and associated m3; NMV P216014, trigonid right m1; NMV P216016, trigonid right m2; NMV P173684, partial right m3 (missing trigonid); NMV P216017, hypolophid right m3; NMV P216007, hypolophid left m4. (*NMV P173685/P200654 and NMV P200653/P200649 are probably from the same individual as they were collected from the same location, share similar stages of wear and type of preservation, and occlusal and interstitial wear patterns align. Each tooth bears two catalogue numbers as the anterior and posterior portions of the teeth were found separately during

collecting carried out in the 1970s and 80s, which were later matched up by the author. They are also thought to be associated with a P3 (P173628) from the same location (note with specimen, C. Hann, 1983).

Remarks. The specimens referred here to *Protetnodon roechus* Owen, 1874 are very similar in morphology, but are towards the lower end of the size range of the type population of *P. roechus* from the Darling Downs, Queensland (fig. 6) (Bartholomai, 1973).

NMV P165457 is the best-preserved and most complete dentary of *Protetnodon* from Nelson Bay (figs. 6A–C). It is broken at the symphysis, just anterior of the mental foramen, and lacks the ascending ramus. It is relatively robust, and is deeper dorso-ventrally than *P. anak*. It is slightly deeper below m1 than below m4. Although difficult to compare, the diastema is possibly slightly shorter and is more robust relative to the length of the molar row than in *P. anak*. The large oval mental foramen is close to p3, and the buccinator fossa extends from p3 posteriorly to below the anterior root of m3.

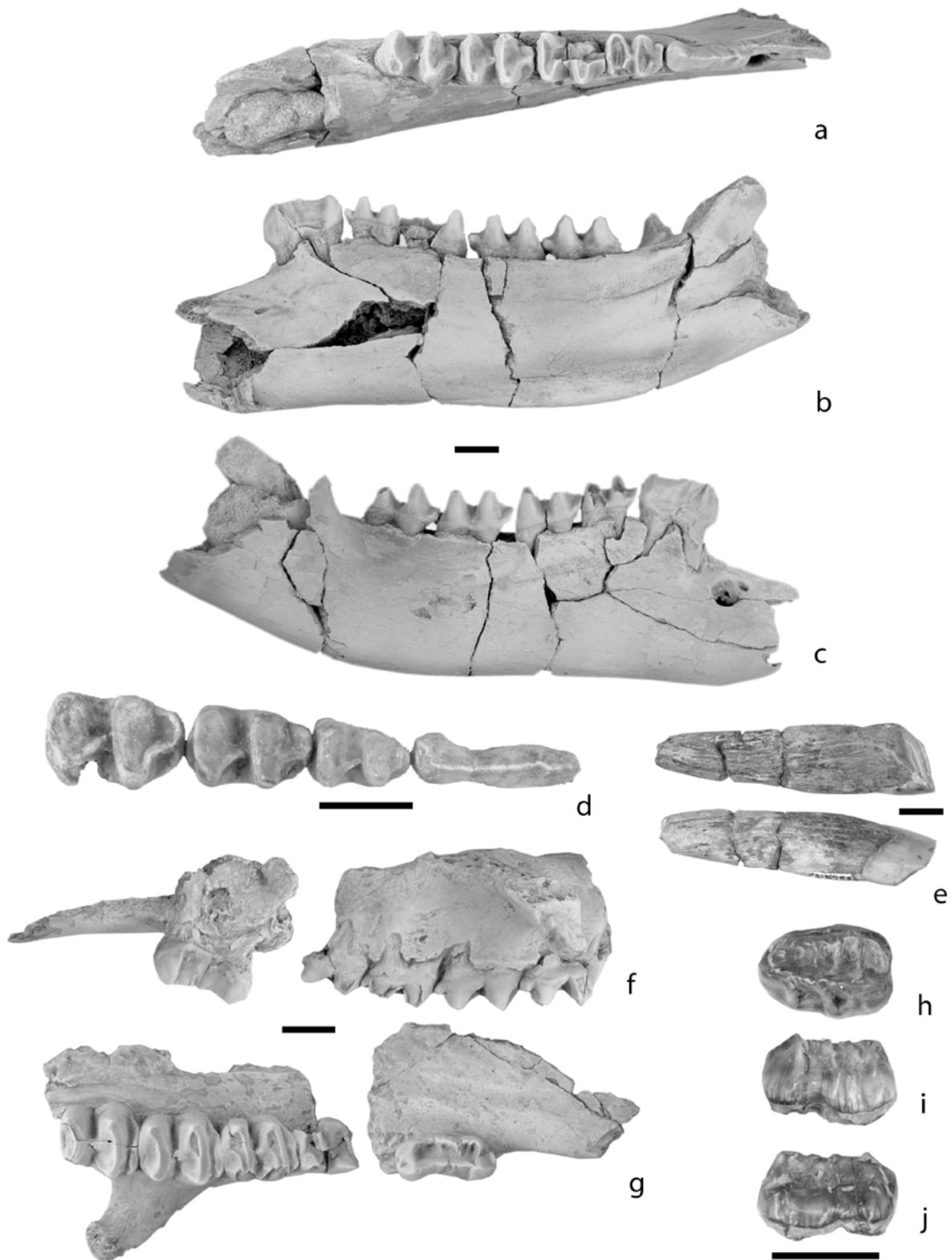


Figure 6. *Protomnodon roechus*: a–c, NMV P165457, right partial dentary with p3, m1–4, occlusal, lingual and labial views; d, NMV P173641, right juvenile tooth row with unerupted p3, dp3, m1–2, occlusal view; e, NMV P215988, left i1, lingual and labial views; f, g, NMV P215986, left partial maxilla with P3, M1–4, labial and occlusal views; h–j, NMV P173645, right dP2, occlusal, labial and lingual views. Scale bars = 10 mm.

Although no unworn i1s are preserved for *P. roechus* from Nelson Bay, the i1 root associated with NMV P173640, and the isolated extremely worn left i1 (NMV P215988) (fig. 6E), are considerably more robust than the i1s referred to *P. sp. cf. brehus* from Nelson Bay, and are more within the expected size range for the species.

In NMV P173642, a poorly developed posterior cingulid is present on all molars but is obscured by interstitial wear in the anterior molars. It is less shelf-like when compared with the posterior cingulid of *P. sp. cf. brehus* from Nelson Bay, and is positioned higher on the hypolophid. A horizontal groove is sometimes developed around the posterior swollen base of the hypolophid. The poor preservation of the enamel in NMV P173642 possibly artificially accentuates such a groove making it appear more shelf-like. The presence of a posterior cingulid on these specimens does not rule out their referral to *P. roechus*, as although the absence of a posterior cingulid on the lower molars is a defining characteristic of *P. roechus*, it does occur very rarely within the species, particularly on dp3 (Bartholomai, 1973, 1977). This pattern of variable development of a posterior cingulid is similar to that seen in *P. anak*, where it is less well developed than in *P. brehus*, and is not always present on all molars within the same individual (Bartholomai, 1973).

dp2 of *P. roechus* has not been reported or described in the literature. NMV P173645 (fig. 6H–J) is tentatively referred to *P. roechus* as it does not fit the descriptions of dp2 for *P. anak* or *P. brehus* given by Bartholomai (1973) and Tedford (1967), and differs from NMV P215995 (from Nelson Bay) here assigned to *P. sp. cf. brehus*. It is sub-triangular in occlusal outline, but is broader and more rounded than NMV P215995. It is composed of a main blade, a very low posterolingual cusp and a wide lingual cingulum. The main blade is positioned more centrally than in NMV P215995. It consists of a prominent anterior and posterior cusp, and two lower intermediate cusps. An anterior ridge descends from the anterior cusp, curving near the base of the crown towards the lingual cingulum, but does not join it. A second strong, sharp ridge descends labially, terminating approximately two-thirds of the way down the crown in a small tubercle. Sharp non-vertical labial ridges also descend from the two intermediate cusps, the posterior one being slightly shorter. They are linked at the bottom by a well-defined cingulum, forming a small pocket. A pocket is also formed by a cingulum that extends from the base of the anterior-most labial ridge towards the first intermediate ridge, the two separated by a tiny tubercle. A short ridge descends labially from the posterior cusp, but remains unconnected by a labial cingulum. The non-tuberculate lingual cingulum runs from the posterolingual cusp to just posterior of the anterior-most tip of the crown, delineating a wide lingual basin. Well-defined ridges in line with the intermediate cusps cross the basin to join to the lingual cingulum, dividing the basin into three sections. A broad ridge descends lingually from the anterior cusp but does not cross to the lingual cingulum, instead forming a constriction in the width of the basin. A strong low ridge descends from the posterior cusp to the very low, poorly defined

posterolingual cusp, and a second ridge descends posteriorly then curves lingually to the base of the posterolingual cusp, defining a large posterior fossette. The dp2 (NMV P215995) referred to *P. sp. cf. brehus* from Nelson Bay differs from NMV P173645 in having less well-defined labial and lingual ridges and labial 'pockets', a narrower lingual basin and a higher, better defined posterolingual cusp, connected to the posterior cusp by a higher ridge.

The P3s here referred to *P. roechus* are all similar morphologically, varying mainly in the continuity of the lingual cingulum. They are very similar to a P3 figured for *P. roechus* from the Darling Downs (Bartholomai, 1973; fig. 7(6), p. 335). They possess a labially concave crown characteristic of *P. roechus*, the lingual cingulum does not extend beyond the prominent anterior cusp and the anterolingual fossette is often poorly defined (Bartholomai, 1973); however, the three well-defined ridges on the labial side of the crest are more vertical than those described for *P. roechus* from the Darling Downs (Bartholomai, 1973).

The upper molars are very similar in both size and morphology in *P. brehus* and *P. roechus*, and are therefore very difficult to distinguish in isolated specimens. However, the specimens here referred to *P. roechus* are done so based on the straight anterior edge of the anterior cingulum and the presence of a variably developed tubercle in the lingual extremity of the median valley, both characteristics of *P. roechus* (Bartholomai, 1973). Other more variable differences noted include: a slightly narrower anterior cingulum, lacking an anterolingual fossette and possessing fewer, less well-developed ridgelets; a less well-developed preparacrista; and a slightly stronger developed postparacrista.

As seen in *P. sp. cf. brehus* from Nelson Bay, the posterior lower molars of the Nelson Bay *P. roechus* are relatively smaller in comparison to other examples of the species from other sites. The Nelson Bay *P. roechus* is smaller overall compared to the type population from the Darling Downs, Queensland, but is similar in size to a single specimen from Cement Mills, Gore (Bartholomai, 1977). Although it bears some similarities to *P. anak*, the proportions of the dentary and some features of the dentition clearly place it closer to *P. roechus*. To date, there has been no study into whether *Protemnodon* was sexually dimorphic, and the small sample size, plus the absence of any larger specimens at Nelson Bay does not allow any further speculation on this matter.

Few *P. roechus* specimens have been described in the literature, and some have been included within descriptions of *P. brehus*, e.g. Bingara and Menindee LFs (Marcus, 1976; Tedford, 1967), causing further confusion. Some authors have suggested that *P. roechus* is synonymous with *P. brehus* (e.g. Hann, 1983; Marshall, 1973; Stirton, 1963), as specimens can possess combinations of the characteristic features of both species, which in themselves are often highly variable. The fact that both species often occur together within the same faunas may offer further support for this theory. The Nelson Bay specimens are here tentatively separated into *P. sp. cf. brehus* and *P. roechus* following Bartholomai (1973) pending a much-needed revision of the Pleistocene species.

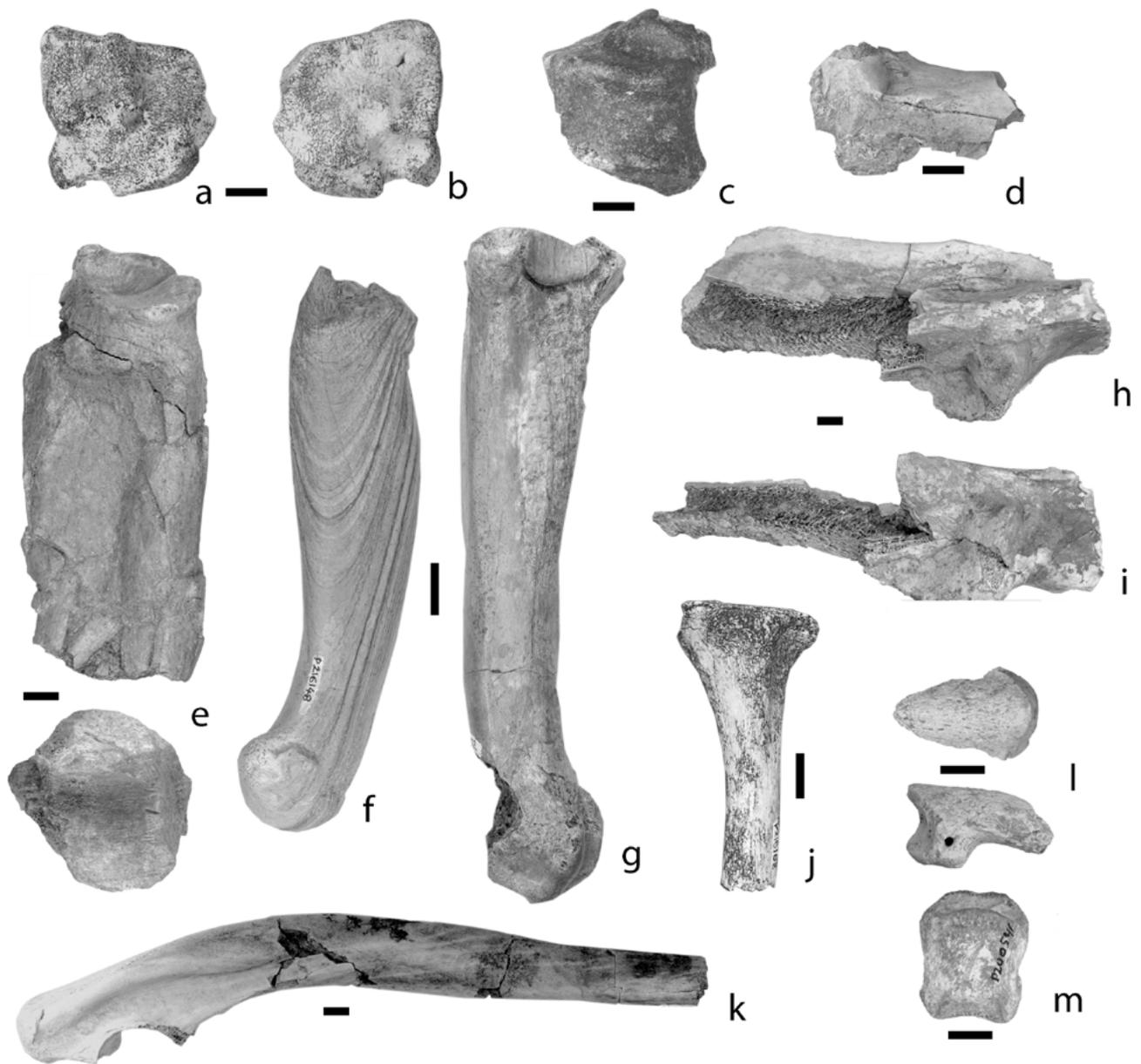


Figure 7. *Protetnodon* sp. postcranial material: a, b, NMV P216160, right cuboid; c, NMV P216155, right astragalus, dorsal view; d, NMV P215118, right partial calcaneum, dorsal view; e, NMV P216071, crushed distal end of left tibia, lateral view; f, NMV P216148, right fifth metatarsal, lateral view; g, NMV P216152, left fourth metatarsal, medial view; h, i, NMV P173675, partial left innominate (ilium), dorsomedial and medial views; j, NMV P216158, proximal end of right fibula; k, NMV P215909, left ulna, lateral view; l, NMV P173669, ungual, dorsal and lateral views; m, NMV P200451, distal phalanx, dorsal view. Scale bars = 10 mm.

Protetnodon large sp. indet.

Referred material. NMV P215990, right I1; NMV P173663, right I1 and I3; NMV P173637, right I2; NMV P218260, left I2; NMV P173688, left and right I3, and left I2; NMV P215992d, right I3; NMV P215993, right I3; NMV P216030, left I3; NMV P216033, right I3; NMV P216034, left I3; NMV P218249, right posterior portion I3. NMV P173675, partial left innominate; NMV P215909; right ulna; NMV P216071, left distal tibia epiphysis and part shaft; NMV

P216154, partial right distal tibia epiphysis; NMV P216158, proximal end right fibula shaft*; NMV P200562, proximal end right fourth metatarsal; NMV P216141, distal end left fourth metatarsal; NMV P216152, left fourth metatarsal; NMV P216148, left fifth metatarsal; NMV P216151, left fifth metatarsal; NMV P216118, partial right calcaneum*; NMV P216155, right astragalus*; NMV P216139, right cuboid*; NMV P216160, partial right cuboid*; NMV P200541, distal phalanx; NMV P216171, distal phalanx; NMV P216200, distal

Table 1. Dimensions of *Protomnodon* n. sp. A upper dentition from the Nelson Bay, Hamilton and Dog Rocks local faunas.

Location	Specimen number	Tooth	Length	Anterior width	Posterior width
Nelson Bay	P216005	dP2	14.5	7.7	8.8
	P200471	dP2	13.6	6.5	7.6
	P187198	P3	21.0	7.0	12.0
	P215998	P3	21.5	9.6	10.3
	P216005	P3	21.7	10.5	11.5e
	P216013	M1	11.0	8.8	9.6
	P200472	M1	12.2	8.8	9.7
	P215788	M1?	-	8.0	-
	P218245	M2	11.9	9.9	10.0
	P216040	M2	-	-	10.6e
	P187192	M3	12.9	11.0	11.4
	P200473	M3	13.8	10.9	11.2
	P200604	M3	12.4	10.8	10.9
P216005	M3	13.2	11.8	12.3	
Hamilton	P160372	dP3	9.9	9.6	10.1
	PM 4429	M2	11.3	10.1	10.6
Dog Rocks	P201862b	M1	11.4	9.0e	10.3
	P201862b	M3	13.8	11.6	11.9

phalanx; NMV 173669, ungual; NMV P216169, ungual, NMV P216195, ungual. *These elements were found in the same location and display a similar state of preservation, therefore are probably from the same individual. †These elements show very similar preservation, and although there is no location data, they were collected by the same person and are probably from the same individual.

Remarks. A number of isolated *Protomnodon* upper incisors are present in the Nelson Bay LF (figs. 5I–K) as well as several postcranial elements (fig. 7); however, owing to the scarcity of *Protomnodon* incisors in the fossil record, their lack of association with other dental material identifiable to species, the scarcity of associated postcranial and dental material, confusion over the validity of *P. roechus* and apparent intraspecific morphological variability, it is not possible to confidently assign any of the Nelson Bay specimens to species. It is probable that both *P. roechus* and *P. brehus* are represented among them.

Protomnodon n. sp. A

cf. *Protomnodon* sp. Turnbull and Lundelius, 1970: 63, pl. XXVIII.

Protomnodon sp. A Whitelaw, 1989: 625.

Protomnodon sp. Flannery, Rich, Turnbull and Lundelius, 1992: 29, figs. 14C–E, 15.

A collection of small *Protomnodon* teeth from Nelson Bay (figs. 8, 9; table 1) show similarities to upper molars and premolars of *Protomnodon* from the early Pliocene Hamilton LF (4.62–4.48 Ma) in

Table 2. Comparison of the ratio of the M1 length to P3 length in species of *Protomnodon*.

	Ratio M1L/P3L
<i>P. n. sp. A</i>	0.54
<i>P. otibandus</i>	0.57
<i>P. chinchillaensis</i>	0.56
<i>P. devisi</i>	0.65
<i>P. snewini</i>	0.66
<i>P. anak</i>	0.67
<i>P. brehus</i>	0.71
<i>P. roechus</i>	0.69
<i>P. hopei</i>	0.66
<i>P. tumbuna</i>	0.69

western Victoria and the late Pliocene Dog Rocks LF, Batesford, Port Philip Basin, Victoria (2.58–1.95 Ma) (Flannery et al., 1992; Turnbull and Lundelius, 1970; Whitelaw, 1991). They probably represent a new species of *Protomnodon*, but without review of the genus, or until more complete material is found, it is not possible to definitively ascertain this and it is therefore not named here.

Nelson Bay referred material. NMV P216005, associated right dP2, unerupted P3 and M3; NMV P200471, right dP2; NMV P187198, right P3; NMV P215998, right P3; NMV P200472, right M1; NMV P216013, right M1; NMV P215785, protoloph left M1; NMV P215788, protoloph left M1?; NMV P218245, left M2; NMV P216040, metaloph right M2; NMV P187192, right M3; NMV P200473, right M3; NMV P200604, left M3; NMV P216009, protoloph left M3.

Hamilton referred material. NMV P160372, left dP3; PM 4429, left M2 (described as dP3 in Turnbull and Lundelius (1970), p. 63–64; pl. XXVII A–E, and M1 in Flannery et al. (1992), p.29); NMV P162896, anterior fragment of left dP2.

Dog Rocks referred material. NMV P201862b, right M1, M3.

Diagnosis. Square, moderately low-crowned upper molars, unconstricted across the median valley, with gently sloping lingual loph margins and swollen loph bases; anterior cingulum square-shaped and restricted lingually, particularly in dP3 and M1. Variably developed postlink present on anterior upper molars in some specimens. Relatively and actually elongate P3 with four intermediate cuspules, of which the centre two are the most distinct.

Differs from all other known species of *Protomnodon*, except *P. otibandus* and *P. chinchillaensis*, in possessing a P3 that is relatively elongate compared to upper molars (see table 2), and from all species in having upper molars that are more rounded in occlusal outline (i.e. unconstricted across the median valley – base of loph expanded lingually and swollen in the labial moiety of the transverse median valley, forming a convex labial margin in occlusal view). Differs from all species except *P. otibandus* and *P. tumbuna* in having gently sloping lingual loph margins and a variably developed postlink on anterior molars in some individuals.

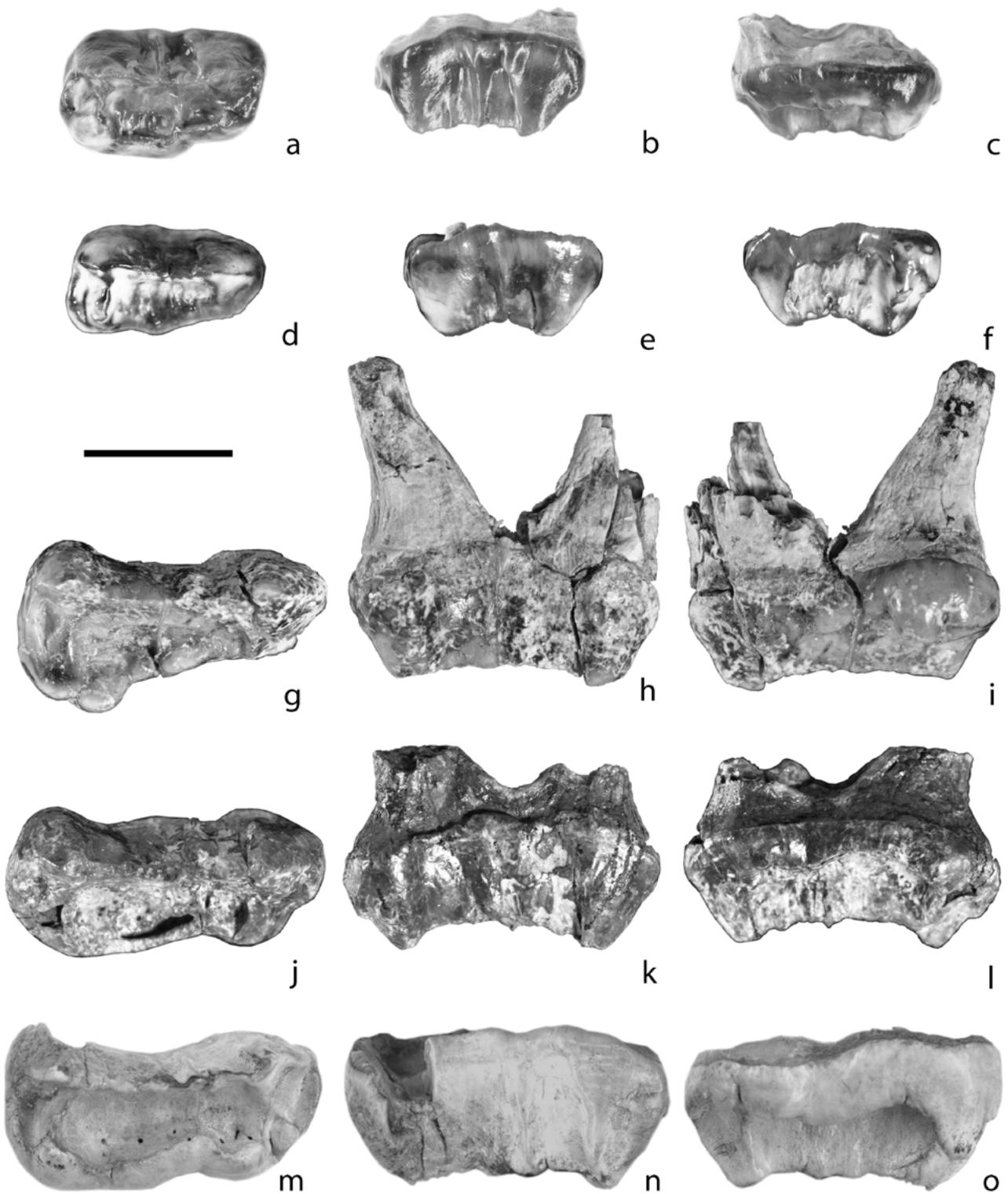


Figure 8. *Protomnodon* n. sp. A from the Nelson Bay LF: a–c, NMV P216005, right dP2, occlusal, labial and lingual views; d–f, NMV P200471, right dP2, occlusal, labial and lingual views; g–i, NMV P187198, right P3, occlusal, labial and lingual views; j–l, NMV P215998, right P3, occlusal, labial and lingual views; m–o, NMV P216005, right unerupted P3, occlusal, labial and lingual views. Scale bar = 10 mm.

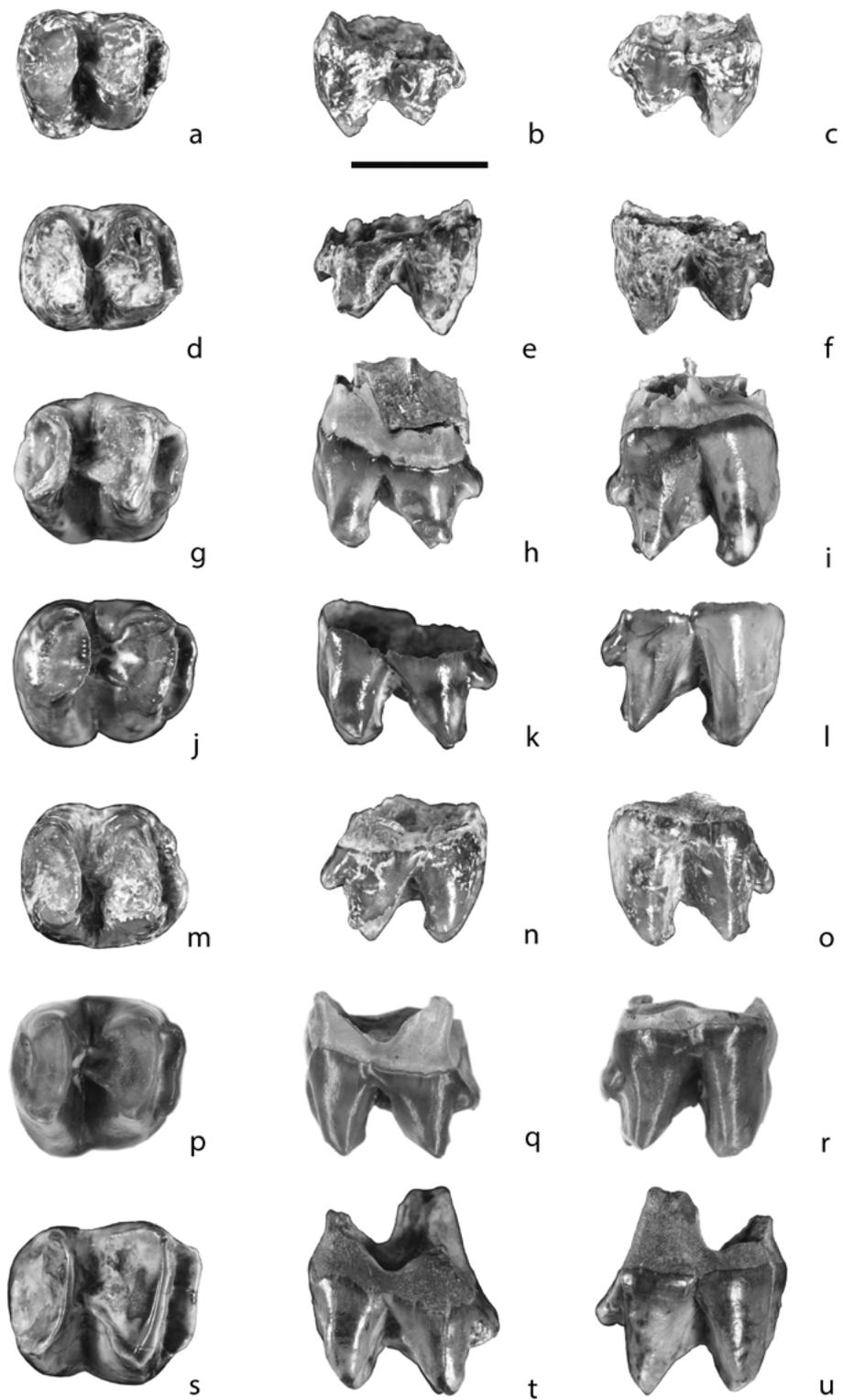


Figure 9. *Protomnodon* n. sp. A from the Nelson Bay LF: a–c, NMV P216013, right M1, occlusal, labial and lingual views; d–f, NMV P218245, left M2, occlusal, labial and lingual views; g–i, NMV P187192, right M3, occlusal, labial and lingual views; j–l, NMV P200473, right M3, occlusal, labial and lingual views; m–o, NMV P200604, left M3, occlusal, labial and lingual views; p–r, NMV P216005, right M3, occlusal, labial and lingual views. *Protomnodon* n. sp. A from the Dog Rocks LF: s–u, NMV P201862b, right M3, occlusal, labial and lingual views. Scale bar = 10 mm.

Differs from *P. anak*, *P. brehus*, *P. roechus* and *P. devisi* in being smaller, in having upper molars with narrower and shorter anterior cinguli, relatively stronger premetacristae and postparacristae, and a tightly V-shaped median valley. The P3 has four intermediate cuspules and labial ridgelets, of which the centre two are most defined (in other species the anterior-most ridgelets are the most distinct) and lacks lingual ridgelets that cross the lingual basin. Differs from *P. brehus*, *P. roechus*, *P. chinchillaensis* and *P. devisi* in having only an occasional single, weak, lingually positioned 'forelink' instead of numerous 'ridgelets' on the anterior cingulum of the upper molars. Differs from *P. chinchillaensis* in having weaker premetacrista in M2–3 and a more square-shaped anterior cingulum.

Differs from *P. otibandus* in being higher crowned, having narrower and longer anterior cinguli on upper molars, and having a premolar with two distinct intermediate labial ridgelets, less distinct lingual ridgelets and a more tuberculate lingual cingulum.

Differs from *P. snewini* in having a stronger postparacrista, premetacrista and midlink, a narrower, more lingually restricted and more basin-like anterior cingulum on upper molars, and a more robust P3.

Differs from *P. nombe* and *P. tumbuna* in being larger, from *P. tumbuna* and *P. hopei* in having relatively narrower upper molars, and from *P. tumbuna* in having a P3 with a less concave buccal margin, a tuberculate lingual cingulum, four intermediate cuspules and ridgelets, and lacking a buccal fossette; and having a much stronger preparacrista on upper molars.

Description. Only the upper dentition is known from Nelson Bay (figs. 8, 9). *Protetnodon* n. sp. A shows many morphological similarities to both *Protetnodon* and *Wallabia*. It falls within the size range of *P. chinchillaensis* and *P. otibandus*, but is closest in morphology to *P. otibandus*. The following description is based primarily on the Nelson Bay specimens, supplemented by elements from the Hamilton and Dog Rocks LFs where available.

The two dP2s (NMV P200471, P216005) from the Nelson Bay LF are complete and only slightly worn. NMV P216005 (figs. 8A–C) is subrectangular in occlusal outline and consists of a main blade positioned slightly labial of the midline, a posterolingual cusp and a well-developed lingual cingulum. The main blade consists of a high anterior cusp, a slightly lower posterior cusp and three lower intermediate cuspules. A strong vertical labial ridgelet ascends from the central intermediate cuspule almost to the base of the crown. Labial ridgelets from the anterior and posterior intermediate cuspules are very short and weak. A strong ridge ascends from the anterior cusp slightly posterolabially to the base of the crown. A second ridge ascends directly anteriorly, curving lingually at the base to terminate on the anterolingual base of the anterior cusp, and does not link to the lingual cingulum. A third, weaker ridge ascends directly lingually terminating at a small cuspule, which marks the start of the lingual cingulum. The lingual cingulum extends posteriorly, defining a wide lingual basin, and terminates at the large, low, rounded posterolingual cusp. The basin is divided into two pockets by a transverse ridge in line with the anterior intermediate

cuspule. The anterior pocket is smaller and narrower than the posterior pocket. The posterolingual cusp is linked to the posterior cusp by a strong, moderately high ridge. A small U-shaped posterior cingulum marks a shallow posterior fossette. NMV P200741 (figs. 8D–F) differs in having a weaker lingual cingulum and shallower lingual basin, weaker labial ridgelets and weaker/absent lingual ridgelets.

There are three P3s present in the current Nelson Bay sample (NMV P187198, P215998 and P216005) (figs. 8G–O). P3 is very long compared to the molars, as in *P. chinchillaensis*, and is slightly longer than those of *P. roechus* from Nelson Bay. The crown is subovate in occlusal outline. It is flattened anteriorly and posteriorly, does not narrow anteriorly, and has a slightly concave labial and straight lingual margin. It is composed of a main blade, a low posterolingual cusp and a wide, low lingual cingulum. The main blade is straight, curving only very slightly labially posteriorly. It consists of a high prominent anterior cusp, a lower posterior cusp and four intermediate cuspules, of which the centre two are much more prominent than the external two. Moderately strong vertical ridgelets ascend labially from the centre two intermediate cuspules almost to the base of the crown. Only very short, weak labial ridgelets ascend from the anterior and posterior intermediate cuspules. The corresponding lingual ridgelets present in other species of *Protetnodon* are either very weakly developed/absent in *Protetnodon* n. sp. A or are removed by wear. A strong ridge and deep groove ascends posterolabially from the anterior cusp, but is not as strong or as continuous as in *P. roechus* and *P. brehus*. A second ridge ascends directly anteriorly curving lingually at the base of the crown to terminate at a small anterolingual cuspule. A weaker ridge also ascends directly lingually linking to the start of the lingual cingulum. The anterolingual cuspule is separated from the lingual cingulum by a groove. The lingual cingulum extends posteriorly, terminating at the high posterolingual cusp defining a lingual basin that widens posteriorly. The lingual cingulum indents slightly opposite the space between the first and second intermediate cuspules, constricting the lingual basin into a small circular anterior pocket and a wider, elongate posterior pocket, but they are not completely divided from one another. The posterolingual cusp is slightly lower than the posterior cusp, the two connected by a moderately high anterolabially trending ridge. The posterior cingulum is low, extending across the entire posterior face of the crown, and defines a large, deep posterior fossette.

NMV P215998 is moderately worn and differs from the unerupted NMV P216005 in that the anterolingual cuspule is absent; therefore, the anterior margin of the crown is more tapered, rather than flat, and the anterior ridge terminates on the anterolingual base of the anterior cusp. The posterolingual cusp is much shorter than the posterior cusp owing to wear. NMV P187198 is also worn and differs from both NMV P215998 and NMV P216005 in that the lingual cingulum narrows rapidly anteriorly resulting in the loss of the small anterior basin, but the lingual ridge from the anterior cusp is retained.

dP3 (NMV P160372) was described and figured by Flannery et al. (1992, p. 29; figs. 14C–E, 15; table 1) from the Hamilton LF. It is not known from the Nelson Bay LF. Two

M1s are known from the Nelson Bay LF (NMV P200472 and NMV P216013) (figs. 9A–C) and one from the Dog Rocks LF (NMV P201862b). The lophs are moderately low crowned and taper towards the crown apices, particularly lingually, owing to the gently sloping slightly concave lingual loph margins. The bases of the lophs are extended lingually and slightly swollen labially. Lophs are strongly concave posteriorly in unworn specimens, and the metaloph is wider and higher than the protoloph. The anterior cingulum is low, short and transversely narrow, extending from the anterior base of the paracone to the anterior base of the protocone. It is truncated abruptly lingually and is near planar. A strong preparacrista closes off the labial end of the anterior cingulum. The postparacrista and premetacrista are relatively strong and meet in some specimens (NMV P201862b) at the base of the median valley about one-half the distance from the midlink to the labial edge, and close off the labial end of the median valley. The lingual and labial moieties of the median valley are tightly V-shaped. The midlink is strong, ascending from the protocone to the centre of the median valley to meet with the weak contribution from the centre of the metaloph. The posterior cingulum consists of a strong, slightly swollen, curved postmetaconulecrista terminating labial of the midline, separated from the weaker postmetacrista by a fissure. A short, weak postlink is present on the posterior face of the metaloph in NMV P201862b and NMV P200472, positioned slightly labial of the midline, but is absent in P216013. M1 differs from dP3 in being higher crowned, relatively more elongate and having a wider protoloph.

Two complete M2s, one from the Hamilton LF (PM 4429) and one from Nelson Bay (NMV P218245) (figs. 9D–F), plus an M2 metaloph (NMV P216040) are known. M2 is as M1 except that it is slightly larger, the metaloph and protoloph are approximately equal width, the postparacrista and particularly the premetacrista are weaker and do not meet, the contribution from the metaloph to the midlink is slightly stronger, and the anterior cingulum is slightly broader transversely, with the lingual third sloping away steeply to the anterolingual base of the protoloph. There is a slight hint of a lingual ‘forelink’. The labial bases of the lophs are strongly swollen, giving the labial margin of the crown a convex appearance in occlusal view as in *Wallabia*. A low rounded crest runs parallel to the edge of the postmetaconulecrista. The Hamilton M1 differs from the Nelson Bay M1 in being slightly lower crowned and possessing a weak postlink (only an extremely weak postlink is present on the isolated metaloph, NMV P216040, from Nelson Bay).

Four complete M3s and one M3 protoloph are known from Nelson Bay (NMV P187192, P200473, P200604, P216005, P216009) (figs. 9G–R) and one complete M3 from the Dog Rocks LF (NMV P201862b) (figs. 9S–U). M3 is as M2 but is slightly larger and the anterior cingulum is squarer, slightly longer and bulbous anteriorly. A weak ‘forelink’ is present near the lingual end of the anterior cingulum in NMV P187192, NMV P216009 and NMV P201862b. The crest parallel to the postmetaconulecrista is strongly swollen. A very weak hint of a postlink is present on NMV P201862b. No M4s are currently recognised in any of the assemblages.

Remarks. Within *Protemnodon* n. sp. A, P3 morphology appears to be quite variable, but this is common within the genus (Bartholomai, 1978). But they are all consistently elongate compared to the molars, and are actually longer than all other species, except for some large individuals of *P. brehus* and *P. roechus* (Bartholomai, 1978) (see table 2). *Protemnodon* n. sp. A is closest overall in size and morphology to *P. otibandus*, sharing features such as an elongate P3, sloping lingual loph margins, a narrow anterior cingulum, poor development of dP3 protoloph and a slight postlink on anterior molars (Flannery et al., 1992; Plane, 1967). It also shares features with *P. chinchillaensis* in the size and relative P3 length (Bartholomai, 1978), and with *P. tumbuna* in the slope of the lingual loph margins and lingually restricted anterior cingulum (Flannery et al., 1983). *P. chinchillaensis* appears to be quite close in morphology to *P. otibandus* differing only in lacking a postlink on the anterior molars (Flannery and Archer, 1984). The postlink is very weak and variably developed in *Protemnodon* n. sp. A, occurring mainly in the specimens from the Pliocene local faunas. The Hamilton specimens also appear to be slightly lower crowned than the Nelson Bay and Dog Rocks specimens. This suggests that a morphological cline exists within this species, with molars becoming higher crowned and losing the postlink with time.

Many questions remain unanswered regarding the morphology and phylogenetic position of *Protemnodon* n. sp. A owing to the lack of complete tooth rows and certainly associated lower dentition. As the Nelson Bay LF appears to be a mixed assemblage of relicts from the Pliocene and Pleistocene/modern species (Piper, 2006a, b; Piper, 2007), it is likely that *Protemnodon* n. sp. A would be more typically found within Pliocene deposits.

Other unidentified macropodid dentition

Referred material. NMV P173646, left M; NMV P173652 left M; NMV P200478, left M; NMV P200479, worn left m; NMV P200480, left m; NMV P200416, right dP2; NMV P187855, left M; NMV P216901, right anterior M.

Remarks. There are several small macropodid molars recovered from the Nelson Bay LF that lack sufficient diagnostic characteristics for complete identification (figs. 10A–E). NMV P173646, NMV P173652, NMV P200478 are moderately low-crowned posterior upper molars (fig. 10A). They bear similarities to *Setonix brachyurus* but have a longer, better developed anterior cingulum, and are slightly larger and proportionally narrower. In these features they are similar to *Lagorchestes leporides*. They also show some similarities to *Thylogale billardierii* but are smaller, have a proportionally narrower metaloph and are more constricted across the median valley. NMV P200479 and NMV P200480 are low-crowned lower molars, again bearing similarities to *Setonix brachyurus* and *Lagorchestes leporides* (fig. 10B). NMV P200416, a small dP2, has a well-defined lingual basin, low crest and two intermediate cusps and ridges (fig. 10C). It is similar to both *Setonix brachyurus* and *Lagostrophus faciatius* but differs in the number of intermediate cusps and the occlusal outline of the crown.

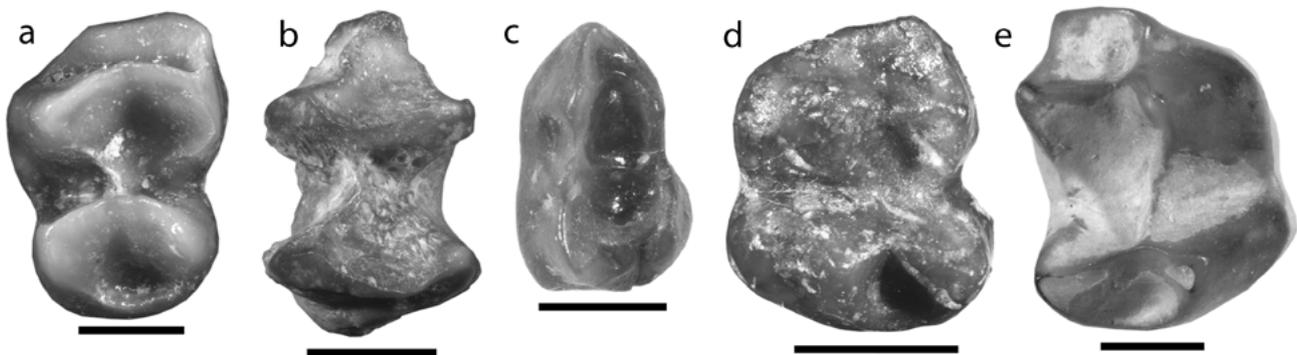


Figure 10. Macropodidae indet.: a, NMV P200478, left M, occlusal view; b, NMV P200480, left m, occlusal view; c, NMV P200416, right dP2, occlusal view; d, NMV P187855, left M, occlusal view; e, NMV P216901, right dP3?, occlusal view. Scale bars = 2 mm.

NMV P187855 is a small, low-crowned upper molar (fig. 10D). The lophs are not well developed, giving it a bunodont appearance. The anterior cingulum is weak, narrow and short with a strong preparacrista connecting to the labial end of the protoloph. The midlink is very weakly developed but the postparacrista and premetacrista are relatively strong and meet at the base of the median valley. The posterior cingulum is well developed and pocket-like. The tooth may represent the deciduous premolar of a small macropodine or may tentatively belong to a member of the Potoroidae.

NMV P216901 is a low-crowned, bunolophodont upper molar with a wide V-shaped median valley labially, a weak midlink and a moderately strong preparacrista connecting to a low, basin-like anterior cingulum (fig. 10E). The lophs are not well developed. The metaloph has interesting wear facets, proceeding almost vertically down the posterior face of each cusp, rather than horizontally as in most macropodids. The protoloph shows little sign of wear. This tooth may represent a deciduous premolar of a small macropodine.

Discussion and remarks on the palaeoecology of the Nelson Bay LF

As described above, the macropodids identified in the Nelson Bay LF are mainly represented by isolated teeth, with the exception of *Baringa nelsonensis*, which dominates the assemblage (43% of all dental and cranial elements; 53% of all elements if postcranial remains are correctly assigned). They represent at least six different genera and 11 species, from small wallaby size (*Macropus* (*Notamacropus*) spp., *Thylogale* cf. *billardierii*, *Baringa nelsonensis*) to the largest kangaroos (*Macropus* (*Macropus*) *giganteus titan*, *Protemnodon* spp., *Simosthenurus occidentalis*).

Protemnodon n. sp. A, like some other members of the Nelson Bay LF (*Palorchestes pickeringii*, *Darcus duggani*, *Pseudokoala*, *Thylacoleo hilli* and possibly *Baringa*), may represent a relictual species from the rainforests/wet forests of the Pliocene (Piper, 2006a; Piper, 2007). The other large Nelson Bay macropodid species are all typical of mid-late Pleistocene assemblages, and became extinct prior to the last glacial maximum or underwent dwarfing (i.e. *Macropus*

(*Macropus*) *giganteus titan*) (Flannery, 1984; Marshall and Corruccini, 1978). *Thylogale billardierii* is now extinct on the mainland, living only in dense wet forests of Tasmania and the larger Bass Strait islands. The other small macropodid species cannot be positively identified, so are not useful for palaeoecological inferences.

The small macropods (*Baringa*, *Thylogale*, *Macropus* (*Notamacropus*)) were likely mixed browser-grazers based on the diets of their extant relatives or dental/cranial morphology (Piper and Herrmann, 2005; Strahan, 1995).

The large macropods have been variously interpreted as grazers or browsers. The simosthenurins filled browser niches throughout temperate woodlands and open forests of the Pleistocene, according to Prideaux (2004). Bartholomai (1973) suggested *Protemnodon* spp. were primarily grazers based on dental morphology, while Flannery (1984) described them as browsers based on dental morphology and preserved gut content of *P. anak* from Morwell, Victoria (coarsely comminuted herbage, including twigs and leaf fragments). A recent study by Butler et al. (2014) utilising dental mesowear analysis classified *Protemnodon* spp. as mixed browser-grazers, with *P. roechus* possibly being a grazer. Carbon isotope analysis of dental enamel from *Protemnodon* sp. indet. from the Pliocene Chinchilla LF, Queensland, shows *Protemnodon* at this location consumed a diet of mainly C₃ plants (shrubs/trees), with some C₄ plants (grasses), supporting its interpretation as a browser-grazer (Montanari et al., 2013).

Macropus (*Macropus*) *giganteus titan* has been classified in the literature as primarily a grazer based on its high-crowned molars and dietary preferences of the extant *M. giganteus* (Bartholomai, 1975; Helgen et al., 2006); however, Butler et al.'s (2014) study suggests *M. giganteus titan* was also a mixed browser-grazer.

A taphonomic analysis of the assemblage from Unit B of the Nelson Bay Formation suggests it is biased towards the preservation of medium- to large-sized animals, yet is generally attritional and autochthonous, meaning the community structure is likely preserved, which gives some strength to palaeoecological inferences (Piper, 2006b; Piper, 2007).

Assuming time-averaging has not greatly affected the composition of the fauna and that it represents a single mammalian community, from an ecological perspective, the Nelson Bay macropodid fauna is extremely rich in comparison to modern macropodid guilds. The most diverse extant macropodid fauna is that of Wallaby Creek, Clarence River Valley, NSW, which contains eight different species (Southwell, 1987). High diversity may be associated with a large variety of vegetation, especially forest close to open grasslands (Southwell, 1987). Niche partitioning among sympatric macropodids is facilitated by habitat and food preference, topography, times of greatest activity and perceived predation risk (Southwell, 1987; le Mar and McArthur, 2005). For example, the large grazing species are often active during the day, moving out from the forests on to the open grassy areas to feed. They form groups and rely on sighting and out-running approaching predators. Smaller, browser-grazers are more active at night and often stay close to the forest edge where there is a greater variety of food and places to hide from predators (Southwell, 1987; Jarman, 1991; le Mar and McArthur, 2005). The abundance of predominantly grazing macropodids in the Nelson Bay LF is low, suggesting grasslands were present but not an extensive component of the ecosystem, but the high macropodid diversity does indicate a mosaic environment of wet and dry sclerophyll forest with abundant food and habitat resources, thus limiting intraguild competition (Southwell, 1987; le Mar and McArthur, 2005).

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Supplementary Material

Table S1: Measurements of lower dentition of Nelson Bay *Protomnodon*. L = length, AW = width of protolophid, PW = width of hypolophid, e = estimated.

	I1 D	P2 L	P2 AW	P2 PW	P3 L	P3 AW	P3 PW	Dp3 L	Dp3 AW	Dp3 PW	M1 L	M1 AW	M1 PW	M2 L	M2 AW	M2 PW	M3 L	M3 AW	M3 PW	M4 L	M4 AW	M4 PW
<i>Protomnodon</i> sp. cf. <i>brehus</i>																						
NMV P216001	-	11.1	5.2	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173647	-	11.7	5.7	6.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P201127 (R)	-	-	-	-	18.3	6.6	7.0	-	-	-	14.4	10.5	10.4	15.5	11.5	11.4	17.7	12.4	11.8	17.9	12.5	11.6
NMV P201127 (L)	-	-	-	-	18.6	-	6.8e	-	-	-	14.6	10.2	10.9	16.7	11.9e	11.5e	17.0	12.2e	12.1e	18.1	12.4	12.4e
NMV P215985	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17.0	12.4	12.1	17.8	12.5	11.8
<i>Protomnodon roechus</i>																						
NMV P165457	-	-	-	-	18.2	5.4	6.6	-	-	-	12.5e	9.0	9.1	15.6	-	10.7	17.3	11.6	11.1	17.4	11.5	9.9
NMV P173642	-	-	-	-	16.4	5.2	5.9	-	-	-	12.4	9.0	9.1	15.0	10.5	10.7	18.0	11.9	12.1	18.1	11.7	10.1
NMV P173640	-	-	-	-	18.7	6.2	6.8	-	-	-	12.3	8.8	9.6	14.7	10.8	11.1	18.5	11.7	11.5	-	-	-
NMV P173641	-	-	-	-	18.8	4.8	5.8	11.4	6.7	7.3	14.1	8.7	9.1	16.2	10.6	10.3	-	-	-	-	-	-
NMV P216016	-	-	-	-	-	-	-	-	-	-	-	-	-	10.8	-	-	-	-	-	-	-	-
NMV P173684	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.6e	11.3	-	-	-	-
NMV P216017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.9	-	-	-	-
NMV P216007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.3e

Table S2: Nelson Bay *Protomnodon* upper dentition measurements. L = length, AW = width of protolophid, PW = width of hypolophid, e = estimated.

	I1 L	I2 L	I3 L	P2 L	P2 AW	P2 PW	P3 L	P3 AW	P3 PW	M1 L	M1 AW	M1 PW	M2 L	M2 AW	M2 PW	M3 L	M3 AW	M3 PW	M4 L	M4 AW	M4 PW
<i>Protomnodon</i> sp. cf. <i>brehus</i>																					
NMV P173663	12.5	-	14.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P215990	12.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P215995	-	-	-	13.0	7.4	7.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Protomnodon roechus</i>																					
NMV P173088 (R)	-	8.6	12.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173088 (L)	-	-	11.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173645	-	-	-	13.1	7.9	8.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173643	-	-	-	-	-	-	20.0	8.3	9.0	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173644	-	-	-	-	-	-	19.5	7.9	8.6	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173628	-	-	-	-	-	-	20.6	7.8	8.3	-	-	-	-	-	-	-	-	-	-	-	-
NMV P215986	-	-	-	-	-	-	19.7	9.3	8.2	12.5	11.3	-	13.6e	12.9	12.1	16.3e	14.2	12.5	16.3e	14.8	11.7
NMV P173682	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P215999	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NMV P173685/P200654	-	-	-	-	-	-	-	-	-	-	-	-	14.8	13.4	13.1	-	-	-	-	-	-
NMV P200653/P200649	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.8	13.1	13.1	-	-	-
NMV P173686 (L)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.0	13.2	11.9
NMV P173686 (R)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13.3	-
NMV P173681	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.2	13.2	12.2e	-	-	-
NMV P216003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.0	13.5	13.0	-	-	-

Table S3. Dimensions of *Thylogale* sp. lower dentition from Nelson Bay. e = estimated.

Specimen number	Tooth	Length	Anterior width	Posterior width
P165469e	p3	6.5	2.4	2.6
P215791	p3	5.7	1.6	2.1
P187860	dp3	3.7	2.1	2.4
P187861	dp3	3.7	2.1	2.5
P187862	dp3	3.8	2.0	2.5
P215964	dp3	-	1.8	-
P215804	m1	4.3	2.8	3.1
	m2	5.0	3.4	3.6
	m3	6.1	3.9	4.2
P200427	m1	-	-	3.3
P200699	m1	4.7	3.3	3.5
P187205	m2	-	-	3.7
P216884	m2	5.1	3.2	3.4e
P173588	m3	5.5	3.8	4.0
P200425	m3	-	-	4.1
P215801	m3	5.7	3.9	3.9
P215851	m3	5.7e	3.9e	4.2e
P215860	m3	-	4.0	-
P218243	m3	-	-	4.1
P200642	m3?	-	4.4	-
P215802	m4?	-	4.0	-
P200426/23	m4?	5.8	4.0	4.0

Table S4. Dimensions of *Thylogale* sp. upper dentition from Nelson Bay. e = estimated.

Specimen number	Tooth	Length	Anterior width	Posterior width
P173573	P3	6.0	-	3.2
P200415	P3	5.9	1.8	2.5
P200417	P3	6.2	2.0	2.8
P200418	P3	6.2	1.7	2.7
P215784	M1	5.2	4.4	4.3
P215779	M1	-	-	4.7
	M2	6.2	5.0	5.1
P215872	M2	6.4	5.4	5.1
P216889	M2	>5.3	5.0e	5.2e
P215778	M3	6.3	4.9	4.9
P200439	M3?	-	4.8	-
P216105	M4?	6.5	4.9	4.2e

Table S5. Dimensions of *Thylogale* sp. upper incisors from Nelson Bay.

Specimen number	Tooth	Occlusal length	Occlusal width
P173658	I1	3.4	1.7
	I1	3.4	1.7
P200485	I1	3.2	2.2
P200486	I1	3.1	1.7
P200487	I1	3.1	2.5
P207870	I1	3.4	2.4
P200484	I2	3.4	1.8
P216260b	I2	3.7	1.9
P187178	I2	3.7	1.9
	I3	4.7	2.1
P200483	I3	4.0	2.1
P200634	I3	5.1	1.7

Table S6. Dimensions of *Macropus* (*Macropus*) sp. upper incisors from Nelson Bay.

Specimen number	Tooth	Occlusal length
P200668	I3	10.6
P216235a	I3	13.6

Table S7. Dimensions of *Macropus* (*Macropus*) sp. lower dentition from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P200697	p2	7.5	3.0	4.4
P173634	m1	13.5	7.5	-
	m2	15.5	-	-
	m3	16.0	10.5	9.5
	m4	17.9	10.0	9.5
P215983	m2	16.9	10.3	9.5
	m3	18.5	10.5	9.4

Table S8. Dimensions of *Macropus* (*Notamacropus*) spp. dentition from Nelson Bay. e = estimated.

Specimen number	Tooth	Length	Anterior width	Posterior width
P187189	DP3?	6.0	4.2	4.6e
P215783	DP3?	-	-	4.3
P173656	DP3?	>3.9	3.8e	3.8e
	M1?	6.2e	4.6	4.4
P200626	M1?	4.5e	3.9	4.0
P187185	M3?	6.9	5.3	4.8
P216887	M3?	7.3	5.5	4.6
P200675	m2?	-	5.2	-
P200606	m3?	-	5.9	-
P215821	m3?	9.7	5.9	5.5

Table S9. Dimensions of *Macropus (Notamacropus)* spp. upper incisors from Nelson Bay.

Specimen number	Tooth	Occlusal length
P173678	I2	5.5
P215807	I2	5.8
P215808	I2	6.0
P215809	I2	5.9
P215814	I2	5.2
P200643	I3	6.3
P215813	I3	7.8
P215815	I3	7.1
P216046	I3	7.6

Table S10. Dimensions of *Simosthenurus* sp. lower dentition from Nelson Bay. e = estimate.

Specimen number	Tooth	Length	Anterior width	Posterior width
P216042	p2	9.9	5.9	7.6
P218251	m	>11.0	9.9e	10.7

Table S11. Dimension of indeterminate small macropodid upper molars from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P173646	M	5.6	4.3	3.4
P173652	M	5.4	4.4	3.6
P200478	M	5.7	4.4	3.6

Table S12. Dimensions of indeterminate small macropodid lower molars from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P200479	m	5.3	3.8	3.5
P200480	m	4.7	3.2	3.3

Table S13. Dimensions of indeterminate small macropodid upper premolar from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P200416	P2	4.3	2.2	2.7

Table S14. Dimensions of indeterminate small macropodid upper molar from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P187855	M	3.8	3.0	3.3

Table S15. Dimensions of indeterminate small macropodid anterior upper molar (dP3?) from Nelson Bay.

Specimen number	Tooth	Length	Anterior width	Posterior width
P216901	M	6.3	4.5	4.8

