

A new 'bone-cracking' dasyurid (Marsupialia), from the Miocene of Riversleigh, northwestern Queensland

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Ganbulanyi djadjinguli gen. et sp. nov. is described on the basis of an upper molar and premolar from an early-late Miocene site in Riversleigh, northwestern Queensland. The paucity of material constrains certainty in the determination of its phylogenetic position. But, among dasyuromorphians, and dependent on the interpretation of tooth homology, this species shows unequivocal synapomorphies only with the derived dasyurine *Sarcophilus*, and/or *Barinya wangala*, a possible sister taxon to the modern dasyurid radiation (i.e., Sminthopsinae, Phascogalinae, Dasyurinae). Other apomorphies, evident in *G. djadjinguli*, are common to both carnivorous thylacinids and dasyurids within the order. Some dental features of *Ganbulanyi djadjinguli* are treated as adaptations to a 'bone cracking' habitus. If this interpretation is correct, then this species represents the only pre-Pliocene Australian taxon known to occupy such a niche and perhaps the smallest specialist 'bone-cracker' within Mammalia.

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RECENT discoveries from Late Oligocene and Miocene deposits of Riversleigh, in northwestern Queensland, have produced a vastly improved fossil record for the Dasyuromorphia (Archer 1982a, b; Muirhead & Archer 1990; Muirhead 1992, 1997; Muirhead & Wroe in press; Wroe 1996a, 1997a, b, in press), the dominant marsupial insectivore-carnivore radiation of Australasia. Surprisingly, analysis of both this and fossil peramelemorphian material (Muirhead 1994; Muirhead & Filan 1995), has shown that the now speciose Dasyuridae was poorly represented in the Miocene rainforests of Riversleigh, with peramelemorphians and thylacinids dominating insectivorous and carnivorous niches, respectively. In fact, only one pre-Pliocene taxon described to date can be confidently placed within Dasyuridae and Wroe (in press) concludes that this species, *Barinya wangala*, represents

the sister taxon to a monophyletic clade which includes all 'modern dasyurids'. The possibility that 'modern dasyurids' (*sensu* Wroe in press) represent the product of a middle to late Miocene radiation must be seriously considered. Wroe (1996a) suggested that the Dasyuridae can not be defined on the basis of dental synapomorphies, and consequently treated several unspecialised fossil taxa, previously placed in Dasyuridae, as Dasyuromorphia *incertae sedis*. Adding to this story of increasing complexity is the new and highly specialised fossil dasyuromorphian taxon described below. Systematics follows Wroe (1996a, 1997a). Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, such that the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4. Specimens are currently held at the University of New South Wales, on loan from the

Queensland Museum, and are denoted by the Prefix QMF.

Systematic palaeontology

Order DASYUROMORPHIA Gill, 1872
Family DASYURIDAE (Goldfuss, 1820)
Waterhouse, 1838

Ganbulanyi gen. nov.

Type species. Ganbulanyi djadjinguli sp. nov.

Etymology. *Ganbulanyi* is a Wanyi Aboriginal word for native cat (Dymock 1993).

Diagnosis. Dasyurid in which the protocone shows a greatly reduced occlusal surface area and a bulbous base with the lingual face steeply inclined, the centrocrista is straight in occlusal view, the postmetacrista is aligned anteroposteriorly, stylar cusp C is present, the major cusps are approximated (i.e., paracone and metacone, the paracone and stylar cusp B, and the metacone and stylar cusp D respectively are at least partially fused), the stylar shelf is greatly reduced, and both the upper molar (M¹ or M²) and premolar (P² or P³) are massive but low-crowned.

Ganbulanyi djadjinguli sp. nov. (Fig. 1)

Diagnosis. As for the genus by monotypy.

Etymology. From the Wanyi Aboriginal words 'djadji' meaning 'to eat' and 'nguli' meaning 'bone' (Dymock 1993). Pronunciation of specific name: jad-jin-guli.

Holotype. QMF 24537, right M¹ or M² With an acute triangular section missing, that is, the posterior portion of metacone and extending to the base of the crown and a small segment of the

lingual face of stylar cusp D.

Type specimen locality and age. Encore Site. Riversleigh World Heritage Estate, northwestern Queensland. This site, from the System C Riversleigh assemblage, has been tentatively dated as early-late Miocene in age (Archer *et al.* 1995).

Referred specimen. QMF 30464, an upper PI or PI, is twin rooted with the posterior root broken away.

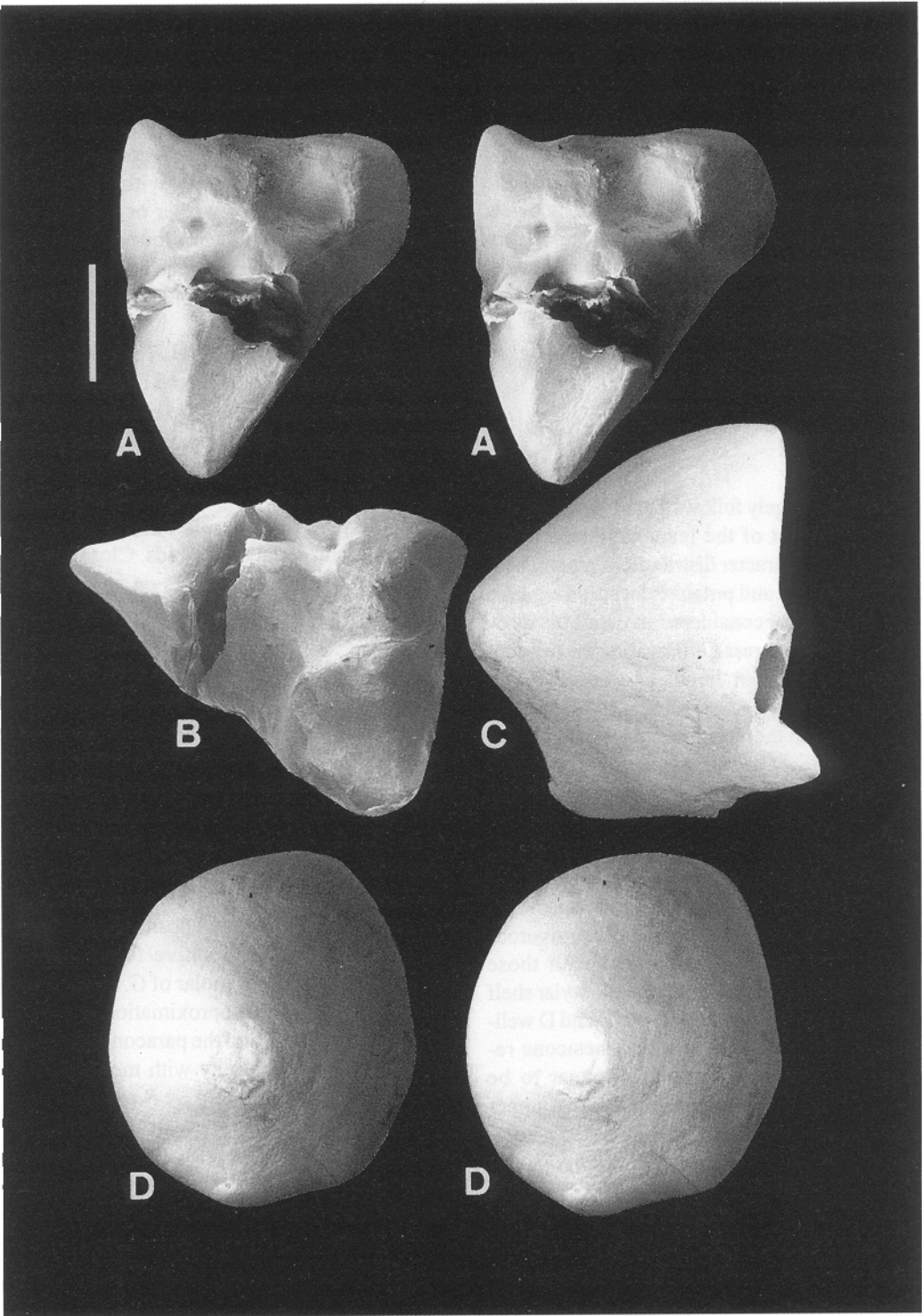
Description of holotype. Right M¹ or M². The posterior face of the metacone and a small part of the lingual face of stylar cusp D are missing. The tooth is tri-rooted. All the major cusps show moderate wear. In order of decreasing height the principle cusps are: metacone, stylar cusp D, paracone, stylar cusp B, stylar cusp C, protocone and metaconule. Stylar cusp E is absent. The occlusal surface area of the protocone is reduced, but the cusp is robust, with a massive base and a steeply inclined lingual face in anterior view. The postmetacrista is the longest shearing crest and oriented anteroposteriorly. All other crests are greatly reduced on the plesiomorphic dasyurid condition (e.g., as in *Murexia*). Stylar cusp D and the metacone are closely approximated, as are the paracone and stylar cusp B, and the paracone and metacone. The stylar shelf is greatly reduced with both stylar cusps B and D positioned lingually. No posterior cingulum, anterior cingulum or protoconule is present. The metaconule is tiny.

Referred specimen. QMF 30464, P² or P³.

Referred specimen locality and age. As for holotype.

Description of referred specimen. QMF 30464 has been referred to *Ganbulanyi djadjinguli* be-

Fig. 1. Ganbulanyi djadjinguli gen. et sp. nov. A, stereo occlusal view of holotype (QMF 24537), right M¹ or M². B, lingual view of QMF 24537. C, lateral view of referred specimen (QMF 30464), an upper P² or P³. D, stereo occlusal view of QMF 30464. Scale = 2.0 mm.



ing from the same local fauna with distinctive low crowned morphology consistent with that of the holotype. The upper premolar may represent P¹ or P² and is near-complete, excepting the posterior root, which is broken away. The principle cusp is positioned centrally and a tiny additional cusp is located at the posterior margin of the crown. In occlusal view the premolar is ovate, almost symmetrical on the long axis, and the anteroposterior dimension slightly exceeds that of the transverse. The tooth is extremely low crowned and robust.

Character analysis

Method

Methodology largely follows that of Wroe (1996a, 1997a). For most of the features treated in the present study, character distributions among both Dasyuromorphia and putative dasyuromorphian outgroup taxa are considered in detail by Wroe (1996a, 1997a, in press), eliminating the need for extensive treatment here. The fossil taxon *Sarcophilus moornaensis* Crabb 1982, has not been included in the character analysis for a number of reasons. Specimens or casts of this species have not been sighted by the author, making direct comparison impossible, furthermore, as judged from the figures published (Crabb 1982), the association made between the upper molar and lower dentition attributed to the species is dubious. The upper molar lacks hypercarnivorous features that would be consistent with those present in the lower dentition, e.g., the stylar shelf is well-developed, with stylar cusps B and D well-separated from the paracone and metacone respectively, but the metaconids appear to be greatly reduced. Moreover, because the upper molar described is of uncertain homology, comparison with that known for *G. djadjinguli*, also of uncertain homology, would be of very limited value.

Morphology of upper premolar. A well-developed P² and P³ are plesiomorphic for Dasyuromorphia, but within the clade both hy-

pertrophy and hypotrophy on these states are derived within the order (Wroe in press). If the premolar of *G. djadjinguli* represents P³, then it shares hyperrobusticity and an ovate outline in occlusal view only with *B. wangala* among Dasyuromorphia. If this tooth represents P² then it shares these states only with *Sarcophilus harrisii*. Regardless of whether or not this tooth represents P² or P³, its very low crowned morphology, relative to transverse and anteroposterior width, is a dasyuromorphian autapomorphy.

Morphology of stylar cusp B. The stylar cusp B of both M¹ and M² is large and distinct from the paracone in most putative sister taxa to Dasyuromorphia, consequently Archer (1976a, 1982b) and Wroe (1996a) treat this as the plesiomorphic state for Dasyuromorphia. This plesiomorphic character state is present in most dasyurids and some thylacinids. Close approximation of these cusps occurs on at least M¹ of most dasyurines. In many derived dasyurines, such as *Dasyurus*, no distinct stylar cusp B is present on the anterobuccal margin of M¹ (Archer (1975) observed the presence of stylar cusp B on M¹ in some *D. hallucatus* and *D. viverrinus*). However, this cusp is present on M² of all Dasyurinae, although it is closely approximated with the paracone in *D. maculatus* and *S. harrisii* in particular. The stylar cusp B of M¹ and M² is present and well separated from the paracone in all Thylacinidae. However, stylar cusp B is both greatly reduced in size and positioned anteriorly in most thylacinids, relative to carnivorous dasyurids. If the upper molar of *G. djadjinguli* is M¹ then the degree of approximation evident between stylar cusp B and the paracone, represents a possible synapomorphy with moderately derived dasyurines (e.g., *Parantechinus*, *Pseudantechinus*). However, if this tooth is M² then the degree of approximation is shared only with *Sarcophilus harrisii* among dasyuromorphians.

Stylar cusp D morphology. The presence of a stylar cusp D which is larger than stylar cusp B is a potential synapomorphy for Dasyuromorphia-

Peramelemorphia, Dasyuromorphia, or Dasyuridae-Thylacinidae (Wroe 1997a). Within Dasyuromorphia stylar cusp D may be reduced through close approximation with the metacone or overall reduction. Close approximation of these cusps is common to *G. djadjinguli* and derived Dasyurinae (e.g. *D. maculatus*, *S. harrisii*), whilst gross reduction represents a possible thylacinid synapomorphy (Wroe 1996a, 1997a). The degree of oppression present in *G. djadjinguli* is greater than that shown any dasyuromorphian, except *S. harrisii*, and may represent an unequivocal synapomorphy uniting the two taxa.

Position of the paracone relative to the metacone. Archer (1976a; 1982b) and Wroe (1996a) treated the presence of a well-separated paracone and metacone as plesiomorphic for the Dasyuromorphia. Approximation of these cusps is evident in some Dasyurinae (e.g. *D. maculatus*, *S. harrisii*), *Planigale*, Thylacinidae (Archer 1976a, 1982b; Muirhead 1992; Wroe 1996a), and *G. djadjinguli*. The presence of this feature in *G. djadjinguli* represents a possible synapomorphy with either a derived dasyurine clade, *Planigale*, or Thylacinidae.

Stylar cusp C morphology. The retention of stylar cusp C is plesiomorphic for Dasyuromorphia (Archer 1976; Muirhead & Archer 1992; Wroe in press). This cusp is present in *G. djadjinguli*, *B. wangala*, and two taxa treated as Dasyuromorphia *incertae sedis* in the present study, i.e., *Ankotarinja tirarensis* and *Keeuna woodburnei*. Archer (1976a) reported that among extant Dasyuridae stylar cusp C is consistently present only in *Murexia*, *Myoictis*, some *Antechinus*, and *Phascosorex*, and variably present in *Sminthopsis virginiae*. Archer (1975) noted the presence of this cusp on single specimens of *Phascogale tapoatafa* and *Planigale maculata*.

Protocone morphology. A large protocone, wherein a broad occlusal surface equals or exceeds the cusp's basal anteroposterior and transverse dimensions is common to Peradectidae,

most Didelphidae, Microbiotheriidae and Peramelemorphia, and is treated as plesiomorphic for Dasyuromorphia in the present study. Within the Order, reduction of the protocone is common to *G. djadjinguli*, some Dasyurinae, and all Thylacinidae. However, the presence of a greatly reduced occlusal surface area on the protocone, which is also basally massive with a lingual face which slopes buccally in anterior view is found only in *G. djadjinguli* and *S. harrisii* among dasyuromorphians.

Orientation of postmetacrista. A postmetacrista which is oriented at about forty-five degrees to the long axis of the maxilla and stylar shelf is plesiomorphic for Dasyuromorphia. In *G. djadjinguli*, some carnivorous Dasyurinae, and Thylacinidae this angle is acute, with the postmetacrista of *G. djadjinguli*, derived dasyurines and thylacinids (i.e. *Sarcophilus* and *Thylacinus*, respectively) almost parallel to the long axis of the stylar shelf.

Discussion

Phylogeny

Uncertainty regarding the homology of teeth referred to *G. djadjinguli* complicates investigation of the taxon's phylogeny. But, regardless of the interpretation favoured, *G. djadjinguli* clearly shares the greatest number of derived features with *S. harrisii* among dasyuromorphians. If the upper premolar (referred specimen QMF 30464) represents P², and the upper molar (holotype QMF 24537) represents M¹, then *G. djadjinguli* shares six apomorphies with *Sarcophilus harrisii* (approximation of the metacone and paracone on M²; anteroposterior orientation of the postmetacrista; approximation of stylar cusp B and the paracone on M¹; approximation of stylar cusp D and the metacone on M¹; reduction of occlusal surface area, basal hypertrophy, and the development of a lingual face which slopes buccally in anterior view on the protocone; and hyperrobusticity and an ovate outline in occlusal view (op2), of which the latter four are unique to these

two species within the Order. If QMF 30464 and QMF 24537 represent P^3 and M^2 , then *G. djadjinguli* and *S. harrisii* shares four apomorphies (approximation of the metacone and paracone on M^2 ; anteroposterior orientation of the postmetacrista; approximation of stylar cusp D and the metacone on M^2 ; reduction of occlusal surface area, basal hypertrophy, and the development of a lingual face which slopes buccally in anterior view on the protocone), of which the latter two are common only to these two species among Dasyuromorphia.

Taken at face value, the presence of at least two, and possibly as many as four, unequivocal synapomorphies in *G. djadjinguli* and *S. harrisii*, might be considered reasonable grounds for concluding monophyly for these two taxa. However, because the homology of both the upper molar and premolar of *G. djadjinguli* cannot be determined definitively, considerable latitude must be given in the inference of phylogeny. At least two factors may confound the acceptance of a special relationship between *G. djadjinguli* and *S. harrisii*. Firstly, interpretations of morphology-based data have favoured a special relationship between *D. maculatus* and *S. harrisii*, with a Pliocene taxon, *Glaucodon ballaratensis* Stirton 1957, flagged as structurally intermediate between the two (Ride 1964; Archer 1982a), a position also supported by molecular studies which indicate that *D. maculatus* and *S. harrisii* are monophyletic (Krajewski *et al.* 1993, 1994). Loss of P^3 is apomorphic within Dasyuromorphia and common to all *Dasyurus*, *Glaucodon*, and *Sarcophilus* (Archer 1976a, 1982a). If QMF 30464 represents P^3 , then either its presence in *G. djadjinguli* is a reversal to a plesiomorphic state, or the loss of P^3 in *Dasyurus* and *Sarcophilus* is homoplasious if monophyly for *G. djadjinguli* and *Sarcophilus* is to be accepted. Secondly, stylar cusp C is lost in all upper molars of extant Dasyurinae, excepting *Myoictis*. *Myoictis* is among the least derived of dasyurine taxa for dental and cranial features (Tate 1947; Archer 1976a, b, 1982a), and lacks many potential synapomorphies uniting *Dasyurus*, *Glaucodon*, and *Sarcophilus*. The presence of a well-developed

stylar cusp C in *G. djadjinguli* also requires the acceptance of apomorphic reversal to a plesiomorphic state in *G. djadjinguli* or independent loss of this feature in *Dasyurus* and *Sarcophilus*, if *G. djadjinguli* and *Sarcophilus* are treated as monophyletic.

That *G. djadjinguli* may be the derived sister taxon of *Barinya wangala* is another hypothesis that must be considered. These taxa may share one unequivocal derived feature (within Dasyuromorphia); extreme hypertrophy and an ovate outline in occlusal view of P^3 . Moreover, because *B. wangala* is less derived for all features, the proposal of a sister taxon relationship is not complicated by the need to accept character state reversals. Finally, the possibility that *G. djadjinguli* represents a thylacinid (which is autapomorphic within the family) or some hereto unknown higher taxon within Dasyuromorphia remains plausible. Although either of these latter two hypotheses would oblige the acceptance of still higher levels of homoplasy within Dasyuromorphia for the few features available for study, so many important characters are unknown for *G. djadjinguli* that neither possibility can be confidently excluded.

Because it shares unequivocal derived features only with *S. harrisii* and *B. wangala* among Dasyuromorphia, *G. djadjinguli* is referred to Dasyuridae. However, in light of the growing complexity of dasyuromorphian phylogeny revealed by the analysis of recent fossil discoveries (Wroe 1996a, 1997a, b) and the demonstration that apomorphies of the basicranium are the most robust indicators of dasyurid affinity available at present (Wroe in press), this decision must be considered tentative pending the discovery of more complete material.

Palaeobiology and biostratigraphy

With the description of *Ganbulanyi djadjinguli* the knowledge of dasyuromorphian diversity during the Miocene is broadened considerably. Basally broad, blunt, conical cusps, such as those on the upper premolar and molar of *G. djadjinguli*, approach the optimal 'design criteria' for the

propagation of cracks in brittle material (Sanson 1991). The development of robust, blunt cusps, particularly on the premolars, is ubiquitous among mammalian taxa that are known to include a high proportion of bone in their diet, such as *Crocota* and *Sarcophilus* (Savage 1977; Van Valkenburgh 1989, 1994; Werdelin 1996). In *G. djadjinguli* the upper premolar, and all cusps of the upper molar, are extremely low crowned relative to their anteroposterior and transverse dimensions. If this morphological similarity is the product of adaptation to a similar niche then *G. djadjinguli* represents the only specialised 'bone-cracking' taxon known from any pre-Pliocene site in Australia. In this context the small size of *G. djadjinguli* is intriguing. *Ganbulanyi djadjinguli* is comparable to *Dasyurus maculatus* in overall dental dimensions. Although *G. djadjinguli* may have been more massive, it is unlikely to have weighed much more than seven kilograms, the maximum weight of *D. maculatus* (Strahan 1995). The author is unaware of any other mammalian 'bone-eating' taxon of such diminutive size.

As noted by Wroe (1997b), a number of unique taxa from Encore Site have been described to date, including *Mayigriphus orbus*, a tiny, derived dasyuromorphian, a giant *Ekaltadeta* (Wroe 1996b), a *Warenja*-like wombat (Archer et al. 1995), and a specialised palorchestid (Black pers. comm.). Both the derived nature of these taxa and the presence of specialisations commonly associated with adaptation to xeric conditions have been treated as supportive of a relatively late age for Encore Site (Wroe 1997b). The dental features of *G. djadjinguli* do not necessarily correlate with adaptation to an arid environment. However, the apparent restriction of this highly distinctive species to Encore Site among Riversleigh localities does provide at least tacit support for the suggestion that unique ecological and climatic conditions prevailed during the depositional episode that produced the site.

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