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# First known extinct feathertail possums (Acrobatidae, Marsupialia): palaeobiodiversity, phylogenetics, palaeoecology and palaeogeography

Prudence R. Fabian, Michael Archer , Suzanne J. Hand , and Robin M.D. Beck 

## ABSTRACT

Four new fossil feathertail possum species (Marsupialia, Diprotodontia, Phalangerida, Petauroidea, Acrobatidae) are described from late Oligocene to middle Miocene fossil deposits in the Riversleigh World Heritage Area, northwestern Queensland. They are the first pre-Pleistocene fossil representatives of this family to be described. Two species are referred to the modern genus *Acrobates* and two to the modern genus *Distoechurus*. These species are distinguished from each other and from the living *Distoechurus pennatus* and *Acrobates pygmaeus* on the basis of qualitative and quantitative characters of the first lower molar (m1), which is the only tooth known for all four fossil species. Fortunately, m1 is morphologically the most variable tooth in the cheektooth row of acrobatids, and it exhibits numerous genus- and species-specific features. Phylogenetic analyses based on dental characters strongly support monophyly of Acrobatidae relative to other petauroids, as well as providing relatively strong support for reciprocal monophyly of *Acrobates* and *Distoechurus*, including the newly described fossil members of these genera. Recognition of species of *Acrobates* and *Distoechurus* in these fossil deposits is broadly congruent with recent estimates for the time of divergence of the two modern genera based on molecular data, and also provides an additional fossil calibration point for future studies of marsupial divergence times. These fossil species provide new insights into the biogeographical and ecological history of this enigmatic family of small possums, specifically that the oldest known species of *Acrobates* occurred in closed forest environments (in contrast to the living species, *A. pygmaeus* and *Acrobates frontalis*, which today inhabit open sclerophyll forests and woodlands) and that *Distoechurus* appears to have originated in Australia, only subsequently dispersing to New Guinea before becoming extinct in its Australian homeland.

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ACROBATIDAE is a highly distinctive family of small, arboreal diprotodontian marsupials. The three extant species—*Acrobates pygmaeus* Desmarest, 1817 and *Acrobates frontalis* (De Vis, 1887) of Australia, and *Distoechurus pennatus* Peters, 1874 of New Guinea—have distinctive elongate hairs that project laterally down the length of the tail, leading to the common names of feathertail gliders for the gliding *Acrobates* Desmarest, 1817 species, and feathertail possum for the non-gliding *D. pennatus* (see Aplin & Archer 1987, Van Dyck & Strahan 2008, Van Dyck *et al.* 2013). *Acrobates* species inhabit coastal sclerophyll forests and tall woodlands in eastern Australia (Van Dyck & Strahan 2008, Van Dyck *et al.* 2013). *Distoechurus pennatus* occurs throughout New Guinea from sea level to 1900 m, where it is widespread in rainforests, as well as in regenerating rainforests (Flannery 1995, Menzies 2011, Aplin & Kale 2011). The three species are omnivorous, feeding on a

mixture of nectar, fruits and invertebrates (Van Dyck & Strahan 2008, Menzies 2011, Van Dyck *et al.* 2013).

Recent estimates for the divergence of Acrobatidae from other petauroids (tarsipedids, petaurids and pseudocheirids), and for the split of *Acrobates* and *Distoechurus* Peters, 1874, vary (Table 1). Most recent molecular clock analyses (which use node dating) have suggested that the acrobatid lineage originated during the Eocene or earliest Oligocene, and that the *Acrobates*–*Distoechurus* split occurred during the Oligocene or latest Miocene (Meredith *et al.* 2009, 2011, Mitchell *et al.* 2014, Duchêne *et al.* 2018). However, the recent node-dating molecular clock analysis of Álvarez-Carretero *et al.* (2022) and the tip-and-node dating total evidence analysis of Beck *et al.* (2022) suggest younger dates, with an entirely Oligocene estimate for the acrobatid lineage, and a latest Oligocene to early Miocene (Álvarez-Carretero *et al.* 2022) or even middle-to-late Miocene (Beck *et al.* 2022) estimate for the *Acrobates*–*Distoechurus* split. Crucially, though, fossil acrobatids have not been used to inform these divergence estimates: to date, the only formally described acrobatid fossils have been from Pleistocene cave deposits, with these specimens concluded to represent the extant species *A. pygmaeus* from caves in Victoria and New South Wales (Long *et al.* 2002, Archer & Hand 2006), and

**Table 1.** Recent divergence time estimates for the divergence of acrobatids from other petauroids, and for the *Acrobates–Distoechurus* divergence, using molecular clock node-dating and total evidence tip-and-node dating.

Study	Data type	Method	Estimated age of divergence of acrobatids from other petauroids	Estimated age of <i>Acrobates–Distoechurus</i> divergence
Meredith <i>et al.</i> (2009)	Molecular (nuclear sequences)	Node dating	40.5 (34.5–46.8)	25.1 (20.2–30.4)
Meredith <i>et al.</i> (2011)	Molecular (nuclear sequences)	Node dating	42.0 (31.5–53.1)	N/A
Mitchell <i>et al.</i> (2014)	Molecular (nuclear and mitochondrial sequences)	Node dating	40.6 (37.3–43.7)	27.2 (22.9–31.3)
Duchène <i>et al.</i> (2018)	Molecular (nuclear sequences)	Node dating	43.1 (39.8–46.1)	28.3 (25.4–31.4)
Álvarez-Carretero <i>et al.</i> (2022)	Molecular (nuclear and mitochondrial sequences)	Node dating	31.8 (30.5–33.0)	23.4 (20.9–25.8)
Beck <i>et al.</i> (2022)	Total evidence (nuclear and mitochondrial sequences and craniodental characters)	Tip-and-node dating	29.0 (26.4–32.7)	14.1 (10.3–18.1)

Dates in brackets represent 95% confidence/credibility intervals.

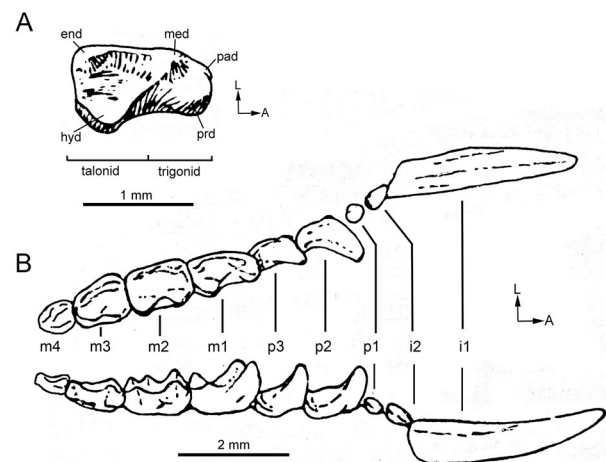
*Acrobates* sp. cf. *A. pygmaeus* from Victoria Fossil Cave in South Australia (Brown & Wells 2000, Reed & Bourne 2000). The existence of acrobatids from the Oligocene and Miocene deposits of the Riversleigh World Heritage Area of northwestern Queensland was noted by Archer *et al.* (1991, 1997, 1999, 2006), and one possible acrobatid specimen has also been identified from the early Miocene Wipajiri Formation of South Australia (Archer & Hand 2006), but these specimens have remained undescribed. Currently, these Oligo-Miocene specimens represent our only fossil insight into acrobatid evolution prior to the Pleistocene.

In this study, we describe four fossil acrobatid species from late Oligocene to middle Miocene (Riversleigh Faunal Zones A–C) faunal assemblages at Riversleigh. Phylogenetic analyses indicate that these fossil species postdate the divergence of the *Acrobates* and *Distoechurus* lineages from each other. As such, they provide a test of existing molecular estimates for the timing of the *Acrobates–Distoechurus* split, and they can be used to calibrate future molecular analyses by providing a minimum age for this divergence. They also illuminate the previously unknown palaeobiogeographical and palaeoecological history of acrobatids.

## Materials and methods

Fossil acrobatid specimens (Supplementary Data 1) have been collected from a range of sites in the Riversleigh World Heritage Area, northwestern Queensland (18°59′–19°08′S, 138°34′–138°43′E). Mammal-bearing fossil deposits at Riversleigh span the late Oligocene to Holocene (Archer *et al.* 1989, 1994, 1995, 1997, 1999, 2006, Arena 2004, Travouillon *et al.* 2006, 2009, Woodhead *et al.* 2016). Riversleigh faunal assemblages containing acrobatids have been allocated on the basis of biocorrelation, superposition, and U/Pb radiometric dates to Riversleigh Faunal Zone (RFZ) A (late Oligocene), B (early Miocene) and C (middle Miocene; Arena 2004, Travouillon *et al.* 2006, Woodhead *et al.* 2016). While faunal assemblages representing Faunal Zones D and E (late Miocene and early Pleistocene, respectively; Woodhead *et al.* 2016) are known, so far these have not produced acrobatids.

Higher level systematic nomenclature follows Aplin & Archer (1987) and Beck *et al.* (2022). Dental terminology



**Figure 1.** Interpreted tooth and cusp homology for acrobatids. A, Lower molar Rm1. B, Lower dentition i1–2 p1–3 m1–4. Abbreviations: A, anterior; end, entocoid; hyd, hypoconid; L, lingual; med, metaconid; pad, paraconid; prd, protoconid. Modified from drawing by M. Woodburne in Archer (1984). [81 mm width].

follows Luckett (1993) for molar and deciduous premolar homology, and Flower (1869) for premolar homology (see also Beck *et al.* 2022). Incisors, canines, premolars and molars are identified by the prefix I/i, C/c, P/p, and M/m respectively, with Ix, Cx, Px and Mx referring to upper teeth, and ix, cx, px and mx indicating lower teeth. L and R are used to indicate whether the teeth are from the left or right side. Cusp nomenclature (Fig. 1) follows Archer (1984). The homologies of the cusps making up the m1 trigonid of acrobatids was considered uncertain by Archer (1984). The fossil specimens described here support Archer's (1984) preferred interpretation—namely that the large buccal trigonid cuspid is the protoconid (not a protostylid), with the metaconid posterolingual to this—because, unlike modern acrobatids, they preserve an obvious crest (the paracristid) extending anterolingually from the large buccal trigonid cuspid, confirming the latter's identity as the protoconid.

Morphological comparisons focused on a single tooth, namely m1, for the following reasons: (1) m1 is the most common (and sometimes only) tooth known for the putative Riversleigh acrobatid species; (2) it is the most distinctive tooth in the cheektooth row of acrobatids, and exhibits the majority of species-specific, qualitative differences in molar morphology between the modern acrobatids *Acrobates* spp.

and *Distoechurus pennatus*; (3) it occupies a key position at the functionally important premolar–molar junction, and is under significant form/functional constraint because it needs to precisely interact with both the very different m2 (posteriorly) and p3 (anteriorly). The more posterior lower molars are less character-rich, relatively more bunodont, and, when found as isolated teeth (as most of the Riversleigh specimens are), it is relatively difficult to identify to specific locus because m2 and m3 are very similar in overall morphology. In addition, although our new fossil species retains an m4, this tooth is absent in the living *D. pennatus* and typically absent in *Acrobates pygmaeus*, precluding comparisons based on this dental locus. Acrobatid upper molars from Riversleigh were not included in this analysis because they are only known as isolated teeth, and hence there is uncertainty regarding both the dental locus and the taxon represented for each of these specimens; the occlusal morphology of acrobatid upper molars is also comparatively simple (Archer 1984; Beck *et al.* 2022). Characterization of the upper dentitions of these taxa must await the discovery of more complete upper tooth rows.

Multiple specimens of *A. pygmaeus* ( $n=44$ ) and *D. pennatus* ( $n=24$ ) were examined to assess the degree of intra-specific dental variation in these extant species, and hence give an indication of the variation that could be expected in fossil acrobatid species. The extant *Acrobates frontalis* has been recently recognized on the basis of genetic data and pedal and tail morphology (Van Dyck *et al.* 2013, Harris 2015). Our comparative sample of 44 *Acrobates* specimens (Supplementary Data 1) was drawn from New South Wales where the distributions of the two species potentially overlap. Dental differences between *A. frontalis* and *A. pygmaeus* have not previously been identified, and we did not detect significant variation in the dental features we examined, including in m1 morphology (see Results). We conservatively refer to all of these specimens as *A. pygmaeus* here.

Dental measurements (Supplementary Data 2) were made to the nearest 0.1 mm using a Leica MZ95 stereomicroscope with 9.5:1 zoom and graticule, and a Wild MMS235 Digital Length Measuring Set attached to a Wild M5A stereomicroscope. Specimens were measured on both instruments, which confirmed the equivalency of measurements made using the two systems. Length (L) was measured as the maximum crown length along the anteroposterior axis of the tooth. Width (W) for premolars was the maximum width of the tooth. Anterior width (AW) of lower molars was the maximum width of the trigonid at right angles to the anteroposterior axis of the tooth. Posterior width (PW) of lower molars was the maximum width of the talonid at right angles to the anteroposterior axis. Crown height was not measured because of individual differences in post-eruption wear. Scanning electron micrographs (SEMs) of gold-plated specimens were taken using an FEI Quanta200 (ESEM) scanning electron microscope in the Electron Microscope Unit of the University of New South Wales.

The coefficient of variation ( $CV = s/\bar{x}$  or  $s/\bar{x} \times 100\%$ , where  $s$  is the standard deviation and  $\bar{x}$  is the mean) was used to calculate variability in dental measurements within three of

the fossil species (excluding those represented by a single specimen). We follow Gingerich (1974) in calculating a separate CV for each tooth measurement. Simpson *et al.* (1960) proposed that CV values between 4 and 10 characterize samples drawn from a single species, with lower values possibly indicating an inadequate sample size, and higher values suggesting that the sample may have been drawn from more than one species. However, the assumption that a  $CV > 10$  indicates the presence of multiple species has been criticized (Plavcan & Cope 2001). We therefore simply compare CVs for the fossil species with those for the modern species *A. pygmaeus* and *D. pennatus*.

In order to determine if the remaining fossil species differ significantly from one another, as well as from the two extant species, in terms of dental dimensions, statistical comparisons were made between the means of each dental measurement for each species. The data were not normally distributed, due to small sample size, and hence did not meet the assumptions for an analysis of variance (ANOVA). Log-transformation of the data set did not result in normality. Thus, statistical comparisons were performed on the non-transformed data using the Kruskal–Wallis test (a non-parametric equivalent of ANOVA), as implemented in PAST v2.17c (Hammer *et al.* 2001), to identify whether there are significant differences in m1 dimensions between at least two of the species analysed. The non-parametric Mann–Whitney test was then performed on species pairs in order to determine exactly which species varied significantly in dental dimensions. A standard  $p$ -value of  $<0.05$  was initially taken to be significant; however, because of the large number of tests ( $n=20$ ; Table 2) carried out, a 5% False Discovery Rate correction (Benjamini & Hochberg 1995) was applied to the initial set of  $p$ -values, using the website <https://multipletesting.com/> (Menyhart *et al.* 2021). A principal components analysis (PCA) was performed on the raw dental measurements of the best represented fossils, together with *A. pygmaeus* and *D. pennatus*, using PAST (Hammer *et al.* 2001).

We assessed evolutionary relationships within Acrobatidae *via* formal phylogenetic analyses of a matrix of qualitative dental characters, many of which were newly identified in the course of this study. These characters are taken from m1 only, because (as noted above) this is the only tooth known for all of the fossil species described here, and because a large number of species-specific, qualitative differences are identifiable based on this tooth, whereas more posterior molars exhibit few species-specific features. Current evidence (see Beck *et al.* 2022 and references therein) indicates that Acrobatidae is a member of the superfamily Petauroidea, which also includes Petauridae (striped possums, gliders and Leadbeater's possum), Pseudocheiridae (ringtail possums) and Tarsipedidae (the Honey possum *Tarsipes rostratus* Gervais & Verreaux, 1842). Pseudocheirids exhibit specialized selenodont molars, while the postcanine dentition of *Tarsipes* comprises minute, degenerate, peg-like teeth that lack evidence of cusps or crests (Archer 1984; Beck *et al.* 2022); thus, both were judged unsuitable for use as outgroup taxa in the

**Table 2.** *p*-values for Mann–Whitney *U* tests comparing m1 length for *A. pygmaeus*, *A. magicus* sp. nov., *A. pettitorum* sp. nov., *D. pennatus*, and *D. georginae* sp. nov.

	M1 length	m1 posterior width
<i>A. pygmaeus</i> versus <i>A. magicus</i> <i>n</i> = 21 versus <i>n</i> = 18	0.0001	0.007527
<i>A. pygmaeus</i> versus <i>A. pettitorum</i> <i>n</i> = 21 versus <i>n</i> = 2	0.0040	0.008
<i>A. pygmaeus</i> versus <i>D. pennatus</i> <i>n</i> = 21 versus <i>n</i> = 11	0.0001	<0.0001
<i>A. pygmaeus</i> versus <i>D. georginae</i> <i>n</i> = 21 versus <i>n</i> = 6	<0.0001	<0.0001
<i>A. magicus</i> versus <i>A. pettitorum</i> <i>n</i> = 18 versus <i>n</i> = 2	0.02632	<b>0.25</b>
<i>A. magicus</i> versus <i>D. pennatus</i> <i>n</i> = 18 versus <i>n</i> = 11	<0.0001	0.0008
<i>A. magicus</i> versus <i>D. georginae</i> <i>n</i> = 18 versus <i>n</i> = 6	<0.0001	0.0075
<i>A. pettitorum</i> versus <i>D. pennatus</i> <i>n</i> = 18 versus <i>n</i> = 11	0.0303	0.0303
<i>A. pettitorum</i> versus <i>D. georginae</i> <i>n</i> = 18 versus <i>n</i> = 6	<b>1</b>	<b>0.0526</b>
<i>D. pennatus</i> versus <i>D. georginae</i> <i>n</i> = 18 versus <i>n</i> = 6	0.0006	<0.0001

Bold indicates non-significance (based on  $p < 0.05$ , corrected with a False Discovery Rate of 5%).

phylogenetic analyses presented here. The following dentally less-specialized taxa were therefore used as outgroups (Supplementary Data 1): the extant sugar glider *Petaurus breviceps* Waterhouse, 1839 (Petauridae, Petaurinae), long-fingered triok *Dactylopsila palpator* Milne-Edwards, 1888 (Petauridae, Dactylopsilinae), and Leadbeater's possum *Gymnobelideus leadbeateri* McCoy, 1867 (Petauridae, Petaurinae), and the fossil *Djaludjangi yadjana* Brammall, 1999, which appears to be a dentally plesiomorphic petaurid or petauroid (Brammall 1999; Roberts 2008). The resultant matrix comprised 25 characters scored for 10 taxa (Supplementary Data 3).

The matrix was analysed using maximum parsimony, as implemented in PAUP\* (Phylogenetic Analysis Using Parsimony\* and Other Methods) version 4.0b10 (Swofford 2002). Both ordered and unordered analyses of the matrix were carried out (see Brocklehurst & Haridy 2021): for the ordered analysis, four multistate characters (characters 7, 13, 14 and 22) that appeared to represent plausible morphoclines were specified as ordered. Multiple most parsimonious trees were summarized by strict consensus. Support values for clades recovered in the strict consensus were calculated using bootstrapping, jackknifing (with 25% deletion of characters), and the decay index (Bremer support; Bremer, 1994). Bootstrap and jackknife values were calculated in PAUP\* using 2000 default search replicates. The decay index was calculated using PAUP\* and PRAP (Parsimony Ratchet Analysis using PAUP) version 1.0 (Müller 2004). Fossil and modern specimens examined in this study are listed in Supplementary Data 1.

### Institutional abbreviations

QM, Queensland Museum, Brisbane, Australia. AM, Australian Museum, Sydney, Australia. AR, Vertebrate Palaeontology Research Collection, University of New South Wales, Sydney, Australia. UNSWZ, Zoological Research

Collection, University of New South Wales, Sydney, Australia.

### Systematic palaeontology

MARSUPIALIA Illiger, 1811  
DIPROTODONTIA Owen, 1866  
ACROBATIDAE Aplin (in Aplin & Archer), 1987  
DISTOECHURUS Peters, 1874  
***Distoechurus jeanesorum* sp. nov.**  
(Fig. 2A–C)

### Diagnosis

This species, which is known from an isolated m1, differs from other fossil *Distoechurus* and *Distoechurus pennatus* in the following combination of features. In terms of occlusal area, it is approximately half the size of the m1 of the extant *D. pennatus*, and approximately 20–25% smaller than that of other fossil *Distoechurus*. The distinct difference between relative trigonid and talonid cusp heights seen in *D. pennatus* is not present. The entoconid is well developed and transversely flattened, whereas in *D. pennatus* this cusp is so reduced that it is barely distinct from the entocristid. The entoconid is more posteriorly situated than in other fossil *Distoechurus*, but less so than in *D. pennatus*. The protoconid is robust and does not exhibit the extreme, almost caniniform condition seen in other fossil *Distoechurus* and *D. pennatus*. The paracristid is present, whereas this crest is absent in *D. pennatus*. The bases of the protoconid and metaconid show a greater degree of confluence than in other fossil *Distoechurus*. The metacristid connecting the protoconid and metaconid is tall and well developed, in contrast to the condition in other fossil *Distoechurus* or *D. pennatus*, where this crest is indistinct or absent. The preentocristid is distinctly notched, whereas it is unnotched in *D. pennatus*. The trigonid is relatively narrow, with a more lingually positioned protoconid than in *D. pennatus*.

### Etymology

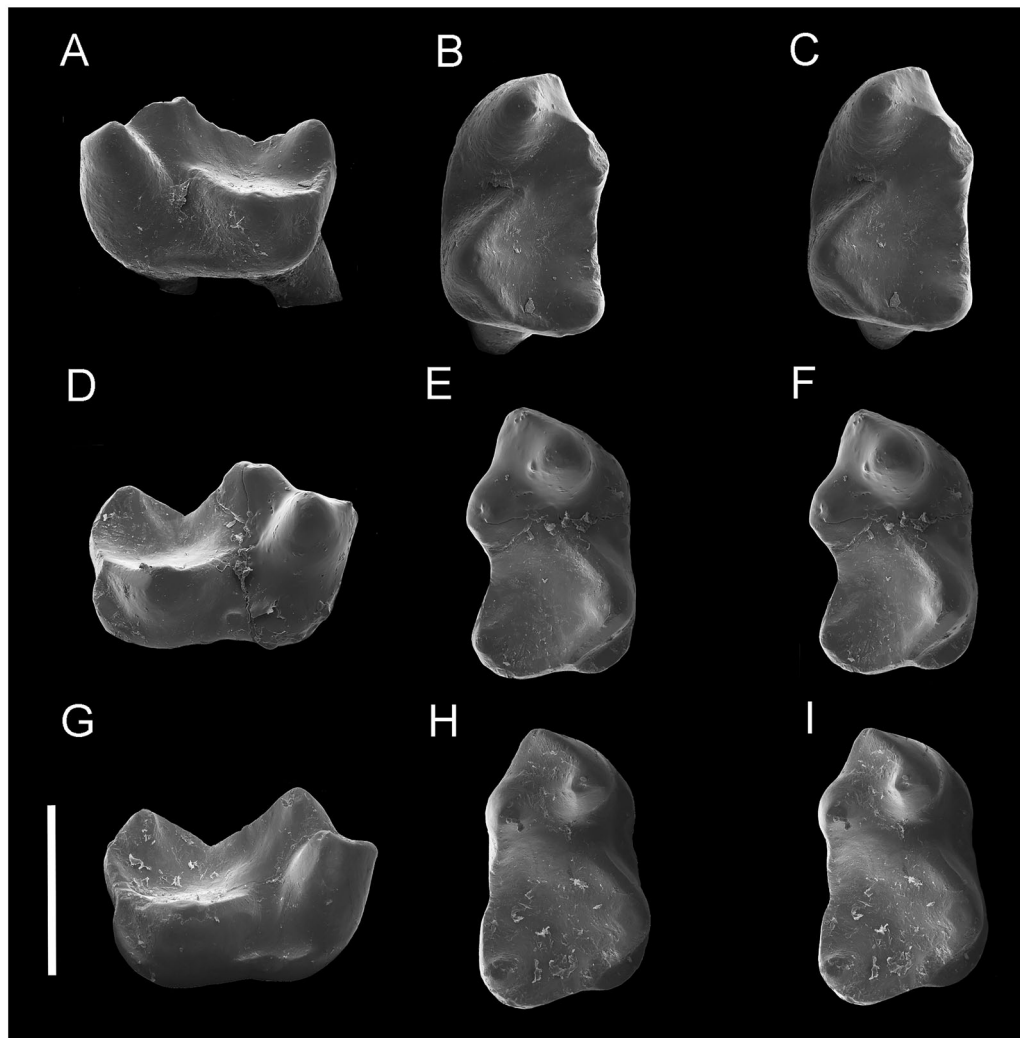
Named in honour of Doug and Ann Jeanes, who have been substantial supporters of the Riversleigh Project, as well as enthusiastic volunteer field hands on field trips to the Riversleigh World Heritage Area, and to White Hunter Site in particular.

### Holotype

QM F61140, isolated Lm1.

### Type locality, unit and age

White Hunter Site, Hal's Hill, D-Site Plateau, Riversleigh World Heritage Area, Boodjamulla National Park, in Waanyi country, northwestern Queensland. The precise coordinates of the type locality are available on application to the QM. White Hunter Site has been interpreted to be late Oligocene in age (Archer *et al.* 1994, 1995, 1999, Creaser 1997, Travouillon *et al.* 2006, Arena *et al.* 2016, Myers *et al.* 2017).



**Figure 2.** A–C, *Distoechurus jeanesorum* sp. nov., QM F61140 holotype, Lm1. A, buccal view. B, C, occlusal stereopair. D–F, QM F61145, Rm1. D, buccal view; E, F, occlusal stereopair. G–I, QM F61144 holotype, Rm1. G, buccal view; H, I, occlusal stereopair. Scale = 1 mm. [169 mm width].

### Description

The only known tooth, m1, is bunoselenodont and has two roots. Four distinct cusps are identifiable, namely the protoconid, metaconid, hypoconid and entoconid. Of these, the protoconid is the tallest, followed by the metaconid, both of which are nearly twice as high as the hypoconid and entoconid, which are subequal in height. The paracristid descends at a steep angle anterolingually from the tip of the protoconid down the anterior margin of the tooth. The metacristid is angled, with the buccal component extending lingually from the tip of the protoconid to the metacristid notch. The lingual component runs anterobuccally from the tip of the metaconid to the metacristid notch, where the two blades meet. The metaconid is transversely narrow and blade-like, and is posteriorly positioned relative to the protoconid. The distance between the anterior tip of the tooth and the metaconid is almost twice the distance from the anterior tip of the tooth to the protoconid. The preentocristid extends anteriorly from the tip of the entoconid to the metaconid, and is distinctly notched. The entoconid is transversely compressed and blade-like. The entoconid and its very short postentocristid are the most posterior parts of the tooth. The postentocristid initially runs in a posterior direction

from the tip of the entoconid to the rear of the talonid, at which point it changes slope and direction to extend buccally, meeting the posthypocristid at an obtuse angle. The posthypocristid extends from the hypoconid in a posterolingual direction to the lingual end of the postentocristid. The cristid obliqua extends in an anterolingual direction towards the longitudinal midline of the tooth, and between the bases of the protoconid and metaconid. A small cingulid is present within the hypoflexid, between the posterobuccal base of the protoconid and the anterobuccal base of the hypoconid.

***Distoechurus georginae* sp. nov.**  
(Fig. 2D–I)

### Diagnosis

This species differs from *Distoechurus jeanesorum* and *Distoechurus pennatus* in the following combination of features of m1. This tooth is significantly smaller than that of *D. pennatus* (which is approximately 1.7 times larger in terms of occlusal area), and approximately 20–25% larger in occlusal area than that of *D. jeanesorum*. It lacks the marked

difference in relative cusp heights seen in *D. pennatus*, and the trigonid is also narrower. The protoconid is more subcaniniform than it is in *D. jeanesorum*, but not as extremely subcaniniform as it is in *D. pennatus*. The bases of the metaconid and protoconid are confluent, but in *D. jeanesorum* these cusps are more intimately fused. The preentocristid is distinctly notched, whereas no such notch is present in *D. pennatus*. The entoconid forms a distinct but transversely flattened blade-like cusp, whereas in *D. pennatus* the entoconid is reduced and almost completely indistinct from the entocristid. The entoconid is more posteriorly positioned than it is in *D. jeanesorum*, but not to the extent that it is in *D. pennatus*. A paracristid extends anterolingually from the tip of the protoconid and is steeply orientated down the anterior surface of the tooth, whereas this crest is not seen in *D. pennatus*. There is no metacristid present, in contrast to the condition in *D. jeanesorum*. The cristid obliqua runs in an anterolingual direction towards the longitudinal midline of the tooth, between the confluent bases of the protoconid and metaconid. There is a posterobuccal cingulid that extends from the posterior margin of the tooth where the postentocristid and posthypocristid meet, and then curves posterobuccally around the posterior flank of the hypoconid. This cingulid is better developed than it is in *D. jeanesorum*, and in *D. pennatus* (in which it is absent).

### Etymology

The species name is in honour of Georgina Hickey (née Clayton) who has been a critically important colleague who collected, processed, prepared and interpreted many of the fossils that have come from the Riversleigh World Heritage area, and edited books and journals focused on Australian vertebrate palaeontology and natural history.

### Holotype

QM F61144, isolated Rm1.

### Referred material

Upper Site: QM F61145, isolated Rm1; QM F61143, isolated Lm1; QM F61142, isolated Rm1. Ringtail Site: QM F23030, isolated Lm1. Gotham City Site: QM F61141, isolated Rm1; QM F30898, isolated Rm1; QM F30920, isolated Rm1; QM F30897, isolated Rm1.

### Type locality, unit and age

Gotham City Site, Riversleigh World Heritage Area, Boodjamulla National Park, in Waanyi country, northwestern Queensland. The precise locality details can be obtained upon application to the QM. All sites are located in the Riversleigh World Heritage area, northwestern Queensland, Australia. Specimens referred here are from Upper Site, Gotham City Site, and Ringtail Site. Upper Site is part of Riversleigh's FZB and has been interpreted to be early Miocene in age, while Gotham City and Ringtail are FZC sites and as such have been interpreted as middle Miocene in age (Hand 1990, Archer *et al.* 1994, 1995, 1999, Creaser

1997, Travouillon *et al.* 2006). Radiometric (U/Pb) dating of speleothem from Ringtail Site provides a middle Miocene age of 13.56 mega-annum [Ma] (Woodhead *et al.* 2016) for that faunal assemblage.

### Description

The m1 is bunoselenodont, with two roots. The protoconid is the tallest cusp, followed by the metaconid, both of which are taller than the similarly sized hypoconid and entoconid. Overall, the trigonid cusps are nearly twice as high as those of the talonid. The trigonid of m1 is very narrow. A paracristid extends anterolingually from the tip of the protoconid, and is steeply orientated down the anterior surface of the tooth. The protoconid is transversely flattened. The lingual surface of the protoconid is flat and forms a smooth, shearing surface. The metaconid is transversely thin and blade-like, and is posteriorly positioned with respect to the protoconid. The preentocristid extends anteriorly from the tip of the entoconid to the tip of the metaconid, and is deeply notched at its midpoint. The distance from the anterior tip of the tooth to the metaconid is almost as long as the distance to the protoconid. The metaconid and protoconid are confluent at their bases, with a deep trigonid basin between the two cusps. The entoconid is transversely compressed and blade-like, and, together with the postentocristid, forms the posterior most part of the tooth. The very short postentocristid initially runs in a posterior direction from the tip of the entoconid to the rear of the talonid, at which point it changes slope and direction to extend buccally, where it joins the posthypocristid at an obtuse angle. The posthypocristid extends from the hypoconid in a posterolingual direction to the lingual end of the postentocristid. The cristid obliqua runs in an anterolingual direction towards the longitudinal midline of the tooth, between the confluent bases of the protoconid and metaconid. A cingulid is present within the hypoflexid, extending from between the posterobuccal base of the protoconid to the anterobuccal base of the hypoconid. There is a posterobuccal cingulid that extends buccally along the buccal third of the posterior margin of the tooth, from below the point where the postentocristid and posthypocristid meet, and then curves anterobuccally around the posterior flank of the hypoconid.

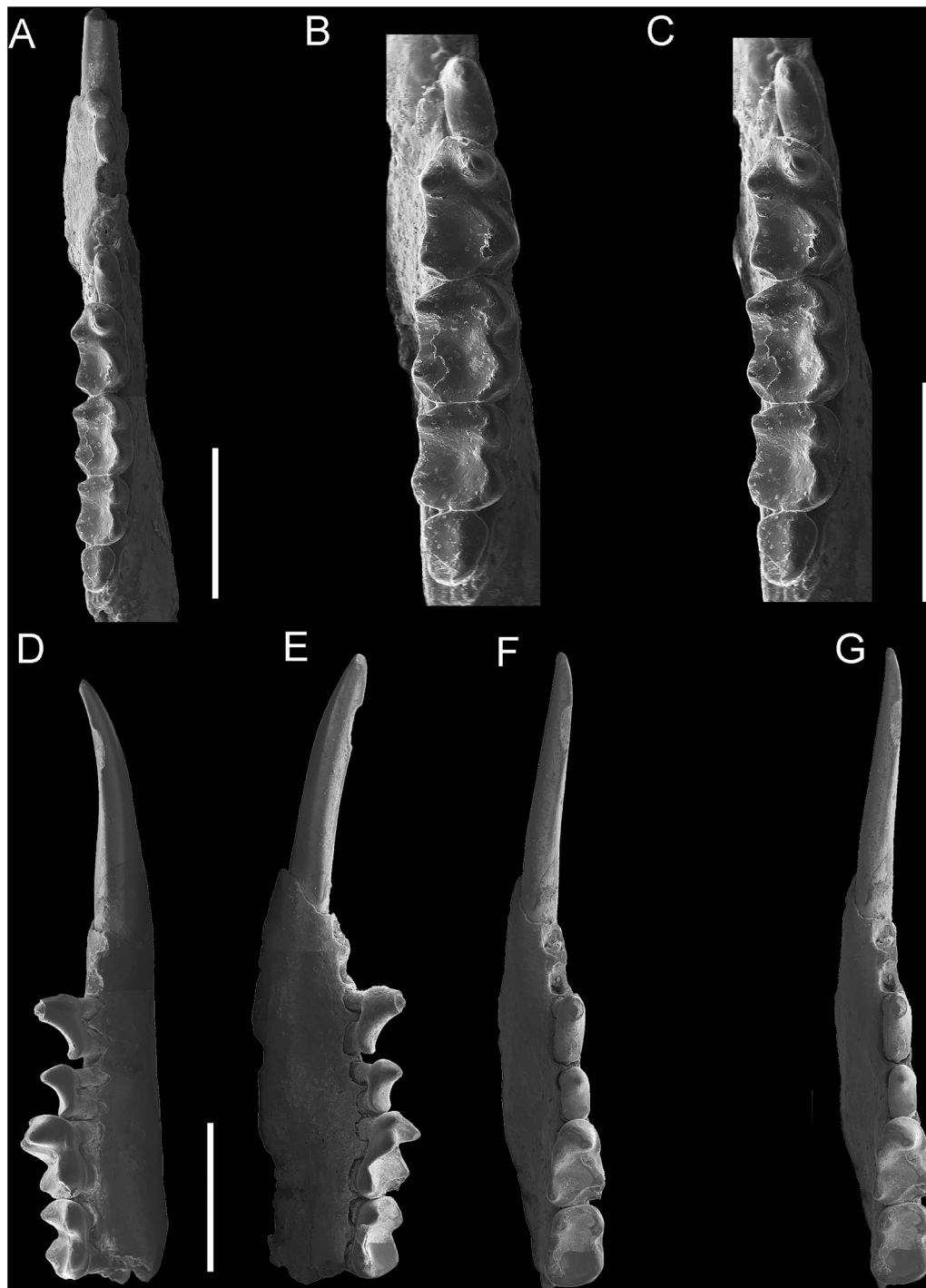
ACROBATES Desmarest, 1817

**Acrobates magicus** sp. nov.

(Fig. 3A–G)

### Diagnosis

*Acrobates magicus* differs from *Acrobates pygmaeus* (including *Acrobates frontalis*, which cannot be differentiated in terms of molar morphology from *A. pygmaeus*; pers. obs.) and other fossil *Acrobates* in the following features of m1: it is nearly a third larger in linear measurements than *A. pygmaeus*, yet smaller than other fossil *Acrobates* (roughly three quarters of the size). It is not as robust as other fossil *Acrobates*. It has a small paraconid that is anterolingual to the protoconid, whereas a paraconid is not present in either



**Figure 3.** *Acrobates magicus* sp. nov. A–C, QM F61153 holotype. A, occlusal view, Ri1–m4; B, C, occlusal stereopair, Rp3–m4. D–G, QM F61154, Ri1, p2–m2. D, buccal view; E, lingual view; F, G, occlusal stereopair. Scale = 2 mm. [169 mm width].

*A. pygmaeus* or other fossil *Acrobates* species. A paracristid extends anterolingually from the tip of the protoconid and steeply dips to the anterior extremities of the tooth, whereas this crest is not present in *A. pygmaeus*. The cristid obliqua terminates between the protoconid and metaconid, whereas in *A. pygmaeus* this crest terminates closer to the base of the protoconid. The metaconid is slightly posteriorly positioned with respect to the protoconid, in contrast to the situation in *A. pygmaeus* where these two cusps are almost directly in line buccolingually. A posterobuccal cingulid extends from the posterior margin of the tooth where the postentocristid

and posthypocristid meet, before curving posterobuccally around the posterior flank of the hypoconid; this cingulid is less developed in other fossil *Acrobates* and is absent in *A. pygmaeus*. The relative lengths of the posthypocristid and cristid obliqua are the same, whereas in other fossil *Acrobates* the cristid obliqua is almost twice the length of the posthypocristid. It has a more lingually positioned entocristid and a wider talonid than *A. pygmaeus*. The trigonid is narrower than the talonid, whereas in *A. pygmaeus* and other fossil *Acrobates* species, this relative difference in the widths of the trigonid and talonid is not as pronounced,



giving the tooth a more rectangular shape. *Acrobates magiscus* has a less well-defined preentocristid than is the case in *A. pygmaeus*. This species also differs from *A. pygmaeus* in the following additional features that do not relate to m1 (other fossil *Acrobates* species are known from the m1 only, so cannot be compared for these features): it has a more robust i1, and the p2 and p3 are shorter and more robust, whereas in *A. pygmaeus* these premolars are taller and subcaniniform. The relative widths of the talonid and trigonid of m3 are the same, in contrast to the condition in *A. pygmaeus* where the talonid is narrower than the trigonid. The m3 is the same size as m2 in *A. pygmaeus*. Finally, there is a fourth molar (m4) present, which is not the case in *A. pygmaeus*.

### Etymology

'Possum Magic' by Mem Fox (Fox 1983) focused on taxonomically ambiguous possums that lived 'Once upon a time... deep in the Australian bush'. We have hereby removed the ambiguity by entangling the identity of these mythical possums with an equally mysterious small possum that lived once upon a time, a very long time ago.

### Holotype

QM F61153, right dentary preserving i1, two small unicuspid teeth of uncertain homology, p2–3, m1–4. It is tentatively assumed here that the two small unicuspid teeth between i1 and p2 represent i2 and p1 (following Archer 1984).

### Referred material

Upper Site: QM F61149, partial right dentary with i1–2 p2–3 m1–3 (p2–3 and m3 broken); QM F61154, partial right dentary with i1 p2–3 m1–2; QM F30954, partial right dentary with i2 p1–3 (cusps of p2–3 broken); QM F20778, partial right dentary with m2 and alveoli present for m3–4; QM F30956, partial left dentary with m1–2; QM F30941, partial right dentary with i1–2 p1–2; QM F61152, partial right dentary with m1–3; QM F61151, partial left dentary with p3–m3 and alveoli for p2; QM F20782, partial right dentary with p2–3 m1–2; QM F61158, isolated Lm1; QM F61159, isolated Lm1; QM F61161, isolated Lm1; QM F61160, isolated Lm1; QM F20797, isolated Rm2; QM F61162, isolated Lm1. Wayne's Wok Site: QM F24315, partial right dentary with m2 and alveoli for m1, 3–4; QM F20727, partial left dentary with m2–3 and alveoli of m4; QM F61150, partial left dentary with i1 p2 and alveoli for i2, p1 and anterior alveolus for p3; QM F30967, partial right dentary with m1–2; QM F61166, partial right dentary with i1 p2–3 m1 and alveoli for i2 and p1; QM F61167, isolated Rm1; QM F61163, isolated Lm1; QM F61165, isolated Rm2; QM F61164, isolated Rm2. R.S.O. Site: QM F61146, partial right dentary with m1–4; QM F61148, partial right dentary with p3 m1 and alveoli for i1–2 p1–2 m2–4; QM F61147, partial left dentary with i1 p3 m3 and alveoli for i2 p1–2 m1–2, 4. Neville's Garden Site: QM F61156, partial right dentary with p3 and m2; QM F23835, partial left dentary with m2–4; QM

F30930, partial right dentary with i1 p3 m1 and alveoli for p2; QM F30928, partial right dentary with p2 m1–3; QM F30796, partial right dentary with m2–4; QM F61157, isolated Lm1. Camel Sputum Site: QM F20734, isolated Lm2. Judith's Horizontal Site: QM F61155, partial dentary with Lm1–2.

### Type locality, unit and age

Upper Site, Godthelp Hill, D-Site Plateau, Riversleigh World Heritage area, Boodjamulla National Park, in Waanyi country, northwestern Queensland. The precise coordinates of the type locality are available upon application to the QM. All sites are located in the Riversleigh World Heritage area, northwestern Queensland, Australia. Specimens referred here are all from Riversleigh's FZB sites: Upper Site, Wayne's Wok Site, Neville's Garden Site, Camel Sputum Site, R.S.O. Site, and Judith's Horizontalis Site. Riversleigh's FZB has been interpreted to be early Miocene in age (Archer *et al.* 1994, 1995, 1999, Creaser 1997, Arena 2004, Travouillon *et al.* 2006, Woodhead *et al.* 2016). Radiometric (U/Pb) dating of speleothem from Neville's Garden Site provides an age of 17.85 Ma for that assemblage, from Camel Sputum Site 17.75 Ma, and from R.S.O. Site an age of 16.55 Ma for that local fauna (Woodhead *et al.* 2016).

### Description

In the dentary, there is a single mental foramen located beneath the anterior root of p3. There are no diastemata present in the dental row. The i1 is a relatively long blade, with a slight convex curve when viewed laterally. The small unicuspid tooth immediately posterior to i1, tentatively identified as i2 following Archer (1984), is smooth and oblong in most specimens, but somewhat variable in shape. A second small unicuspid tooth is present between i2 and p2, and is tentatively identified as p1; it resembles i2 in overall morphology. The p2 is bicuspid, double-rooted and subcaniniform in shape, with the major cusp positioned anteriorly. The second cusp is located directly posterior to the major cusp and is joined to it by a shallow crest that runs in a buccal-lingual direction. The anterior cusp widens towards the base where it joins the posterior cusp, which then narrows posteriorly. The p3 resembles p2, but differs in that it is somewhat shorter in height and length (see Appendix 2).

The m1 is bunoselenodont, with two roots. The protoconid is the tallest cusp, followed by the metaconid, then the paraconid, and lastly the similarly-sized hypoconid and entoconid. The protoconid is nearly twice as tall as the talonid cusps. The m1 has a small paraconid anterior to the protoconid and metaconid; the paraconid is slightly shifted lingually from the anteroposterior midline. The paracristid extends downward from the protoconid in an anterolingual direction towards the paraconid. The metaconid is approximately a third shorter than the robust protoconid. These cusps occur at roughly equal distances from the longitudinal midline of the tooth, but the metaconid is positioned slightly posterior to the protoconid. The trigonid basin between the

protoconid and metaconid is shallow because these two cusps are basally partially confluent.

The entoconid is posterolingually positioned, being almost twice the distance from the midline compared with the position of the metaconid, and is slightly more posteriorly positioned than is the hypoconid. The preentocristid extends from the tip of the entoconid to the tip of the metaconid, and is deeply notched at its midpoint. The postentocristid runs from the entoconid along the posterior margin of the tooth. The cristid obliqua runs in an anterolingual direction from the hypoconid tip, towards the longitudinal midline of the tooth, and terminates between the protoconid and the metaconid. The posthypocristid runs in a posterolingual direction along the posterior margin of the talonid, and continues to the base of the entoconid. The posthypocristid and cristid obliqua meet in an angular fashion. There is a cingulid within the hypoflexid region, extending from between the posterobuccal base of the protoconid to the anterobuccal base of the hypoconid. There is a posterobuccal cingulid that begins from below the point on the posterior margin of the tooth where the postentocristid and posthypocristid meet, and then curves posterobuccally around the posterior flank of the hypoconid.

The m2 resembles m1 with the following differences. It is slightly smaller in size and more rectangular in shape. Only four cusps are present; the paraconid is absent. There is no significant difference in the relative heights of the cusps. The paracristid curves in an anterolingual direction from the protoconid to the anterior tip of the tooth. The meta-cristid curves posterolingually from the protoconid towards the tip of the metaconid. The anterior margin of the tooth, in front of the protoconid and metaconid, is approximately semicircular, but is slightly skewed buccally. The cristid obliqua and the posthypocristid are of similar length and meet each other at a right angle. The posthypocristid is not as steeply angled from the hypoconid as it is in m1, but instead curves in a gentle manner in a posterolingual direction from the tip of the hypoconid. The posterior margin of the tooth curves in a semicircle, with the posterior most point buccal to the midline. The hypoflexid cingulid and posterobuccal cingulid are still present, although they are less pronounced. The m3 resembles m2, with the following differences. It is smaller in size and more rectangular. The talonid is only marginally wider than the trigonid. The junction of the posthypocristid and postentocristid at the posterior edge of the tooth is much straighter, whereas in m2 it is curved. The m4 resembles m3 with the following differences. There is no entoconid. It is much smaller in size, roughly half the size of m1 in linear dimensions. The m4 is also more variable than the other teeth in terms of size.

***Acrobates pettitorum* sp. nov.**  
(Fig. 4A–C)

### Diagnosis

This species differs from *Acrobates pygmaeus* (including *Acrobates frontalis*, which is dentally indistinguishable in terms of molar morphology from *A. pygmaeus*) and

*Acrobates magicus* in the following features of m1. This tooth is almost twice as large in terms of occlusal area as that of *A. pygmaeus*, and roughly 25% larger than that of *A. magicus*. It lacks a paraconid, whereas this cusp is present in *A. magicus*. A paracristid is present, whereas this crest is absent in *A. magicus*. The cristid obliqua terminates at the base of the protoconid, whereas in *A. pygmaeus* it terminates at a point between the protoconid and the metaconid. A posterobuccal cingulid extends from the posterior margin of the tooth at the junction of the postentocristid and the posthypocristid and then around the posterior flank of the hypoconid; whereas this cingulid is absent in *A. pygmaeus*. The cristid obliqua is almost twice as long as the posthypocristid, whereas these crests are of approximately equal length in *A. magicus* and *A. pygmaeus*. The cristid obliqua forms a taller, more sharply defined crest than occurs in *A. pygmaeus* or *A. magicus*. There is a steeply inclined crest extending from the centre of the cristid obliqua in an anterobuccal direction down the buccal side of the tooth towards the buccal base of the protoconid; this is not present in *A. magicus* or *A. pygmaeus*. A buccal crest runs anteroposteriorly from the external buccal base of the protoconid to the anterobuccal base of the metaconid; this crest is not present in *A. magicus* or *A. pygmaeus*. The trigonid is almost as wide as the talonid, whereas in *A. magicus* and *A. pygmaeus* the talonid is narrower because the protoconid is located in a more lingual position. The talonid is also wider than that of *A. pygmaeus* and *A. magicus* because the entoconid is situated in a relatively more lingual position. The preentocristid is better defined than in *A. pygmaeus*. The hypoconid sits almost transversely in line with the entoconid, the entoconid being only slightly posterior to the hypoconid, whereas in *A. pygmaeus* the entoconid is situated further posterior relative to the hypoconid.

### Etymology

The species name is honour of Ken and Margaret Pettit, who have generously supported the Riversleigh Project via the CREATE Fund at UNSW to enable establishment of the Pettit CREATE Preparator position at UNSW.

### Holotype

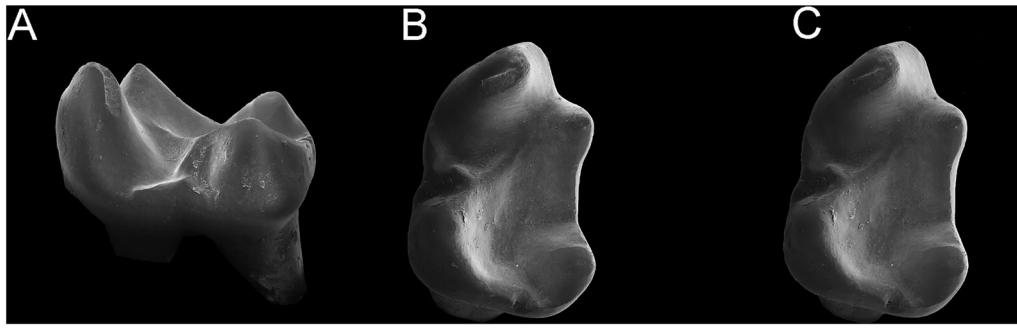
QM F61169, isolated Lm1.

### Referred material

Gotham City Site: QM F61168, Rm1.

### Type locality, unit and age

Gotham City Site, Gag Plateau, Riversleigh World Heritage area, Boodjamulla National Park, in Waanyi country, north-western Queensland. Precise coordinates of the type locality are available on application to the QM. Fossil sites are located in the Riversleigh World Heritage Area, north-western Queensland, Australia. As a RFZC site, Gotham City Site is interpreted to be middle Miocene in age (Hand 1990,



**Figure 4.** *Acrobates pettitorum* sp. nov., QM F61169 holotype, Lm1. A, buccal view; B, C, occlusal stereopair. Scale = 1 mm. [169 mm width].

Archer *et al.* 1994, 1995, 1999, Creaser 1997, Travouillon *et al.* 2006, Arena *et al.* 2016, Myers *et al.* 2017).

### Description

The m1 is bunoselenodont, with two roots. Four cusps are identifiable on the occlusal surface which are, from tallest to shortest: the protoconid, metaconid, hypoconid, and entoconid. The steeply dipping paracristid runs from the tip of the protoconid in an anterolingual direction to the anterior base of the trigonid at the anterior margin of the tooth. The protoconid is robust. The trigonid is nearly as wide as the talonid. The metaconid is only slightly posterior to the protoconid. The postmetacristid steeply inclines in a posterior direction where it meets the preentocristid at the trigonid/talonid junction. The trigonid basin between the protoconid and metaconid is shallow. The transverse mid-section of the tooth at the talonid/trigonid junction is wide. In occlusal view, the entoconid is lingually directed and only slightly posteriorly positioned with respect to the hypoconid. The preentocristid runs gently up to the tip of the entoconid from a notch between the talonid/trigonid junction where it joins the postmetacristid. The postentocristid runs from the back of the talonid in a lingual direction to the posterior base of the entoconid, then in an anterior direction to the tip of the entoconid. The hypoconid is robust. In occlusal view, the tip of the hypoconid is buccally directed. The hypoconid sits almost transversely in line with the entoconid. The entoconid is only slightly anterior to the hypoconid. The cristid obliqua runs in an anterolingual direction from the hypoconid tip to the longitudinal midline of the tooth, terminating before it reaches a point midway between the bases of the protoconid and metaconid. The posthypocristid inclines in a posterolingual direction to the rear of the talonid, where it joins the postentocristid. There is a crest extending from the centre of the cristid obliqua, which is steeply inclined in the anterobuccal direction, down the buccal side of the tooth facing the external base of the protoconid. This is not present in *A. magicus* or *A. pygmaeus*. There is a buccal crest that runs anteroposteriorly from the external buccal base of the protoconid to the anterobuccal base of the metaconid; this crest runs along the edge of the buccal cingulid that extends between the protoconid and the hypoconid. There is a pronounced buccal cingulid that extends from below the base of the protoconid to the base of the hypoconid. There is a posterobuccal cingulid that

extends from the junction between the postentocristid and posthypocristid and around the posterior flank of the hypoconid.

### Results

#### Qualitative comparisons

Based on qualitative differences in m1 morphology (discussed in the species diagnoses and descriptions above), the Riversleigh acrobatid fossils appear to fall into four distinct morphotypes. Given the degree of intraspecific variation in m1 morphology seen in the modern acrobatids *Acrobates pygmaeus* and *Distoechurus pennatus*, these four fossil morphotypes are interpreted here as representing four new species. We refer two species to *Acrobates* (*Acrobates magicus* and *A. pettitorum*) and two to *Distoechurus* (*Distoechurus jeansorum* and *D. georginae*). These generic assignments are supported by the results of our phylogenetic analyses (see below).

#### Quantitative comparisons

Raw data for tooth measurements are given in [Supplementary Data 2](#). Univariate statistics for *Acrobates pygmaeus*, *Acrobates magicus* and *Acrobates pettitorum* are shown in [Table 3](#), and those for *Distoechurus pennatus* and *Distoechurus georginae* are in [Table 4](#).

CV values calculated for dental measurements of the three fossil acrobatid species known from multiple specimens, namely *A. magicus*, *D. jeansorum* and *D. georginae*, are comparable with those of the extant species *A. pygmaeus* and *D. pennatus*, and are in most cases somewhat lower (although this may be because of the smaller sample sizes for the fossil species). This suggests that the sets of specimens referred here to *A. magicus*, *D. jeansorum* and *D. georginae* each represent no more than one species. In *A. magicus* (the only fossil species known from intact cheek-tooth rows), measurements for m4 showed the greatest CV values. This may be because this tooth—which has been lost in both *A. pygmaeus* and *D. pennatus*—was under relatively reduced constraint in terms of size because of its diminishing functional value in *A. magicus*. However, the high variability may also reflect the posterior position of this tooth in the molar row. It is striking that CV values for dental measurements in *A. magicus* become larger with increased

**Table 3.** Univariate statistics for *Acrobates pygmaeus*, *Acrobates magicus* sp. nov. and *Acrobates pettitorum* sp. nov. Measurements (mm).

<i>Acrobates pygmaeus</i>						<i>Acrobates magicus</i>						<i>Acrobates pettitorum</i>					
Lower Teeth	N	OR	Mean	SD	CV	Lower Teeth	N	OR	Mean	SD	CV	Lower Teeth	N	OR	Mean	SD	CV
p2 L	21	0.72–1	0.86	0.07	8.58	p2 L	7	0.87–0.98	0.92	0.04	3.89	p2 L	–	–	–	–	–
p2 W	21	0.26–0.46	0.35	0.05	15.40	p2 W	7	0.4–0.48	0.44	0.03	7.08	p2 W	–	–	–	–	–
p3 L	21	0.72–0.94	0.81	0.05	6.15	p3 L	10	0.74–0.84	0.79	0.04	4.49	p3 L	–	–	–	–	–
p3 W	21	0.36–0.55	0.43	0.05	11.25	p3 W	10	0.39–0.44	0.42	0.02	3.87	p3 W	–	–	–	–	–
m1 L	21	0.87–1.03	0.95	0.04	4.27	m1 L	18	1.2–1.39	1.26	0.05	3.67	m1 L	2	1.38	0.07	5.12	
m1 PW	21	0.57–0.71	0.65	0.04	5.83	m1 PW	18	0.73–0.9	0.81	0.05	5.70	m1 PW	2	0.93	0.08	8.41	
m2 L	21	0.9–1.03	0.95	0.03	2.98	m2 L	21	1.12–1.33	1.18	0.05	4.22	m2 L	–	–	–	–	–
m2 AW	21	0.64–0.79	0.72	0.04	5.28	m2 AW	21	0.7–0.9	0.81	0.05	5.89	m2 AW	–	–	–	–	–
m2 PW	21	0.6–0.83	0.73	0.05	7.15	m2 PW	21	0.81–0.92	0.86	0.03	3.74	m2 PW	–	–	–	–	–
m3 L	21	0.79–0.98	0.87	0.04	4.86	m3 L	9	0.95–1.07	1.00	0.04	3.54	m3 L	–	–	–	–	–
m3 AW	21	0.63–0.8	0.69	0.04	5.85	m3 AW	9	0.7–0.84	0.76	0.05	6.00	m3 AW	–	–	–	–	–
m3 PW	21	0.54–0.75	0.60	0.05	8.48	m3 PW	8	0.66–0.83	0.76	0.05	7.00	m3 PW	–	–	–	–	–
m4 L	–	–	–	–	–	m4 L	4	0.61–0.72	0.68	0.05	8.07	m4 L	–	–	–	–	–
m4 AW	–	–	–	–	–	m4 AW	4	0.47–0.63	0.57	0.07	13.06	m4 AW	–	–	–	–	–
m4 PW	–	–	–	–	–	m4 PW	4	0.33–0.49	0.43	0.08	17.55	m4 PW	–	–	–	–	–
m1–2 L	21	1.57–2.06	1.90	0.10	5.40	m1–2 L	8	2.35–2.46	2.40	0.042	1.75	m1–2 L	–	–	–	–	–
m1–3 L	21	2.63–2.94	2.81	0.07	2.51	m1–3 L	3	3.33–3.41	3.36	0.044	1.30	m1–3 L	–	–	–	–	–
Average Variation Coefficient					6.71	Average Variation Coefficient					5.93	Average Variation Coefficient					6.77

Abbreviations. N, number of specimens; OR, observed range; SD, standard deviation; CV, coefficient of variation; L, length; W, width; AW, anterior width; PW, posterior width.

**Table 4.** Univariate statistics for *Distoechurus pennatus* and *Distoechurus georginae* sp. nov. Measurements (mm).

<i>Distoechurus pennatus</i>						<i>Distoechurus georginae</i>					
Lower Teeth	N	OR	Mean	SD	CV	Lower Teeth	N	OR	Mean	SD	CV
p2 L	11	1.41–1.69	1.56	0.092	5.90	p2 L	–	–	–	–	–
p2 W	11	0.53–0.68	0.6	0.047	7.89	p2 W	–	–	–	–	–
p3 L	–	–	–	–	–	p3 L	–	–	–	–	–
p3 W	–	–	–	–	–	p3 W	–	–	–	–	–
m1 L	11	1.73–2.01	1.84	0.082	4.47	m1 L	6	1.3–1.48	1.37	0.07	4.78
m1 PW	11	1.01–1.2	1.08	0.058	5.41	m1 PW	6	0.84–0.94	0.86	0.04	4.38
m2 L	11	1.49–1.76	1.64	0.089	5.39	m2 L	–	–	–	–	–
m2 AW	11	1.01–1.23	1.1	0.061	5.53	m2 AW	–	–	–	–	–
m2 PW	11	0.97–1.15	1.045	0.049	4.69	m2 PW	–	–	–	–	–
m3 L	11	1.8–1.4	1.29	0.068	5.23	m3 L	–	–	–	–	–
m3 AW	11	0.86–0.97	0.92	0.037	4.06	m3 AW	–	–	–	–	–
m3 PW	11	0.72–0.89	0.81	0.049	6.13	m3 PW	–	–	–	–	–
m4 L	–	–	–	–	–	m4 L	–	–	–	–	–
m4 AW	–	–	–	–	–	m4 AW	–	–	–	–	–
m4 PW	–	–	–	–	–	m4 PW	–	–	–	–	–
m1–2 L	11	3.31–3.72	3.46	0.13	3.75	m1–2 L	–	–	–	–	–
m1–3 L	11	4.48–4.95	4.7	0.17	3.55	m1–3 L	–	–	–	–	–
Average Variation Coefficient					5.17	Average Variation Coefficient					4.58

Abbreviations. N, number of specimens; OR, observed range; SD, standard deviation; CV, coefficient of variation; L, length; W, width; AW, anterior width; PW, posterior width.

distance from m1, which may represent evidence that increased variability is a function of distance from the molar/premolar interface. Principal Component Analysis (PCA) supported these conclusions about species boundaries by similarly demonstrating clear size separation between *A. magicus*, *A. pygmaeus* and *D. pennatus* (Fig. 5, Table 5). It further demonstrated that m1 length was the most important measurement in determining species boundaries.

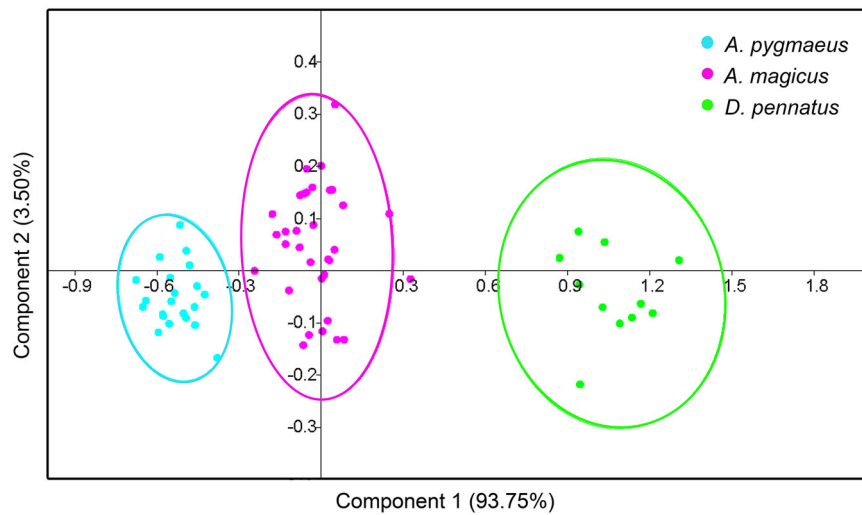
The fact that m1 displays the least intraspecific variability of any of the teeth measured supports our decision to focus on this tooth to reveal species-level differences in size and morphology. However, it is noteworthy that in our *A. pygmaeus* sample, which potentially could represent a mixed sample of *A. pygmaeus* and *A. frontalis*, CVs for m1 length and width were as expected for a single species (4.27 and 5.83 respectively) but were high for p2 width and p3 width (15.40 and 11.25 respectively).

This also gives further support to the results of the Mann–Whitney U tests (Table 2). Multiple Mann–Whitney

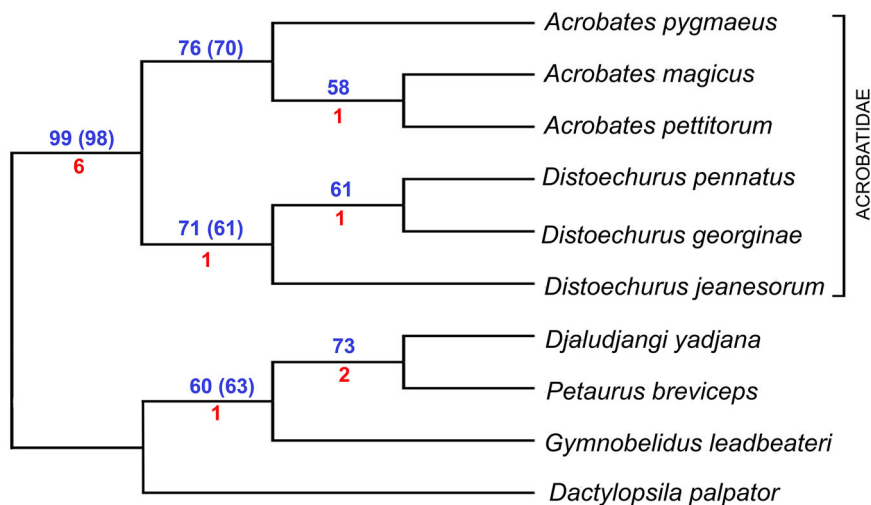
**Table 5.** Summary statistics of principal components analysis using 10 measurements of p2 and m1–3 of *A. pygmaeus*, *A. magicus* sp. nov. and *D. pennatus*.

Component	1	2
Eigenvalue:	0.288381	0.0107495
% Variance	93.745	3.4944
Cumulative percent	93.745	97.2394
Eigenvectors:		
p2 length	0.4475	–0.664
p2 width	0.1563	0.09813
m1 length	0.5588	–0.02785
m1 posterior width	0.2654	0.2437
m2 length	0.4352	0.05916
m2 anterior width	0.2436	0.05218
m2 posterior width	0.1964	0.2793
m3 length	0.2624	0.1557
m3 anterior width	0.1443	0.1693
m3 posterior width	0.1249	0.5934

U tests were performed because the Kruskal–Wallis, a non-parametric equivalent of ANOVA, can only determine if there was an overall statistically significant difference in size



**Figure 5.** Results of Principal Component Analysis (PCA) of 10 dental measurements of p2 and m1–3 for *Acrobates pygmaeus*, *Acrobates magicus* sp. nov. and *Distoechurus pennatus*. [81 mm width].



**Figure 6.** Single most parsimonious tree from the unordered analysis with bootstrap, jackknife and Bremer support values given. Bootstrap and jackknife support values in blue, with jackknife values given in parentheses, Bremer support values given in red. No jackknife value is given when support value is below 50. [169 mm width].

among the species being compared; it does not indicate exactly which species differ significantly from each other. By performing numerous Mann-Whitney tests, corrected for multiple testing using a False Discovery Rate of 5%, it was possible to determine that all taxa were significantly different from one another in at least one size component, either m1 length or m1 posterior width, with the exception of *A. pettitorum* and *D. georginae*. These were, however, distinguished from one another by distinctive qualitative features as noted above. Despite relatively small sample sizes for these two species, the results of the Mann-Whitney tests do not contradict their recognition as distinct species.

### Phylogenetic analyses

Characters and character states used in the phylogenetic analyses are listed in [Appendix 3.1](#). Maximum parsimony analysis of the morphological character–taxon matrix ([Appendix 3.2](#)) with all characters unordered and equally

weighted resulted in one most parsimonious tree (tree length = 38 steps; CI= 0.7419, RI= 0.8261, RC= 0.6522; [Fig. 6](#)). The tree was rooted assuming that the three extant petaurid outgroup taxa (i.e., *Dactylopsila palpator*, *Gymnobelidus leadbeateri* and *Petaurus breviceps*) form a clade (in agreement with recent molecular data); this rooting decision resulted in the fossil *Djaludjangi yadjana* clustering within Petauridae as sister-taxon to *Petaurus* Shaw, 1791. A sister-taxon relationship between *Petaurus* and *Djaludjangi* Brammall, 1999 to the exclusion of *Dactylopsila* Gray, 1858 and *Gymnobelidus* McCoy, 1867 is feasible, as some molecular clock studies suggests that *Petaurus* diverged from other extant petaurids during the late Oligocene or early Miocene (Meredith *et al.* 2009, Mitchell *et al.* 2014, Álvarez-Carretero *et al.* 2022; but see Beck *et al.* 2022, p. 244, who estimated a somewhat younger date for this divergence), and *Djaludjangi* is known from Riversleigh’s FZB (early Miocene) and FZC (middle Miocene) sites (Brammall 1999). However, it should be emphasized that the character matrix and associated phylogenetic analysis presented here was

intended to resolve relationships within Acrobatidae only, and so relationships among the petaurid outgroup taxa should be treated with circumspection. The tree topology is illustrated in Fig. 6 with bootstrap, jackknife and Bremer support values indicated.

Acrobatidae (i.e., all species of *Acrobates* and *Distoechurus*) is the most strongly supported clade in this analysis (bootstrap = 99%, jackknife = 98%, Bremer = 6), and is supported by the following unambiguous synapomorphies (all based on m1): protoconid and metaconid form distinctly separate cusps (ch. 1 1→0; ci = 1); absence of a protocristid (ch. 10 1→0; ci = 1); absence of a premetacristid (ch. 12 1→2; ci = 1; reversed in *Distoechurus jeanesorum*); buccal placement of the protoconid without transverse compression (ch. 13 0→2; ci = 1); cristid obliqua terminates at a point between the protoconid and the metaconid (ch. 14 0→1; ci = 1; reversed in *Acrobates magicus* + *Acrobates pettitorum*); buccal cingulid present (ch. 17 1→0; ci = 1); posthypocristid and the cristid obliqua are approximately equal in length (ch. 23 1→0; ci = 0.5).

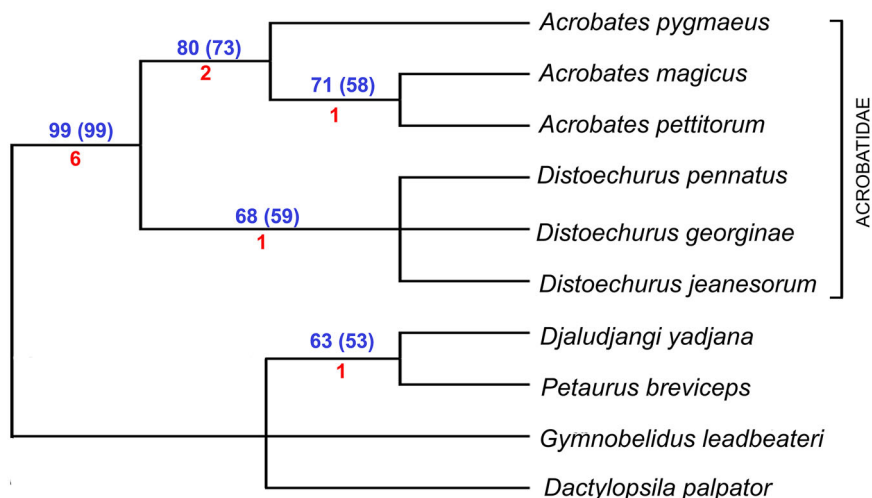
Monophyly of *Acrobates* (i.e., the extant *Acrobates pygmaeus*, plus the fossil *A. magicus* and *A. pettitorum*) also receives relatively strong support values (bootstrap = 76%, jackknife = 70%, Bremer = 2). It is characterized by the following unequivocal synapomorphies: the entoconid is rounded, rather than transversely compressed (ch. 4 0→1; ci = 0.5); the anterolingual surface of the protoconid is rounded (ch. 11 0→1; ci = 1.0); the protoconid and metaconid are transversely in line (ch. 19 1→0; ci = 1); the posthypocristid is posterolingually orientated then lingually deflected (ch. 20 0→1; ci = 1). Monophyly of *A. magicus* and *A. pettitorum* to the exclusion of the extant *A. pygmaeus* is only weakly supported (bootstrap = 58%, jackknife <50%, Bremer = 1), and is characterized by a single unambiguous synapomorphy: the direction of the cristid obliqua, which approaches the protoconid base (ch. 14 1→2; ci = 1.0).

Monophyly of *Distoechurus* (i.e., the extant *Distoechurus pennatus* and the fossil *D. jeanesorum* and *Distoechurus georginae*) receives weak-to-moderate support (bootstrap =

71%; jackknife = 61%, Bremer = 1), and is characterized by the following unequivocal synapomorphy: entoconid is posteriorly placed with regards to the hypoconid (5 0→1; ci = 1.0). Monophyly of *D. pennatus* and *D. georginae* to the exclusion of *D. jeanesorum* (bootstrap = 61%, jackknife < 50%, Bremer = 1) is relatively weakly supported and is characterized by a single unambiguous synapomorphy: entoconid distinctly shorter than the hypoconid (ch. 21 0→1; ci = 0.5).

Maximum parsimony analysis of the morphological matrix with all characters equally weighted and four multi-state characters representing plausible morphoclines ordered resulted in three most parsimonious trees (tree length = 40; CI 0.7143; RI = 0.800; RC = 0.6000). As for the unordered analysis, the trees were rooted assuming that the extant petaurid outgroup taxa form a clade; again, this resulted in the inclusion of *Djaludjangi* within Petauridae, as the sister to *Petaurus*. The strict consensus of the three most parsimonious trees is shown in Fig. 7, with bootstrap, jackknife and Bremer support values indicated.

Monophyly of Acrobatidae is strongly supported in this analysis (bootstrap = 99%; jackknife = 98%; Bremer = 7). Synapomorphies (Fig. 7) for this clade are: protoconid and metaconid form separate cusps (1.1→0; ci = 1); paracristid runs in an anterolingual direction from the tip of the protoconid (7.1→0; ci = 1); absence of the protocristid (10.1→0; ci = 1); absence of the premetacristid (12.0→2; ci = 1; reversed in *D. jeanesorum*); protoconid buccally placed relative to the anteroposterior midline of the tooth (13.0→2; ci = 0.667); buccal cingulid present (17.1→0; ci = 1); cristid obliqua and posthypocristid are approximately equal length (23.1→0; ci = 0.5). Monophyly of *Acrobates* receives relatively strong support (bootstrap = 80%; jackknife = 73%; Bremer = 2). Synapomorphies for this clade are: entoconid does not exhibit transverse flattening, cusp has rounded sides (4.0→1; ci = 0.5); all sides of the protoconid are rounded (11.0→1; ci = 1); metaconid is in line with or only slightly posterior in regards to the protoconid (19.1→0; ci = 1); posthypocristid is posterolingually directed then lingually



**Figure 7.** Strict consensus of the three most parsimonious trees in the ordered analysis. Bootstrap and jackknife support values in blue, with jackknife values given in parentheses and Bremer support values given in red. No jackknife value is given when support value is below 50. All character transformations are listed. [169 mm width].

deflected (20.0→1;  $ci = 0.5$ ). A clade comprising the fossil species *A. magicus* and *A. pettitorum* receives moderate support (bootstrap = 71%, jackknife = 58%, Bremer = 1) and is supported by a single synapomorphy: cristid obliqua approaches the protoconid base (14.1→2;  $ci = 1$ ).

Monophyly of *Distoechurus* receives moderate support (bootstrap = 68, jackknife = 59, Bremer = 1). This clade is supported by a single synapomorphy: entoconid is posteriorly placed in regards to the hypoconid (5.0→1;  $ci = 1$ ). This clade is supported by an additional synapomorphy under ACCTRAN: entoconid distinctly shorter than the hypoconid when viewed dorsally (21.0→1;  $ci = 0.333$ , reversed in *D. jeanesorum*). However, relationships within *Distoechurus* are unresolved in the strict consensus.

In summary, both the unordered and unordered analyses provide strong support for monophyly of Acrobatidae, and moderate-to-strong support for monophyly of both *Acrobates* (including *A. magicus* and *A. pettitorum*) and *Distoechurus* (including *D. jeanesorum* and *D. georginae*).

## Discussion

### Origin of Acrobatidae and timing of the *Acrobates–Distoechurus* divergence

The oldest acrobatid species described here, *Distoechurus jeanesorum*, is known from the Riversleigh FZA White Hunter Site, which is currently interpreted to be late Oligocene in age (~25 Ma: Archer *et al.* 1994, 1995, 1999, Creaser 1997, Myers & Archer 1997, Travouillon *et al.* 2006, Black *et al.* 2012, 2012, Arena *et al.* 2016, Myers *et al.* 2017); this species is referred to the modern genus *Distoechurus*. The oldest *Acrobates* species, *Acrobates magicus*, is slightly younger: it occurs in multiple FZB sites at Riversleigh, which are radiometrically dated and/or interpreted as early Miocene in age. Our phylogenetic analyses confirm that *D. jeanesorum* appears to be more closely related to *Distoechurus pennatus* than to *Acrobates pygmaeus*, implying that the *Distoechurus–Acrobates* split occurred prior to ~25 Ma.

This is in reasonable agreement with the molecular clock analyses of Meredith *et al.* (2009), Mitchell *et al.* (2014) and Duchêne *et al.* (2018), all of which have point estimates for the *Distoechurus–Acrobates* split that are >25 Ma (Table 1). The point estimate for the molecular clock analysis of Álvarez-Carretero *et al.* (2022) is only 23.4 Ma, but the maximum bound of the 95% Highest Posterior Density (HPD) estimate is 25.8 Ma (Table 1). By contrast, the total evidence tip-and-node dating estimate of Beck *et al.* (2022) is markedly younger than 25 Ma (Table 1), but divergence dates in this study were consistently younger than those of recent molecular clock analyses (which use node-dating and molecular data only). The m1 of *D. jeanesorum* exhibits multiple synapomorphies of *Distoechurus*, and referral of *D. jeanesorum* to *Distoechurus* receives relatively strong support (as measured by bootstrap, jackknife and Bremer values) in our phylogenetic analyses, suggesting that the *Acrobates–Distoechurus* split may predate the age of *D. jeanesorum* (late Oligocene; ca 25 Ma) by a considerable margin; thus,

the fossil specimens described here are more congruent with the molecular clock analyses of Mitchell *et al.* (2014) and Duchêne *et al.* (2018) in particular (Table 1).

Indeed, our study suggests that the Riversleigh acrobatids are suitable for use as a fossil calibration point to provide a minimum date for the age of the *Acrobates–Distoechurus* split. Specifically, we argue that this divergence can be calibrated based on QM F61140, the holotype (and currently only known specimen) of *D. jeanesorum*. This specimen is from the Riversleigh's FZA White Hunter Site at Riversleigh, which is currently interpreted as ca 25 Ma old based largely on biocorrelation (Myers & Archer, 1997, Travouillon *et al.* 2006, Black *et al.* 2012, 2012, Arena *et al.* 2016, Myers *et al.* 2017). However, in the absence of published absolute dates for this or other Riversleigh FZA sites, we argue that 23.03 Ma (the Oligocene–Miocene boundary) represents a conservative minimum for calibrating the age of *Acrobates–Distoechurus* divergence.

The divergence of acrobatids from other petauroids must be older than the age of Riversleigh's FZA (~25 Ma), but presumably postdates the age of the 54.6 Ma old Tingamarra Local Fauna, from which definitive diprotodontians (let alone representatives of specific diprotodontian families) appear to be absent. Thus, the molecular clock estimates for this divergence from the analyses of Meredith *et al.* (2009, 2011), Mitchell *et al.* (2014) and Duchêne *et al.* (2018)—all of which date to the Eocene or earliest Oligocene – appear plausible based on the evidence at hand. The molecular clock estimate of Álvarez-Carretero *et al.* (2022) is considerably younger (early Oligocene), but still broadly compatible with the fossil evidence. By contrast, the total evidence clock estimate of Beck *et al.* (2022) for this divergence appears less plausible, because definitive pseudocheirids are also known from Riversleigh's FZA (Roberts 2008) and the Etadunna Formation in central Australia (Woodburne *et al.*, 1987; Roberts, 2008), and so all four modern petauroid families must have diverged from each other and acquired family-specific apomorphies by 25 Ma at the latest. Beck *et al.* (2022) did not include any fossil petauroids in their phylogenetic analyses, which were restricted to taxa known from relatively well-preserved cranial material, and it remains to be seen what impact their inclusion would have on the divergence time estimates. Regardless, it appears that acrobatids originated during one of the major 'dark ages' in the fossil record of mammals in Australia, spanning from the early Eocene to the late Oligocene (Archer *et al.* 1999, Beck 2017).

### Palaeoecological and palaeobiogeographical implications

Today, *Acrobates pygmaeus* and *Acrobates frontalis* are confined to open sclerophyll forests and woodlands (Strahan 1983, 1995) in eastern Australia, while *Distoechurus pennatus* occurs in closed forests (Aplin & Kale 2011; Aplin pers. comm. 2012) in New Guinea. Archer (1984) hypothesized that this difference in habitat explains why the *Acrobates* lineage evolved gliding adaptations while *Distoechurus* did not.

Gliding allows efficient locomotion in open forests where canopies do not interlock, and has evolved independently in open forest inhabitants of two other families of phalangeridan possums (Petauridae and Pseudocheiridae). However, the oldest known representative of the *Acrobates* lineage, *Acrobates magicus*, is first known from the early Miocene FZB, which is interpreted as a closed rainforest environment (Travouillon *et al.* 2009), and open sclerophyll forests and woodlands do not appear to have become widespread in Australia until the late middle Miocene (Martin 1994). Thus, the earliest members of the *Acrobates* lineage may not have been gliders; gliding adaptations may instead have evolved subsequently, in response to the gradual opening up of Australia's forests from the middle Miocene onwards. The *Distoechurus* lineage, on the other hand, appears to have maintained a preference for closed forest habitats over the last 25 Ma. This hypothesis could be tested by the identification of postcranial indicators of gliding that are present in *A. pygmaeus* but absent (presumably plesiomorphically) in *D. pennatus*, and the discovery of postcranial remains of acrobatids at Riversleigh; if our hypothesis is correct, then osteological correlates of gliding should be absent in the Riversleigh acrobatids. However, at present, no postcranial specimens have been found at Riversleigh that can be unequivocally referred to acrobatids.

Only small areas of land appear to have been emergent north of the Australian continent before the middle Miocene (Quarles van Ufford & Cloos 2005), with the orogeny that led to the formation of the major Central Range of New Guinea occurring ~12 Ma (Quarles van Ufford & Cloos 2005). This is considerably younger than the oldest species of *Distoechurus* described here, namely *Distoechurus jeansorum*, which is from Riversleigh's FZA (late Oligocene; ~25 Ma). Consequently, it appears that the *Distoechurus* lineage originated in Australia, dispersed to New Guinea some time later (most likely after the New Guinean Central Range orogeny, *ca* 12 Ma), and then went extinct in Australia after the middle Miocene (the age of the youngest Riversleigh *Distoechurus* species described here, *Distoechurus georginae*, which is from Riversleigh's FZC). Curiously, *Acrobates* does not appear to have colonized New Guinea (but see Helgen 2003), although the New Guinean fossil record is currently insufficiently known to rule out this possibility.

It is interesting to note that the only living species of *Acrobates*, *A. pygmaeus* and *A. frontalis*, do not inhabit the closed forest habitat inferred for the oldest known member of the genus, *A. magicus*. This might be understandable if Australian closed forests, now more limited in geographic area than they were in the Miocene, had retained other acrobatids that competitively excluded species of *Acrobates*. However, as far as can be determined from the fossil record, this did not occur. Although the post-Miocene fossil record of closed forest mammal communities in Australia is relatively limited (e.g., the early Pliocene Hamilton Fauna in Victoria and the middle Pleistocene Mount Etna Fauna in eastern Queensland), what there is provides no evidence for species of *Distoechurus* in Australia after the middle

Miocene (Long *et al.* 2002, Hocknull 2005, 2009, Black *et al.* 2012). Alternatively, loss of closed forest species of *Acrobates* in Australia, and concomitant evolution of the open-forest-adapted *A. pygmaeus*, may have been the result of increasing climatic variability and hence vegetation changes in the late Cenozoic. Because of their lower latitudinal position and higher annual rainfall, the closed forests of New Guinea would have been characterized by relatively greater stability since the middle Miocene, which may explain why *Distoechurus* survived there but not in Australia. Much more information is required, however, about the post-middle Miocene evolution of Australia's closed forest mammal communities before these seeming palaeogeographical/palaeoecological mysteries can be resolved.

## Conclusions

The fossils described here provide the first fragmentary glimpse into the pre-Pleistocene evolutionary history and diversity of acrobatids, and indicate that the divergence between the two modern genera (*Acrobates* and *Distoechurus*) predates the Miocene. Discovery of more complete (cranial and postcranial) acrobatid material in fossil sites at Riversleigh or elsewhere has the potential to give major insights into other aspects of acrobatid biology, including the evolution of their uniquely derived auditory system (Aitkin and Nelson 1989; Aplin 1990; Archer *et al.* 2019; Beck *et al.* 2022: character 62), and the precise timing of origin of gliding specializations in the *Acrobates* lineage.

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No potential conflict of interest was disclosed by the author(s).

## Supplemental data

Supplementary research materials for this article can be accessed at <https://doi.org/10.1080/03115518.2023.2242439>

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**Appendix 1. Fossil and extant specimens examined in this study****A1.1. Materials listing for Riversleigh fossil specimens**

List of Riversleigh fossil specimens used in the morphometric and phylogenetic analyses

<b>Specimens referable to <i>Distoechurus jeanesorum</i></b>		
<b>Specimen</b>	<b>Specimen description</b>	<b>Site</b>
QM F61140 (holotype)	Isolated molar, Lm1	White Hunter
<b>Specimens referable to <i>Distoechurus georginae</i></b>		
<b>Specimen</b>	<b>Specimen description</b>	<b>Site</b>
QM F61141	Isolated molar, Rm1	Gotham City
QM F30898	Isolated molar, Rm1	Gotham City
QM F30920	Isolated molar, Rm1	Gotham City
QM F61144 (holotype)	Isolated molar, Rm1	Gotham City
QM F30897	Isolated molar, Rm1	Gotham City
QM F23030	Isolated molar, Lm1	Ringtail
QM F61145	Isolated molar, Rm1	Upper
QM F61142	Isolated molar, Rm1	Upper
QM F61143	Isolated molar, Lm1	Upper
<b>Specimens referable to <i>Acrobates magicus</i></b>		
<b>Specimen</b>	<b>Specimen description</b>	<b>Site</b>
QM F61146	Partial dentary, Rm1–4.	RSO
QM F61147	Dentary Li1, p3, m3, alveoli present for i2, p1–2, m1–2, 4.	RSO
QM F61148	Partial dentary, Rp3, m1, alveoli present for i1–2, p1–2, m2–3, 4, damage to m1.	RSO
QM F61149	Partial dentary, Ri1–2, p2–3, m1–3 (p2–3 and m3 broken).	Upper
QM F61150	Partial dentary, Li1, p2, alveoli present for i2, p1 and anterior alveolus of p3	Wayne's Wok
QM F61151	Partial dentary, Lp3, m1–3, alveoli present for p2.	Upper
QM F61152	Partial dentary, Rm1–3.	Upper
QM F61153 (holotype)	Partial dentary, Ri1, p1,3, m1–4, alveoli present for p2	Upper
QM F61154	Partial dentary, Ri1, p2–3, m1–2, alveoli present for i2, p1.	Upper
QM F30941	Partial dentary, Ri1–2, p1–2.	Upper
QM F61155	Dentary fragment, Lm1–2	Judith's Horizontal
QM F61156	Partial dentary, Rp3, m2, alveoli present for m1.	Neville's Garden
QM F61157	Isolated molar, Lm1.	Neville's Garden
QM F61158	Isolated molar, Lm1.	Upper
QM F61159	Isolated molar, Lm1.	Upper
QM F61160	Isolated molar, Lm1.	Upper
QM F61161	Isolated molar, Lm1	Upper
QM F61162	Isolated molar, Lm1.	Upper
QM F61163	Isolated molar, Lm1.	Wayne's Wok
QM F61164	Isolated molar, Rm2.	Wayne's Wok
QM F61165	Isolated molar, Rm2.	Wayne's Wok
QM F61166	Partial dentary, Ri1, p2–3, m1, with alveoli present for i2, p1	Wayne's Wok
QM F61167	Isolated molar, Rm1	Wayne's Wok
QM F20727	Partial dentary, Lm2–3, alveoli present for m4	Wayne's Wok
QM F20734	Isolated molar, Lm2	Camel Sputum
QM F20778	Partial dentary, Rm2, alveoli present for m3–4.	Upper
QM F20782	Partial dentary, Rp2–3, m1–2.	Upper
QM F20797	Isolated molar, Rm2.	Upper
QM F23835	Partial dentary, Lm2–4.	Neville's Garden
QM F24315	Partial dentary, Rm2, alveoli present for m1, 3–4.	Wayne's Wok
QM F30796	Partial dentary, Rm2–4.	Neville's Garden
QM F30928	Partial dentary, Rp2, m1–3	Neville's Garden
QM F30930	Partial dentary, Ri1, p3, m1, alveoli present for p2	Neville's Garden
QM F30954	Partial dentary, Ri2, p1–3, p2–3 cusps broken.	Upper
QM F30956	Partial dentary, Lm1–2	Upper
QM F30967	Partial dentary, Rm1–2	Wayne's Wok
<b>Specimens referable to <i>Acrobates pettitorum</i></b>		
<b>Specimen</b>	<b>Specimen description</b>	<b>Site</b>
QM F61168	Isolated molar, Rm1	Gotham City
QM F61169 (holotype)	Isolated molar, Lm1	Gotham City

## A1.2 Materials listing for extant species

List of specimens used for morphometric and phylogenetic analyses in this study

### *Acrobates pygmaeus*

Specimen	Specimen description	Site
AMS M1192	Skull and dentary, sex unknown.	Gunnedah, NSW.
AMS M2436	Skull and dentary, sex unknown.	No Data.
AMS M2495	Skull and dentary, sex unknown.	Marrangaroo, NSW.
AMS M2614	Skull and dentary, sex unknown.	Uralla, NSW.
AMS M2695	Skull and dentary, sex unknown.	Narellan, nr Camden, NSW.
AMS M2723	Skull and dentary, sex unknown.	Revesby, Sydney, NSW.
AMS M2751	Skull and dentary, sex unknown.	Bankstown, Sydney, NSW.
AMS M3001	Skull and dentary, male.	Belltrees, Scone, NSW.
AMS M3048	Skull and dentary, female.	New Forest, Newnes Junction, NSW.
AMS M3294	Skull and dentary, sex unknown.	Cox River, Lithgow, NSW.
AMS M3295	Skull and dentary, sex unknown.	Cox River, Lithgow, NSW.
AMS M3297	Skull and dentary, male.	Cox River, Lithgow, NSW.
AMS M3298	Skull and dentary, sex unknown.	Cox River, Lithgow, NSW.
AMS M3299	Skull and dentary, sex unknown.	Brown's Paddock, Lithgow, NSW.
AMS M3723	Skull and dentary, female.	Portland, NSW.
AMS M4197	Skull and dentary, sex unknown.	No Data.
AMS M5060	Skull and dentary, male.	Avondale, Burragate, NSW.
AMS M5072	Skull and dentary, male.	Lindfield, Sydney, NSW.
AMS M5356	Skull and dentary, female.	St. Ives, Sydney, NSW.
AMS M5377	Skull and dentary, male.	Martinsville, Lake Macquarie, NSW.
AMS M5522	Skull and dentary, male.	"Wellingrove Station", Glen Innes, NSW.
AMS M6151	Skull and dentary, female.	Balgowlah, Sydney, NSW.
AMS M6162	Skull and dentary, male.	Bylong, nr Rylestone, NSW.
AMS M8170	Skull and dentary, female.	Empire Bay, nr Woy Woy, NSW .
AMS M8172	Skull and dentary, female.	Curlewis, 10mls S of Gunnedah, NSW.
AMS M8175	Skull and dentary, sex unknown.	Maitland, NSW.
AMS M8175	Skull and dentary, male.	Maitland, NSW.
AMS M8176	Skull and dentary, female.	Carcoar, NSW.
AMS M8326	Skull and dentary, male.	Maraylya, nr Windsor, NSW.
AMS M14020	Skull and dentary, female.	Windana Warkton nr. Coonabarabran, NSW.
AMS M23465	Skull and dentary, sex unknown.	Martindale valley, 30km SSE of Denman, NSW.
AMS M26218	Skull and dentary, sex unknown.	No Data.
AMS M31801	Skull and dentary, female.	Kosciusko National Park, NSW.
AMS M33822	Skull and dentary, sex unknown.	No Data.
AMS M33986	Skull and dentary, sex unknown.	Armidale, NSW.
AMS M34528	Skull and dentary, sex unknown.	Timbarra Plateau, NSW.
AMS M35824	Skull and dentary, female.	No Data.
AMS M37592	Skull and dentary, sex unknown.	No Data.
AMS M37593	Skull and dentary, female.	Niagara Park, NSW.
AMS M37594	Skull and dentary, female.	Mordi, Central Coast, NSW.
AMS M37595	Skull and dentary, male.	Bungawalbin River, NSW.
AMS M39443	Skull and dentary, sex unknown.	Gosford, NSW.
AMS M40178	Skull and dentary, sex unknown.	Wybong district, owl pellet, NSW
AMS M42732	Skull and dentary, female.	Failford, NSW.

### *Distoechurus pennatus*

Specimen	Specimen description	Site
AMS M01921	Skull and dentary, male.	PNG.
AMS M04148	Skull and dentary, female.	Mt Lamington District. Northern Province PNG.
AMS M07055	Skull and dentary, male.	Dobodura PNG
AMS M09554	Skull and dentary, male.	Mageh, nth slopes Wahgi Divide, Jimi Valley PNG.
AMS M09555	Skull and dentary, female.	Mageh, nth slopes Wahgi Divide, Jimi Valley, PNG.
AMS M13745	Skull and dentary, male.	Maliaala Creek. 1 km.S.of Yuro, E. Mt Karimui, S. Simbu Province, PNG.
AMS M13747	Skull and dentary, female.	Yuro, E. side Mt. Karimui, Sth Simbu Province, PNG.
AMS M14600	Skull and dentary, male.	Wigote, Torricelli Mts West Sepik Province.
AMS M14752	Skull and dentary, female.	Homwe Village, vicinity of Yuro, East Mt. Krarimui Sth. Simbu, PNG.
AMS M15306	Skull and dentary, female.	Maliaala Ck. 1 km.S. of Yuro, E.Mt Karimui, S. Simbu Province, PNG.
AMS M16694	Skull and dentary, sex unknown.	Bobole, Southern Highland Province, PNG.
AMS M18522	Skull and dentary, male.	Bobole Village Southern Highlands Province PNG.
AMS M01921	Skull and dentary, male.	PNG.
AMS M04148	Skull and dentary, female.	Mt Lamington District. Northern Province PNG.
AMS M07055	Skull and dentary, male.	Dobodura PNG
AMS M09554	Skull and dentary, male.	Mageh, nth slopes Wahgi Divide, Jimi Valley PNG.
AMS M09555	Skull and dentary, female.	Mageh, nth slopes Wahgi Divide, Jimi Valley, PNG.
AMS M13745	Skull and dentary, male.	Maliaala Creek. 1 km.S.of Yuro, E. Mt Karimui, S. Simbu Province, PNG.
AMS M13747	Skull and dentary, female.	Yuro, E. side Mt. Karimui, Sth Simbu Province, PNG.
AMS M14600	Skull and dentary, male.	Wigote, Torricelli Mts West Sepik Province.
AMS M14752	Skull and dentary, female.	Homwe Village, vicinity of Yuro, East Mt. Krarimui Sth. Simbu, PNG.
AMS M15306	Skull and dentary, female.	Maliaala Ck. 1 km.S. of Yuro, E.Mt Karimui, S. Simbu Province, PNG.
AMS M16694	Skull and dentary, sex unknown.	Bobole, Southern Highland Province, PNG.
AMS M18522	Skull and dentary, male.	Bobole Village Southern Highlands Province PNG.

### A1.3 Outgroup taxa

List of specimens used for outgroup comparisons in the phylogenetic analysis

Specimen	Specimen description	Species
AR02912	Cast of upper and lower dentition	<i>Dactylopsila palpator</i>
AR11985	Right dentary	<i>Djaludjangi yadjana</i>
AR17565	Skull and dentary	<i>Gymnobelideus leadbeateri</i>
AR19703	Skull and dentary	<i>Petaurus breviceps</i>

## Appendix 2: Raw data for tooth measurements

The following are linear measurements (in mm) for lower cheek teeth. Abbreviations: p2 = second lower premolar, p3 = third lower premolar, m1 = first lower molar, m2 = second lower molar, m3 = third lower molar, m4 = fourth lower molar; L = length, W = width, AW = anterior width, PW = posterior width.

### A2.1 Tooth measurements of Riversleigh fossil acrobatid specimens

#### *Acrobates magicus*

Specimen	p2		p3		m1		m2			m3			m4			m1-2 L	m1-3 L	m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW			
QM F61146	-	-	-	-	1.27	0.86	1.15	0.9	0.89	1.01	0.84	0.83	0.72	0.63	0.49	2.38	3.34	4.06
QM F61147	-	-	0.81	0.43	-	-	-	-	-	1.01	0.76	0.74	-	-	-	-	-	-
QM F61148	-	-	0.81	0.44	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QM F61149	0.98	0.48	0.84	0.42	1.31	0.88	1.14	0.83	0.91	1.06	-	-	-	-	-	2.46	-	-
QM F61150	0.95	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QM F61151	-	-	0.77	0.4	1.29	0.73	1.16	0.73	0.82	0.97	0.7	0.66	-	-	-	2.44	3.41	-
QM F61152	-	-	-	-	1.27	0.79	1.17	0.8	0.85	1.02	0.78	0.78	-	-	-	-	-	-
QM F61153	-	-	0.84	0.41	1.29	0.75	1.13	0.76	0.84	0.95	0.76	0.77	0.65	0.55	0.42	2.44	3.33	3.99
QM F61154	0.92	0.43	0.76	0.42	1.22	0.87	1.15	0.8	0.92	-	-	-	-	-	-	2.39	-	-
QM F30941	0.94	0.42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QM F61155	-	-	-	-	1.2	0.79	1.14	0.73	0.86	-	-	-	-	-	-	2.35	-	-
QM F61156	-	-	0.74	0.41	-	-	1.19	0.81	0.89	-	-	-	-	-	-	-	-	-
QM F61158	-	-	-	-	1.27	0.82	-	-	-	-	-	-	-	-	-	-	-	-
QM F61159	-	-	-	-	1.27	0.79	-	-	-	-	-	-	-	-	-	-	-	-
QM F61160	-	-	-	-	1.28	0.83	-	-	-	-	-	-	-	-	-	-	-	-
QM F61161	-	-	-	-	1.39	0.9	-	-	-	-	-	-	-	-	-	-	-	-
QM F61162	-	-	-	-	1.22	0.83	-	-	-	-	-	-	-	-	-	-	-	-
QM F61163	-	-	-	-	1.26	0.78	-	-	-	-	-	-	-	-	-	-	-	-
QM F61164	-	-	-	-	-	-	1.19	0.85	0.86	-	-	-	-	-	-	-	-	-
QM F61165	-	-	-	-	-	-	1.21	0.84	0.9	-	-	-	-	-	-	-	-	-
QM F61167	-	-	-	-	1.29	0.79	-	-	-	-	-	-	-	-	-	-	-	-
QM F61166	0.92	0.42	0.79	0.42	1.29	0.79	-	-	-	-	-	-	-	-	-	-	-	-
QM F20727	-	-	-	-	-	-	1.26	0.82	0.88	1.07	0.75	0.81	-	-	-	-	-	-
QM F20734	-	-	-	-	-	-	1.19	0.78	0.85	-	-	-	-	-	-	-	-	-
QM F20778	-	-	-	-	-	-	1.33	0.9	0.91	-	-	-	-	-	-	-	-	-
QM F20782	0.91	0.43	0.78	0.42	1.2	0.84	1.22	0.8	0.81	-	-	-	-	-	-	2.36	-	-
QM F20797	-	-	-	-	-	-	1.22	0.83	0.83	-	-	-	-	-	-	-	-	-
QM F23835	-	-	-	-	-	-	1.16	0.77	0.85	0.99	0.7	0.73	0.61	0.47	0.33	-	-	-
QM F24315	-	-	-	-	-	-	1.19	0.83	0.85	-	-	-	-	-	-	-	-	-
QM F30796	-	-	-	-	-	-	1.18	0.83	0.88	0.99	0.79	0.79	0.72	0.62	0.49	-	-	-
QM F30928	0.9	0.42	-	-	-	-	1.14	0.79	0.86	0.97	0.72	-	-	-	-	-	-	-
QM F30930	-	-	0.79	0.39	1.27	0.79	-	-	-	-	-	-	-	-	-	-	-	-
QM F30954	0.87	0.48	0.75	0.44	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QM F30956	-	-	-	-	1.26	0.78	1.12	0.74	-	-	-	-	-	-	-	2.37	-	-
QM F30967	-	-	-	-	1.2	0.77	1.13	0.77	0.82	-	-	-	-	-	-	-	-	-

#### *Acrobates pettitorum*

Specimen	p2		p3		m1		m2			m3			m4			m1-2 L	m1-3 L	m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW			
QM F61168	-	-	-	-	1.33	0.87	-	-	-	-	-	-	-	-	-	-	-	-
QM F61169	-	-	-	-	1.43	0.98	-	-	-	-	-	-	-	-	-	-	-	-

#### *Distoechurus georginae*

Specimen	p2		p3		m1		m2			m3			m4			m1-2 L	m1-3 L	m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW			
QM F30920	-	-	-	-	1.32	0.85	-	-	-	-	-	-	-	-	-	-	-	-
QM F61141	-	-	-	-	1.3	0.85	-	-	-	-	-	-	-	-	-	-	-	-
QM F30898	-	-	-	-	1.35	0.85	-	-	-	-	-	-	-	-	-	-	-	-

(continued)

Continued.

*Distoechurus georginae*

Specimen	p2		p3		m1		m2			m3			m4			m1-2 L	m1-3 L	m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW			
QM F61144	-	-	-	-	1.48	0.94	-	-	-	-	-	-	-	-	-	-	-	-
QM F61145	-	-	-	-	1.38	0.85	-	-	-	-	-	-	-	-	-	-	-	-
QM F61142	-	-	-	-	1.27	0.74	-	-	-	-	-	-	-	-	-	-	-	-
QM F61143	-	-	-	-	1.26	0.79	-	-	-	-	-	-	-	-	-	-	-	-
QM F23030	-	-	-	-	1.41	0.84	-	-	-	-	-	-	-	-	-	-	-	-
QM F30897	-	-	-	-	1.22	-	-	-	-	-	-	-	-	-	-	-	-	-

*Distoechurus jeanesorum*

Specimen	p2		p3		m1		m2			m3			m4			m1-2 L	m1-3 L	m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW			
QM F61140	-	-	-	-	1.24	0.76	-	-	-	-	-	-	-	-	-	-	-	-

**A2.2 Tooth measurements of extant acrobatid species***Acrobates pygmaeus*

Specimen	p2		p3		m1		m2			m3			m4		m1-2 PW	m1-3		m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW		L	L	
AMS M02695	0.89	0.33	0.85	0.42	0.92	0.61	0.98	0.64	0.71	0.86	0.74	0.58	-	-	-	1.93	2.81	-
AMS M02751	0.82	0.36	0.75	0.36	0.87	0.57	0.92	0.67	0.68	0.89	0.69	0.61	-	-	-	1.78	2.86	-
AMS M03294	0.94	0.34	0.82	0.44	0.97	0.71	0.97	0.79	0.8	0.86	0.69	0.65	-	-	-	2.02	2.93	-
AMS M03295	0.9	0.34	0.83	0.49	0.98	0.71	0.95	0.74	0.78	0.79	0.67	0.57	-	-	-	1.57	2.78	-
AMS M03297	0.91	0.37	0.78	0.46	0.95	0.68	0.93	0.71	0.83	0.83	0.68	0.57	-	-	-	1.96	2.8	-
AMS M03298	0.72	0.35	0.72	0.38	0.97	0.64	0.96	0.67	0.7	0.9	0.69	0.6	-	-	-	1.94	2.85	-
AMS M03299	0.86	0.43	0.79	0.46	0.9	0.64	0.95	0.72	0.72	0.91	0.72	0.6	-	-	-	1.88	2.76	-
AMS M042732	0.78	0.26	0.83	0.42	0.93	0.61	0.93	0.68	0.6	0.87	0.65	0.6	-	-	-	1.86	2.73	-
AMS M05060	0.88	0.42	0.75	0.46	0.92	0.65	0.96	0.72	0.75	0.88	0.72	0.75	-	-	-	1.86	2.78	-
AMS M06162	0.88	0.33	0.83	0.36	0.92	0.6	0.91	0.68	0.69	0.9	0.69	0.62	-	-	-	1.88	2.75	-
AMS M08170	0.92	0.31	0.78	0.38	0.95	0.66	0.94	0.78	0.77	0.92	0.8	0.65	-	-	-	1.93	2.85	-
AMS M08175	0.77	0.37	0.8	0.41	0.97	0.66	0.94	0.74	0.78	0.88	0.66	0.55	-	-	-	1.93	2.83	-
AMS M31801	0.88	0.33	0.84	0.43	0.97	0.7	0.93	0.75	0.8	0.84	0.71	0.69	-	-	-	1.89	2.76	-
AMS M34528	0.73	0.31	0.73	0.48	0.9	0.65	0.9	0.71	0.74	0.79	0.65	0.56	-	-	-	1.83	2.63	-
AMS M37593	1	0.45	0.83	0.47	1.03	0.68	1.03	0.71	0.72	0.88	0.63	0.56	-	-	-	2.06	2.85	-
AMS M37594	0.83	0.28	0.84	0.37	0.95	0.66	0.96	0.74	0.71	0.88	0.68	0.58	-	-	-	1.93	2.84	-
AMS M37595	0.85	0.33	0.78	0.47	0.93	0.66	0.93	0.69	0.73	0.86	0.64	0.56	-	-	-	1.84	2.77	-
AMS M39443	0.86	0.33	0.85	0.45	1.02	0.71	0.97	0.74	0.74	0.87	0.74	0.54	-	-	-	2	2.85	-
AMS M42732	0.89	0.29	0.81	0.44	0.9	0.62	0.93	0.7	0.68	0.85	0.67	0.59	-	-	-	1.86	2.73	-
UNSWZ 142	0.74	0.4	0.78	0.39	0.94	0.65	0.97	0.76	0.76	0.98	0.74	0.64	-	-	-	1.94	2.94	-
UNSWZ 152	0.92	0.46	0.94	0.55	0.99	0.68	0.94	0.72	0.69	0.91	0.69	0.57	-	-	-	1.96	2.84	-

*Distoechurus pennatus*

Specimen	p2		p3		m1		m2			m3			m4		m1-2 PW	m1-3		m1-4 L
	L	W	L	W	L	PW	L	AW	PW	L	AW	PW	L	AW		L	L	
AMS M02695	1.6	0.67	-	-	1.91	1.13	1.65	1.11	1.09	1.39	0.88	0.75	-	-	-	3.43	4.51	-
AMS M02751	1.54	0.59	-	-	1.83	1.05	1.68	1.12	1.03	1.23	0.88	0.78	-	-	-	3.39	4.69	-
AMS M03294	1.53	0.58	-	-	1.76	1.05	1.59	1.01	1.04	1.27	0.93	0.83	-	-	-	3.39	4.56	-
AMS M03297	1.5	0.6	-	-	1.73	1.11	1.7	1.12	1.08	1.33	0.96	0.84	-	-	-	3.37	4.81	-
AMS M06162	1.63	0.54	-	-	1.86	1.03	1.51	1.05	0.97	1.18	0.86	0.72	-	-	-	3.34	4.6	-
AMS M08170	1.69	0.62	-	-	1.85	1.2	1.76	1.23	1.15	1.4	0.97	0.89	-	-	-	3.59	4.95	-
AMS M08175	1.64	0.53	-	-	1.85	1.01	1.68	1.06	1.01	1.33	0.97	0.83	-	-	-	3.53	4.8	-
AMS M37593	1.41	0.58	-	-	1.89	1.1	1.49	1.06	1.07	1.23	0.91	0.86	-	-	-	3.38	4.57	-
AMS M42732	1.62	0.68	-	-	1.86	1.05	1.73	1.09	1.02	1.3	0.94	0.79	-	-	-	3.59	4.8	-
UNSWZ Dp1	1.41	0.63	-	-	1.73	1.01	1.58	1.08	1.01	1.27	0.92	0.8	-	-	-	3.31	4.48	-
UNSWZ Dp2	1.6	0.58	-	-	2.01	1.11	1.7	1.17	1.03	1.28	0.93	0.78	-	-	-	3.72	4.93	-

**Appendix 3. Characters, character states, and data matrix used in the phylogenetic analyses.****A3.1 Characters and character states used in the phylogenetic analyses, with characters for which states were ordered denoted by an asterisk (i.e., ch. 7, 13, 14, 22).**

1. Metaconid and protoconid on m1 are distinctly separate cusps (0); metaconid and protoconid are completely or almost completely merged on m1, forming a single cusp (1).
2. Paraconid on m1 absent (0); paraconid present (1).
3. Entoconid on m1 absent or barely distinguishable from the entocristid (0); entoconid present and distinct (1).
4. Entoconid is transversely flattened (0); entoconid not transversely flattened, maintains a rounded form (1).
5. Hypoconid and entoconid on m1 are transversely in line or almost in line (symmetrical) (0); entoconid is posteriorly placed relative to the hypoconid (asymmetrical) (1).
6. Paracristid absent (0) paracristid present (1).
7. \*Paracristid runs anterolingually from tip of protoconid (0); paracristid runs anteriorly from tip of the protoconid (1); paracristid runs anterobuccally from the tip protoconid (2). Taxa lacking a paracristid (ch. 6) were scored as inapplicable for the character.
8. Buccal and lingual component of the postprotocristid aligned at a gentle angle in m1 (0); buccal and lingual component of the postprotocristid deflect at a sharp angle (1). (Modified from Woodburne et al. 1987).
9. m1 buccal postprotocristid and lingual postprotocristid form an angle of only slightly less than 90° (0); m1 buccal postprotocristid and lingual postprotocristid form an angle of considerably less than 90° (1). (Modified from Woodburne et al. 1987).
10. Protocristid absent (0); protocristid present (1)
11. Anterolingual surface of the protoconid on m1 forms a flat, shearing, blade-like surface (0); anterolingual surface is rounded (1).
12. m1 premetacristid is strongly developed with the buccal side of the metacristid crest running from the tip of the protoconid down to the metacristid notch and the lingual side of the metacristid running down from the tip the metaconid in an anterobuccal direction to the metacristid notch (0); weakly developed with lingual component of the postprotocristid and metacristid completely merged or almost completely merged (1); absent (2).
13. \*m1 trigonid compressed transversely such that the protoconid is on the lingual half of the tooth (0); protoconid is centrally located on the anterior margin of the tooth (1); trigonid of m1 not compressed transversely with the protoconid placed buccally (2). (Modified from Archer 1984)
14. \*Cristid obliqua on m1 terminates at the metaconid base (0); cristid obliqua terminates between the metaconid and the protoconid (1); cristid obliqua terminates at the protoconid base (2).
15. m1 has a shallow talonid valley (0); m1 talonid valley deep (1).
16. Anterobuccal cingulid present as a small notch on the anterobuccal face of m1 (0); anterobuccal cingulid absent (1).
17. Buccal cingulid present on the buccal side of m1 extending from the base of the protoconid to the base of the hypoconid (0); buccal cingulid absent (1)
18. Posterobuccal cingulid present on m1, extending from the junction between the postentocristid and posthypocristid and around the posterior flank of the hypoconid (0); posterobuccal cingulid absent (1).
19. Metaconid is in line with the protoconid or only slightly posterior (0); metaconid is distinctly posterior to protoconid (1).
20. Posthypocristid is posterolingually directed on m1 (0); posthypocristid is posterolingually directed then lingually deflected (1).
21. Entoconid and hypoconid are same height, or entoconid only slightly smaller (0); entoconid distinctly smaller (1).
22. \*Postmetacristid and entocristid on m1 form a continuous crest, no notch visible at the talonid/trigonid junction (0); gentle notch (1); distinct notch, where the postmetacristid and preentocristid meet at the talonid/trigonid junction (2).
23. m1 cristid obliqua and posthypocristid approximately the same length (0); cristid obliqua almost twice the length of the posthypocristid (1).
24. Transverse crest on m1 entoconid present (1); weak or absent (0).
25. Transverse crest on m1 hypoconid present (1); weak or absent (0).

**A3.2 Data matrix for phylogenetic analyses. Character states: 0, 1, 2, '?' denotes an unknown or inapplicable character.**

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Acrobates pygmaeus</i>	0	0	1	1	0	0	?	?	?	0	1	2	2	1	0	0	0	1	0	1	0	2	0	0	0
<i>Acrobates magicus</i>	0	1	1	1	0	1	0	?	?	0	1	2	2	2	0	0	0	0	0	1	0	2	0	0	0
<i>Acrobates pettitorum</i>	0	0	1	1	0	1	0	?	?	0	1	2	2	2	0	0	0	0	0	1	0	2	1	0	0
<i>Distoechurus pennatus</i>	0	0	0	0	1	0	?	?	?	0	0	2	2	1	0	0	0	1	1	0	1	0	0	0	0
<i>Distoechurus jeanesorum</i>	0	0	1	0	1	1	0	?	?	0	0	0	2	1	0	0	0	0	1	0	0	2	0	0	0
<i>Distoechurus georginae</i>	0	0	1	0	1	1	0	?	?	0	0	2	2	1	0	0	0	0	1	0	1	2	0	0	0
<i>Djaludjangi yadjana</i>	1	0	1	0	0	1	1	1	0	1	?	1	1	0	0	1	1	1	?	1	1	2	1	1	1
<i>Gymnobelideus leadbeateri</i>	1	0	1	0	0	1	1	0	1	1	?	1	0	0	1	0	1	1	?	0	0	1	1	0	0
<i>Petaurus breviceps</i>	1	0	1	1	0	1	1	1	0	1	?	1	1	0	1	0	1	1	?	0	0	2	1	1	0
<i>Dactylonax palpator</i>	1	0	1	0	0	1	2	0	0	1	?	1	0	0	0	0	1	0	1	0	0	2	1	0	0