

## New material of *Gumardee pascuali* Flannery et al., 1983 (Marsupialia: Macropodiformes) and two new species from the Riversleigh World Heritage Area, Queensland, Australia

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### Abstract

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New specimens of the late Oligocene macropodiform, *Gumardee pascuali*, are described, as well as two new late Oligocene to early Miocene species, *G. springae* sp. nov. and *G. richi* sp. nov. Species of *Gumardee* exhibit a unique combination of features, including very long upper and lower third premolars, partially lophodont molars and, in dorsoventral plane, concave lower molar row and convex upper molar row. We combined two morphological matrices to assess the phylogenetic relationships of these species. Our analysis recovered species of *Gumardee* as a well-supported monophyletic group, nested within Potoroinae. *Gumardee richi* and *G. pascuali* appear to be more derived than *G. springae* in having a more strongly developed posthypocristid that is almost hypolophid-like.

### Keywords

Macropodiform; systematics; late Oligocene; early Miocene; new species.

### Introduction

Flannery et al. (1983) described *Gumardee pascuali* from a single maxilla containing worn P3-M4. The holotype was found at D-Site, in the Riversleigh World Heritage Area (WHA), north-western Queensland, Australia. Current understanding of biostratigraphy in the Riversleigh WHA suggests that D-Site is part of Faunal Zone A, which is interpreted to be late Oligocene in age (Archer et al., 1989; Archer et al., 1997; Creaser, 1997; Travouillon et al., 2006, 2011). Three other Riversleigh Faunal Zones, B, C and D, have been interpreted to be early, middle and early late Miocene in age, respectively (Archer et al., 1989; Archer et al., 1997; Creaser, 1997; Travouillon et al., 2006, 2011).

Additional specimens of *Gumardee* were reported from the Namba Formation of Lake Pinpa, South Australia (Flannery and Rich, 1986). However, due to the fragmentary nature of the fossils recovered (mostly isolated teeth), they were referred to *Gumardee* sp., and await re-assessment when additional material is known.

Flannery et al. (1983) suggested that *G. pascuali* was a potoroine because it had ‘bunodont’ molars, a greatly reduced

M4 (their M5) and an elongate P3, aligned with the molar row and with buccal and lingual cingula and 11 buccal and lingual transcristae. Its relationship with potoroines was further supported by Flannery et al. (1984), who discussed the monophyly of this group in which they also included other Oligo-Miocene taxa such as *Purtia*, *Wakiewakie*, *Bulungamaya* and *Wabularoo* (Archer, 1979; Case, 1984; Flannery et al., 1983; Woodburne, 1984). However, monophyly of potoroines, and including these extinct taxa, have not been found in more recent morphological phylogenies (Kear et al., 2007; Kear and Pledge, 2008; Prideaux and Warburton, 2010; Travouillon et al., 2014).

Here we describe new material of *Gumardee pascuali*, as well as two new species of the same genus, from the Riversleigh WHA. We re-assess the phylogenetic relationships of all three *Gumardee* taxa, using a new combined morphological matrix.

### Materials and methods

The new specimens of *Gumardee pascuali* and of the two new species were collected from Riversleigh WHA, north-western Queensland (18°59'–19°08'S, 138°34'–138°43'E). All specimens are registered in the Queensland Museum fossil

collection, Brisbane, Australia (prefix **QM F**). All dental measurements were taken with digital vernier callipers.

Terminology follows Lockett (1993) for cheek tooth homology, Archer (1984) and Cooke (1997a, b) for dental morphology, Meredith et al. (2009) and Prideaux and Warburton (2010) for higher systematic nomenclature (using Macropodiformes sensu Meredith et al., 2009; and using subfamilies Potoroinae, Macropodinae, Lagostrophinae and Sthenurinae as part of Macropodidae, sensu Prideaux and Warburton, 2010), and Travouillon et al. (2006, 2011, 2013) for biostratigraphic nomenclature (see also Archer et al., 1989, 1997; Creaser, 1997; Arena, 2004).

In a previous attempt to analyse the phylogenetic relationship of basal macropodiforms, using the matrix of Kear and Pledge (2008), the tree recovered was highly unresolved (Travouillon et al., 2014). We suggested that combining the matrices of Kear and Pledge (2008), and of Prideaux and Warburton (2010), might provide better resolution of macropodiform relationships. Here, we combined those two matrices, using the matrix of Prideaux and Warburton (2010) as the base, because it included more taxa and contained all macropodid subfamilies (Lagostrophinae was not represented in Kear and Pledge, 2008). We added four new out-group species, including the Miocene bandicoot *Galadi speciosus* (Travouillon et al., 2010), the extant Common Brushtail Possum *Trichosurus vulpecula*, the extant Common Ringtail Possum *Pseudocheirus peregrinus*, and the Miocene Pygmy Possum *Burramys brutyi* (Brammall and Archer, 1997). We also added several other fossil and extant macropodiform taxa as follows:

-Hypsiprymnodontidae: *Hypsiprymnodon bartholomaii* Flannery and Archer, 1987a, *H. philcreaseri* Bates et al., 2014, *Ekaltadeta ima* Archer and Flannery, 1985, *Jackmahoneya toxoniensis* Ride, 1993 and *Propleopus oscillans* De Vis, 1888.

-Balbaridae: *Nambaroo saltavus* and *N. tarrinyeri* Flannery and Rich, 1986, *N. couperi* Cooke, 1997b, *N. gillespieae* Kear et al., 2007, *Wururoo dayamayi* Cooke, 1997b, *Balbaroo gregoriensis* and *B. camfieldensis* Flannery et al., 1983, *B. fangaroo* Cooke, 2000, *Ganawamaya acris*, *G. ornata* and *G. aediculis* Cooke, 1992.

-Basal macropodiforms: *Bulungamaya delicata*, *Purtia mosaicus* Case, 1984, *Wakiewakie lawsoni* Woodburne, 1984, *Ganguroo bites* Travouillon et al., 2014, *Wabularoo naughtoni* Archer, 1979, *Gumardee pascuali* Flannery et al., 1983, *G. richi* sp. nov. and *G. springae* sp. nov. (this work).

-Potoroinae: *Bettongia moyesi* (Flannery and Archer, 1987b), and the extant Rufous Bettong *Aepyprymnus rufescens*.

-Lagostrophinae: *Tjukuru wellsi* (Prideaux and Tedford, 2012).

From the Kear and Pledge (2008) matrix, we added to our matrix only cranial and dental characters (postcranial characters were omitted because associated postcranials are not known for most basal taxa) that were not already in the Prideaux and Warburton (2010) matrix. These included characters 1-6, 8-10, 12, 16-23, 25-26, 28-32, 37-39, 41, 45, and 105 (see supplementary information for character descriptions). We also redefined or added new character states for some characters (characters 17, 23, 34, 38 and 40 in Prideaux and Warburton, 2010; characters 4, 10, 12, 21, 23, 25-26, and 32 in Kear and Pledge, 2008; see

supplementary information for details), and added additional characters to the matrix (see characters 115-119 in supplementary information). One such character appears to be particularly important for distinguishing basal taxa from other macropodiforms: 'molar morphology' (character 23), which we redefined to be applicable to the whole range observed. 'Bunodont' taxa (e.g. *Burramys* and *Hypsiprymnodon* spp.) have poorly defined lateral crests (no distinct loph or lophids). 'Bunolophodont' taxa (e.g. *Trichosurus*, *Ekaltadeta*, *Aepyprymnus* spp.) have defined lateral crests, but these crests not functioning as loph or lophids (no physical connection between the crest and the opposing cusp). 'Partially lophodont' taxa (e.g. *Bulungamaya*, *Purtia*, *Ngamaroo* and *Gumardee* spp.) have functional anterior lophids (well-developed lophid connecting protoconid to metaconid) and posterior lophs (well-developed loph connecting metacone to metaconule), but incomplete (non-functional) posterior lophids (entoconid and hypoconid are not connected by a well-developed lophid) and anterior lophs (protocone and paracone are not connected by a well-developed loph). 'Bilophodont' taxa (e.g. *Gangaroo*, *Wabularoo*, and all balbarids, sthenurines and macropodines) have fully functional anterior and posterior lophs/lophids. Our combined matrix has a total of 119 characters.

The parsimony analysis was performed using 1,000 heuristic replicates, saving ten trees per replicates, and the analysis repeated using the saved trees. The analysis resulted in multiple parsimonious trees, which were summarised as a strict consensus tree. Bootstrap values were calculated using 1000 replicates of ten random addition sequence replicates. The analysis was done in the software PAUP\* 4.0b10 (Swofford, 2002). Decay indices were calculated in the software TreeRot. v3 (Sorenson and Franzosa, 2007).

## Systematic palaeontology

### Macropodidae Gray, 1821

#### Potoroinae Trouessart, 1898

#### *Gumardee* Flannery et al., 1983

*Type species.* *Gumardee pascuali* Flannery et al., 1983

*Additional species.* *Gumardee richi* sp. nov. and *G. springae* sp. nov.

*Revised generic diagnosis.* Potoroine with elongated and narrow sectorial P3/p3 aligned with molar row, buccal and lingual cingulae on the medial portion of P3, concave lower molar row and convex upper molar row in dorsoventral plane, buccinator sulcus on the dentary, reduced m4/M4 (smaller than m3/M3), and partially lophodont (see definition in methods) molars.

Species of *Gumardee* differ from all hypsiprymnodontids in having elongated sectorial premolars, aligned with the tooth row, and having partially lophodont molars. They differ from *Wabularoo*, *Ganguroo*, balbarids, sthenurines, macropodines and lagostrophines in having a greatly reduced M4, concave lower molar row and convex upper molar row in dorsoventral plane and having partially lophodont molars. They differ from *Purtia*, *Ngamaroo*, *Bulungamaya*, *Wakiewakie* and all

Table 1. Measurements of the upper and lower dentition of *Gumardee pascuali*, in mm. L = anteroposterior length, AW = anterior width, PW = posterior width, p = premolar, m = molar.

Specimen	Site	P2		dP3		P3		M1			M2			M3			M4		
		L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F10646	D-Site					10.29	4.6	5.5	5.79	4.98	5.98	6.09	5.19	6.01	5.7	4.72	4.6	4.72	3.09
QM F30421	Dirk's Towers	6.24	3.86	5.36	4.25	10.38		5.68	5.7	4.62									
				p3		m1		m2			m3			m4					
				L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F45107	Bone Reef			10.17	4.67														
QM F12422	D-Site					5.33	3.93	4.73	6.11	4.68	4.95	7.02	5.14	5.21	6.25	4.66	3.97		

potoroines, in buccal and lingual cingulae on the medial portion of P3 and being much larger in size.

### *Gumardee pascuali* Flannery et al., 1983

Table 1, Figure 1

*Holotype.* QM F10646, partial right maxilla with worn P3 and M1-4.

*Additional material.* QM F30421, right juvenile maxilla with P2, dP3, P3 removed from crypt, M1; QM F45107, right p3; QM F12422, left dentary with m1-4.

*Revised species diagnosis.* *Gumardee* with 11 cuspules and associated lingual and buccal transcrisetae on the occlusal margin of P3/p3, deep buccinator sulcus, six cuspules on P2, no StC (stylar cusp C) on M2-3, postprotocrista not connected to the metaconule on upper molars, and metaloph connects metacone to metaconule on M4.

*Age and distribution.* All specimens are from the Riversleigh World Heritage Area, north-western Queensland, Australia (18°15'35"S, 138°06' 41"E). The holotype (QM F10646) and QM F12422 are from D-Site. QM F30421 is from Dirk's Towers Site and QM F45107 is from Bone Reef Site. D-Site's Riversleigh Local Fauna and Bone Reef Local Fauna are part of Riversleigh's Faunal Zone A (interpreted to be late Oligocene in age), and Dirk's Towers is part of Faunal Zone B (early Miocene in age) as distinguished by Archer et al. (1989); Archer et al. (1997), Arena (2004) and Travouillon et al. (2006, 2011).

*Remarks.* QM F12422 was first assigned to *Wabularoo naughtoni* by Flannery et al. (1984). The specimen is heavily worn and damaged, making comparisons difficult. Nevertheless, dental size and shape of QM F12422 are quite different from those of the holotype of *W. naughtoni*, suggesting that it represents a different taxon. Further, the molar row in *W. naughtoni* is straight in lateral view, but is it is convex in QM F12422, as it is in all *Gumardee* specimens. We assign this specimen to *G. pascuali* because it is from the type locality and its lower molar dimensions match those for the holotype's upper molars. The length and width of the p3 roots also match those of QM F45107 from Bone Reef Site.

*Description.* The maxilla and upper dentition was described by Flannery et al. (1983), including P3, M1-4. However, the holotype is very worn (figs. 1A–C), and thus most of the dental features are obscured. Here we describe an unworn juvenile specimen (QM F30421) referred to this taxon from Dirk's Towers Site.

P2 is almond shaped in occlusal view, almost plagiulacoid-like in shape, but with a straight occlusal outline (figs. 1D–F). The tooth is almost as wide as it is long with its lingual margin steeper than its buccal margin. The occlusal ridge increases in height posteriorly, and has six cuspules present along its length, with the anterior five having associated lingual and buccal transcrisetae. The posterior cuspule is the largest.

The dP3 is molariform, and almost square in occlusal outline (figs. 1D–F). The paracone is the tallest cusp on the crown, followed in decreasing order by the metacone, neometaconule, metaconule and protocone. A slight anterior cingulum is present just lingual to the preparacrista. The preparacrista is almost horizontal as it runs from the paracone anteriorly. The postparacrista descends the posterior face of the paracone, and meets an anteriorly directed premetacrista from the metacone in the interloph valley. No stylar cups are present on the buccal margin of the tooth. The protoloph runs from the protocone buccally, rising gently for half its length and then steeply before contacting the paracone. The postprotocrista runs posterobuccally before curving posteriorly midway in the interloph valley, forming a mid-link contacting the anterior face of the metaloph. A large neometaconule occurs midway along the metaloph, with an associated postlink descending the metaloph posteriorly. The postmetaconulecrista is posterobuccally directed before curving buccally to meet the postmetacrista.

A cap of P3 is represented and matches the description by Flannery et al. (1983) in having 11 cuspules on its occlusal edge (figs. 1D–F). Buccal and lingual transcrisetae are associated with each cuspule. The posterolingual-most transcriseta is likely to be equivalent to the posterolingual ridge found in most Riversleigh macropodoids (e.g. *Ganguroo* species) but this transcriseta is not as well developed here and contributes much less to the posterolingual heel of the tooth.

M1 is almost square in occlusal outline, but slightly wider anteriorly (figs. 1D–F). The paracone is the tallest cusp followed in decreasing order by the protocone, metaconule, metacone,

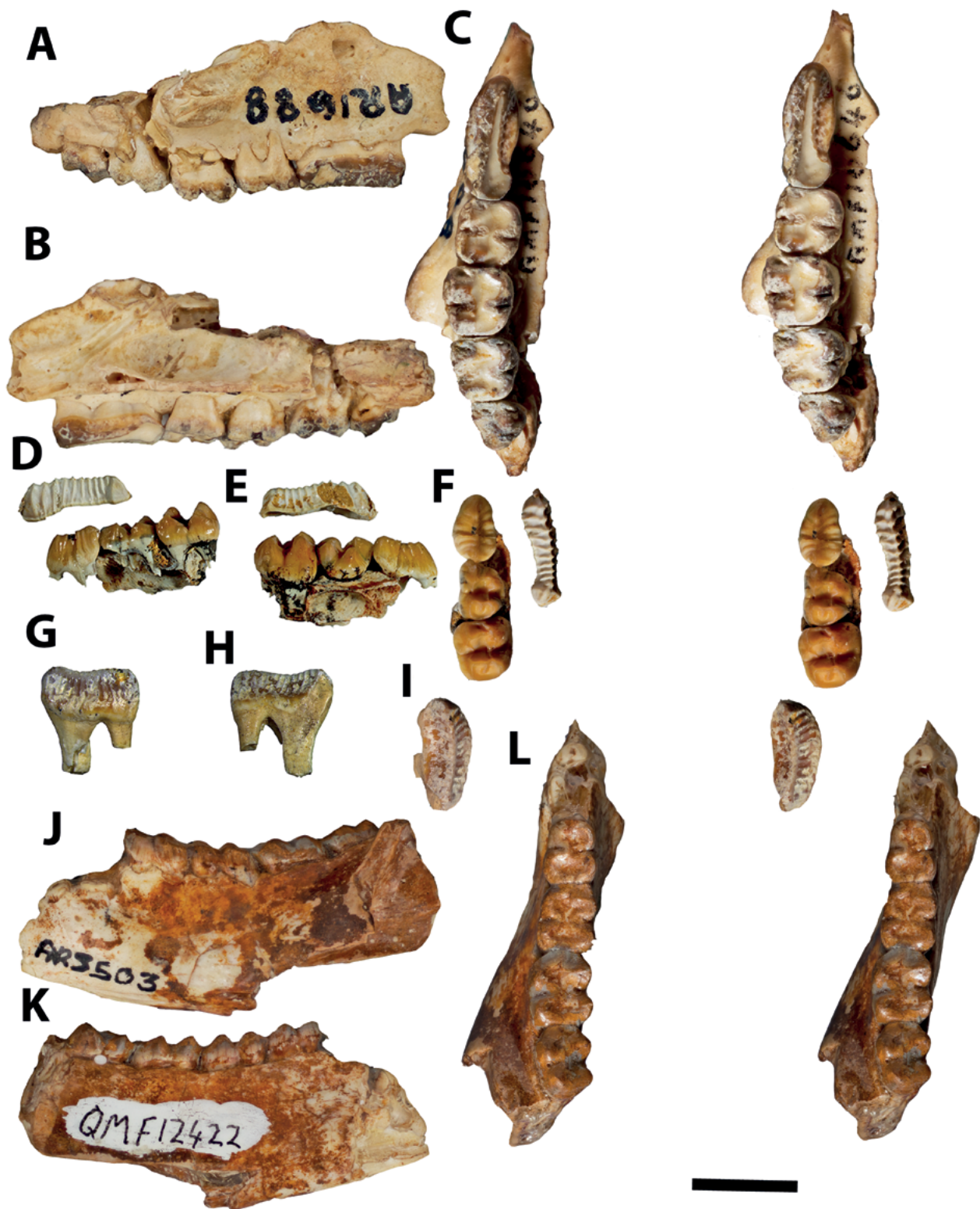


Figure 1. *Gumardee pascuali*, holotype QM F10646, right maxilla with P3, M1-4: A, buccal, B, lingual, and C, occlusal (stereopair) views; QM F30421, right juvenile maxilla with P2, dP3, P3 removed from its crypt, M1: D, buccal, E, lingual, and F, occlusal (stereopair) views; QM F45107, right p3: G, buccal, H, lingual, and I, occlusal (stereopair) views; QM F12422, left dentary with m1-4: J, buccal, K, lingual, and L, occlusal (stereopair) views. Scale bar equals 10 mm.

Table 2. Measurements of the upper and lower dentition of *Gumardee richi*, in mm. L = anteroposterior length, AW = anterior width, PW = posterior width, p = premolar, m = molar.

Specimen	Site	P2		dP3		P3		M1			M2			M3			M4		
		L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F57631	Dirk's Towers	5.61	3.84	4.47	3.95			5.46	4.98	4.35	5.39	5.36	4.29						
QM F57632	Dirk's Towers							5.28	5.25	4.7	5.51	5.5	4.76	5.18	5.36	4.33	4.84	4.91	3.13
		p2		dp3		p3		m1			m2			m3			m4		
		L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F24723	Quantum Leap	4.04	3.49	4.54	3.25			4.69	3.61	3.99									
QM F30698	Dirk's Towers										4.98	4.17	4						
QM F30875	Dirk's Towers							4.49	3.49	3.95	4.97	4.06	4.05	5.15	3.91	3.8			
QM F36313	Dirk's Towers							4.71	3.6	3.95	5.08	3.96	3.87						

neometaconule and StC. The preparacrista is straight and runs anteriorly from the paracone to the anterior margin of the tooth. The postparacrista is straight for the first half of its length and slopes directly posteriorly from the paracone apex. There, it forms a T intersection where it meets a crest connecting to a well-developed and buccally positioned StC. The second half of the postparacrista curves lingually toward the interloph valley where it connects to a straight and steep premetacrista. The protoloph is short, slightly inflated on its anterior side and steeply descends the lingual flank of the paracone until it meets the preprotocrista at about one third of its length from the protocone. The preprotocrista runs from the protocone anterobuccally, and curves slightly more anteriorly where it meets the protoloph. An anterior cingulum is present anterior to the protoloph and is bordered by the preparacrista buccally and preprotocrista lingually. A short and low precingulum is present lingual to the preprotocrista. The postprotocrista descends posterobuccally from the protocone toward the interloph valley where it forms a distinct wall before rising posteriorly toward the metaloph but ends before reaching it. The metaloph is parallel to the protoloph and descends the lingual flank of the metacone to connect to a tall metaconule. The neometaconule is present midway along the metaloph, with an associated postlink. The postmetacrista runs posteriorly from the apex of the metacone to connect close to the crown base the postmetaconulecrista which sweeps across the posterior face of the loph.

The dentary is damaged anteriorly and posteriorly (figs. 1J–L). The ventral margin is convex in lateral view, and the dorsal margin is concave, with the posterior molars elevated above the anterior molars. A deep but narrow buccinator sulcus is present on the buccal side of the dentary and runs from below the root of p3 to level with the anterior root of m2. The full depth of the masseteric canal is preserved and ends below m2.

The p3 is a sectorial tooth, longer than it is wide (figs. 1G–I). The anterior portion of the tooth is wider than its posterior portion. In lateral view, the occlusal edge is straight and slightly more elevated posteriorly, but in occlusal view, the main crest is posterolingually curved. The posterior part of

the tooth is damaged on the lingual side, preventing an accurate assessment of the number of cuspids on the crown. There are at least 11 cuspids with associated coarse lingual and buccal transcrisids, descending for two thirds the crown height. The lingual flank of the tooth is much steeper than the buccal flank. A short cristid descends anteriorly from the anterior end of the occlusal margin, but damage prevents an assessment of the presence of a posteriorly orientated cristid.

The m1 is heavily worn (figs. 1J–L). Very little of its morphology can be discerned. The tooth is roughly rectangular in occlusal outline but the talonid is wider than the trigonid. In occlusal view, dentine has been exposed through most of the occlusal surface, except for a thin layer of enamel on the margin of the tooth. The buccal cuspids seem more worn than the lingual.

The m2 is similar to m1 except as follows (figs. 1J–L): the tooth is longer and wider; the trigonid is almost as wide as the talonid; and a precingulid and anterior cingulid are present.

The m3 is similar to m2 except as follows (figs. 1J–L): the tooth is longer and wider; the talonid and trigonid are almost the same width; the tooth is less worn, revealing some of its morphology, such as the presence of a postmetacristid and preentocristid, and the posthypocristid was not connected to the buccal crest from the entoconid.

The m4 is similar to m3 except as follows (figs. 1J–L): the tooth is shorter and narrower; and the trigonid is much wider than the talonid.

#### *Gumardee richi* sp. nov.

Table 2, Figures 2 and 3

*Holotype.* QM F57631, partial left juvenile maxilla with P3 in crypt, dP2-3 and M1-2.

*Paratypes.* QM F24723, left juvenile dentary with broken i1, p2, dp3, m1, m3 in crypt; QM F36313, partial juvenile right dentary with m1-2; QM F57632, left maxilla with M1-4.

*Additional material.* QM F30698, left dentary with m2, m4 in crypt; QM F30875, left dentary with m1-3.

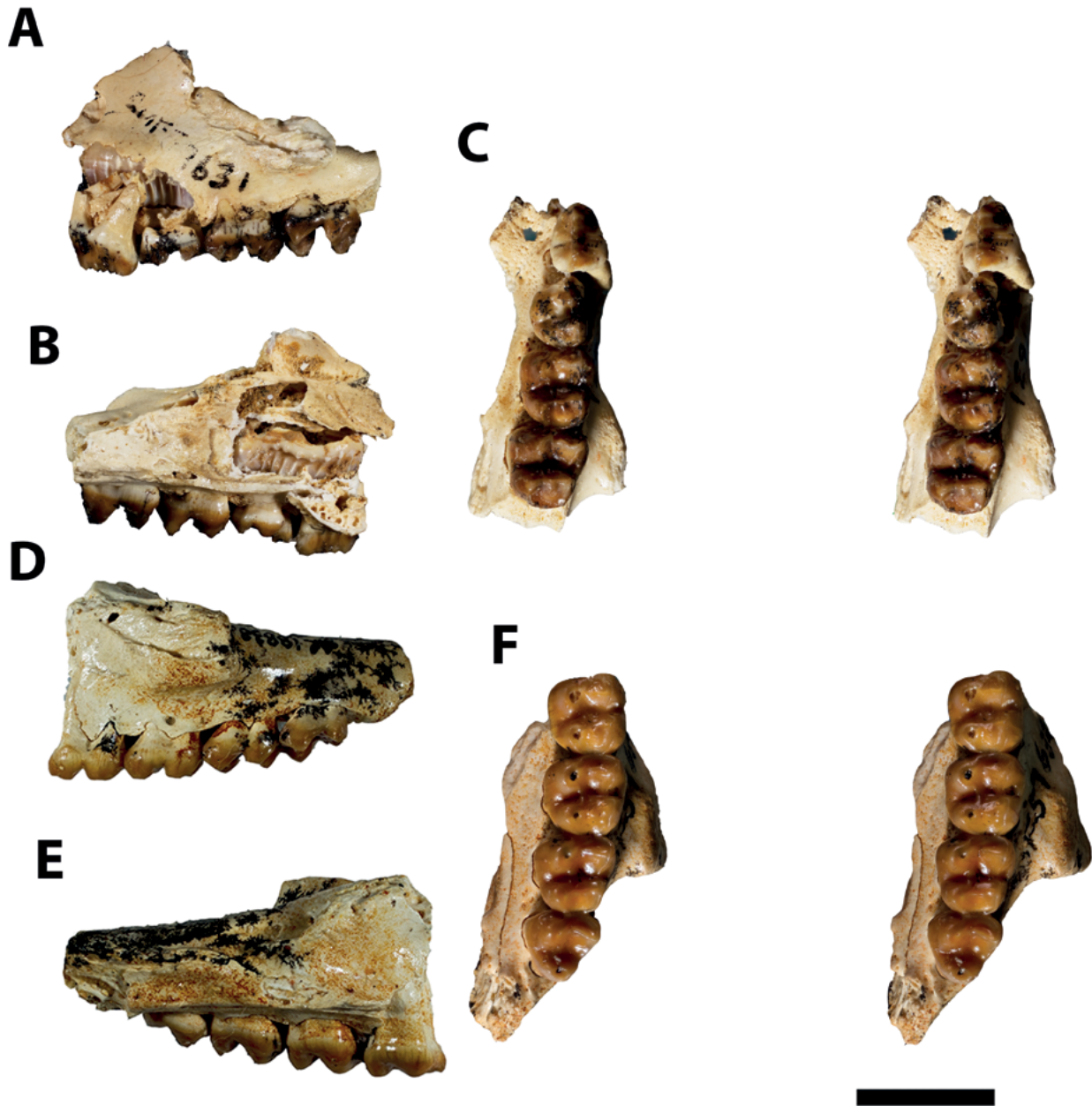


Figure 2. *Gumardee richi* sp. nov., holotype QM F57631, partial left juvenile maxilla with P3 in crypt, dP2-3 and M1-2: A, buccal, B, lingual, and C, occlusal (stereopair) views; paratype QM F57632, left maxilla with M1-4: D, buccal, E, lingual, and F, occlusal (stereopair) views. Scale bar equals 10 mm.

**Diagnosis.** *Gumardee* with five cuspsules on P2, StC present on M2-3, eight lingual and buccal transcrisetae on the occlusal margin of P3, shallow buccinator sulcus, postprotocrista not connected to the metaconule on any upper molars, metaloph joins metacone to metaconule on M4, and the posthypocristid is tall, joined to the entoconid, forming an almost complete hypolophid on all lower molars and dp3.

**Etymology.** Named after Dr Thomas H. Rich, vertebrate palaeontologist and senior curator at Museum Victoria, for his long and significant contribution to Australian palaeontology.

**Age and distribution.** All specimens are from Dirk's Towers Site, except for paratype QM F24723 which is from Quantum Leap Site. Dirk's Towers and Quantum Leap Sites are on D-Site Plateau, Riversleigh World Heritage Area, north-western

Queensland, Australia (18°15'35"S, 138°06' 41"E) and are part of Faunal Zone B (interpreted to be early Miocene in age) as distinguished by Archer et al. (1989), Archer et al. (1997), Arena (2004), Travouillon et al. (2006) and Travouillon et al. (2011).

*Description.* P2 is ovoid in shape in occlusal view, and almost as wide as it is long (figs. 2A–C). There are five cuspules on the occlusal margin. The anterior four cuspules have associated lingual and buccal transcrisetae. The posterior-most cuspule is the largest. The occlusal margin is straight, but increases in height posteriorly. The lingual margin of the tooth is steeper than its buccal margin.

The dP3 is molariform but with rounded edges in occlusal view (figs. 2A–C). The paracone is the tallest cusp on the crown, followed in decreasing order by the metacone, neometaconule, metaconule and protocone. The preparacrista is straight and descends the anterior face of the paracone. On its lingual side, a steep but short anterior cingulum is present. The postparacrista descends the posterior face of the paracone to meet in the interloph valley an anteriorly directed premetacrista from the metacone. There are no stylar cusps on the buccal margin of the tooth. The protoloph runs buccally from the protocone, rising gently for the first half of its length, then steeply to ascend the tall paracone. The postprotocrista is a weak crest that runs posterobuccally from the protocone and ends in the interloph valley. The metaloph connects the metacone to the metaconule via a large neometaconule, present midway with an associated postlink descending the metaloph posteriorly. The postmetaconulecrista is posterobuccally directed before curving buccally to meet the postmetacrista.

P3 is in its crypt with only the anterior and lateral sides visible (figs. 2A–B). There are 8 transcrisetae visible on the buccal and lingual sides of the crown. The tooth is as long as the combined length of P2 and dP3 and widest anteriorly at approximately one third its length. It narrows distinctively level with the 7<sup>th</sup> and 8<sup>th</sup> transcrisetae. A narrow cingulum is present on the lingual side of the crown. A tall posterolingual crest is present.

M1 is trapezoidal in occlusal outline, with its anterior portion wider than its posterior portion (figs. 2A–F). The paracone is the tallest cusp followed in decreasing order by the metacone, neometaconule, metaconule, protocone and StC. The molar is lophodont, having a fully formed metaloph (connecting metacone to metaconule) but an underdeveloped protoloph, which does not connect to the protocone. The preparacrista descends the paracone anteriorly before curving lingually and joining an anterobuccally directed preprotocrista from the protocone. An anterior cingulum is present between these two crests and the protoloph. No precingulum is present. StC is a gentle inflation on the buccal side of the crown. The postparacrista is straight and descends the posterior face of the paracone before ending in the interloph valley. The postprotocrista runs posterobuccally from the protocone toward the interloph valley before posteriorly ascending half way up the anterior flank of the metaloph. No distinct premetacrista is present. The metaloph is approximately twice the length of the protoloph and parallel to it. A neometaconule and associated postlink are present midway along the length of

the metaloph. The postmetaconulecrista and postmetacrista connect at the posterior margin of the crown.

M2 is similar in morphology to M1 except as follows (figs. 2A–F): the tooth is wider anteriorly; the protoloph is longer; the anterior cingulum is wider; a small precingulum is present just lingual to the preprotocrista; the protocone and metaconule are taller.

M3 is similar in morphology to M2 except as follow (figs. 2D–F): the dimensions of the tooth are reduced both in length and width, especially posteriorly; the postparacrista is more posteriorly orientated; the precingulum is wider; StC and the neometaconule are reduced.

M4 is similar in morphology to M3 except as follow (figs. 2D–F): the tooth is smaller in all dimensions and the posterior cusps and posterior width of the tooth are highly reduced; the anterior cingulum and precingulum are wider; the postparacrista and premetacrista are more buccally directed; StC is absent; the postmetacrista and postmetaconulecrista are shortened; there is no neometaconule or postlink on the reduced metaloph.

Description of the morphology of the dentary and lower dentition are based on QM F24723, QM F30698 and QM F36313 (fig. 3).

In buccal view, the ventral margin of the horizontal ramus is lightly convex with no distinct digastric eminence (figs. 3A–B). The dorsal margin of the horizontal ramus is markedly concave posteriorly, resulting in posterior teeth being higher than anterior teeth. The horizontal ramus decreases in height anteriorly below p2, so that this tooth slants forward. Two mental foramina are present; one large below the anterior root of p2 and one small below m1. The small posterior mental foramen is more posteriorly positioned in adults, below m2. A distinct buccinator sulcus is present on the buccal margin of the dentary. In lingual view, the symphysis is relatively smooth and extends as far posteriorly as the posterior of dp3. The ascending ramus is inclined at an angle approximately 125 degrees from the horizontal ramus. The masseteric canal is a large ovoid opening which projects anteriorly to below the anterior molars. It is confluent through the masseteric foramen with the dental canal for most of its length. The mandibular foramen is ovoid and posterobuccally orientated.

The i1 is partially preserved. It is a tear-shaped tooth with distinct dorsal and ventral enamel flanges (figs. 3A–C). Enamel is confined to the buccal surface of the tooth. An alveolus for i2 is present posterior to i1, but this tooth is not preserved.

The p2 is plagiaulacoid-like with the occlusal surface, in lateral view, straight but steadily increasing in height posteriorly (figs. 3A–C). In occlusal view, the buccal margin is more convex and much less steep than the lingual margin. Five cuspids with associated buccal and lingual transcrisetae are present on the crown, anterior to a large posterior cuspid. Short cristids descend the crown anterior to the anterior-most cuspid and posterior to the posterior-most cuspid.

The dp3 is a molariform tooth, wider posteriorly than anteriorly, its anterior portion being elevated where it buttresses p2 (figs. 3A–C). The tallest cusp on the crown is the protoconid, followed in decreasing order by the metaconid, entoconid, paraconid, hypoconid and protostylid. The trigonid is narrow,

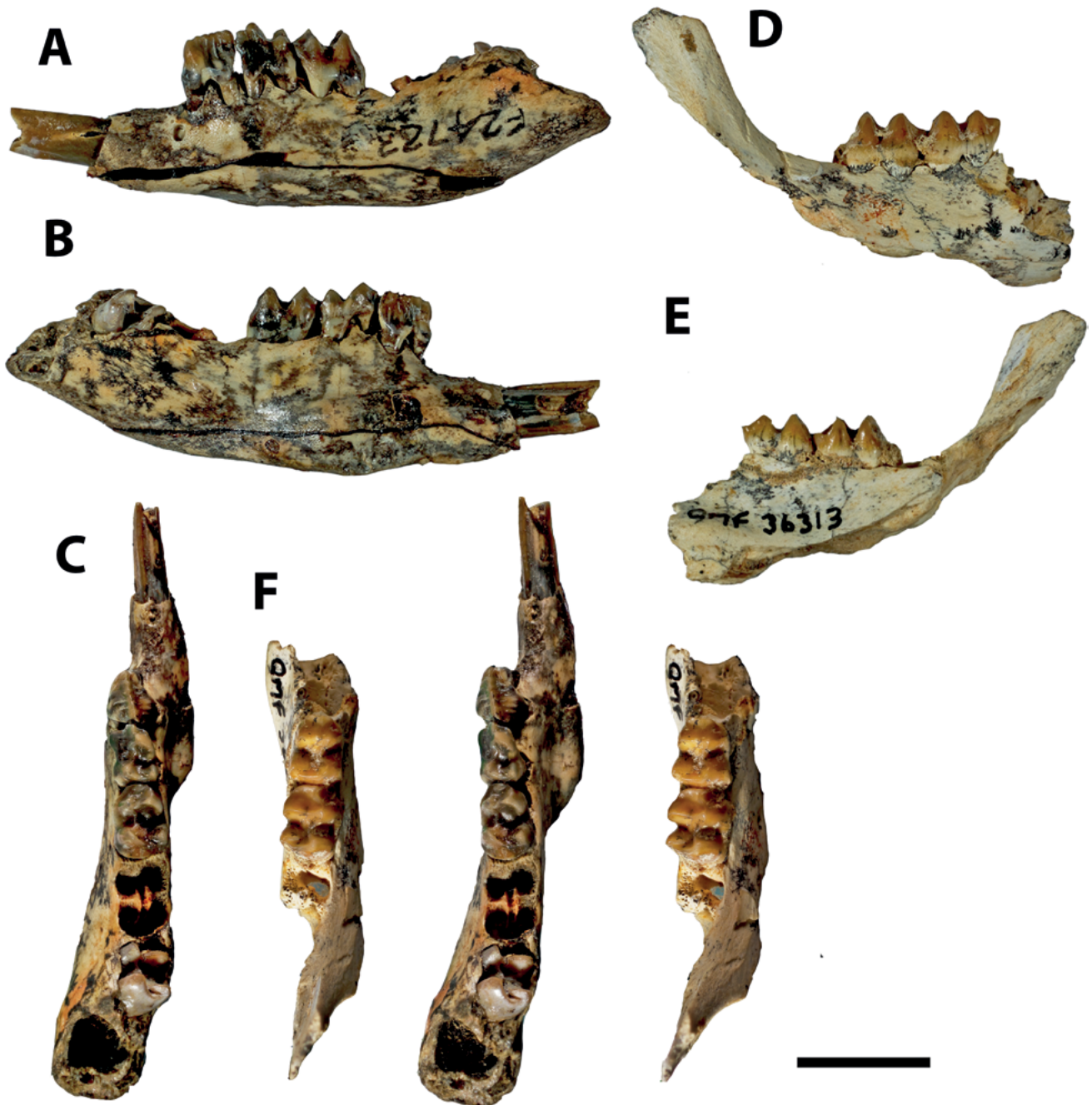


Figure 3. *Gumardee richi* sp. nov., paratype QM F24723, left juvenile dentary with broken i1, p2, dp3, m1, m3 in crypt: A, buccal, B, lingual, and C, occlusal (stereopair) views; paratype QM F36313, partial juvenile right dentary with m1-2: D, buccal, E, lingual, and F, occlusal (stereopair) views. Scale bar equals 10 mm.

with the paraconid, protoconid and metaconid in an almost linear formation, with a posterolingually directed crest running from anterior to the paraconid to posterior to the metaconid, and ending at the base of the trigonid in the interlophid valley. A protostylid is present on the buccal margin of the trigonid, just buccal to the protoconid. There is a faint wear facet connecting

the protoconid and protostylid and a distinct ridge connecting the protostylid to the cristid obliqua, which descends the posterior flank of the trigonid into the interlophid valley before ascending the talonid posterobuccally to the tip of the hypoconid. The posthypocristid descends the hypoconid posterolingually, and then ascends the posterobuccal flank of the entoconid.



Table 3. Measurements of the upper dentition of *Gumardee springae*, in mm. L = anteroposterior length, AW = anterior width, PW = posterior width, p = premolar, m = molar.

Specimen	Site	P2		dP3		P3		M1			M2			M3			M4		
		L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F18948	White Hunter					9.42	4.45	5.19	5.07	4.94				5.29	5.37	4.48	5.04	4.59	3.45
QM F18948	White Hunter					9.13	4.05	5.18	5.06	4.86	5.57	5.5	4.74	5.23	5.31	4.32	4.43	4.61	3.55
QM F19633	White Hunter					8.6	3.46	4.72	4.95	4.7	5.37	5.24	4.43	4.79	4.99	4.08	4.33	3.94	3.04
QM F19634	White Hunter							5.42	5.34	4.91	5.7	5.52	4.51	5.47	4.84	3.89			
QM F19679	White Hunter					9.79	4.36	5.41	5.58	5.02	5.46	5.54	4.73	5.29	5.3	4.43			
QM F19680	White Hunter							5.26	5.32	4.71	5.8	5.81	4.92						
QM F19681	White Hunter			4.28	3.83			5.6	5.11	4.73									
QM F19874	White Hunter										5.88		4.53				4.53	4.08	3.08
QM F19990	White Hunter							5.32	5.3	4.98	5.63	5.62	4.68	5.21		4.16			
QM F19999	White Hunter					8.88	3.99	5.26	5.02	4.74	5.62	5.56							
QM F20291	White Hunter							5.16	5.08	4.89	5.39	5.41	4.87	5.59	5.34	4.27	4.61	4.57	3.08
QM F50432	White Hunter							5.24			5.67			6.03					
QM F50432	White Hunter					9.58		5.55	5.15	4.77	6.07	6.01	4.99	5.73	5.44	4.48			
QM F52815	White Hunter							5.07	6.01	5.09	5.24	5.72	4.77	5.29	4.57	4.13			
QM F52816	White Hunter					9.37	4.2	5.1	5.15	4.74	5.93	5.46	4.81	5.82	5.28	4.29			
QM F52816	White Hunter	4.83	3.57	4.61	3.99			5.35	5.19	4.7	5.77	5.34	4.64	5.25	5.41	4.27			
QM F52816	White Hunter			4.63	4.11	9.48		5.19	5.31	4.76	5.69	5.11	4.5	5.55	4.9	3.99			
QM F57552	White Hunter					9.76	4.63	5.24	5.05	4.7	5.57	5.21	4.47	5.44	5.12	4.06			
QM F57557	White Hunter	4.88	4.12	4.27	4.31			5.09	5.57	4.92	6	5.52	4.72						
QM F57557	White Hunter	4.63	4.04	4.33	4.3			5.63	5.37	4.81	5.98	5.72	5.01						
QM F57613	White Hunter							5.08	5.18	5.15	5.94	5.59	4.81	5.26	4.9	4.27			
QM F57784	White Hunter					8.83	3.5	5.42	4.98		5.65	5.36	4.52	4.86	5.23	4.54			

There is no distinct postentocristid. A crest runs from the tip of the entoconid buccally. A preentocristid is present, descending the anterior flank of the entoconid to the interlophid valley.

The m1 is similar to dp3 in morphology except as follows (figs. 3A–F). The tooth is larger in length and width. The entoconid is the tallest cuspid followed by the metaconid, hypoconid, protoconid and paraconid. The protostylid is absent. The trigonid is wider with the protoconid more buccally placed, forming a 45 degree angle with the paraconid and metaconid. A precingulid is present buccal to the paraconid, and an anterior cingulid is present on its lingual side. Both the precingulid and anterior cingulid are bordered anteriorly by a crest which runs from the anterobuccal corner of the tooth to the anterior flank of the metaconid, through the paraconid. A premetacristid is present, connecting the metaconid to the anterior crest bordering the precingulid and anterior cingulid. The sinuous protolophid descends buccally from the metaconid before connecting to the protoconid. The cristid obliqua connects the protoconid to the hypoconid via the interlophid. The posthypocristid is lower and connects to a

postentocristid. The buccal crest from the entoconid is more developed but ends below the entoconid buccally.

The m2 is similar in morphology to m1 except as follows (figs. 3D–F). The tooth is larger in length and width. The protoconid is the tallest cusp, followed in decreasing order by the hypoconid, metaconid, entoconid and paraconid. The precingulid and anterior cingulid are wider. Both the protolophid and posthypocristid are taller.

The m3 is similar in morphology to m2 except as follows (figs. 3A–F). The tooth is longer and wider, with all cuspids taller and crests longer.

The m4 is only preserved in its crypt in QM F30698, with its morphology obscured.

#### *Gumardee springae* sp. nov.

Tables 3–4, Figures 4–6

*Holotype*. QM F52816, partial juvenile skull with left associated P2, dP3, left and right P3 in crypt, M1–3 and associated left maxilla with dP3, P3 in crypt, M1–3.

Table 4. Measurements of the lower dentition of *Gumardee springae*, in mm. L = anteroposterior length, AW = anterior width, PW = posterior width, p = premolar, m = molar.

Specimen	Site	p2		dp3		p3		m1			m2			m3			m4		
		L	W	L	W	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QM F19604	White Hunter													6.29	4.61	4.59			
QM F19606	White Hunter	4.08	3.18	4.4	3.52	8.96		5.04	3.77	4.06	5.77	3.89							
QM F19819	White Hunter					8.81	3.76	4.83	3.82	4.09	5.25	4.51	4.49	5.78	4.58	4.53	5.05	4.21	3.55
QM F19872	White Hunter					8.55	3.7	4.87	3.75	4.06	5.17	4.45	4.43	5.66	4.55	4.57	4.9	4.4	3.75
QM F19922	White Hunter													6.09	4.68	4.52			
QM F19995	White Hunter					8.77													
QM F30292	White Hunter							4.46	3.6	3.83	5.68	4.19	4.12	5.8	4.44	4.18	5.08	4.17	3.46
QM F31549	White Hunter					8.92	3.8	4.75	3.88	4.23	5.08	4.31	4.48	5.73	4.9	4.91	5.27	4.27	3.74
QM F31556	White Hunter							4.79	3.7	4.29	6.08	4.49	4.64	6.14	4.97	4.71			
QM F31559	White Hunter							4.86	4.19	4.12	5.39	4.45	4.37	5.41	4.54	4.23			
QM F41199	White Hunter										5.39	4.32	4.14	5.73	4.44	4.3	5.17	3.99	3.28
QM F41286	White Hunter					8.46	3.8	4.91	4.11	4.02	5.02	4.45	4.26	5.6	4.55	4.34	4.97	4.17	3.36
QM F57551	White Hunter					9.17	3.89	4.17	3.71	4.03	5.33	4.47	4.69						
QM F57553	White Hunter										5.36	4.36	4.37	5.94	4.35	4.42			
QM F57554	White Hunter	4.25	3.5			8.81	3.19	4.63	3.84	3.84	5.42	4.05	4.1	5.94	4.24	4.23			
QM F57555	White Hunter			4.43	3.75	9.14	3.78	5.12	4.12	4.24	5.72	4.5	4.64						
QM F57556	White Hunter					8.94	3.62	4.99	3.88	4.17	5.46	4.46	4.33	5.68	4.74	4.36	5.53	4.44	3.5
QM F57610	White Hunter	4.08	3.18	4.69	3.69			5.39	3.94	4.23		3.96							
QM F57611	White Hunter	4.11	3.01	4.26	3.58			4.92	3.99	4.05									
QM F57612	White Hunter							4.85	3.66	3.91	5.49	4.21	4.19	5.79	4.42	4.18			
QM F57783	White Hunter									4.18	5.22	4.38	4.44	5.83	4.37	4.29			

*Paratypes.* QM F19606, right juvenile dentary with p2, dp3, p3 in crypt, m1-2; QM F19633, left maxilla with P3, M1-4; QM F19872, left dentary with p3, m1-4; QM F19874, right juvenile maxilla with broken M2, M4 in crypt; QM F31549, right dentary with i1, p3, m1-4; QM F57554, right dentary with p2, p3, m1-3; QM F57557, partial juvenile skull with left and right P2, dP3, M1-2; QM F57611, right dentary with i1, p2, dp3, m1, m2 in crypt.

*Referred material.* QM F57552, left maxilla with P3, M1-3; QM F18948, associated maxillae with right P3, M1, M3-4, left P3, M1-4; QM F19634, left maxilla with M1-3; QM F19679, left maxilla with P3, M1-3; QM F19680, right maxilla with M1-2; QM F19681, left juvenile maxilla with dP3, P3 in crypt, M1; QM F19990, right maxilla with M1-2, broken M3; QM F19999, left maxilla with P3, M1-2, broken M3; QM F20291, right maxilla with worn M1-4; QM F50432, associated left and right maxillae, with P3, M1-3; QM F52815, partial juvenile skull with broken right dP3, M1-3, M4 in crypt; QM F57613, right maxilla with M1-3; QM F57553, right dentary with m2-3; QM F57551, right dentary with p3, m1-2; QM F57555, left dentary with dp3, p3, m1-2; QM F57612, left dentary with m1-3; QM F57610, left dentary with p2, dp3, m1, broken m2; QM F57556, left dentary with p3, m1-4; QM F19604, right dentary with broken m2, m3, broken m4; QM F19819, right dentary with p3, m1-4; QM F19922, left juvenile dentary with m3, m4 in crypt; QM F19995, right juvenile dentary with

p3 in crypt; QM F30292, associated left m1-4; QM F31556, left dentary with m1-3; QM F31559, right dentary with m1-3; QM F41199, right dentary with m2-4; QM F41286, right dentary with p3, m1-4; QM F57783, right dentary with partial m1, m2-3; QM F57784, left maxilla with P3, partial M1, M2-3.

*Diagnosis.* *Gumardee* with postprotocrista connected to the metaconule on all upper molars, metaloph does not connect metacone to metaconule on M4, shallow buccinator sulcus, nine cuspules/cuspids with eight transcristae/transcristids on P3/p3, five cuspules on P2, no St C on M2-3, and buccal crest from entoconid well-developed as a hypolophid, with low posthypocristid on all lower molars and dp3, well developed protostylid on dp3, no premetacristid on m1, and well developed paracristid on m1.

*Etymology.* Named after Kirsten Spring, collection manager of the Geosciences Program at the Queensland Museum, Brisbane, Australia, in recognition of her skilled and careful management of the large and diverse Riversleigh fossil collections.



Figure 4. *Gumardee springae* sp. nov., holotype QM F52816, partial juvenile skull with left loose P2, dP3, left and right P3 in crypt, M1-3 and associated left maxilla with dP3, P3 in crypt, M1-3: A, dorsal, and B, ventral views. Scale bar equals 10 mm.

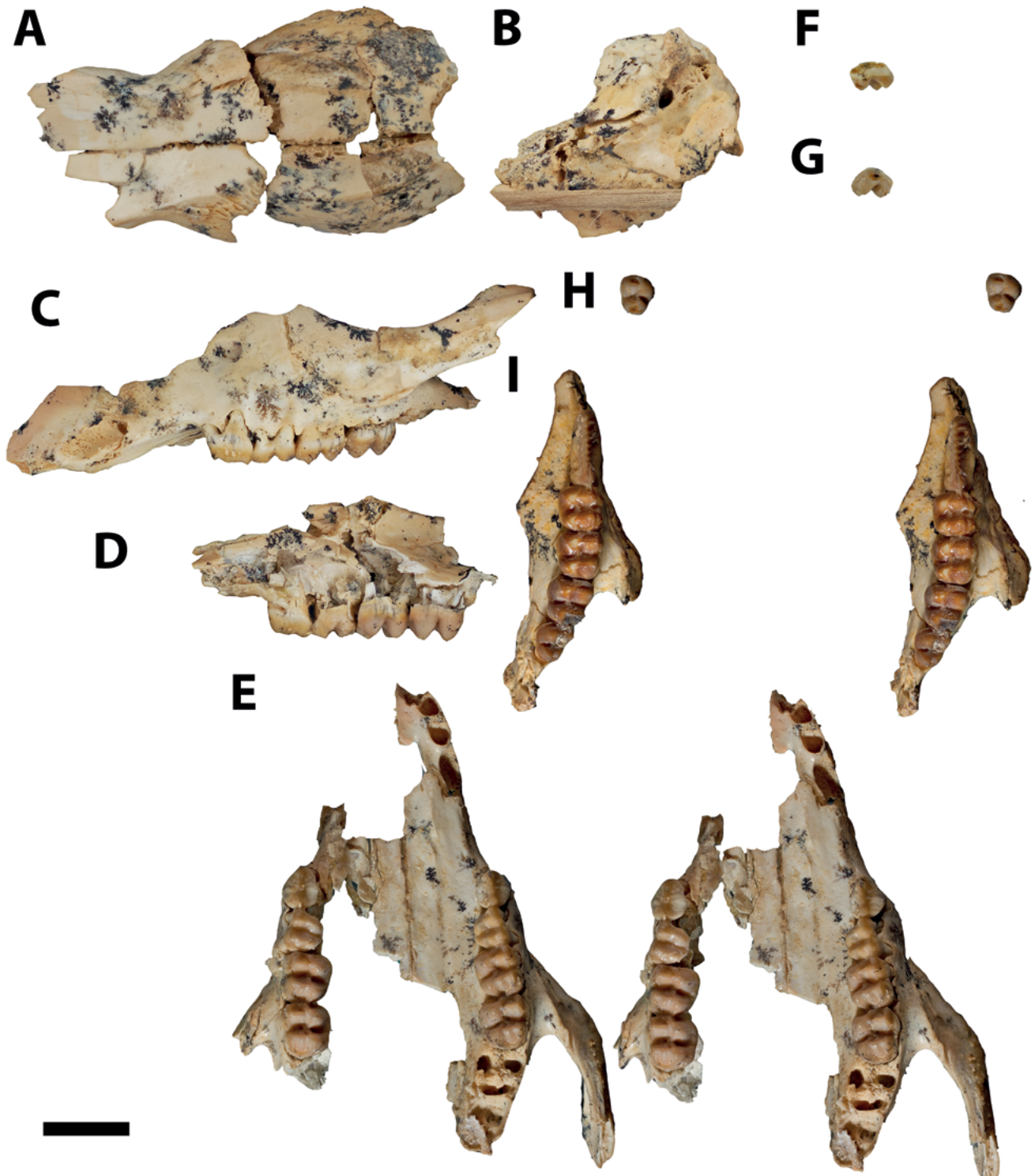


Figure 5. *Gumardee springae* sp. nov., paratype QM F57557, partial juvenile skull with left and right P2, dP3, M1-2: A, dorsal view of neurocranium; B, ventral view of basioccipital, occipital condyle and supraoccipital; C, buccal, D, lingual, and E, occlusal (stereopair) views of palate; paratype QM F19874, right M4: F, buccal, G, lingual, and H, occlusal (stereopair) views; QM F19633, left maxilla with P3, M1-4: I, occlusal (stereopair) view. Scale bar equals 10 mm.

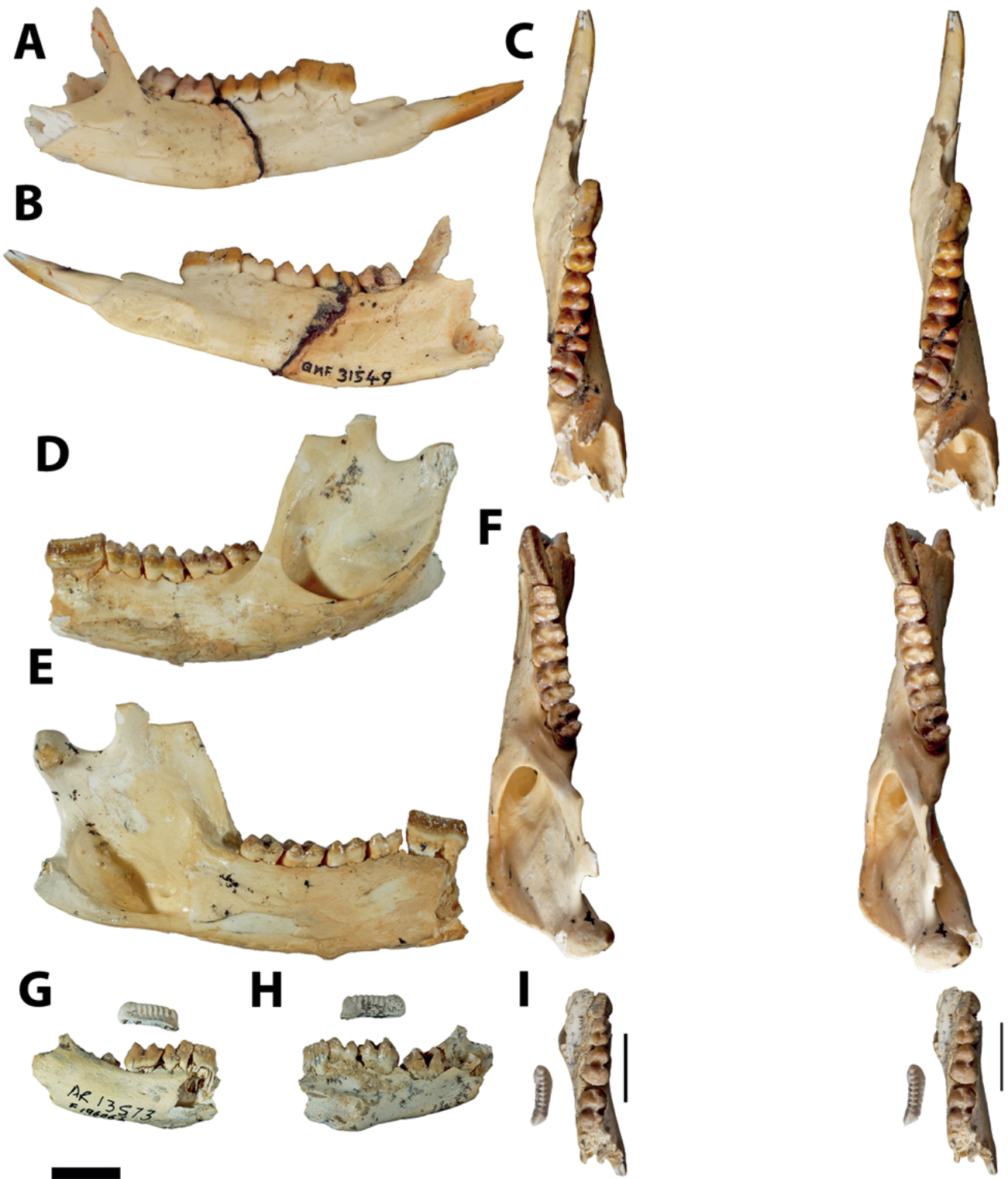


Figure 6. *Gumardee springae* sp. nov., paratype QM F31549, right dentary with i1, p3, m1-4: A, buccal, B, lingual, and C, occlusal (stereopair) views; paratype QM F19872, left dentary with p3, m1-4: D, buccal, E, lingual, and F, occlusal (stereopair) views; paratype QM F19606, right juvenile dentary with p2, dp3, p3 in crypt, m1-2: G, buccal, H, lingual, and I, occlusal (stereopair) views. Scale bar equals 10 mm.

*Age and distribution.* All specimens are from White Hunter Site, D-Site Plateau, Riversleigh World Heritage Area, north-western Queensland, Australia (18°15'35"S, 138°06' 41"E). White Hunter Site is part of Riversleigh's Faunal Zone A, interpreted to be late Oligocene in age on the basis of biocorrelation of those faunas with Ngama Local Fauna, Etadunna Formation, South Australia, as distinguished by Archer et al. (1989), Archer et al. (1997), Arena (2004) and Travouillon et al. (2006, 2011).

*Description.* The skull morphology description is based on holotype QM F52816 and paratype QM F57557 (figs. 4–5). The premaxilla is partly preserved in QM F57557 (fig. 5). The alveoli for I1–3 and C1 are present. The alveolus for I1 is the largest for the incisors and ovoid in shape and laterally compressed. The alveoli for I2 and I3 are squarer and the alveolus for I2 is slightly smaller than the alveolus of I3. The alveolus for C1 is almost twice the size as that of I1, but the lateral wall of the alveolus is damaged, preventing full assessment of its size. The alveolus for C1 is bordered by the maxilla posteriorly. An incisive fenestra is present medial to I3 and C1, but only the anterior and lateral portion of its wall are preserved, with the maxilla contributing to the posterolateral wall.

The maxilla is the best preserved part in both specimens (figs. 4–5). The palate is concave in lateral view, contrasting with the molar row that is convex. In ventral view, the molar row curves posteromedially. The lateral borders of the maxillopalatine fenestrae are present, extending as far anteriorly as the midpoint of M1, and as far posteriorly as the posterior of M4. The palatine is preserved in QM F52816, bordering the right maxillopalatine fenestra from M3 to M4. In lateral view, a small ovoid infraorbital canal is present above the posterior root of P2 in QM F57557, and dorsal to the middle of P3 in QM F52816. The maxillary-jugal suture is relatively smooth. A masseteric process is present ventral to the maxillary-jugal suture as a short ridge. In lateral view, the dorsal margin of the frontal is perfectly flat. Distinct ridges border the dorsal margins of the frontals, narrowing posteriorly, past the postorbital constriction of the skull, and are at their narrowest at the frontal-parietal sutures. These ridges continue through the parietals and widen posteriorly. There is no distinct sagittal crest at the sagittal suture. Portions of the squamosal, alisphenoid, basisphenoid and ectotympanic are poorly preserved in QM F52816.

Part of the basioccipital, occipital condyle and supraoccipital are preserved in QM F57557 (fig. 5B). The preserved portion of the basioccipital is relatively flat. The occipital condyle is ovoid in ventral view, about twice as wide as it is long. Two foramina lie within the ventral condyloid fossae. The anterior-most foramen, the hypoglossal foramen, is about half the size of the posterior foramen, the condylar foramen. These foramina lead to short canals which open posteriorly into the foramen magnum. Posterolateral to the condylar foramen, another round foramen is present. The posterior wall of the jugular foramen is present just anterolateral to the condylar foramen.

The description of the upper dentition is based on holotype QM F52816 and paratypes QM F19633, QM F19874 and QM F57557.

P2 is a plagiulacoid-like tooth almost as wide as it is long (figs. 5C–E). In occlusal view, its lingual margin is steeper than its buccal margin, and the tooth is widest at about midlength. The occlusal ridge increases in height posteriorly. There are six cuspules present on the occlusal margin. Lingual and buccal transcrisetae are associated with the anterior five cuspules. The posterior cuspule is the largest and is much taller than the other cuspules on the occlusal ridge.

dP3 is molariform, and almost square in occlusal view (figs. 5C–E). The paracone is the tallest cusp, followed in decreasing order by the metacone, metastyle?, neometaconule, protocone and metaconule. There is no distinct anterior cingulum or precingulum. The preparacrista is almost horizontal as it runs from the paracone anteriorly. The postparacrista descends the posterior face of the paracone, and meets an anteriorly directed premetacrista from the metacone. No stylar cups are present on the buccal margin of the tooth. The protoloph runs from the protocone buccally, rising gently for the first half of its length and then steeply before contacting the paracone. The postprotocrista runs posterobuccally before curving posteriorly midway in the interloph valley, forming a mid-link contacting the anterior face of the metaloph. A large neometaconule is present midway along the metaloph, with an associated postlink descending the metaloph posteriorly. The postmetaconulecrista is posterobuccally directed before curving buccally to meet a distinctive cusp (metastyle?) at the posterobuccal corner of the tooth. The postmetacrista connects this cusp to the metacone anteriorly.

P3 is an elongate sectorial tooth approximately one and half times to almost twice the length of M1 (fig. 5I). In occlusal view, the tooth is widest midlength, with a distinctive kink, with the tooth narrowing just before the posterior-most cuspule. There are nine cuspules on the crown, with the anterior eight having associated transcrisetae. The posterior-most cuspule is about twice the size of the anterior cuspules. The occlusal crest is straight and runs from the most anterior corner of the tooth through all cuspules to the posterior-most corner of the tooth. Both the lingual and buccal margins of the occlusal ridge are very steep, before reaching rounded lingual and buccal cingula. There are no distinct lingual or buccal cuspules or ridges on either side of the posterior-most cuspule, other than a slight inflation, more prominent on the lingual than buccal side.

M1 is relatively square in occlusal outline, only slightly wider anteriorly (figs. 5E, I). The paracone is the tallest cusp followed in decreasing order by the metacone, protocone and metaconule. The preparacrista is straight and runs anteriorly from the paracone to the anterior margin of the tooth. The postparacrista is straight and slopes directly posteriorly from the paracone apex to the interloph valley where it connects to a straight and steep premetacrista. In most specimens observed, a minute StC is present just buccal to the postparacrista, except in the holotype QM F52816, QM F19634, QM F19874 and QM F18948, where this cusp is absent. The protoloph is short and steeply descends the lingual flank of the paracone until it meets the preprotocrista at about one third of its length from the protocone. The preprotocrista runs from the protocone anterobuccally, and curves slightly

more anteriorly where it meets the protoloph. An anterior cingulum is present anterior to the protoloph and is bordered by the preparacrista buccally and preprotocrista lingually. A short and low precingulum is present lingual to the preprotocrista. The postprotocrista descends posterobuccally from the protocone toward the interloph valley where it forms a distinct wall before connecting to the premetaconulecrista which connect posterolingually to the metaconule. The metaloph is parallel to the protoloph and descends the lingual flank of the metacone to connect to the low metaconule. The neometaconule is present midway along the metaloph, with an associated postlink or neometaconule crista which extends half way down the posterior face of the metaloph. The postmetacrasta runs posteriorly from the apex of the metacone to connect close to the crown base with the postmetaconulecrista, which sweeps across the posterior face of the loph.

M2 is similar in morphology to M1 except as follows (figs. 5E, I): the tooth is slightly longer and wider anteriorly, increasing the length of all anterior cristae; the protoloph is taller and less steep; the anterior cingulum is longer; StC is absent; the precingulum is twice as wide as it is on M1; and the preparacrista is anterobuccally curved.

M3 is similar in morphology to M2 except as follows (fig. 5I): the tooth is smaller in all dimensions but more greatly reduced posteriorly; the precingulum is longer and wider, extending almost to the lingual corner of the tooth; the postparacrista and premetacrasta are weak crests that do not meet in the interloph valley; and the neometaconule is greatly reduced to a small inflation on the posterior flank of the metaloph.

M4 is similar in morphology to M3 except as follows (figs. 5F–I): the tooth is further reduced in all dimensions; the protoloph does not connect to the preprotocrista; the postparacrista and premetacrasta are barely visible; the metaloph does not connect to the metaconule, instead it is anterolingually orientated and meets the premetaconule crista just anterior to the metaconule; and the precingulum is larger and extends to the lingual corner of the tooth.

Description of the morphology of the dentary is based on paratypes QM F31549 and QM F19872, unless otherwise stated (fig. 6). The ventral margin of the horizontal ramus is slightly convex in buccal view. There is no distinct digastric eminence, but the ramus is at its tallest just below the anterior root of m3. The dorsal margin of the horizontal ramus is markedly concave posteriorly, resulting in posterior molars being elevated with respect to p3 and anterior molars. Anteriorly, the horizontal ramus decreases in height below p3, such that this tooth slants forward. Anterior to p3, the horizontal ramus is straight and constant in depth throughout the diastema. A distinct buccinator sulcus is present on the buccal margin of the dentary, and extends from level with the anterior of m1 to level with the middle of m2. A large ovoid anterior mental foramen is present just below the anterior root of p3, close to the dorsal edge of the diastema. No posterior mental foramen is present in the majority of the specimens observed, but a small posterior mental foramen is present in the juvenile QM F19606 (below the anterior root of m1), QM F57551 (below m2), and two to three posterior mental foramina are present in QM F57556 and QMF19819 (below m1 and m2).

In lingual view, the symphysis is relatively smooth and extends posteriorly to the middle of p3. The ascending ramus is inclined at an angle approximately 125 degrees to the horizontal ramus. The masseteric fossa is buccally expanded. The masseteric canal is a large ovoid opening which projects anteriorly from the masseteric fossa to the level of the anterior of m3 and is confluent through the masseteric foramen with the dental canal for most of its length. The mandibular foramen is ovoid in shape and is posterobuccally orientated. The pterygoid fossa is wide and deep. The condyle is barrel-shaped.

Description of the morphology of the lower dentition is based on the least worn adult paratype QM F31549, and unworn juveniles QM F19606, QM F57554 and QM F57611.

The i1 is a short tear-shaped tooth, with a distinct dorsal enamel flange but less distinct ventral enamel flange (figs. 6A–C). The occlusal crest is slightly sinuous. Enamel is confined to the buccal surface of the tooth and extends further ventrally than dorsally. The crown is ovoid in cross-section.

The p2 is plagiulacoid-like (figs. 6G–I). In lateral view, the occlusal margin is straight but steadily increases in height posteriorly. In occlusal view, the buccal margin is more convex and much less steep than the lingual margin. Four cuspids with associated buccal and lingual transcrisids are present on the crown, anterior to a large posterior cuspid. Short cristids descend the crown anterior to the anterior-most cuspid and posterior to the posterior-most cuspid.

The dp3 is a molariform tooth, wider posteriorly than anteriorly, its anterior portion being elevated where it buttresses p2 (figs. 6G–I). The tallest cusp is the protoconid, followed in decreasing order by the entoconid, hypoconid, metaconid, paraconid and protostylid. The trigonid is narrow, with the paraconid, protoconid and metaconid in an almost linear formation, with a posterolingually directed crest running from anterior to the paraconid to posterior to the metaconid, ending at the base of the trigonid in the interlophid valley. A protostylid is present on the buccal margin of the trigonid, just buccal to the protoconid. There is a faint connection between the protoconid and protostylid (possibly due to wear), and another connection between the protostylid and cristid obliqua, which descends the posterior flank of the trigonid into the interlophid valley before ascending the talonid posterobuccally to the tip of the hypoconid. The posthypocristid descends the hypoconid posterolingually, and then curves anterolingually to connect to the postentocristid, which descends from the tip of the entoconid posteriorly. A preentocristid is present, descending the anterior flank of the entoconid to the interlophid valley. A crest runs from the tip of the entoconid buccally.

The p3 has a semilunar occlusal outline and is aligned with the molar row (figs. 6A–F). The occlusal edge lies lingual to the midline and is slightly lingually concave. In lateral view, the occlusal edge is straight and more elevated posteriorly. In the juveniles, nine cuspids are present on the occlusal edge, with the anterior eight cuspids having associated buccal and lingual transcrisids, descending only halfway down the crown. In adults, cuspids and transcrisids are obscured by heavy wear on the crown. The lingual flank of the tooth is nearly vertical while the buccal flank is less steeply sloping. A short cristid

descends anteriorly from the anterior end of the occlusal margin and a much longer cristid runs from the posterior margin, curving to the lingual side of the crown base.

The molar row is straight in occlusal view but concave in lateral view. Molars are bunolophodont with central molars larger than terminal ones.

The m1 is similar to dp3 in morphology except as follows (figs. 6A–I). The tooth is larger in length and width. The hypoconid is the tallest cuspid followed by the entoconid, metaconid, protoconid and paraconid in juveniles. In the adult QM F31549, buccal cupids are worn well below the level of lingual cuspids, with the metaconid being the tallest cuspid followed by entoconid, protoconid, hypoconid and paraconid (also seen on m2 and m3). The protostylid is absent. The trigonid is wider with the protoconid more buccally placed, forming a 45 degree angle with the paraconid and metaconid. A precingulid is present buccal to the paraconid, and an anterior cingulid occurs on its lingual side. Both the precingulid and anterior cingulid are bordered anteriorly by a crest which runs from the anterobuccal corner of the tooth to the anterior flank of the metaconid, through the paraconid. The sinuous protolophid descends buccally from the metaconid before connecting to the protoconid. The cristid obliqua connects the protoconid to the hypoconid via the interlophid. The buccal crest from the entoconid, the hypolophid, is taller and loph-like and almost reaches the posthypocristid posteriorly. In the adult QM F31549, the buccal side of the tooth is so worn that the hypolophid looks as if it was connected to the hypoconid (also seen on m2 and m3).

The m2 is similar in morphology to m1 except as follows (figs. 6A–I). The tooth is larger in all dimensions. The protoconid is the tallest cusp, followed in decreasing order by the hypoconid, entoconid, metaconid and paraconid. The precingulid and anterior cingulid are larger. A premetacristid is present, connecting the metaconid to the anterior crest bordering the precingulid and anterior cingulid. Both the protolophid and hypolophid are taller.

The m3 is similar in morphology to m2, apart from it being longer and wider, with all cuspids taller and crests longer (figs. 6A–F).

The m4 is similar in morphology to m3 except as follows (figs. 6A–F). The tooth is smaller in all dimensions. The talonid is greatly reduced, especially the entoconid and the hypolophid, which are half the size and length of that of m3.

### Results of Phylogenetic Analysis

Our analysis resulted in 860 most parsimonious trees (tree length = 590; consistency index = 0.3492; retention index = 0.7616), summarised as a strict consensus tree (fig. 7). Hypsiprymmodontidae was recovered as monophyletic and as the sister group to all other taxa within Macropodiformes, but with low support values (bootstrap = <50; Bremer = 0). Balbaridae forms a paraphyletic group, basal to Macropodidae, but also with low support values. Both *Balbaroo* and *Nambaroo* are polyphyletic.

Within Macropodidae, Potoroinae was recovered as a monophyletic group, sister to all other macropodids, with low support values (bootstrap = <50; Bremer = 0). Within

Potoroinae, *Bulungamaya delicata* occurs as the most basal member, and species of *Gumardee* are recovered as a monophyletic group with moderately good support (bootstrap = 68; Bremer = +1) and as the sister group to a clade containing *Purtia mosaicus*, *Ngamaroo archeri*, *Wakiewakie lawsoni*, *Bettongia moyesi* and all extant potoroines. Species of *Bettongia* are not reciprocally-monophyletic.

Species of *Ganguroo* and *Wabularoo* occur as basal members of a clade containing lagostrophines, sthenurines and macropodines (with low support). Lagostrophinae, Sthenurinae and some macropodines (fig. 7) were recovered with strong support values.

### Discussion

The phylogenetic analysis supports the original attribution of species of *Gumardee* to Potoroinae (Flannery et al., 1983, 1984). The analysis also recovers Potoroinae as a monophyletic group, including extant taxa and a number of fossil taxa such as *Purtia mosaicus*, *Ngamaroo archeri*, *Wakiewakie lawsoni*, *Bettongia moyesi* and *Bulungamaya delicata*. Both *P. mosaicus* and *W. lawsoni* were originally placed in Potoroinae by Case (1984) and Woodburne (1984), respectively, but this placement was not supported by recent phylogenetic analyses, in which they form a clade with *N. archeri* outside of Potoroinae (Kear and Pledge, 2008; Travouillon et al., 2014). In other phylogenetic analyses (Prideaux and Tedford, 2012; Prideaux and Warburton, 2010), *P. mosaicus* and *W. lawsoni* were not included and *N. archeri* and *B. delicata* (their *Nowidgee* matrix; see Travouillon et al., 2014) occur as basal members, sister to lagostrophines, sthenurines and macropodines. They are all recovered in our analysis within Potoroinae, though with low support. The phylogenetic relationship of *Bettongia moyesi* has been rarely tested since its description (Flannery and Archer, 1987b). It appears to form a clade with *W. lawsoni*, rather than other *Bettongia*, suggesting that its generic attribution may need to be revised. It was placed in this genus because the jugal extends high onto the face anterior to the orbit as in all other species of *Bettongia* and Flannery and Archer (1987b) suggested that it was very similar in morphology to *B. lesueur*. However, the authors also suggested that the similarities between these two species could be retained primitive features and therefore not necessarily indicative of close relationship. Our results support this latter assessment. Due to low support values, it is difficult to assess whether this clade warrants subfamily level (Potoroinae) within Macropodidae (sensu Prideaux and Warburton, 2010) or as a family of its own (Potoroidae, e.g. sensu Kear and Cooke, 2001; Meredith et al., 2009).

Potoroinae, as a monophyletic group, is characterised by the following features: long sectorial P3/p3 with many fine ridges (>5 ridges); strongly developed preprotocrista confluent with precingulum; distinct postmetacristid and postprotocristid on lower molars; cristid obliqua restricted to buccal side of lower molars; postentocristid distinct and connecting to large posthypocristid posteriorly and low hypocingulid present between entoconid and posthypocristid; no digastric eminence on the dentary, with a convex ventral margin. Two additional features unique to this clade, excluding *Bulungamaya delicata*, include the masseteric canal extending below the anterior molars



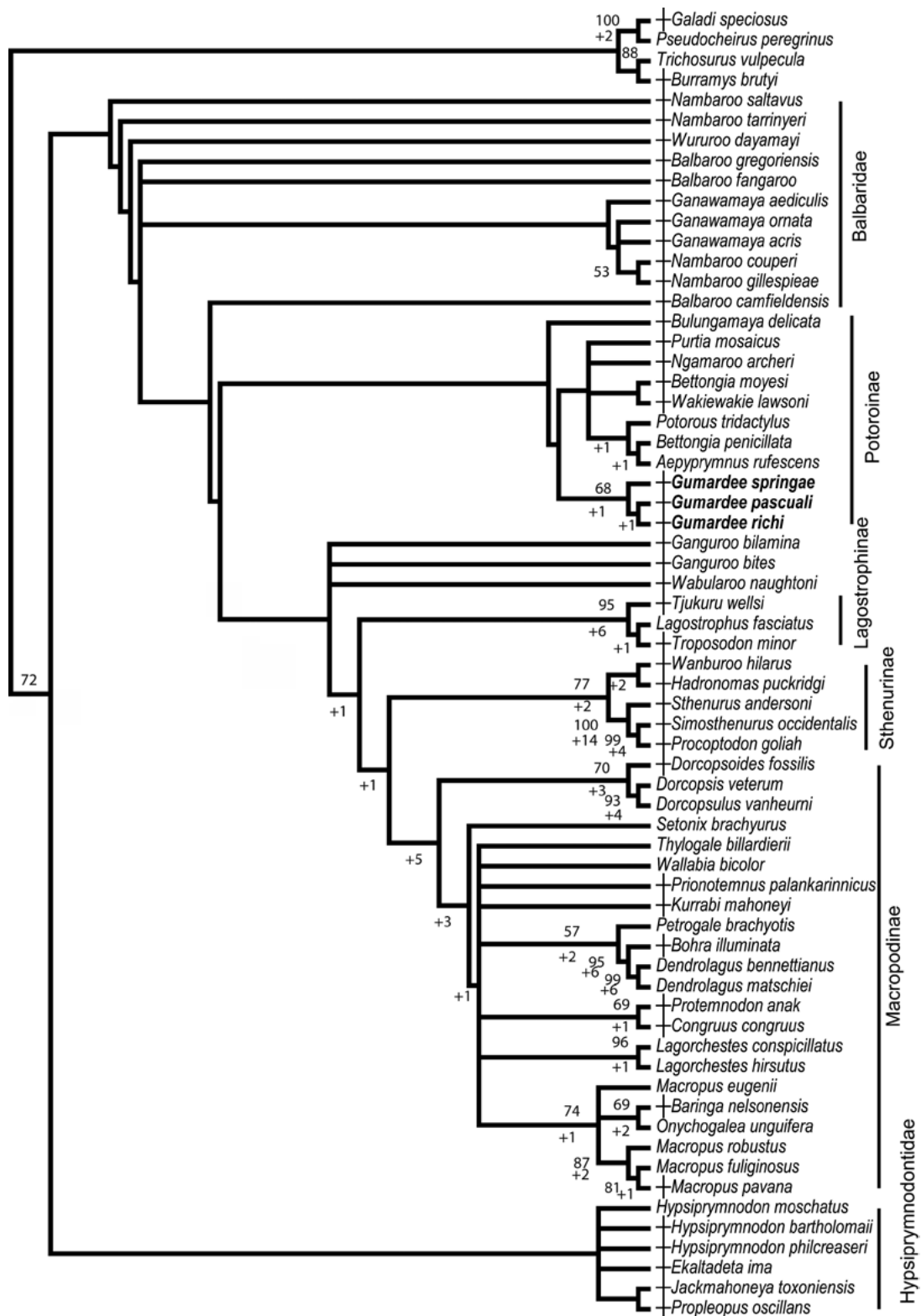


Figure 7. Strict consensus of 860 most parsimonious trees (tree length = 590; consistency index excluding uninformative characters = 0.3492; retention index = 0.7616) from maximum parsimony analysis of our matrix containing 119 characters, assessing the phylogenetic relationship of *Gumardee* species. Numbers above branches represent bootstrap values (1000 replicates); numbers below branches represent decay indices. Fossil taxa are indicated by †. Species of *Gumardee* are highlighted in bold.

and the cheek tooth row being concave in the dorsoventral plane. The majority of the characters defining the crown-group Potoroinae (*Bettongia* + *Potoroo*) are cranial and postcranial characters which are not assessable in the fossil taxa, except for five characters (one cranial and four dental): frontal-squamosal contact (fossil potoroine taxa have a parietal-alisphenoid contact); absence of a lingual cingulum on P3 (present in *Gumardee*); absence of a lateral constriction on P3 (present in *Gumardee*); postprotocrista restricted to the lingual side of the tooth in upper molars (extends in interloph valley in *Gumardee*); and postprotocrista is short and thick (fine and low in *Gumardee*). The position of *Bulungamaya delicata* as a basal potoroine is quite surprising but it is supporting Prideaux and Warburton (2010)'s conclusions that the subfamily Bulungamayinae (included *Bulungamawa*, *Ganguroo* and *Wanburroo*) is paraphyletic and should no longer be used. However, considering that the position of *Bulungamaya delicata* has very low support values (bootstrap = <50), this position could be an artefact of missing cranial and postcranial scores, which are needed to accurately assess its phylogenetic relationship.

Our phylogenetic analysis also recovers Hypsiprymnodontidae as a monophyletic group. Wroe (1996) suggested that propleopines (e.g. *Ekaltadeta* and *Propleopus*) were the sister taxa to species of *Hypsiprymnodon*. A review of the systematics of this group by Kear and Cooke (2001) supported this placement. However, several studies did not support the monophyly of Hypsiprymnodontidae, finding Propleopinae to be the sister taxon to Balbaridae (Kear and Pledge, 2008; Travouillon et al., 2014). Our analysis does not support a close relationship between Balbaridae and Propleopinae; instead, Balbaridae is a paraphyletic group, with *Balbaroo camfieldensis* being the sister taxon to Macropodidae. Considering that support values are low, these results should be interpreted cautiously.

The new identified specimens of *Gumardee pascuali* and the two new taxa have increased the temporal range of the genus, although the sample size for *G. pascuali* (n=4) and *G. richi* (n=6) remains low. *Gumardee springae* has a much higher sample size (n=38), but seems to occur only at White Hunter Site, and is the most abundant macropodiform at this locality. White Hunter Site is part of Riversleigh Faunal Zone A, and interpreted to be late Oligocene in age (Archer et al., 1997; Myers and Archer, 1997; Travouillon et al., 2006, 2011), as are D-Site and Bone Reef Site, where *G. pascuali* instead occurs. *Gumardee pascuali* also occurs at Dirk's Towers Site (Faunal Zone B, early Miocene in age; Travouillon et al., 2006, 2011), extending the temporal range of this taxon. *Gumardee richi* also occurs at Dirk's Towers Site, as well as Quantum Leap Site in the same Faunal Zone (Travouillon et al., 2011, 2013). *Gumardee springae* is more archaic than either *G. pascuali* or *G. richi* in having a postprotocrista connected to the metaconule on all upper molars (not connected in the other two species); its metaloph does not connect the metacone to the metaconule on M4 (connected in the other two species); its buccal crest from the entoconid is well-developed as a hypolophid, with its posthypocristid lying low on all lower molars and dp3 (buccal crest weaker in the other two species and their posthypocristid is taller, almost so as to form a functional hypolophid); it has a well-developed protostylid on dp3 (absent on the other two taxa); no premetacristid on m1

(present in the two other taxa); and a well-developed paracristid on m1 (reduced in other taxa). This would suggest that *G. springae* may be ancestral to both *G. pascuali* and *G. richi*, and White Hunter Site could be older than Dirk's Towers and Quantum Leap Site, and also possibly older even than D-Site and Bone Reef Site.

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