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A review of the late Cenozoic genus *Bohra* (Diprotodontia: Macropodidae) and the evolution of tree-kangaroos

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Abstract

Tree-kangaroos of the genus *Dendrolagus* occupy forest habitats of New Guinea and extreme northeastern Australia, but their evolutionary history is poorly known. Descriptions in the 2000s of near-complete Pleistocene skeletons belonging to larger-bodied species in the now-extinct genus *Bohra* broadened our understanding of morphological variation in the group and have since helped us to identify unassigned fossils in museum collections, as well as to reassign species previously placed in other genera. Here we describe these fossils and analyse tree-kangaroo systematics via comparative osteology. Including *B. planei* **sp. nov.**, *B. bandharr* comb. nov. and *B. bila* comb. nov., we recognise the existence of at least seven late Cenozoic species of *Bohra*, with a maximum of three in any one assemblage. All tree-kangaroos (Dendrolagina subtribe nov.) exhibit skeletal adaptations reflective of greater joint flexibility and manoeuvrability, particularly in the hindlimb, compared with other macropodids. The Pliocene species of *Bohra* retained the stepped calcaneocuboid articulation characteristic of ground-dwelling macropodids, but this became smoothed to allow greater hindfoot rotation in the later species of *Bohra* and in *Dendrolagus*. Tree-kangaroo diversification may have been tied to the expansion of forest habitats in the early Pliocene. Following the onset of late Pliocene aridity, some tree-kangaroo species took advantage of the consequent spread of more open habitats, becoming among the largest late Cenozoic tree-dwellers on the continent. Arboreal Old World primates and late Quaternary lemurs may be the closest ecological analogues to the species of *Bohra*.

Key words: Australia, New Guinea, Biogeography, Marsupial, Pliocene, Pleistocene, Phylogeny, Adaptation, Extinction

Introduction

Kangaroos and their relatives (Macropodoidea) are the dominant mammalian herbivores of the Australian continent and the most diverse group of marsupial herbivores ever to have evolved. Molecular-clock estimates place the divergence of macropodoids from arboreal phalangeriform (possums) at 55–45 million years (Ma) ago (Meredith *et al.* 2009; Duchêne *et al.* 2018; Cascini *et al.* 2019), whereas a recent total evidence tip-dating analysis (Beck *et al.* 2022) suggests that this occurred more recently (38–29 Ma ago). Currently, there are no known occurrences for any diprotodontian marsupials reported from prior to the late Oligocene (Black *et al.* 2012; Crichton *et al.* 2023). Thus, we know nothing of perhaps the first third of macropodoid evolution, which includes the transition to life on the ground. As macropodines (kangaroos and wallabies) diversified through the late Miocene and Pliocene (Couzens & Prideaux 2018; Cascini *et al.* 2019), tree-kangaroos moved into the trees. Given the comparatively recent nature of this event, and the fact that macropodines are better represented in the fossil record from the late Miocene onward than any other Australian marsupial group (Megirian *et al.* 2010; Prideaux & Warburton 2010), one might expect that a reasonable understanding of the evolution of tree-kangaroos to present a systematic framework and a model for the evolution of the group, including the likely timing and environmental drivers of the shift into the trees.

Tree-kangaroos are among the most fascinating, enigmatic and threatened of all marsupials. The vast majority of what we know about them has come from studies of species within the sole extant genus, *Dendrolagus* Müller, 1840. Two species (*D. bennettianus* DeVis, 1887; *D. lumholtzi* Collett, 1884) occupy well-wooded habitats within a peripheral strip of northeastern Queensland (Martin 2005), while the other eight inhabit the rainforests of New Guinea (Flannery 1990; Eldridge *et al.* 2018). Although tree-kangaroos have been the subject of several taxonomic reviews over the past 80 years (Rothschild & Dollman 1936; Groves 1982; Flannery *et al.* 1996; Martin 2005), improvements in our knowledge of their biology have come slowly, and our understanding of the ecology of most extant species is poor. This is due to a combination of the inaccessibility of their habitats, their arboreal nature, and their increasing rarity. Several species are at serious risk of extinction from habitat destruction and over-hunting (Eldridge *et al.* 2018).

Extant species of *Dendrolagus* range in mean adult body mass from 7.1 kg (female) and 8.6 kg (male) for *D. lumholtzi*, to 10.2 kg (female) and 16.9 kg (male) for *D. inustus* Müller, 1840 (Flannery *et al.* 1996; Martin 2005). Tree-kangaroos today are primarily, if not wholly, selective browsers of dicot material, which, at least in *D. lumholtzi*, may consist of leaves, flowers, fruits, mosses, lichens and ferns (Coombes 2005; Heise-Pavlov 2017). They spend most of their time in the canopy, although *D. mbaiso* Flannery *et al.*, 1995 is purported to spend more time on the ground than its congeners (Flannery *et al.* 1996). Tree-kangaroos mostly hop bipedally when on the ground, but may move quadrupedally when climbing, using their hindlimbs alternately or in unison (Proctor-Gray & Ganslosser 1986; Heise-Pavlov 2017).

The earliest deliberation upon the evolutionary relationships of tree-kangaroos of which we are aware was made by DeVis (1887:13): "Were we to suffer ourselves to be guided by general similarity and a certain resemblance in seating and balancing faculties, we should trace the tree-kangaroo to the rock wallaby, since, superficially considered, the passage from the one into the other may appear of easy accomplishment by insensible degrees." But in the next sentence, DeVis laid out what he believed was the more likely scenario: "it is almost certain that *Dendrolagus* is not a modified *Petrogale*, but stands in the relation of either ancestor or descendant of the kangaroo-rats" (i.e., potoroines) due to the shared presence of a blade-like premolar and small canine. For the next century most authorities leaned toward an alliance between *Dendrolagus* and the New Guinea forest wallabies *Dorcopsis* Schlegel & Müller, 1845 and *Dorcopsulus* Matschie, 1916 (e.g., Bensley 1903; Raven & Gregory 1946; Tate 1948; Kirsch 1977), although by the 1980s, the suspicion had arisen that the oft-mentioned dental similarities (e.g., blade-like premolars, simple low-crowned molars) were actually symplesiomorphies (Archer 1984; Flannery 1989). Since then, results from several molecular studies (e.g., Baverstock *et al.* 1989; Campeau-Péloquin *et al.* 2001; Westerman *et al.* 2002, 2022; Meredith *et al.* 2009; Mitchell *et al.* 2014), our earlier osteological analysis (Prideaux & Warburton 2010), and a total-evidence analysis (Beck *et al.* 2022) have supported a sister relationship between rock-wallabies and tree-kangaroos in the tribe Dendrolagini.

The first palaeontological insights into tree-kangaroos were provided in the early 1980s when several hindlimb elements collected during the late 19th century from the Wellington Caves, central eastern New South Wales, were recognised as belonging to a new genus and species of 'giant' tree-kangaroo, *Bohra paulae* Flannery & Szalay, 1982.

Three further species of *Bohra* were described in the 2000s: *B. wilkinsonorum* Dawson, 2004a from the late Pliocene of southeastern Queensland on the basis of a single maxilla fragment, and *B. illuminata* Prideaux & Warburton, 2008 and *B. nullarbora* Prideaux & Warburton, 2009 from the Pleistocene of south-central Australia on the basis of much of the skeleton. None of these species originate from assemblages indicative of rainforest palaeohabitats, which contrasts with the modern distributions of tree-kangaroo species. Indeed, some of these assemblages point to relatively dry woodland habitats (e.g., Prideaux *et al.* 2007). Nevertheless, it is clear from functional analyses of limb morphology of *B. paulae, B. illuminata* and *B. nullarbora* that they were adapted for climbing trees (Warburton & Prideaux 2010; Warburton *et al.* 2011, 2012).

Using the skeletons of *B. illuminata* and *B. nullarbora* as a guide, we scoured museum collections in search of isolated teeth and bones of fossil tree-kangaroos. Some specimens that we have censused here had hitherto been identified as belonging to tree-kangaroos (Flannery & Archer 1984; Flannery *et al.* 1992; Hocknull 2005a, b; Prideaux & Warburton 2008, 2009), whereas some had been attributed to taxa other than tree-kangaroos, while others had not been identified at all. The main objectives of this paper are to provide: 1) a taxonomic review of all of the fossil material referable to *Bohra*, which includes descriptions of one new species, generic reallocation of two species, and recognition of the tree-kangaroo clade as a discrete taxonomic unit: Dendrolagina subtribe nov.; 2) an osteology-based phylogenetic analysis of tree-kangaroo interrelationships; 3) body-mass estimates for extinct species; and 4) an appraisal of the ecomorphology and evolutionary patterns apparent within the group.

Materials and methods

Abbreviations and timescale

Dentition. Upper teeth are designated by upper case abbreviations (e.g., P3, M2); lower teeth by lower case abbreviations (e.g., i1, m3). Deciduous premolars are denoted by the prefix 'd', e.g., dP2, dp3 (following Luckett *et al.* 1993). L, length; AW, anterior width; PW, posterior width; AH, anterior height; PH, posterior height (as defined in Prideaux 2004). Molar crown height was measured only for minimally worn specimens (i.e., no dentine exposed).

Hindlimb. CL, calcaneus length; CTD, calcaneus tuber depth; CTW, calcaneus tuber width; FC, femur circumference (as defined in Warburton & Prideaux 2010 and below).

Institutions and prefixes. AM F, Palaeontology Collection, Australian Museum, Sydney; AM M, Mammal Collection, Australian Museum, Sydney; AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; ANWC, Australian National Wildlife Collection, Canberra; FMNH PM, Department of Paleontology, Field Museum of Natural History, Chicago; NHMD, Natural History Museum of Denmark, Copenhagen; NMV C, Mammal Collection, Museum Victoria, Melbourne; QM F, Vertebrate Palaeontology Collection, Department of Geosciences, Queensland Museum, Brisbane; SAMA P, Palaeontology Section, South Australian Museum, Adelaide; UCMP, University of California Museum of Paleontology, Berkeley; WAM, Palaeontology Collection, Department of Earth and Planetary Sciences, Western Australian Museum, Perth.

Geological timescale. Geochronologic intervals: late Miocene, 11.63 to 5.33 Ma ago; early Pliocene, 5.33 to 3.60 Ma ago; late Pliocene, 3.60 to 2.58 Ma ago; early Pleistocene, 2.58 to 0.78 Ma ago; middle Pleistocene, 780 to 126 thousand years (ka) ago; late Pleistocene, 126 to 11.7 ka ago; Holocene, 11.7 ka ago to present; late Quaternary, 126 ka ago to present (following Walker & Geissman 2022). Biochronologic intervals (Australian land mammal ages): Tirarian, 4.5 to c. 3 Ma ago; Naracoortean, c. 3 Ma ago to present (Megirian *et al.* 2010). LF, Local Fauna.

Locality information

Here we provide geographic, stratigraphic and chronological information for the localities (Figure 1) that have produced evidence of extinct tree-kangaroos.

Bone Gulch and Fisherman's Cliff, southwestern New South Wales

Bone Gulch (34°11' S, 141°63' E) and Fisherman's Cliff (34°06' S 141°40' E) are located on the northern bank of the Murray River, southwestern New South Wales, c. 10 km west of the junction with the Darling River Anabranch (Gill 1973). The Bone Gulch LF originates from interbedded sands and clays within the Blanchetown Clay (Gill 1973; Marshall 1973), the age of which has been constrained using magnetic polarity stratigraphy to 2.4–1.9 Ma ago (Whitelaw 1991). However, recent luminescence dating suggests a younger age within the early Pleistocene (L. Arnold, pers. comm., 2019). The Fisherman's Cliff LF originates from stratigraphically below the Bone Gulch section, in a zone of normal magnetic polarity, previously suggested on that basis to represent the late Pliocene Gauss Chron (Whitelaw 1991). However, marked faunal similarity between the assemblages suggests a short age gap, which points rather to accumulation within one of the shorter normal-polarity intervals within the Matuyama Chron.

Bow, central eastern New South Wales

The Bow fossil locality (32°07' S, 150°09' E) lies immediately west of Bow Creek on the Merriwa–Cassilis Road, 12 km west of Merriwa in the upper Hunter Valley. The fossil assemblage, which composes the Bow LF, originates from unnamed fluviatile sediments exposed in a road cutting in front of the former Bow Post Office (Skilbeck 1980). The deposit has not been directly dated, but stage-of-evolution biochronology and biocorrelation of the Bow LF with assemblages elsewhere suggest a Pliocene age (e.g., Flannery & Archer 1984; Tedford *et al.* 1992; Dawson *et al.* 1999).



FIGURE 1. Map of Australia and New Guinea showing localities that have produced fossils attributable, or potentially attributable, to species of *Bohra*.

Childers Cove, southern Victoria

Childers Cove (38°29' S, 142°40' E) lies c. 20 km east of Warrnambool on the south coast of Victoria. Fossil vertebrate material, which is largely composed of fragmented bone and isolated teeth, originates from an unnamed sedimentary unit composed of bands of calcareous nodules and gravel in a matrix of silty sand (Rich *et al.* 2006). Currently under study by Lisa Nink (Flinders University), the Childers Cove LF is largely undescribed and undated, but provisional biocorrelation with other assemblages has been interpreted to suggest a late Pliocene or early Pleistocene age (Rich *et al.* 2006).

Curramulka Quarry, Yorke Peninsula, South Australia

Several decades of mining operations in Curramulka Quarry, located on the southern edge of Curramulka (34°41' S, 137°42' E), central Yorke Peninsula, have episodically exposed sediment-filled fissures within the limestone, at least some of which contain vertebrate fossils (Pledge 1992). One fissure fill, RF95, was discovered, prospected and screened for fossils by James McNamara (South Australian Museum) in the mid-1990s. The fauna from this undated deposit is largely undescribed, but those taxa that have been identified to species level have predominantly Pleistocene records elsewhere (Prideaux 2004). The exception is the megapode *Garrdimalga mcnamarai*, which is known only from RF95 (Shute *et al.* 2017).

Darling Downs, southeastern Queensland

Many creeks and rivers across the Darling Downs region of southeastern Queensland cut through older fluviatile deposits that have produced late Cenozoic vertebrate remains (Bartholomai 1976a; Molnar & Kurz 1997).

Chinchilla. Chinchilla is a small town in the western Darling Downs. It lends its name to a region from which vertebrate fossils have been collected since the 19th century. Although the exact stratigraphic and geographic provenance of most fossils collected before the 1960s is uncertain (Bartholomai 1963, 1975), most are believed to have originated from the Chinchilla Sand, a series of fluviatile deposits representing multiple depositional episodes exposed along the Condamine River (Bartholomai & Woods 1976; Louys & Price 2015). The main locality prospected for fossils since the mid-20th century is composed of a series of gullies within the bounds of the Chinchilla Rifle Range (26°48' S, 150°41' E), which is located on the north bank of the Condamine River at Chinchilla (Wilkinson *et al.* 2021). The Chinchilla Sand has not been directly dated, but stage-of-evolution biochronology and biocorrelation of the Chinchilla LF with assemblages elsewhere suggest a late Pliocene age (e.g., Tedford *et al.* 1992; Dawson *et al.* 1999; Louys & Price 2015).

Darling Downs (site not specified). Fossil deposits of late and presumably also middle Pleistocene age occur across the Darling Downs (Bartholomai 1976a; Molnar & Kurz 1997). However, much of the material in the 'Old Collection' of the Queensland Museum was collected in the late 19th century and has no site provenance data associated with it.

New Kalamurina, Warburton River, South Australia

New Kalamurina (UCMP V72058; 27°43' S, 138°14' E) is located on the Warburton River in the eastern Lake Eyre Basin. The site has not been directly dated, but the Katipiri Formation, from which the assemblage originates, is considered to be of middle to late Pleistocene age (Nanson *et al.* 2008).

Speaking Tube Cave, Mount Etna, eastern Queensland

Fossil-bearing infill sediments in the Speaking Tube Cave system were intersected by quarrying operations on the western side of Mount Etna (23°09'S, 150°27'E), near Rockhampton, in the early 21^{st} century (Hocknull 2005b). Units C–D are of middle Pleistocene age, with a maximum age of 326 ± 22 ka provided by uranium–thorium dating of an underlying flowstone (Hocknull *et al.* 2007).

Stirton Quarry and SAM Hill, Lake Kanunka, South Australia

The Pompapillina Member of the Tirari Formation crops out near the northern end of a dissected escarpment on the western side of Lake Kanunka (28°46' S, 138°25' E) in the eastern Lake Eyre Basin (Tedford *et al.* 1992). The main fossil site is Stirton Quarry (= Lake Kanunka Site 1, UCMP V5772), which is excavated into the eastern end of the UC Hill bluff. The channel fill also runs through the adjacent, isolated SAM Hill (= Lake Kanunka Site 2, UCMP V5773). Fossils are typically sourced as float on the surface of SAM Hill and in the intervening saddle (Tedford *et al.* 1992). This assemblage is the Kanunka LF, one of Australia's two most diverse Pliocene vertebrate assemblages, along with the Chinchilla LF (Prideaux & Tedford 2012; Louys & Price 2015). Its age is considered to be late Pliocene, possibly around 3.6 Ma, according to magnetostratigraphy and biocorrelation (Tedford *et al.* 1992).

Thylacoleo Caves, Nullarbor Plain, Western Australia

Three caves discovered in 2002 in the one area of the central Nullarbor Plain (31°26'S, 127°56'E) are known collectively as the Thylacoleo Caves, and have produced remains of a diverse range of vertebrate species (Prideaux

et al. 2007). Many are represented by associated or articulated skeletons. Two of the caves have produced specimens of tree-kangaroos.

Leaena's Breath Cave. Fossils collected from this cave between 2002 and 2014 originated from atop or within the interstitial spaces between boulders, and atop or entombed within infill sediments. Uranium–thorium dating of calcite crusts on cave-floor specimens and optically stimulated luminescence dating of infill sediments suggest accumulation in the middle Pleistocene (Prideaux *et al.* 2007).

Last Tree Cave. Fossils collected from this cave between 2002 and 2014 originated from atop or between boulders and within sediment formed within the cave from limestone breakdown. Similarities in species composition with the other Thylacoleo Caves assemblages suggest a similar age (Prideaux *et al.* 2007).

Awe Localities, Papua New Guinea

A series of fossil localities are known within the late Pliocene Otibanda Formation, which crops out along the Watut and Bulolo Rivers, in the Upper Watut and Bulolo Valleys, respectively (Plane 1967; Hoch & Holm 1986). Potassium–argon dating of a sample of pyroclastic rock collected by Ella Hoch in 1983 from an outcrop of the Otibanda Formation on the eastern bank of the river, 200–300 m downstream from Awe Fauna Type Locality, i.e., close to Watut 3, has produced an age of 2.9 ± 0.4 Ma (Hoch & Holm 1986). This falls close to the boundary of the Tirarian and Naracoortean land mammal ages (Megirian *et al.* 2010). Due to erosional changes to the landscape between 1963 and 1983, it was not possible to relate the stratigraphic origin of the dating samples to the section sampled by Plane (E. Hoch, pers. comm., 8 September 2016).

Awe Fauna Type Locality. The Awe Fauna Type Locality (= Watut 1, UCMP V6234) is located on the Watut River (7°13' S, 146°32' E), near Yauwipu, in a "blue to grey claystone on a cliff about 20 feet above the western bank of the Watut River" (Plane 1967: 63).

Charlie Lawrence Locality. Before becoming submerged by a pond, Charlie Lawrence Locality (UCMP V6172) was located on the lower stretch of Wiganda Creek, near its confluence with the Watut River, a few hundred metres west of Awe Fauna Type Locality and Watut 3 (Plane 1967).

Watut 3. Watut 3 (UCMP V6356) lies around 500 m northeast and downstream of the Awe Fauna Type Locality, on the eastern bank of the Upper Watut River (Plane 1967).

Widubosh Goldmine. Widubosh Goldmine (7°06' S, 146°36' E) is located on the Bulolo River, c. 10 km north of Bulolo.

Wellington Caves, central eastern New South Wales

The Wellington Caves (32°36' S, 148°55' E) are located 6 km south of Wellington, and 1 km east of the Bell River, on the western slopes of the Great Dividing Range. Several of the caves contain vertebrate fossil deposits, two of which, Cathedral and Mitchell (= Breccia) Caves, were first sampled 190 years ago (Dawson 1985). Tree-kangaroo remains have originated from at least three deposits within the Wellington Caves.

Big Sink Doline. Pale red-orange, consolidated sediments adhering to the south wall of the Big Sink doline comprise the Big Sink unit (Osborne 1997). The deposit has not been directly dated, but stage-of-evolution biochronology and biocorrelation of the Big Sink LF with dated assemblages elsewhere suggest a Pliocene age (Dawson *et al.* 1999).

Cathedral Cave. Fossil-bearing infill sediments in the floor of the main chamber have been the subject of several excavations, beginning with Sir Thomas Mitchell in 1830 (Dawson 1985). The stratigraphic origins of most specimens collected in the 19th century were not recorded, but Ramsay's Shaft No. 2, positioned in the alcove south of the 'Altar' (a large calcite column) in the main chamber, produced much of the larger fossil material collected in 1881 (Ramsay 1882). Optically stimulated luminescence of sediments and radiocarbon dating of charcoal samples from the upper 4.2 m of the sequence accumulated during two intervals: from c. 72 to 38 ka ago and from 7 ka to 400 years ago (Fusco *et al.* 2023). However, no reliable dates exist for the lower part of the sequence, and its age may extend into the middle Pleistocene.

Bone Cave / **Phosphate Mine.** The largest and most complex cave at Wellington is the Bone Cave / Phosphate Mine system. It contains multiple chambers filled with fossil-bearing infill sediments referable to several different stratigraphic units. Excluding the Pliocene Big Sink and Koppa's Pool deposits, which were not excavated until the late 20th century, the remaining sediments are considered to be of Pleistocene age. An early Pleistocene age has been suggested for the Bone Cave deposit (Dawson 1995; Dawson & Augee 1997), but no dates have yet been published.

Wellington Caves (site not specified). Fossil deposits of early Pliocene through Holocene age occur within

the Wellington Caves complex (Dawson & Augee 1997; Dawson *et al.* 1999). However, much of the material in the 'Old Collection' of the Australian Museum has no site provenance data associated with it (Dawson 1985). Most of this material likely originates from the Pleistocene deposits of Cathedral and Mitchell Caves, where much of the 19th century collecting was focused. No fossils are known to have been collected from either of the two recognised Pliocene deposits until the late 20th century (Dawson *et al.* 1999; Nipperess 2000).

Tunnel Cave, southwestern Western Australia

Tunnel Cave (34°05' S, 115°02'E) in the Leeuwin–Naturaliste region of southwestern Australia contains a late Pleistocene–Holocene archaeological deposit (spanning 22–4 ka ago), which preserves a diverse vertebrate assemblage (Dortch 2004). Vertebrate species have been identified from both morphological analysis of skeletal material and ancient DNA retrieved from morphologically nondescript scraps of fossil bone (Murray *et al.* 2013).

Nomenclature and mensuration

Description style, terminology and mensuration follow Murray (1995), Wells & Tedford (1995), Prideaux (2004), Prideaux & Warburton (2008, 2009, 2010), Warburton & Prideaux (2010, 2021), and Nomina Anatomica Veterinaria (2017). Line drawings of diagnostically key elements with anatomical features annotated are presented in Figs 2–10 for *Dendrolagus bennettianus*, a representative modern tree-kangaroo.

Serial designation of the cheek dentition follows Flower (1867) and Luckett (1993). All measurements (Tables 1–7) are in millimetres and were taken with Mitutoyo digital callipers (Kawasaki, Japan). Femur circumferences used for body-mass calculations were measured by wrapping a piece of string around the shaft, immediately below the distal edge of the m. quadratus femoris tubercle, marking the string with a pen where the ends overlapped, and then straightening out the string and measuring the distance between the marks to the nearest millimetre. Dentary depth and width are measured below the abutment of m2 and m3.

Taxonomic review structure

Synonym list. Junior synonyms, alternative attributions, misspellings, identifications made only to genus level (for species), and/or nominal combinations different from those proposed here.

Type specimens. Specimens in the type series and who collected them and when (if known).

Type locality. Brief information on the origin of the holotype. More detailed information on all localities producing remains of species of *Bohra* is presented in 'Locality information'.

Referred specimens. A list of specimens ordered by site, and a basic description of each. The terms 'juvenile' and 'adult' are only an approximate guide to ontogenetic age; a fully erupted dentition, closed sutures and/or fused epiphyses are considered to indicate 'adultness'.

Diagnosis. An ensemble of osteological features that allow a species to be differentiated from those that it might most readily be confused with, including unique traits, proportional differences and/or a unique combination of traits known individually in other species.

Description and comparisons. A description followed by a comparison with other taxa, organised element by element. Because each species of *Bohra* is known from so few specimens, most element descriptions pertain to only one specimen. However, in those few cases where n > 1, we reflect on any variation observed within the description. Descriptions are not included for elements for which adequate published descriptions exist. However, we do present new images of many specimens for which photographs have previously been published at a lower resolution or in grayscale.

Remarks. A synthesis of information composed of one or more of the following: consideration of the grounds for element associations or the referral of specimens to a species; deductions about localities; inferences about geographic distribution; taxonomic implications of placement within *Bohra*; and reflections on past analyses of key specimens.

Photography

Most specimens were photographed at Flinders University by Grant Gully using a Visionary Digital LK imaging system (Dun, Inc.) with a Canon EOS 5DSR camera coupled with either a Canon EF 100 mm or 65 mm f2.8 IS USM macro lens. Multiple images were compiled into a single image using Zerene Stacker 1.04 software. Other specimens were photographed with a standard DSLR camera or phone.

Phylogenetic analysis

The phylogenetic analysis largely re-uses the matrix of Prideaux & Warburton (2010), but with additional tree-kangaroo and rock-wallaby species included and some taxa deemed superfluous for this study excluded (e.g., *Ngamaroo archeri, Sthenurus andersoni, Macropus pavana*), on the grounds that they would otherwise represent extra species in parts of the tree that are not in focus here. The sole extant member of the macropodoid family Hypsiprymnodontidae (*Hypsiprymnodon moschatus* Ramsay, 1875) is the outgroup. We also included *Watutia novaeguineae* Flannery *et al.*, 1989, which was not included in the prior analysis. Character states for species were scored from direct observation of specimens, with the exception of *Bulungamaya delicata* Flannery *et al.*, 1983a and *Ganguroo robustiter* Cooke *et al.*, 2015. These taxa occupy the same relative positions in the analysis as *Nowidgee matrix* Cooke, 1997 and *Ganguroo bilamina* Cooke, 1997 do in Prideaux & Warburton (2010), but *N. matrix* has subsequently been recognised as a junior synonym of *B. delicata* (Travouillon *et al.* 2014), while postcranial material previously referred to *G. bilamina* (Kear *et al.* 2001) has since been shown to belong to *G. robustiter* (Cooke *et al.* 2015).

A total of 85 osteological characters were chosen, 50 craniodental and 35 postcranial (Appendix 1). Most characters and states are the same as those used in Prideaux & Warburton (2010), but some are new and others have been deleted because they were poorly defined or uninformative in light of the adjusted taxonomic composition of the matrix. In addition, states for several have been refined and mis-scorings for some taxa have been corrected.

Characters are unweighted and unordered, except for characters 1, 3, 14, 25, 53, 62, 64, 67, 76 and 78, which we hypothesise are morphoclinal and are, therefore, ordered in the phylogenetic analysis. The character matrix (Appendix 2) was assembled in Winclada (Nixon 2002), exported as a Nexus file and then subjected to heuristic parsimony analysis in PAUP4.0a150 (Swofford 2002) using standard settings, tree bisection–reconnection (TBR) branch swapping, 1,000 random addition replicates per search, and no character-state optimization. When discussing synapomorphies, we use the qualifier 'unique' to indicate that a character state change occurs nowhere else on the tree, and 'homoplastic' to indicate that attainment of a particular state typifies more than one clade due to character reversal or parallelism. Synapomorphies identified are common to both Accelerated and Delayed Transformation optimisation. Branch-support values were calculated using bootstrap analyses in PAUP using heuristic searches (1,000 replicates, maxtrees 4,000).

Body-mass estimates

Dimensions of load-bearing bones are often tightly positively correlated with body mass in terrestrial vertebrates, both within and between species (Anderson *et al.* 1985; Anyonge 1993; Reynolds 2002). One common measure is femur circumference, which has previously been used to estimate body mass in some large extinct macropodids (Helgen *et al.* 2006), and thus can be used for estimating body mass in fossil tree-kangaroos. We also explored the potential of the calcaneus for predicting body mass, partly because of its pivotal role in both locomotion and weight bearing in macropodids (Marshall 1974), and also because calcanei have a higher frequency in the fossil record than most skeletal elements due to their robustness.

Here we compiled a dataset for extant macropodines to create predictive equations and model body mass in extinct species. One femoral and three calcaneal dimensions were collected from adult macropodine specimens (n = 63; 23 species) of known body mass available in Australian wildlife collections (Table 9). Adult status was determined on the basis of cranial suture closure, dental eruption and/or limb-bone epiphyseal fusion. We generated two separate regressions, one based on a tree-kangaroo-only sample (n = 14; six species) and the other on the entire macropodine sample.

Two- and three-dimensional calcaneal variables were generated from linear measurements (CL \times CTW; CL \times CTD; CL \times CTD \times CTW). Body-mass and both calcaneal and femoral measurements were logarithmically

transformed (\log_{10}) to improve the 'fit' of data to regression lines. To model relationships between body mass and each variable we applied the least-squares regression method to datasets using the following equation:

 $\log_{10}(M_{est}) = m(\log_{10}\text{measurement}) + c$

where M_{est} = body-mass estimate, m = regression coefficient and c = y-intercept. Coefficient of determination (r^2) and p values were identified for each slope.

We determined the regression coefficient and y-intercept for each regression (Table 10) and then used these values to predict M_{est} for each extinct tree-kangaroo specimen by entering the transformed variable into the relevant equation. From an assessment of the scaling of the predictor variable in extant tree-kangaroo specimens, it is reasonable to assume that scaling will be similar for the extinct tree kangaroos. Logarithmically transformed values were then retransformed $(10^{[\log 10(Mest)]})$ to actual values of predicted body-mass estimates in kg (Table 11). To correct for biasing introduced by logarithmic transformation, we derived a 'smearing estimator' using a ratio estimator (RE), which was calculated as mean observed mass values \div mean retransformed predicted mass values (Table 10; for further details see Smith 1993). Corrected mass estimates were determined by multiplying RE and the retransformed mass estimate (i.e., corrected $M_{est} = \text{RE} \times M_{est}$).

Results

Systematic palaeontology

Diprotodontia Owen, 1877

Phalangeriformes Szalay, 1982 sensu Woodburne, 1984

Macropodidae Gray, 1821

Macropodinae Gray, 1821

Dendrolagini Flannery, 1989

Dendrolagina subtribe nov.

Included genera. Bohra Flannery & Szalay, 1982; Dendrolagus Müller, 1840 (tree-kangaroos).

Diagnosis. Distinguished from other members of the Dendrolagini by the following combination of skeletal features: robust cranial rostrum; broader than deep occiput; absence of large palatal fenestrae; slightly broadened I1; broad lingual cingulum on P3; low-crowned molars; fine, low postprotocrista on upper molars; masseteric canal extends to posterior cheek teeth and separate from dental canal; posterobuccal eminence on main crest of p3; rectus femoris origin positioned immediately adjacent to acetabular rim; short, broad iliopubic process; medially displaced quadratus femoris scar; short, broad calcaneus with posteromedially expanded, dorsoventrally compressed tuber calcanei; large, medially expanded sustentaculum tali, extending far beyond the medial margin of the articular facets; relatively large, transversely broad calcaneofibular ligaments; relatively broad calcaneocuboid articulation; transversely broad, short, dorsoventrally compressed talus with shallow trochlea; relatively short, transversely broad, dorsoventrally compressed metatarsals IV and V.



FIGURE 2. Cranium (adult) of *Dendrolagus bennettianus* (QM JM19863). Note that all incisors except for the left 11 are missing, as are the left and right C1 and right P3. The posterior root of the right dP2 remains in place. A: left lateral view. B: dorsal view. C: palatal view. D: anterior view. E: posterior view. BOC, basioccipital; BSP, basisphenoid; BUF, buccinator fossa; EAM, external auditory meatus; ECT, ectotympanic; EGP, ectoglenoid process; EOR, eye orbit; FOM, foramen magnum; FRO, frontal; GLF, glenoid fossa; IBP, incisor-bearing portion of premaxilla; IFO, incisive foramen; INP, interparietal; IOF, infraorbital foramen; JUG, jugal; LAC, lacrimal; MAP, masseteric process; MAX, maxilla; MPO, medial pterygoid origin; MPP, mastoid process of the periotic; MPS, maxilla–palatine suture; MVC, median vertical crest; NAP, narial aperture; NAS, nasal; NCD, neurocranial dome; NUC, nuchal (lambdoid) crest; OCC, occipital condyle; PAL, palatine; PAR, parietal; PGP, postglenoid process; PLF, posterior lacerate foramen; TEC, temporal crest; UVP, upright (vertical) portion of premaxilla; ZPS, zygomatic process of the squamosal.



FIGURE 3. Dentary (left, adult) of *Dendrolagus bennettianus* (QM JM19863). A: lateral view. B: mesial view. C: occlusal view. AMC, alveolar margin of the cheek-tooth row; AMF, anterior mental foramen; APR, angular process; ARA, anterior root of ascending ramus; ARM, anteroventral rim of masseteric fossa; BUS, buccinator sulcus; COP, coronoid process; DIA, diastema; DIE, digastric eminence; DIS, digastric sulcus; HOR, horizontal ramus; ILP, insertion for the lateral pterygoid muscle; IMF, inferior mandibular foramen; ISM, insertion area for the internal superficial masseter muscle; MAC, mandibular condyle; MAF, masseteric fossa; MFO, masseteric foramen; MHG, mylohyoid groove; MNO, mandibular notch; MPF, medial pterygoid fossa; MSP, mandibular symphyseal plate; PAS, postalveolar shelf.



FIGURE 4. Cheek-tooth rows of *Dendrolagus bennettianus* (QM JM19863) in stereo occlusal view. A: left P3, M1–4. B: right p3, m1–4.



FIGURE 5. Humerus (right, adult) of *Dendrolagus bennettianus* (QM JM19863). A: cranial view. B: medial view. C: caudal view. D: lateral view. E: proximal view. F: distal view. CAP, capitulum; COF, coronoid fossa; DEL, deltoid crest; GRT, greater (lateral) tubercle; HHE, humeral head; ITG, intertubercular (bicipital) groove; LET, lesser (medial) tubercle; LEP, lateral epicondyle; MEP, medial epicondyle (missing epiphysis); MLD, insertion of m. latissimus dorsi; MPE, insertion of m. pectoralis superficialis; OLF, olecranon fossa; RAF, radial fossa; SCF, supracondylar foramen; SCR, (lateral) supracondylar ridge; TRO, trochlea.



FIGURE 6. Innominate (right, adult) of *Dendrolagus bennettianus* (QM JM19863). A: dorsolateral view. B: ventrolateral view. C: ventromedial view. D. dorsomedial view. ACE, acetabulum; AUS, auricular surface; GLF, gluteal fossa; ICT, iliocotylar tubercle; ILB, iliac body; ILC, iliac crest; IPE, iliopubic eminence; IPR, ishiopubic ramus; ISC, ischiocotylar tubercle; ISD, descending ramus of ischium; IST, ischiatic tuberosity; LCI, lateral crest of the ilium; OBF, obturator foramen; PCT, pubocotylar tubercle; PUS, pubic symphysis; RET, tubercle of the m. rectus femoris.



FIGURE 7. Femur (right, adult) of *Dendrolagus bennettianus* (QM JM19863). A: cranial view. B: caudal view. C: medial view. D: lateral view. E: proximal view. F: distal view. AFO, fossa for m. adductors; FHE, femoral head; FTR, femoral trochlea; GTR, greater trochanter; ICF, intercondylar fossa; ITF, intertrochanteric fossa; LCO, lateral condyle; LEP, lateral epicondyle; LTC, lateral trochanteric crest; LTR, lesser trochanter; LSF, lateral supracondylar fossa (for m. flexor digitorum superficialis); MCO, medial condyle; MEP, medial epicondyle; MSF, medial supracondylar fossa (for m. gastrocnemius); TQF, tubercle for m. quadratus femoris.



FIGURE 8. Tibia (right, adult) of *Dendrolagus bennettianus* (QM JM19863). A: cranial view. B: caudal view. C: medial view. D: lateral view. E: proximal view. F: distal view. DFF, distal fibular facet; ICE, intercondylar eminence; IOB, interosseous border; LCO, lateral condyle; LFO, lateral fossa; MCO, medial condyle; MMA, medial malleolus; PFF, proximal fibular facet; TAS, talar articular surface; TCR, tibial crest.



FIGURE 9. Calcaneus and talus (right, adult) of *Dendrolagus bennettianus* (QM JM19863). Calcaneus (A–E). A: dorsal view. B: plantar view. C: medial view. D: cranial view. E: lateral view. Talus (F–K). F. plantar view. G: medial view. H: dorsal view. I: caudal view. J: lateral view. K: cranial view. AHN, head of talus (articular facet for navicular); APT, anterior plantar tuberosity; ATF, anteromedial facet for head of talus; CFA, articular facet for cuboid; CPS, calcaneal plantar surface; DMF, dorsomedial facet of calcaneal-cuboid articulation; DLF, dorsolateral facet of calcaneal-cuboid articulation; FGS, flexor groove of sustentaculum tali; FIB, fibular articular surface; FIL, tubercles for fibular ligaments; LCS, lateral calcaneal facet; LTF, lateral facet for talus; LTC, lateral trochlear crest; MCF, medial calcaneal facet; MFO, malleolar fossa; MMA, medial malleolus; MTC, medial trochlear crest; MTF, medial facet for talus; PVP, posteroventral process; STA, sustentaculum tali; TCA, tuber calcanei; TCE, epiphysis of tuber calcanei; TPS, transverse plantar sulcus; TRO, trochlea (talo-crural joint); VMF, ventromedial facet of calcaneal-cuboid articulation.



FIGURE 10. Metatarsals (right, adult) of *Dendrolagus bennettianus* (QM JM19863). Metatarsal IV (A–D). A: dorsal view. B: plantar view. C: medial view. D: lateral view. Metatarsal V (E–H). E: dorsal view. F: plantar view. G: medial view. H: lateral view. CUB, articular facet for cuboid; FCL, fossa for collateral ligaments; HMT, head of metatarsal; MIIIF, articular facet for metatarsal III; MIVF, facet for metatarsal IV; MVF, articular facet for metatarsal V; PLP, proximolateral process; PSF, facet for plantar sesamoid (proximal plantar process); IOC, crest for interosseous ligaments; IOS, sulcus for interosseous ligaments.

Bohra Flannery & Szalay, 1982

Type species. Bohra paulae Flannery & Szalay, 1982.

Revised diagnosis. Species of *Bohra* are distinguished from those of *Dendrolagus* based on the following craniodental features: larger check teeth relative to the size of the cranium; higher-crowned upper incisors; narrower P3, which lacks a large, distinct posterobuccal accessory cusp and deep cleft posterior to the anterior cusp of the main crest; relatively narrower molars, with a better developed postparacrista and no parametacristid. All known species of *Bohra* are also larger than those of *Dendrolagus*. *Bohra* most closely resembles *Dorcopsis* and *Watutia* in molar morphology, but the premetacristid, cristid obliqua and postprotocrista are less developed than in *Dorcopsis*, and the molars are narrower relative to their length than in *Watutia*.

Species of *Bohra* may be distinguished from those of *Dendrolagus* on the basis of the following postcranial features: slightly less robust humerus, with a more pronounced pectoral crest, a slightly less developed deltoid tubercle, and a larger, more projecting medial epicondyle; relatively more robust femoral diaphysis; less sinuous tibial diaphysis with a relatively longer distal fibular facet; less obliquely orientated trochlear crests and groove on the talus; shorter and more robust metatarsals IV and V.

Etymology. According to a legend of the Euahlayi people of inland eastern Australia, *Bohra* was a kangaroo that went about on four limbs and possessed canines before men removed them (Parker 1953). Flannery & Szalay (1982) considered this evocative of extant tree-kangaroos, which have relatively more equally proportioned foreand hindlimbs and retain small canines. They did not designate a gender, but with the naming of *B. illuminata*, Prideaux & Warburton (2008) inferred that it was feminine.

Temporal and geographic distribution. Late Pliocene of southeastern Queensland, central eastern New South Wales, northern South Australia, and Papua New Guinea. Early and/or middle Pleistocene of central eastern New South Wales and southern South Australia. Middle Pleistocene of eastern Queensland, southeastern Western Australia and northern South Australia. See Figure 1.

Bohra paulae Flannery & Szalay, 1982

Bohra pauli: Dawson (2004a), p. 271, table 1; lapsus calami.

Holotype. AM F62099 / AM F62100, right adult calcaneus and talus. The holotype was originally based solely on the calcaneus (AM F62099); the talus was listed and described separately as a referred specimen (AM F62100). However, given their precise anatomical fit and similar preservation, it is beyond reasonable doubt that these two elements belong to the same individual.

Type locality. Wellington Caves (site not specified), New South Wales. No specific locality or collection details are associated with the holotype of *B. paulae*. However, the type locality is very likely a Pleistocene deposit (see 'Locality information').

Referred specimens. Cathedral Cave, Wellington Caves. AM F62101, left tibia. AM F62102, left tibia (proximal half). Collected by Henry Barnes of the Australian Museum in 1881 (Ramsay 1882). The stratigraphic origins of the tibiae are unknown, but Ramsay's Shaft No. 2, positioned in the alcove south of the 'Altar' formation in the main chamber, evidently produced much of the larger fossil material collected from Cathedral Cave in 1881 (Ramsay 1882).

Wellington Caves (site not specified). AM F103802, adult right metatarsal V. AM F104075, left juvenile metatarsal IV. AM F104092, adult right metatarsal V. AM F104550, juvenile left metatarsal IV. These specimens are part of the 'Old Collection' of the Australian Museum (Dawson 1985), and probably originate from a Pleistocene deposit based on the same line of reasoning as for the holotype.

Etymology. Named in honour of Flannery & Szalay's draftsperson Paula Kendall.

Revised diagnosis. A large species of *Bohra*, closest in size to *B. wilkinsonorum* in calcaneal dimensions. The species is distinguished by the following combination of calcaneal features: dorsal half of tuber calcanei barrel-shaped; plantar aspect less flared posteriorly, particularly laterally, than in the similarly large *B. wilkinsonorum*; medial and lateral talar facets of calcaneus continuous anteriorly but with facet contours distinct; calcaneocuboid articulation transversely broad, with step between dorsal facets smoothed, and confluent with ventromedial facet;

talar and cuboid articular surfaces separated by short distance. The talus is distinguished from that of other species of *Bohra* by having a shallow trochlear groove that is slightly deeper medially, and a very short talar neck. The tibia is relatively more robust than in *B. illuminata* and *B. nullarbora*, particularly distally. The metatarsals IV and V are more robust than those of *B. illuminata* and *B. nullarbora*, and the metatarsal IV diaphysis is proportionally deeper anteriorly than in *B. nullarbora*.

Description and comparisons. Tibia. The tibia of *B. paulae* (Figure 11) is significantly larger (Table 8) and more robust than that of *B. illuminata* and is more similar to species of *Dendrolagus* (Figure 8) in its stockiness. Other aspects of its morphology, including the relative size of the anterior tibial crest (Figure 8A), the curvature of the shaft, and the length of distal fibular facet (Figure 8B) are similar between *B. paulae* and *B. illuminata*, although the proximal fibular facet (Figure 8D) is more pronounced in *B. paulae*. The tibial crest is shorter and the lateral fossa for m. tibialis cranialis (Figure 8D) is deeper in both *B. paulae* (Figure 11) and *B. illuminata* than in species of *Dendrolagus*. Caudolaterally, the interosseous border of the tibia is more sinuous than that of *B. illuminata* and *B. nullarbora*, but less so than in species of *Dendrolagus*. The tibial diaphysis is more flared distally than in *B. illuminata* and *B. nullarbora*. The distal articular surface of AM F62101 has sustained significant post-mortem damage from rodent gnawing (Figure 11F), but the relatively short medial malleolus reflects the corresponding morphology of the talus.

Calcaneus. The plantar surface of the holotype calcaneus was evidently expanded posteromedially, but the specimen is abraded in this area (Figure 12B). It is also abraded on the lateral side (Figure 12C), but the contour of the surrounding bone allows us to infer that it was flared to a lesser degree than in *B. wilkinsonorum* (Figure 20A–B). Indeed, the tuber calcanei of *B. paulae* is distinctly barrel-shaped in dorsal view (Figure 12A), and not as constricted anteriorly as in other tree-kangaroo species. Otherwise, the calcaneus is similar in general proportions and size to that of *B. wilkinsonorum* (Table 8). The distance between the talar and cuboid facets is even shorter in *B. paulae* than in other tree-kangaroos, e.g., *D. bennettianus* (Figure 9A). Although extended medially, the sustentaculum tali is relatively short, not extending as far posteriorly as in other tree-kangaroo species (Figure 9A–B). The plantar surface is flat, only slightly rugose, and very broad anteriorly (Figure 12B). The non-rugose flexor groove is shallow and wide, but not as wide as in *D. lumholtzi* (Figure 9B).

The medial and lateral talar facets in *B. paulae* are broadly continuous (Figure 12B, E) and more smoothed than in *D. bennettianus* (Figure 9A), *D. lumholtzi*, *B. illuminata* and *B. nullarbora*. The lateral facet is only slightly tapered mesially, and the medial facet is large, ovoid and almost transverse in alignment (Figure 12A). The calcaneocuboid articulation is relatively shallow, and the characteristic macropodid 'step' between the medial and lateral facets is not much more than an undulation (Figure 12B, E, H; cf. Figure 9A). The ventromedial facet is broad and completely continuous with the medial and lateral facets (cf. Figure 9D). Overall, the cranial end of the calcaneus closely resembles that of *D. lumholtzi*. The sulcus for the m. flexor digitorum longus is short and narrow compared with all other species (cf. Figure 9B).

Talus. The talus of *B. paulae* is short and wide, but the medial crest is moderately high and steep, and the lateral crest is low and broad, resulting in a moderately shallow but asymmetrical trochlear groove (Figure 12H, J). This marked asymmetry in crest contour is similar to that observed in *D. lumholtzi*, but less so in *D. bennettianus* (Figure 9H, K) and other species of *Bohra*, where the crests are more equally pronounced. The talar neck is very short (Figure 12K, N, L), shorter in fact than in all other tree-kangaroos for which the talus is known (e.g., Figure 9H). The navicular facet is slightly deeper relatively than that of *D. lumholtzi*, and most similar to that of *D. bennettianus* (Figure 9K). The malleolar fossa is broad and shallow in comparison to the conditions observed in *B. nullarbora*, *D. bennettianus* and the species of *Dorcopsulus*, *Petrogale* Gray, 1837, *Setonix* Lesson, 1842 and *Thylogale* Gray, 1837. The posteroventral process is similar in its posterior extension to the condition observed in *B. illuminata*, *B. nullarbora*, *D. lumholtzi* and *D. bennettianus* (Figure 9G), but more extended than in *B. planei* (Figure 33J).

Metatarsals. Two juvenile metatarsal IV specimens are referred to *B. paulae* (Figure 13A–J) on the basis of their overall proportions and relative robustness, and the transversely wide, conjoined articular facet for metatarsal V, as in species of *Dendrolagus* (Figure 10B). AM F104075 is more robust and slightly shorter, and has a broader, more posteriorly restricted plantar ridge compared with AM F104550. Otherwise, they are very alike and morphologically distinct from the *B. illuminata* holotype metatarsal IV, which is also not fully grown and missing the distal epiphysis, and from the *B. nullarbora* holotype metatarsal IV, which is fully grown and has a fused distal epiphysis. The proximal articular facet for the cuboid is convex dorsally, while the peninsula of the cuboid facet that extends ventrally onto the posterior face of the plantar tuberosity is concave (Figure 13E, J). In comparison, the dorsolateral



FIGURE 11. Tibia of *Bohra paulae*. AM F62102, left adult tibia (A–F). A: cranial view. B: caudal view. C: medial view. D: lateral view. E: proximal view. F: distal view. AM F62101, partial left adult tibia (G–J). G: cranial view. H: caudal view. I: medial view. J: lateral view.



FIGURE 12. Calcaneus and talus (right, adult) of the holotype of *Bohra paulae* (AM F62099–F62100). Calcaneus (A–E). A: dorsal view. B: plantar view. C: medial view. D: lateral view. E: cranial view. Calcaneus and talus in articulation (F–I). F: dorsal view. G: medial view. H: cranial view. I: lateral view. Talus (J–O). J: cranial view. K: dorsal view. L: medial view. M: caudal view. N: plantar view. O: lateral view.



FIGURE 13. Metatarsals IV and V of *Bohra paulae*. AM F104075, left juvenile metatarsal IV (A–E). A: dorsal view. B: plantar view. C: lateral view. D: medial view. E: proximal (caudal) view. AM F104550, left juvenile metatarsal IV (F–J). F: dorsal view. G: plantar view. H: lateral view. I: medial view. J: proximal (caudal) view. AM F104092, right adult metatarsal V (K–N). K: dorsal view. L: plantar view. M: medial view. N: lateral view. AM F103802, right adult metatarsal V (O–R). O: dorsal view. P: plantar view. Q: medial view. R: lateral view.

corner of the cuboid facet is more pointed in *B. illuminata*, while the ventral peninsula of the facet is much broader in *B. nullarbora*. In *B. paulae*, the plantar sesamoid facet on the anteroventral face of the plantar tuberosity abuts the conjoined metatarsal V facets (AM F104550) or is separated from them by a 1-mm gap (AM F104075), as in the *B. illuminata* holotype, while the gap is closer to 2 mm in the *B. nullarbora* holotype and *D. bennettianus* (Figure 10B). The metatarsal IV of *B. paulae* is more robust (broader relative to length) than that of the *B. illuminata* holotype. AM F104550 and the *B. nullarbora* holotype are very similar in size and general proportions, despite the ontogenetic difference between the specimens. However, the diaphysis of AM F104550 is comparatively deeper cranially (less concave ventrally).

Two metatarsal V specimens are referred to *B. paulae* (Figure 13K–R) on the basis of their absolute size, proportions and distinctive robustness. Both are complete and fully grown with fused distal epiphyses. The proximal articular facet for the lateral facet of the cuboid is roughly triangular and concave, sweeping up onto the broad proximolateral process. The proximomedial surface has a single broad articular facet for metatarsal IV. There only noteworthy differences between them are that AM F103802 is 11% larger than AM F104092. AM F103802 and AM F104092 are 25% and 15% larger, respectively, than the *B. nullarbora* holotype metatarsal V (Table 8), and slightly broader posteriorly (evident primarily in the plantar rugosity). Other points of morphological distinction in metatarsal V morphology between *B. paulae* and *B. nullarbora* include a relatively larger surface area of the metatarsal IV facet, shorter proximolateral process and commensurately less deeply flexed cuboid facet in *B. paulae*. From the smaller, ontogenetically younger *B. illuminata* holotype, *B. paulae* differs by having a more rounded medial end of the metatarsal IV facet and a more rugose interosseous ligament attachment (Figure 13M, Q).

Remarks. We are confident that the only known calcaneus and talus of *Bohra paulae* once articulated with each other and, as Flannery & Szalay (1982) originally suggested, that the two referred left tibiae belong to the same species as the tarsal bones. Both tibiae were collected from Cathedral Cave within the Wellington Caves complex (Figure 1), likely from Ramsay's Shaft No. 2. Subsequent excavations within this area of the cave led by Lyndall Dawson & others in 1982–1986 (Dawson & Augee 1997) and by Diana Fusco and GJP since 2016 have revealed close spatial associations between limb elements of large macropodid individuals. It is conceivable that the holotype not only came from Shaft No. 2, but also belongs to the same individual as one of the referred tibiae.

By contrast, 'Wellington Caves' is the only provenance information associated with the four metatarsals. Their larger size and morphological distinction from the metatarsals of *B. illuminata* and *B. nullarbora* prompt us to refer them to *B. paulae* rather than *B. bandharr*. Basic metrics (Table 8) reinforce this: the holotype calcaneus of *B. paulae* is 23% longer than that of *B. nullarbora*, while metatarsal V length (mean of AM F103802 and AM F104092) is also 23% greater than that of *B. nullarbora*. Similarly, calcaneus length to metatarsal V length (*B. paulae* holotype against mean of AM F103802 and AM F104092) is 0.72, as it is for the *B. nullarbora* holotype.

Bohra bandharr (Dawson, Muirhead & Wroe, 1999) comb. nov.

Protemnodon bandharr Dawson, Muirhead & Wroe, 1999. Long et al. (2002), p. 1050. Silvaroo bandharr: Dawson (2004b), pp. 275, 284–288, table 1. Dawson (2006), p. 114. Eldridge et al. (2019), p. 822.

Holotype. AM F69830, partial right adult dentary (preserving m4).

Type locality. Big Sink doline, Wellington Caves, New South Wales. Big Sink unit. Pliocene.

Paratypes. AM F69828, left adult maxilla fragment (preserving M3–4); AM F69829, right adult maxilla fragment (preserving P3, M1). Big Sink doline (Big Sink unit). A third paratype (AM F69827, left i1) of this species was identified from the Big Sink LF (Dawson *et al.* 1999), but it is deemed here to belong to a species of *Congruus* McNamara, 1994.

Referred specimens. BC1 site, Bone Cave, Wellington Caves, New South Wales. AM F146754, left P3. Collected by Michael Augee and others in the 1990s or 2000s.

Bone Cave / Phosphate Mine (probable), Wellington Caves. FMNH PM1586, right adult maxilla (preserving M1–4). This specimen was collected by Wendell B. Swanson in 1953 and donated to the Field Museum, Chicago, in 1956, along with numerous other specimens from the Wellington Caves. An origin within Bone Cave / Phosphate Mine system seems likely, given that this is where Leslie Marcus made a collection in 1954 of fossils now deposited in the University of California Museum of Paleontology, Berkeley, and was the main focus of palaeontological attention at Wellington in the mid-20th century (Dawson 1985).

Etymology. In the Wiradjuri language of central New South Wales bandharr means 'kangaroo'.

Revised diagnosis. A large species of *Bohra* with upper molars intermediate in size between those of the larger *B. wilkinsonorum* and smaller *B. bila* and *B. illuminata*. The upper molars are slightly more rectangular in occlusal outline than in other species of *Bohra*, while all secondary crests, including the postparacrista, are very weakly developed. The P3 is most similar in size and morphology to that of *B. wilkinsonorum*, but lacks the large posterobuccal eminence of that species. The postalveolar shelf of the dentary is longer and more rounded than in all other species of *Bohra* for which the dentary is known. The lophid sides of m3–4 are markedly convex.



FIGURE 14. Maxilla and upper cheek teeth of *Bohra bandharr*. FMNH PM1586, partial right adult maxilla (A–C). A: lateral view. B: mesial view. C: stereo occlusal view. AM F146754, left P3 (D–H). D: stereo occlusal view. E: buccal view. F: anterior view. G: lingual view. H: posterior view.

Description and comparisons. Maxilla and palatine. Despite being the most complete of the three maxillary specimens, very little is preserved of the maxilla of FMNH PM1586 (Figure 14A–C). However, there is sufficient to suggest that, although broken off, the base of the masseteric process was positioned above the anterior root of M3 in lateral view. A portion of the palatine bone is attached to the maxilla adjacent to M3–4. It is orientated anteroposteriorly before inflecting anterolingually mesial to the M3 metaloph (Figure 14C).

The position of the masseteric process relative to M3 matches that observed in adult specimens of *B. nullarbora*, *B. bila* and *B. planei*. The process is slightly more anteriorly located in the holotype of *B. illuminata*, but this is very likely because of its ontogenetically slightly younger age, the M4 having only just come into occlusion. The fusion to the maxilla of a solid portion of palatine points to the presence of an entirely bony (non-fenestrate) secondary palate in *B. bandharr*, which is an attribute of dendrolaginans within the Dendrolagini.

Upper dentition. Two specimens preserve P3: the paratype AM F69829 (Figure 15G) and the referred specimen AM F146754 (Figure 14D–H). Crown posterior width is similar (Table 1), and crown length may be inferred to have been (enamel is missing from the anterior end of AM F69829). AM F146754 is narrower anteriorly than in AM



FIGURE 15. Craniodental specimens of *Bohra bandharr*. AM F69830 (holotype) right, adult dentary (A–F). A: lateral view. B: mesial view. C: occlusal view. D: stereo occlusal view of m4 and postalveolar shelf. E: posterior view. F: anterior view of m4. G: AM F69829, partial right adult maxilla (P3–M1) in stereo occlusal view. H: AM F69828, partial left adult maxilla (M3–4), stereo occlusal view.

L AW	4W	· · · ·	P3 PW	ΗH	Hd	Г	AW	M1 PW	AH I	H	L A	M P	12 W A	H b	H	Γ	M P	13 W AI	H PF	L	AW	M4 PW	AH	Hd
2.18 4.78 6.77 5.59 5.77	4.78 6.77 5.59 5.77	6.77 5.59 5.77	5.59 5.77	5.77												~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	26 7.	26 -	I	9.82	7.77	6.39	I	
1.7^{*} 5.85 6.55 8.26 8.03 8.	5.85 6.55 <u>8.26 8.03 8.</u>	6.55 <u>8.26</u> 8.03 8.	8.26 8.03 8.	- 8.26 8.03 8.	8.26 8.03 8.	8.03 8.	\sim 1	28	ı		t	t				c č		t						
2.90 6.93	7.90 6.93 7	7.90 6.93 7	7.90 6.93 7	7.90 6.93 7	1.90 6.93 7	0.93		,08		- ح	.17 7.1	95 7.	- 099		۲	81 8	12 7.	27 -	1	10.03	7.85	.6.59	4.76	4.62
L AW PW AH PH L AW F	aw pw ah Ph L aw F	p3 r PW AH PH L AW F	AH PH L AW F	PH L AW F	L AW F	AW F	~	M N	AH I	На	L A	ч М	V A	Η	— н	L	W P	13 W AI	H PE	L	AW	PW PW	ЧH	Hd
							1													9.53	6.92	1	4.83	1
-tooth dimensions (mm) of <i>Bohra</i> sp. cf. <i>B.</i> ba	dimensions (mm) of <i>Bohra</i> sp. cf. <i>B. ba</i>	sions (mm) of <i>Bohra</i> sp. cf. <i>B. ba</i>	(mm) of <i>Bohra</i> sp. cf. <i>B. ba</i>	of Bohra sp. cf. B. ba	"a sp. cf. <i>B. ba</i>	:f. <i>B. ba</i>	a	ndhai	γ.															
P3 M	P3 M	P3 M	W		W		\geq	=					M2					M3				M4		
L AW PW AH PH L AW P	AW PW AH PH L AW P	PW AH PH L AW P	AH PH L AW P	PH L AW P	L AW P	AW P	Ч	M	HΗ	ΡΗ	L A	W H	A W	H F	H	L ,	AW I	W A	H PI	I L	AW	ΡW	AH	Ηd
00 2	00 2	00 2																		8.98	7.26	6.16	3.68	4.11
		00.0	1	1							7.56 6.	.76 6	.61			.33 6	.88	.51 3.5	50 3.5	0				
															~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	.35 6	.87 6	- 15.	1	8.56	1	5.74	ı	ı
																				9.50	7.28	5.94	3.69	4.12
											8.12 6.	.65 6	.51											
																•	.47	- 4.(	)3 -					
															∞	.43 6	.69 6	.37	3.(	90				
6.2	6.2	6.2	6.2	6.2	6.2	- 6.2	6.2	4	ı	1														
p3 m	p3 m	p3 m		m	m	m	В	_				1	m2				-	n3				m4		
L AW PW AH PH L AW PW	AW PW AH PH L AW PW	PW AH PH L AW PW	AH PH L AW PW	PH L AW PW	L AW PW	AW PW	ΡМ	1	AH	ΡΗ	L A	W H	A Mo	H F	H	L /	AW F	W A	H PI	I L	AW	ΡW	AH	Ηd
6.73 1.93 2.53 3.64 3.50	1.93 2.53 3.64 3.50	2.53 3.64 3.50	3.64 3.50	3.50																				
3.41 5.86 - 4	- 3.41 5.86 - 4	3.41 5.86 - 4	5.86 - 4	- 5.86 - 4	5.86 - 4	- 4	4	.89	ı	-	5.99 5.	.52 5	<u>4</u> 4.	ı	-	.72 5	69 5	- 72	1	8.50	5.66	5.27	ī	ı
																.74	- 9	- 43	1	9.15	69.9	'	4.51	ı
															6	.48 6	.10 6	- 90.	1	9.67	6.05	5.69	4.68	4.79

F69829, and its posterobuccal eminence is slightly better developed. The following description is primarily based on AM F146754 because it is much less worn. The main crest is straight for its length, except for the anterior- and posterior-most cuspules, which are slightly buccally offset. The main crest is composed of five cuspules (Figure 14D). No ridgelets ascend from them on the lingual side, but a coarse buccal ridgelet is associated with the anterior-most cuspule, while a fine ridgelet ascends from the second cuspule and a very fine ridgelet ascends from the third cuspule (Figure 14D–E). Each of the latter two ridgelets terminates at a small cingular cuspule, while a third cuspule is located posterior to them. The lingual cingulum is low but distinct, and inflects toward the tooth midline midway along the crown. It continues anteriorly to a position adjacent to the anterior cusp of the main crest, before again inflecting buccally and terminating at the anterior end of the crown. A very small, triangular posterior basin is present at the posterior end of the crown, separated by a coarse ridge that represents a continuation of the lingual cingulum from the expanded posterolingual portion of the crown.

The P3 is most similar to that of *B. wilkinsonorum* in size and morphology, but is distinguished by being relatively narrower anteriorly, and by having a much less pronounced posterobuccal eminence and three buccal cingular cuspules. Although *B. nullarbora* also has an anteriorly broad P3, the crown is slightly narrower posteriorly and much smaller overall.

The M1 of AM F69829 is so worn that it consists of little more than a dentine basin surrounded by a thin border of enamel (Figure 15G), but the molars of FMNH PM1586 are only slightly worn, with dentine breached only slightly on the loph crests of M1–2, and the lingual cusps of M3 (Figure 14C). The molars are low crowned, with very fine, low secondary crests, including the postparacrista and postprotocrista. The protoloph of M1 is slightly narrower than the metaloph, but is slightly wider on M2 and increasingly wider on M3 and M4 (Figures 14C, 15H). M1–2 are distinctly flat-sided, producing an overall quite rectangular crown shape in occlusal view. M3–4 are similar, but very slightly more convex adjacent to the interloph valley. The more posterior portion of the postmetaconulecrista forms a small but distinct shelf on the M4 posterior face. The interloph valley of M4 is bordered by a fine, low, lingual cingulum on the metaloph anterior face.

The upper molars of *B. bandharr* are smaller than those of *B. wilkinsonorum*, but larger than those of *B. bila* and *B. illuminata* (Tables 1, 3–5). They are distinguishable from other species of *Bohra* by being more rectangular in occlusal outline (flat-sided). Even taking into account the wear sustained by FMNH PM1586, the secondary crests, most notably the postparacrista, postprotocrista and premetacrista, are very weakly developed, which is also characteristic of *B. nullarbora* and *B. planei*.

Dentary. The holotype (AM F69830) and only known dentary (Figure 15A–F) has been adequately described previously (Dawson *et al.* 1999). The specimen is missing much of the ascending ramus and anterior end of the dentary, and has been slightly distorted by crushing. It is shallower relative to its width than in *B. bila*, a trait more reminiscent of *B. illuminata*. The ventral profile of the dentary and the highly reduced nature of the digastric eminence and sulcus are shared with *B. bila*, which also has a similarly proportioned and rugose anterior insertion area for the internal superficial masseter muscle. The form of the postalveolar shelf of the dentary differs from that of all other species of *Bohra* for which the dentary is known. It is longer than in *B. bila* and *B. illuminata*, and has a more rounded mesial border than in *B. bila* and *B. nullarbora*, lacking any sign of a mesial process.

Lower dentition. The holotype preserves only the m4 and even that is missing the posterobuccal portion of the crown (Figure 15A–F). The m4 is intermediate in size between those of the smaller *B. nullarbora* and the larger *B. bila* and *B. illuminata* (Tables 1, 4–5). The convexity of the lophid sides, effectively the manner in which they are "bowed strongly outwards" (Dawson *et al.* 1999, p. 280), is greater than that in all other species of *Bohra*. It is worth noting that two points of difference between *B. bandharr* and *B. bila* identified previously – "*Silvaroo bandharr*...differs from *S. bila* in lacking a posterior cingulum or basal swelling on the posterior hypolophid of m4, [and] in having a much narrower (buccally curtailed) anterior cingulum on m4" (Dawson 2004b, p. 285) – do not hold on closer examination. There is a low, narrow postcingulid on the m4 of *B. bandharr* (Figure 15E), and the apparently greater buccal extent of the m4 precingulid in the holotype of *B. bila* is an artefact of the greater wear it has sustained by comparison.

**Remarks.** Among the seven named species of *Bohra*, *B. bandharr* and *B. bila* are founded on holotypes that preserve the fewest diagnostic attributes, with *B. bandharr* the closest to being a *nomen dubium*. The holotype of *B. bandharr*, from the Pliocene Big Sink LF, is a partial, distorted dentary preserving one incomplete molar encompassing three diagnostic traits. These are also manifested in a partial dentary from the Pliocene Chinchilla LF ('bowed' buccal lophid sides, broad molars, long, rounded postalveolar shelf) herein referred to *B.* sp. cf. *B. bandharr*. Maxillary fragments from the Big Sink LF and Pleistocene Bone Cave deposit within the same cave complex in the

Wellington Caves system (Figure 1) are referred to *B. bandharr* on the grounds of commensurate size and *Bohra* morphology. Among the species of *Bohra*, the cheek teeth of *B. bandharr* are second only to *B. wilkinsonorum* in size, and it may be significant that the holotype calcaneus of *B. paulae*, also from the Wellington Caves, is second only in size to the calcaneus referred to *B. wilkinsonorum* in the Chinchilla LF. As further specimens of fossil tree-kangaroos are collected from the Wellington Caves and analysed, the prospect of *B. bandharr* being a junior synonym of *B. paulae*, which has been described to date only from hindlimb elements, will need to be considered.

The isolated left i1 (AM F69827) from the Big Sink LF listed as a paratype of *B. bandharr* (Dawson *et al.* 1999) is deemed here to be referable to a species of *Congruus* (see Warburton & Prideaux 2021), as is the paratype left i1 (QM F43292) referred to by Dawson (2004b) to *Silvaroo bila* (herein, *B. bila*).

#### Bohra sp. cf. B. bandharr

cf. Dendrolagus sp. 1: Flannery & Archer (1984), pp. 358-359, 361-362, figure 1F-G, table 1. Rich (1991), p. 1049.

cf. *Dendrolagus* sp. 2: Flannery & Archer (1984), pp. 358–359, 362–363, figure 1F–G, table 1. Rich (1991), p. 1049. Tedford *et al.* (1992), p. 187.

cf. Dendrolagus: Tedford et al. (1992), p. 190, table 3; partim.

Protemnodon ?cf. bandharr: Dawson et al. (1999), pp. 281, 287, table 10.

Dendrolagus sp. 2: Dawson et al. (1999), p. 281.

Dendrolagus sp.: Dawson (2004a), pp. 267, 270-272, table 1; partim.

Silvaroo sp. indet. 1: Dawson (2004b), pp. 283, 286, figure 3.

Silvaroo sp. 1: Dawson (2004b), p. 288, table 2.

*Dendrolagus* sp. indet.: Prideaux & Warburton (2008), pp. 463–464, figure 1; partim. *Silvaroo* sp.: Louys & Price (2015), pp. 565, 567, 569, figure 8N.

**Referred specimens.** Chinchilla Rifle Range (site not specified), Queensland. QM F43281, partial right adult dentary (preserving m3–4). QM F58665, partial right adult dentary (preserving m3–4); QM F61040, right i1. Collected by Doris and Cecil Wilkinson.

Probably Chinchilla. QM F4750, partial right adult dentary (preserving incomplete p3, m1–4). This specimen retains no associated locality information. Chinchilla Sand is suggested by preservation (chocolate-brown bone, bluegrey enamel and yellow- to orange- to chocolate-brown adhering matrix), which has been used to retrospectively, albeit tentatively, differentiate Chinchilla Sand specimens from other Darling Downs material (e.g., Bartholomai 1963, 1975; Bartholomai & Woods 1976; Louys & Price 2015). Collection details are unknown, but it was very likely collected in the late 19th century. The specimen was ascribed the number 8808 in De Vis's catalogue.

Bow, New South Wales. AM F59576, partial right adult maxilla (preserving M2–3); AM F64004, posterior half of left P3; AM F64007, right M4; AM F64075, partial left maxilla (preserving very worn M2–4). AM F64245, left M4.

Fisherman's Cliff, Warrananga Station, New South Wales. NMV P38267, left M2; MNV P38351, left M3 metaloph; NMV P38325, right p3. Collected by Edmund Gill and others in the late 1960s or James Warren and others in the early 1970s.

FUPS Quarry, Bone Gulch, Moorna Station, New South Wales. NMV P257273, partial left P3; NMV P257274, left M3; NMV P257275, right M1 metaloph. These specimens were picked from concentrate sieved from sediment collected by a team led by GJP. NMV P257273 was collected on 14 February 2016, NMV P257274 on 16 August 2015, and NMV P257275 on 15 February 2016.

**Remarks.** An assortment of specimens have been grouped under this limbo nomen (Figure 16–18) because they share dentary or cheek-tooth traits with specimens of *B. bandharr* (e.g., comparatively rectangular upper molars, dentary with a long, rounded postalveolar shelf), but differ by having narrower, much smaller molars (Table 2). NMV P38325, by contrast, is a p3 from the early Pleistocene Fisherman's Cliff LF (Figure 1) referred to *B.* sp. cf. *B. bandharr* by association with several loose molars, and the general similarity of its form (Figure 18J–L) to that of the only other unworn p3 known for a species of *Bohra*, that of the paratype of *B. illuminata* (Figure 24D).

The barrier to defining a species from among this collective is the lack, in any one specimen, of sufficient diagnostic attributes that would permit its selection as a reliable holotype. Obtaining further tree-kangaroo fossils from the Chinchilla and Bow localities (Figure 1) may offer the greatest chance of solving this impasse. Nevertheless, although it lacks a name, it would be reasonable to assume that within the sample referred to *B*. sp. cf. *B. bandharr* there is yet another late Cenozoic species of *Bohra*.



**FIGURE 16.** Dentary specimens of *Bohra* sp. cf. *B. bandharr*. QM F4750, partial right adult dentary (A–C). A: lateral view. B: mesial view. C: stereo occlusal view. QM F58665, partial right adult dentary (D–F). D: lateral view. E: mesial view. F: stereo occlusal view. QM F61040, right i1 (G–H). G: buccal view. H: lingual view. QM F43281, partial right adult dentary (I–K). I: lateral view. J: mesial view. K: stereo occlusal view.



**FIGURE 17.** Maxillary and upper dental specimens of *Bohra* sp. cf. *B. bandharr*. AM F64075, partial left adult maxilla (A–B). A: lateral view. B: stereo occlusal view. AM F59576, partial right adult maxilla (C–E). C: lateral view. D: mesial view. E: stereo occlusal view. AM F64007, right M4 (F–J). F: buccal view. G: lingual view. H: anterior view. I: posterior view. J: stereo occlusal view. K: AM F64245, left M4, stereo occlusal view. AM F64004, posterior half of left P3 (L–P). L: lingual view. M: buccal view. N: anterior view. O: posterior view. P: stereo occlusal view.

## Bohra wilkinsonorum Dawson, 2004a

Holotype. QM F43277, right juvenile maxilla fragment (preserving dP2-3, M1-2; P3 removed from crypt).

**Type locality.** Chinchilla Sand, Chinchilla Rifle Range (site not specified), north bank of the Condamine River, Chinchilla, western Darling Downs, Queensland. The holotype was collected by Doris and Cecil Wilkinson.

**Referred specimens.** Probably Chinchilla. QM F675, right adult calcaneus. This specimen retains no associated locality or collection information, although it was likely collected in the late 19th century. Chinchilla Sand is suggested by preservation. See earlier comments on specimens referred to *B*. sp. cf. *B. bandharr* putatively from Chinchilla.



**FIGURE 18.** Cheek teeth of *Bohra* sp. cf. *B. bandharr*. NMV P257274, left M3 (A–E). A: stereo occlusal view. B: anterior view. C: posterior view. D: lingual view. E: buccal view. NMV P38267, left M2 (E–G). F: stereo occlusal view. G: anterior view. H: anterior view. I: NMV P257273, partial left P3, stereo occlusal view. NMV P38325, right p3 (J–L). J: buccal view. K: lingual view. L: stereo occlusal view.

Childers Cove, Victoria. NMV P221950, left P3. Collected by David Pickering and others on 24 November 2011. NMV P222378, right M1. Collected by David Pickering and Wayne Gerdtz on 3 or 4 August 2004.

**Etymology.** Named in honour of Doris and Cecil Wilkinson for their fossil collecting efforts at the Chinchilla Rifle Range locality.

**Revised diagnosis.** The largest-known species of *Bohra* based on molar and calcaneal dimensions. The P3 is similar in size and morphology to that of *B. bandharr*, but is less markedly narrowed anteriorly. The postpara- and premeta-cristae on M2 are strongly developed and incurved, more so than in any other species of *Bohra*. The slight convexity of the buccal side and distinct interloph concavity of the lingual side of the M1–2 crown resembles that of the much smaller *B. nullarbora*.

The species is also distinguished by the following combination of calcaneal features: massive, dorsoventrally compressed tuber calcanei; plantar aspect very broad and strongly flared posteriorly, particularly on the lateral aspect of the epiphysis; medial and lateral talar facets of the calcaneus discontinuous; pronounced and strongly demarked crest from the caudomesial border of the medial talar facet for the posterior talocalcaneal ligament; calcaneocuboid facets transversely broad, with oblique, moderately deep step; ventromedial facet separated from dorsomedial facet by deep fossa.

**Description and comparisons.** Maxilla. Essentially all that is preserved of the holotype maxilla is that portion bearing the erupted dP2–3 and M1–2, the unerupted P3, and the masseteric process (Figure 19A–C). With its extremity positioned adjacent to the M2 protoloph in this juvenile specimen, the masseteric process is posteroventrally orientated and bears a low, slightly rugose crest along its anterolateral edge (Figure 19C).

The juvenile maxilla is known for no other species of *Bohra*, and so no direct morphological comparisons are possible due to the changes that can occur from the ontogenetic stage where M2 has just come into occlusion versus a full adult where M4 is in occlusion. Nevertheless, it is worth noting that in *D. bennettianus*, the molars progress anteriorly relative to the position of the masseteric process between these two ontogenetic stages. When M2 first comes into occlusion, its protoloph is positioned adjacent to the masseteric process, but in adults the abutment of M2–3 is adjacent to the masseteric process. The same may well have been the case for *B. wilkinsonorum*. In shape, the masseteric process is more rounded than in *B. illuminata* and *B. bila*.

Upper dentition. Previously described in detail (Dawson 2004a).

The dP2–3 remain unknown for other species of *Bohra*, but comparisons with the much smaller *D. bennettianus* and *D. inustus* reveal very similar general crown outlines, although those of *D. bennettianus* are the closest match. Their dP2 crowns are relatively flat-sided oval shapes, and they share a low weak buccal cingulum. However, *B. wilkinsonorum* differs by lacking the large anterior cusp of the main crest bordered posteriorly by a deep cleft

(Figure 19A–C), which is characteristic of both the dP2 and P3 of species of *Dendrolagus*. These species are also very similar in dP3 morphology, sharing: a strongly developed postparacrista, which abuts the end of the dP2 main crest; well-developed postpara- and premeta-cristae, which are anteroposteriorly orientated and confluent, rather than incurved as on M1–2; and a distinct preprotocrista that marks the lingual end of the transversely narrow precingulum. No preprotocrista is evident on the holotype M1, but there is a slight preprotocrista present on the unworn (unerupted) referred specimen, NMV P222378 (Figure 19L). There is a stylar eminence in the region of cusp C on M1, but not M2 (Figure 19C). Whether a urocrista (of which there is a slight manifestation in *D. bennettianus* and a very distinct expression in *D. inustus*) was also present in *B. wilkinsonorum* cannot be ascertained due to extensive wear of the metaloph.



**FIGURE 19.** Maxillary and upper dental specimens of *Bohra wilkinsonorum*. QM F43277 (holotype) right juvenile maxilla (A–F). A: lateral view. B: mesial view. C: occlusal view. D: stereo occlusal view of unerupted P3 (cast). E: lingual view of unerupted P3 (cast). F: stereo occlusal view of dP2–3, M1–2 (cast). NMV P221950, left P3 (G–K). G: stereo occlusal view. H: anterior view. I: lingual view. J: posterior view. K: buccal view. NMV P222378, right M1 (L–P). L: stereo occlusal view. M: buccal view. N: lingual view. O: anterior view. P: posterior view.

TABLE 3. Ch	eek-tooth din	nensio	ns (mr	n) of <i>E</i>	3ohra v	wilkins	vonor	·m·																
		dP2					dP3					P3					M1					M2		
	L AW	PW	ΗV	Hd	Г	AW	PW	ΗV	Hd	Г	AW	$\mathbf{PW}$	ΗV	Hd	Г	AW	PW	HΗ	Hd	Г	AW	ΡW	ΗV	Hd
QM F43277	7.38 5.19	5.30	ı	ı	7.27	5.93	6.72	ı	ı	12.28	5.26	6.43	5.99	6.08	8.93	7.88	8.42	4.35	4.74	10.20	8.72	8.31	4.56	5.32
NMV P221950										12.48	5.40	6.73	7.25	5.15										
NMV P22378															9.17	7.85	7.99	5.16	5.14					
TARLE 4 Ch			um) su	n) of <i>F</i>	Sohra P		ata fo	MO	-4740	is from	Barth	iemolo iemolo	9761											
							n 10							<i>u</i> ).										
		M1					M2					M3					M4							
	L AW	ΡW	ΗH	Hd	Γ	AW	ΡW	ΗH	Hd	L	AW	ΡW	ΑH	Hd	Γ	AW	PW	AH	Ηd					
QM F4740					8.6	7.4	7.3	I	I	9.6	7.7	7.0	ı	I	9.7	7.2	6.2	I	ı					
QM F43276	7.36 7.21	7.30	ı	ı	8.66	7.51	7.11	I	I	9.35	7.96	6.75	4.67	4.67	9.13	7.3	5.45	4.07	4.17					
QM F58667					8.42	7.53	7.17	4.62	4.89						-									
	dj	p3				p3				ml				m				ц	13				m4	
	L AW P	W Aj	Hd H	IL	AW	PW	HΗ	Hd	L AI	W PW	HΗ	Hd	LA	W PW	/ AH	Hd	L	AW P	W AF	Hd H	Γ	AW	PW /	H PH
QM F4749	6.03 3.47 4.	.09 3.1	19 3.4	6					- 5.0	)2 -	ı	ı												
QM F43280				10.6	1 4.17	4.56	I	-	.43	5.40	ı	1	8.30 6.	01 6.0	4	I	9.91	7.13 6.	91 -	I	10.51	7.15	6.26	ı ı
QM F58668								~	.11 5.1	14 5.52	5.27	6.05												
QM F58669																	9.60	5.72 6.	68 6.0	2 6.48				
*Bohra wilkinsonorum* is most similar in P3 size and morphology to *B. bandharr* (Tables 1, 3). It differs by narrowing less markedly anteriorly, possessing three buccal cingular cuspules and bearing a slightly less pronounced posterobuccal eminence. Although the holotype P3 bears an anterior crest on the posterobuccal eminence (Figure 19D–E), this is lacking from NMV P221950 (Figure 19G–K).

In M1–2 occlusal outline (Figure 19C, F, L), *B. wilkinsonorum* resembles the much smaller *B. nullarbora*. They share a slightly convex, but essentially quite flat, buccal side of the crown, a trait that also characterises *B. bandharr*. However, the lingual sides of M1–2 of *B. bandharr* are also flat lingually, rather than convex adjacent to the interloph valley. The strongly developed and incurved form of the postpara- and premeta-cristae on M2 distinguishes *B. wilkinsonorum* from all other species of *Bohra*. Absence from M2 of a stylar crest in the region of cusp C is a condition shared with *B. bandharr*, *B. illuminata* and *B. nullarbora*, but not *B. bila* and *B. planei*, in which this crest is distinct.

Calcaneus. The referred calcaneus, QM F675, is well preserved and complete except for the caudolateral extremity of the tuber calcanei (Figure 20B, D). The calcaneus is large, stout, broad, stout and dorsoventrally flattened, with clearly defined articular surfaces and rugged ligamentous insertions. The tuber calcanei is strongly flared caudally (Figure 20B). From the plantar view, the medial margin diverges from the long axis more continuously along its length, in comparison to the lateral margin, which widens distinctly at the epiphysis. The rugose plantar surface is broad cranially, with a large anterolateral tubercle (Figure 20A). The transverse sulcus that separates the cranial margin of the rugose surface from the cuboid articulation is slightly oblique from medial to lateral sides. The sustentaculum tali is deep (from medial view), medially expanded and very slightly convex (Figure 20C).



FIGURE 20. Calcaneus (right, adult) of *Bohra wilkinsonorum* (QM F675). A: plantar view. B: dorsal view. C: medial view. D: lateral view. E: cranial view.

The medial and lateral talar facets are separated by a narrow but distinct, non-articular area (Figure 20B, E). The lateral facet is barrel-shaped (Figure 20B). The fibular facet is broad and rounded, and projects over the deep sulci for the posterior calcaneofibular ligament (Figure 20B, D). The tubercle and sulcus for the anterior calcaneofibular ligament are large, laterally expanded and rugose. The posterior margin of the oval medial talar facet projects dorsally and expands onto the dorsal surface toward the base of the calcaneal tubercle, with a marked projection for posterior talocalcaneal ligament (Figure 20B). Cranial to the talar facets, the mid-dorsal surface is has a deep scar for the ligamentum cervicis tali. The calcaneocuboid articulation is transversely very broad (laterally extending beyond the margin of the fibular facet; Figure 20B); and dorsoventrally compressed in cranial view (Figure 20E). The step between the rectangular dorsomedial and rounded dorsolateral facets is distinct, obliquely aligned and moderately smoothed (Figure 20A). The ventromedial facet is transversely broad, but dorsoventrally relatively shallow (Figure 20E). It is smoothly continuous with the dorsolateral facet but separated by a deep transverse groove from the dorsomedial facet.

The lateral flaring of the tuber calcanei epiphysis is more pronounced than in all other species of *Bohra*, especially the similarly large *B. paulae* (Figure 12B). The transverse plantar sulcus is relatively deep and long in comparison to all other species of *Bohra*, in particular *B. paulae* and QM F51762 (*Bohra* sp. indet. 1), and is much deeper than in the species of *Dendrolagus* (Figure 9B). The expanded medial plantar margin of the sustentaculum

tali accentuates the moderately deep flexor sulcus of the sustentaculum tali to a greater extent than in *B. paulae*, *B.* sp. indet. 1 and the species of *Dendrolagus*, though it is not as deeply flared as in *B. planei*. The gap between the medial and lateral talar facets resembles that observed in *B. nullarbora*, but differs from the condition seen in other species of *Bohra* and species *Dendrolagus* (Figure 9A), in which the facets are confluent. The calcaneocuboid articulation is transversely much broader than in any other species (Figure 20B, E cf. Figure 9B, D). The profile of the calcaneocuboid step and complete separation of the ventromedial and dorsomedial facets is most like *B. planei*, while the rounded and laterally expanded of the dorsolateral facet is more like other species of *Bohra*, in contrast to *B. planei* (Figure 33C).

**Remarks.** The recognition of *B. wilkinsonorum* as a second member of the genus *Bohra* on the basis of one juvenile maxilla fragment (Dawson 2004a) was a highly perceptive deduction given that the type species was described and is still known only from hindlimb elements from a locality 665 km to the south (Flannery & Szalay 1982). Based on the dimensions of these specimens (Table 8), *B. wilkinsonorum* and *B. paulae* are the two largest species of *Bohra*, and one might be able to hypothesise on those grounds that the fossils belong to the same species. However, the recognition from the Darling Downs region (indeed, probably from the type locality) of a very large calcaneus clearly referable to a species of *Bohra* that is morphologically distinct from that of *B. paulae* supports its taxonomic separation. This calcaneus is much larger than, and differs in morphology from, the other two calcanei from the Chinchilla LF, which we refer to *B.* sp. indet. 1. Referral to *B. wilkinsonorum* of a loose upper premolar and molar from the putatively late Pliocene or early Pleistocene Childers Cove LF of southern Victoria (Rich *et al.* 2006) represents a major range extension of 1,500 km to the south (Figure 1).

### Bohra bila (Dawson 2004b) comb. nov.

Wallabia indra (De Vis, 1895): Bartholomai (1976b), pp. 375, 378 (partim), plate 53: figures 1–3. Not W. indra (De Vis, 1895).

Silvaroo bila Dawson, 2004b: Dawson (2006), p. 114. Piper & Herrmann (2006), p. 130. Louys & Price (2015), pp. 565, 567–568, figure 8M. Piper (2016), p. 238. Eldridge *et al.* (2019), p. 822.

Holotype. QM F43280, partial left adult dentary (preserving p3, m1-4).

Type locality. Chinchilla Rifle Range (site not specified), north bank of the Condamine River, Chinchilla, western Darling Downs, southeastern Queensland. Chinchilla Sand. Pliocene. Collected by Doris and Cecil Wilkinson.

**Paratypes.** QM F43276, partial left maxilla (preserving M1–4). Chinchilla Rifle Range (site not specified). Collected by Doris and Cecil Wilkinson. A second paratype (QM F43292, left i1) from Chinchilla is deemed here to be referable to a species of *Congruus*.

**Referred specimens.** Lion Hill, Chinchilla Rifle Range, Queensland. QM F58668, left m1; QM F58669, left juvenile dentary fragment (preserving m3). Collected by Doris and Cecil Wilkinson.

Chinchilla Sand, Chinchilla Rifle Range (site not specified). QM F58667, left M2. Collected by Doris and Cecil Wilkinson.

Chinchilla (presumably Chinchilla Sand). QM F4740, partial left adult maxilla (preserving M2–4). Collected by Kendall Broadbent in 1887.

Probably Darling Downs, Queensland. QM F4749, partial left juvenile dentary (preserving dp3, m1 trigonid). No locality details are associated with this specimen.

**Etymology.** In the Wiradjuri language of central New South Wales, *bila* means 'river', a reference to the surmised riparian habitat of this species.

**Revised diagnosis.** *Bohra bila* is distinguished from all other species of *Bohra* by having the palatine extend anteriorly to a position mesial to the M2 protoloph. The upper molars are similar in size to those of *B. bandharr* and *B. illuminata*, but its M4 is slightly smaller. They are most similar in morphology to those of the slightly smaller *B. planei*. They differ by having the cusp C region of the stylar crest diverge from the postparacrista closer to the paracone apex, and by lacking any sign of the stylar crest on M3. The ventral margin of the dentary is very smoothly curved posteriorly in lateral profile, lacking the digastric eminence of *B. illuminata* and *B. nullarbora*. It differs from that of *B. bandharr* by being deeper and having a shorter postalveolar shelf, which bears a small mesial process. The lower molars are similar in size and morphology to those of *B. illuminata*, but they lack a distinct premetacristid and the lophids are thinner in buccal view. The p3 is large and robust.

**Description and comparisons.** Maxilla and palatine. QM F4740 is a chunk of maxilla that retains M2–4 and the complete masseteric process, and has attached to it a thin strip of palatine (Figure 21D–E). QM F43276 retains M1–4, but the end of its masseteric process is abraded off. It also has a thin strip of palatine fused to it, which extends anteriorly to a position mesial to the M2 anterior root (Figure 21B). The masseteric process of QM F4740 is triangular in lateral view. Its tip aligns with the M3 interloph valley (Figure 21D), and its leading edge is slightly twisted anterolaterally. Although the tip of the masseteric process is missing in QM F43276, we can extrapolate that it would have been positioned adjacent to the M3 protoloph.

In *B. bila*, the maxilla–palatine suture extends anteriorly to a position adjacent to the M2 anterior root, but in *B. nullarbora, B. illuminata, B. planei* and *B. bandharr* it stops and inflects lingually at or posterior to a position mesial to the anterior edge of M3. The position of the masseteric process in *B. bila* is consistent with that observed in adult specimens of *B. nullarbora, B. planei* and *B. bandharr*. The form of the masseteric process is a good match for that of *B. illuminata*, but in the holotype of that species it is instead positioned adjacent to the M2 metaloph. This may be an artefact of its younger ontogenetic age (M4 is in the process of rotating into occlusion).



**FIGURE 21.** Maxillary and upper dental specimens of *Bohra bila*. QM F43276, partial left adult maxilla (A–C). A: lateral view. B: mesio-occlusal view. C: stereo occlusal view (cast). QM F4740, partial left adult maxilla (D–E). D: lateral view. E: stereo occlusal view. QM F58667, left M2 (F–J). F: stereo occlusal view. G: lingual view. H: buccal view. I: anterior view. J: posterior view.



**FIGURE 22.** Dentary and lower dental specimens of *Bohra bila*. QM F43280 (holotype) left adult dentary (A–C). A: lateral view. B: mesial view. C: stereo occlusal view (cast). QM F4749, partial left juvenile dentary (D, H, L). D: stereo occlusal view. H: lateral view. L: mesial view. QM F58669, left juvenile dentary fragment (E, I, K, O–P). E: stereo occlusal view. I: lateral view. K: mesial view. O: anterior view. P: posterior view. QM F58668, left m1 (F–G, J, M–N). F: stereo occlusal view. G: buccal view. J: lingual view. M: anterior view. N: posterior view.

Upper dentition. Previously described in detail for QM F43276 (Dawson 2004b). The referred unworn M2, QM F58667 (Figure 21F–J), is indistinguishable from the M2 of QM F43276 in size and morphology, except for possessing a very slightly weaker cusp C region of the stylar crest.

*Bohra bila* is a close match for *B. bandharr* and *B. illuminata* in upper molar size, but it has a slightly smaller M4 (Tables 1, 4–5). In morphology, including general shape of the crown outline, *B. bila* is most similar to *B. planei*, and to a slightly lesser degree, *B. nullarbora*, both of which have smaller molars. In contrast to that of *B. planei*, the cusp C region of the stylar crest diverge from the postparacrista closer to the paracone apex in *B. bila* rather than further up the paracone. In addition, there is no manifestation of this stylar crest region on M3 in *B. bila*. The upper molars of *B. bila* differ from those of *B. nullarbora* by having a cusp C region of the stylar crest on M1–2, incurved postpara- and premeta-cristae, and a broader, more open posterior metaloph face on M4.

Dentary. Previously described in detail for the holotype, QM F43280 (Dawson 2004b). The two referred juvenile dentary fragments are too incomplete to add to the knowledge of dentary morphology, but QM F58669 does confirm the absence of a digastric eminence.

The holotype dentary of *B. bila* (Figure 22A–C) is most similar in overall form to that of *B. nullarbora*, but its ventral margin has a much more evenly curved profile due to the barely discernible digastric sulcus and absence of a digastric eminence (Figure 22A–B). It also has a larger and more rugose anterior insertion area for the internal superficial masseter muscle, and a more distinct buccinator sulcus (Figure 22A). The latter feature is also characteristic of the smaller *B. bandharr*, which is distinguished by its longer, rounded postalveolar shelf. A postalveolar shelf that bears a mesial process is shared with *B. nullarbora*, but the process on the latter is more pronounced.

Lower dentition. The lower check teeth of the holotype have been described (Dawson 2004b), but the molars are heavily worn. Here we describe the teeth of three referred specimens, which have sustained little to no wear, one of which (QM F4749) preserves the previously unknown dp3.

The dp3 is narrow, especially anteriorly due to the compressed form of the trigonid (Figure 22D). The protolophid is very narrow and inflects at the protoconid into a paracristid that rises to a point anteriorly that matches the protoconid in height. From there a crest descends lingually to the anterolingual corner of the crown. If this is a continuation of the paracristid, then its terminus is likely the position of the paraconid; however, it is also conceivable that the high point on the paracristid marks the paraconid (Figure 22H, L). The buccal face of the crown is sheer; there is no distinct cingulum, although the crown bulges slightly near to the base. There is no parastylar crest. The metaconid is higher than the protoconid and gives rise to short, fine pre- and post-metacristids (Figure 22D). Although broader than protolophid, the hypolophid is quite narrow relative to the m1 protolophid, and sits substantially lower than it in buccal view. Like the protolophid, the hypolophid slopes slightly buccally, resulting in the hypoconid being noticeably lower than the metaconid. The cristid obliqua descends into the interlophid valley and smoothly ascends to the protoconid apex, such that there is no distinct postprotocristid (Figure 22D). The posterior face of the hypolophid is smooth and featureless.

QM F58668 is a complete, isolated, unworn m1 crown (Figure 22F–G, J, M–N), whereas QM F4749 is missing the m1 talonid. The only slight difference is that the most posterior portion of the paracristid is slightly inflected in QM F58668 and straight in QM F4749. The m1 protolophid is narrower than the hypolophid, and its crest is straight for much of its length, as opposed to posteriorly convex like the hypolophid. The paracristid trends anterolingually from the protoconid apex before turning lingually, forming a distinct anterior shelf with a rounded lingual border (Figure 22F, M). The small precingulid is at a distinctly lower level than the anterior portion of the paracristid (Figure 22M). A short, distinct parametacristid is directed anterobuccally from the metaconid apex, but terminates high on the protolophid anterior face. The cristid obliqua terminates low on the protolophid is broadly convex on the lingual side. The posterior face of the hypolophid is smooth and featureless, except for a slight bulge low on the crown on the buccal side (Figure 22F, N).

The m3 is generally similar in form to the much smaller m1, but differs in the following ways: the lophid sides are more convex, the protolophid is not as narrow relative to the hypolophid, the precingulid is broader, and the parametacristid is very low and barely discernible (Figure 22E–F).

The dp3 is not known for any other species of *Bohra*. It is closest in overall morphology to that of the much smaller *Setonix brachyurus* (Quoy & Gaimard, 1830), with these species sharing a very similar trigonid topology. The main difference is that *S. brachyurus* lacks the crest that descends lingually to the anterolingual corner of the crown from the anterior high point on the paracristid. In addition, the base of the crown is not as narrow anteriorly relative

to posteriorly in *S. brachyurus*, and the hypolophid curves more smoothly into the cristid obliqua and premetacristid than in *B. bila*. In species of *Dendrolagus* and dorcopsins, there is no distinct protolophid and paracristid, but rather a single crescentic crest (paralophid), which is met halfway along its length by the cristid obliqua. Species of *Dendrolagus* (e.g., *D. bennettianus*) may also have a distinct parastylar crest, but this is absent from *B. bila*. The p3 of *B. bila* is large and robust relative to the molars compared with its proportions in *B. illuminata* and *B.* sp. cf. *B. bandharr*, which are the only other species of *Bohra* for which p3 is known. The lower molars of *B. bila* are similar in size and morphology to those of *B. illuminata* (Tables 4–5), but the lophids are thinner in buccal view and the m3 lacks a distinct premetacristid.

**Remarks.** *Bohra bila* is known definitively only from the Pliocene Chinchilla LF of southeastern Queensland (Figure 1). The referred specimen QM F4749 is from the Darling Downs, and is probably from Chinchilla, judging from the preservation of the bone, teeth and adhering sediment. This species is one of three in the Chinchilla LF, which is the most of any known assemblage.

By recognising that *Silvaroo bila* Dawson, 2004b belongs in *Bohra* Flannery & Szalay, 1982, we render *Silvaroo* Dawson, 2004b a junior synonym of *Bohra*, because *S. bila* is its type species (Dawson 2004b). Furthermore, we recognise that the species originally named *Protemnodon bandharr* Dawson, Muirhead & Wroe, 1999, before it was shifted to *Silvaroo* by Dawson (2004b), also belongs in *Bohra*. *Silvaroo* sp. indet. 1 and *Silvaroo* sp. indet. 2 of Dawson (2004b) include specimens referable to *B. bandharr* and *B. planei*, respectively. The one remaining species that was allocated to *Silvaroo* is *Protemnodon buloloensis* Plane, 1967 from the Pliocene Awe LF of Papua New Guinea. Because it lacks the generic attributes of *Protemnodon* Owen, 1874 (Dawson 2004b; Kerr & Prideaux 2022), and because *Silvaroo* is a junior synonym of *Bohra*, the generic allocation of this species is uncertain. Although resolving this problem is outside of the scope of this work, it is worth noting that the form of the p3 is dorcopsin-like: it is markedly elongate relative to the molars and broader anteriorly before constricting just forward of the posterior end of the tooth. It is within the size range of *Watutia novaeguineae*, which is likewise from the Awe LF (Flannery *et al.* 1989), but it is clearly distinct from it, minimally at the species level.

### Bohra illuminata Prideaux & Warburton, 2008

Bohra sp. nov. 1: Prideaux (2006), p. 1524. Prideaux et al. (2007), p. 423, table 1.

Bohra sp. indet.: Prideaux & Warburton (2008), pp. 463–464, figure 1 (partim). Prideaux & Warburton (2009), p. 166, figure 1 (partim).

**Holotype.** WAM 03.5.10, partial adult skeleton including cranium, partial left and right dentaries. Minimal wear on P3 and M4 indicate that these teeth had only recently erupted. This reveals that the specimen is a young adult not yet fully grown as confirmed by the unfused epiphyses of vertebrae and limb elements. Postcranial elements: four cervical, four thoracic, five lumbar, and eight caudal vertebrae; numerous partial ribs; proximal fragments of right and left scapulae; left clavicle; right humerus (missing proximal epiphysis); right ulna; fragments of radius; triquetrum, hamatum; metacarpals; manual phalanges; innominate fragments, including partial left and right ilia with acetabular fossa; fragments of left femur and near-complete right femur; left and right tibiae; left calcaneus; right talus; right cuboid; partial left and right metatarsals IV; partial left metatarsal V; pedal phalanges, including left digits IV–V.

**Revised diagnosis.** *Bohra illuminata* is distinguished from *B. nullarbora* and the species of *Dendrolagus* in the following cranial features: a distinct buccinator fossa; a less distinct supraorbital crest above the posterior end of the eye orbit; a broad groove between the supraorbital crest and superior lacrimal rugosity, which produces a constriction of the frontals; a relatively shallow zygomatic arch; a strongly domed dorsal neurocranial surface; a distally broader, more anteriorly hooked postglenoid process. The cheek teeth are large relative to the dimensions of the palate. P3 bears a distinct posterolingual cusp, but only the slightest hint of a thin cingulum anterior to it, which distinguishes *B. illuminata* from all other species for which P3 is known. The dentary is shallower relative to the height of the lower molars than in all other tree-kangaroo species. The il of *B. illuminata* has thicker dorsal and ventral enamel flanges than in *B. nullarbora*. Lower molars bear a strongly developed premetacristid.

Compared with that of *B. nullarbora*, the clavicle of *B. illuminata* is more gracile and flattened, with less expanded articular facets and a more medially positioned anterior inflection. The humerus is more gracile with a weaker pectoral crest, deltoid ridge, bicipital groove and spinodeltoid insertion than in *B. nullarbora*, but with a

			P3					MI					M2					M3					M4		
	Γ	AW	ΡW	ЧH	Hd	Γ	AW	ΡW	ЧH	Hd	Г	AW	ΡW	НИ	Hd	Γ	AW	ΡW	HΗ	Hd	Γ	AW	ΡW	ΗV	Hd
WAM 02.7.16	9.95		4.96	3.84	3.88	7.46	6.61	69.9	4.06	4.42	8.29	6.85	6.85	4.57	4.70										
WAM 03.5.10	9.40	4.02	5.24	5.69	5.27	7.17	6.99	69.9	ı	ı	8.82	7.50	6.93	4.05	4.65	9.41	7.81	7.04	4.40	4.74	10.00	7.65	6.49	4.68	5.25
SAMA P55401																					9.24	7.53	5.78	4.20	4.41
SAMA P55402																					ŀ	ı	6.12	ı	5.05
SAMA P55403																					9.57	7.23	6.00	4.04	4.81
SAMA P55406																9.24	7.31	6.70	4.36	4.63					
SAMA P55416						7.19	5.93	6.27	3.43	3.89															
			p3					ml					m2					m3					m4		
	Γ	AW	ΡW	ЧH	Hd	Γ	AW	$\mathrm{PW}$	ΗH	Hd	Г	AW	ΡW	ЧH	Hd	Γ	AW	PW	HΗ	Hd	Γ	AW	ΡW	ΗH	Hd
WAM 02.7.16	8.10	2.48	3.40			7.59	4.81	5.17	4.97	5.81	8.54	5.63	5.94	6.08											
WAM 03.5.10						I	4.61	5.14	·	ı	8.34	5.58	5.71	3.67	4.61	10.65	6.56	6.81	5.30	5.87	10.72	6.61	6.28	5.86	6.59
SAMA P55408						7.72	4.90	5.23	5.39	6.44															
SAMA P55409											8.26	4.95	5.46	4.68	6.23										
SAMA P55410						7.08	4.43	5.02	4.27	5.24															

TABLE 5 Cheek-tooth dimensions (mm) of Rohra illuminata

higher m. teres major insertion. The distal articular surface of the humerus is relatively broad. The ilium is relatively narrower anteroposteriorly, with a straighter medial border compared with that of *B. nullarbora*. The distinct long adductor muscle grooves on the medial aspect of the femur distinguish *B. illuminata* from *B. nullarbora* and *B. planei*, and in this attribute resembles the species of *Dendrolagus*. The tibia of *B. illuminata* is smaller and more gracile than that of *B. paulae*, and the interosseous margin is less sinuous in cranial view. The talar articular surface on the calcaneus is wider and the medial malleolus is more obliquely orientated in distal view than in *B. planei*. The calcaneus has a longer anterior plantar sulcus than in *B. nullarbora*, and more confluent talar facets with a mesially tapered lateral talar facet. The cuboid facets on the calcaneus are smoothly confluent and the calcaneocuboid step is very shallow and smoothed. Metatarsal IV is less robust than in *B. nullarbora*, with a smaller cuboid facet, a more medially constricted facet for metatarsal V, and a more rounded, distally orientated sesamoid facet. Metatarsal V is less robust.

**Type Locality.** Metasthenurus Chamber, Last Tree Cave, Nullarbor Plain, southeastern Western Australia. Most of the holotype was collected from a small grotto on the north side of the chamber by John A. Long, Lindsay M. Hatcher and GJP in July 2002 and April 2003. However, the right femur and several non-descript postcranial fragments were collected by Lindsay M. Hatcher and GJP in April 2014. Fossils from the floor of Last Tree Cave, although previously inferred to be of early middle Pleistocene age (Prideaux *et al.* 2007), are actually undated, but include specimens of several species known from well-dated middle and late Pleistocene sites elsewhere. At this point, the type locality age is best considered conservatively as Pleistocene. The precise location from which the holotype was collected is recorded with the Department of Earth and Planetary Sciences, Western Australian Museum.

**Paratype.** Main Chamber, Last Tree Cave. WAM 02.7.16, partial juvenile skeleton. Craniodental elements: left P3, M1–2, right maxilla fragment (preserving M1); left i1, partial right dentary (preserving m1–2 in occlusion, m3 in crypt, isolated p3); Postcranial elements: fragments of numerous vertebrae including 14 caudal vertebrae; numerous rib fragments; proximal fragment of left scapula; proximal fragment of right humerus; numerous carpals and metacarpals; innominate fragments including left and right ilia with acetabula, right ischium and epipubic; proximal fragment of femora; distal epiphysis of right fibula; fragments of right and left proximal tibia epiphyses; distal fragment and epiphysis of right tibia; left and right calcanei (right with separate epiphysis); left talus; left cuboid; left navicular; left and right metatarsals IV; right metatarsal V (missing distal epiphysis); left proximal, left and right medial and distal phalanges of digit IV, plus several other distal phalanges. This specimen was collected by GJP on 7 July 2002 from beneath a boulder overhang on the east side of the southern end of the chamber, the deepest point in the cave at 40 m depth.

**Referred specimens.** RF95 fissure fill, Curramulka Quarry, Yorke Peninsula, South Australia. SAMA P55401, right M4; SAMA P55402, right M4; SAMA P55403, left M4; SAMA P55406, left M3; SAMA P55408, left m1, right m1 (these teeth are identical in morphology, wear and preservation, so are considered to belong to the same individual); P55409, right m2; SAMA P55410, right m1; SAMA P55416, left M1. These specimens were collected by James A. McNamara (South Australian Museum) in the mid-1990s. The deposit is considered to be of Pleistocene age.

New Kalamurina, Warburton River, South Australia. SAMA P59526, left i1. Collected by Neville S. Pledge (South Australian Museum), 9 March 1972. Middle to late Pleistocene.

**Etymology.** This refers to the insights provided by the holotype, the first-known specimen of a species of *Bohra* represented by associated hindlimb and cranial elements. This confirmed that *Bohra paulae*, known only from hindlimb elements, and *B. wilkinsonorum*, known only from one partial maxilla, were indeed congeneric, as argued by Dawson (2004a).

**Description and comparisons.** Cranium. Previously described in detail (Prideaux & Warburton 2008). The incisor-bearing portion of the premaxilla (Figure 23A) is similar in proportion and relative depth to that observed in *Dendrolagus bennettianus* and *D. inustus*, but is shallower than in *B. nullarbora* and relatively longer than in most species of *Dendrolagus*. The narial aperture is slightly broader than deep (Figure 23B), as in *B. nullarbora*, but the lateral margins are more concave than in species of *Dendrolagus*. The buccinator fossa is moderately deep (Figure 23A), much more distinct than in *B. nullarbora* and species of *Dendrolagus*, in which there is only the barest hint of a concavity immediately above the diastema. The masseteric process is small, extending ventrally to about the level of the basal enamel margin of M2, as in species of *Dendrolagus*. Above the posterior extremity of the eye orbit, there is a swelling of the frontal, triangular in lateral view, that is bounded dorsally by a slight supraorbital crest (Figure 23A). Above the centre of the orbit, a broad groove (Figure 23A, C) separates the supraorbital crest from the superior lacrimal rugosity.

This groove manifests itself in dorsal view as a constriction of the frontals. This combination of supraorbital features distinguishes *B. illuminata* from all other tree-kangaroo species. Posteriorly, the supraorbital crest is more markedly projected laterally in *B. nullarbora*, and much smoother and lower over its entire length in species of *Dendrolagus*.



**FIGURE 23.** Cranium and partial dentaries of the holotype of *Bohra illuminata* (WAM 03.5.10). A: right lateral view. B: anterior view. C: dorsal view. D: palatal view. E: posterior view. F: posterior end of right dentary in lateral view. G: mesial view. H: partial left dentary in lateral view. I: mesial view.



**FIGURE 24.** Craniodental specimens of *Bohra illuminata*. WAM 03.5.10, holotype (A, G–J). A: left upper cheek-tooth row in stereo occlusal view. G: right m4 in stereo occlusal view. H: left lower cheek-tooth row in stereo occlusal view. I: left i1 in buccal view. J: left i1 in lingual view. WAM 02.7.16 (B–F). B: incomplete, unerupted right P3 in stereo occlusal view. C: left M1 in in stereo occlusal view. D: right p3 in stereo occlusal view. E: right m1 in stereo occlusal view. F: right m2 in stereo occlusal view. SAMA P59526, left i1 (K–L). K: buccal view. L: lingual view.

The zygomatic process of the squamosal (Figure 23A–B, E) is shallower relative to the depth of the cranium than in all other tree-kangaroo species. The marked doming of the dorsal surface of the neurocranium, which is typically a feature of young juvenile macropodid individuals, is unique to *B. illuminata* among young adults or

subadults of tree-kangaroo species. The relatively narrow ectoglenoid process (Figure 23D) and the manner in which the postglenoid process is broad at its distal extremity and curved anteriorly, providing the glenoid fossa with a semi-circular shape when viewed laterally (Figure 23A), are unique among tree-kangaroo species.

Upper dentition. *Bohra illuminata* is most easily distinguished from all other tree-kangaroo species by having larger cheek teeth relative to the overall proportions of the palate and a weakly developed lingual cingulum on P3, but with a distinct cuspule on the anterolingual corner of the crown (Figures 23D, 24A). In addition, the central cuspules of the P3 main crest are very small and only just distinguishable (Figure 24A–B). The upper molars of *B. illuminata* (Figures 24A, C, 25A–J, Table 5) are most similar in size and morphology to those of *B. bandharr*, differing only by being marginally less flat-sided buccally. The upper molars are also similar to those of *B. nullarbora*, but differ by being slightly larger overall and longer relative to their width, by having a flatter lingual side of the crown base, and by having a low cingulum bordering the interloph valley lingually. They differ from those of *B. bila* by lacking any remnant cusp C region of the stylar crest, and by having a less incurved postparacrista.

Dentary. The horizontal ramus of *B. illuminata* (Figure 23F–I) is shallower relative to the height of the lower molars than in *B. nullarbora*, *B. bila* and the species of *Dendrolagus*, although this may be because the holotype is a subadult. The mandibular condyle is not positioned as high above the level of the molar row as in *B. nullarbora*. The digastric sulcus is less distinct in *B. illuminata* than in *B. nullarbora* and *B. bila*, and the anterior insertion area for the internal superficial masseter muscle is thinner and restricted to the rim of the masseteric fossa. The general profile of the posterior end of the dentary is otherwise similar between these three species.



**FIGURE 25.** Molars of *Bohra illuminata*. SAMA P55406, left M3 (A–E). A: stereo occlusal view. B: lingual view. C: buccal view. D: posterior view. E: anterior view. SAMA P55401, right M4 (F–J). F: stereo occlusal view. G: lingual view. H: buccal view. I: posterior view. J: anterior view. SAMA P55408, left m1 (K–O) and right m1 (N). K: stereo occlusal view. L: lingual view. M: buccal view. N: posterior view. O: anterior view.

Lower dentition. Although similar in size and overall morphology, the i1 of *B. illuminata* (Figure 24I–K) has thicker dorsal and ventral enamel flanges than that of *B. nullarbora*. The unerupted p3 of the paratype, WAM 02.7.16 (Figure 24D), although lacking its full complement of enamel, was clearly swollen posteriorly, but the posterobuccal eminence is not as large as in the holotype of *B. bila*. The lower molars (Figures 24E–H, 25K–O) closely resemble those of *B. nullarbora*, but they are larger and the premetacristid is more strongly developed, especially on m3–4, a morphology reminiscent of the condition seen in the species of *Dorcopsis*. The lophids of *B. illuminata* are slightly more swollen than in *B. nullarbora*, and the buccal and lingual sides of the interlophid valleys are less concave.

Clavicle. The clavicle is more gracile and dorsoventrally flattened than in *B. nullarbora*, with reduced articular facets and a less laterally positioned cranial inflection.

Humerus. The humerus is less robust than in *B. nullarbora*, with a weaker pectoral crest, deltoid ridge, bicipital groove and spino-deltoid insertion, and a higher teres major insertion.

Ilium. The ilium is relatively narrower craniocaudally than in *B. nullarbora*, with a less sinuous medial border.

Femur. The holotype right femur is abraded near its proximal epiphyseal margin, and the proximal and distal articular epiphyses are missing (Figure 26). The distal end of the lateral trochanteric crest terminates craniad of the distal margin of the lesser trochanter (Figure 26A). The trochanteric fossa is relatively open (Figure 26B), as in species of *Dendrolagus* (Figure 5A). The shaft is cranially convex (Figure 26C–D), less robust than in *B. nullarbora*, and tending to ovoid in cross-section rather than circular, reminiscent of the species of *Dendrolagus* (Figure 5A–D). Highly distinct muscle scars - one on the proximocaudal surface immediately distal to the trochanteric fossa and two elongate, depressed scars on the medial surface of middle third of the femur – appear to correspond to the three portions of the mm. adductores femoris (Figure 26C). These are much more strongly marked than in B. nullarbora, which has no sign of the proximal one, and B. planei in which the adductor scars are more rugose than depressed and more caudally than medially positioned, but are similarly strongly developed in species of Dendrolagus (Figure 7C; Warburton et al. 2012). The quadratus femoris tubercle is more raised than in B. nullarbora and B. planei. The distal fossa for the medial gastrocnemius is very shallow, even shallower than in species of Setonix and Thylogale, and most similar to those of *B. nullarbora* and species of *Dendrolagus* (Figure 7C). This is also the case with the very shallow popliteal fossa. The distal epiphysis resembles that of the species of *Dendrolagus* (Figure 7F), but the fibular groove of the lateral condyle is less reduced and the cranial epiphyseal width is only slightly less than the caudal width in B. illuminata.



**FIGURE 26.** Right femur of the holotype of *Bohra illuminata* (WAM 03.5.10). A: cranial view. B: caudal view. C: medial view. D: lateral view.

Tibia. The tibia of *B. illuminata* is smaller and more gracile than that of *B. paulae* (Figure 11). The two species are similar in the relative size of the tibial crest, curvature of the shaft and length of fibular contact, but the proximal fibular facet of *B. illuminata* is less pronounced than in *B. paulae*. In cranial view, the interosseous margin of the tibia is less sinuous than in *B. nullarbora*, and particularly in *B. paulae*. From the distal view, the talar articular surface is wider and the medial malleolus set at a more oblique angle in *B. illuminata* than in *B. planei* (Figure 32).

Calcaneus. The calcaneocuboid step is much shallower and more smoothed than in all other species of *Bohra*, with the possible exception of *B. paulae*. Compared with that of *B. nullarbora*, the calcaneus of *B. illuminata* is smaller (which in part is very likely due to its younger ontogenetic age), lacks a partial separation of the talar facets, and has a longer anterior plantar sulcus, a poorer developed plantar tuberosity, a narrower sustentaculum tali, and a relatively wider, more mesially tapered lateral talar facet. Distinguished from that of *B. paulae* by being smaller, with a relatively shorter and less barrel-shaped tuber calcanei, shorter and wider talar facets, a longer sustentaculum tali, a larger anteroplantar tuberosity, a relatively smaller ventromedial cuboid facet and relatively wider dorsolateral cuboid facet. The calcaneus of *B. illuminata* is distinguished from that of *B. wilkinsonorum* in being much smaller in absolute size (Table 8), with much smoother and confluent talar and cuboid facets. The transversely wider, smoother, and more confluent cuboid facets similarly set the calcaneus of *B. illuminata* apart from that of *B. planei* (Figure 33).

Talus. The holotypes of *B. illuminata* and *B. nullarbora* are very similar in talar morphology, but two clear differences are evident. The facets for articulation with the calcaneus on the ventral surface are smoothly conjoined in *B. illuminata*, whereas they are separated by a distinct groove in *B. nullarbora*. In addition, the malleolar fossa in *B. illuminata* is narrower than in *B. nullarbora*. Although the talus of *B. illuminata* is smaller and has a shallower trochlear groove, both of these differences may well be due to its younger ontogenetic age. All other differences evident between the two specimens appear to be superficial and the result of the incompleteness of several features due to post-depositional abrasion or breakage. By comparison, *B. paulae* (Figure 12K) and *B. planei* (Figure 33I) are characterised by a shorter talar neck and shallower malleolar fossa from the dorsal view, and a broader, less obliquely orientated navicular facet in cranial view.

Metatarsals. The metatarsal IV of the *B. illuminata* holotype is less robust than in *B. nullarbora* and *B. paulae*, and the metatarsal V facet is more medially constricted. In *B. illuminata*, the dorsolateral corner of the cuboid facet is more pointed than in *B. nullarbora* and *B. paulae*, while the ventral peninsula of this facet is intermediate in relative breadth between the conditions manifested in the other two species. The proximity of the plantar sesamoid and metatarsal V facets in *B. illuminata* is intermediate between that observed in *B. nullarbora* and *B. paulae*.

The metatarsal V of the *B. illuminata* holotype is less robust than that of *B. nullarbora*, but this may simply be because it is not fully grown. It also differs by having a relatively broader metatarsal IV facet. By comparison with *B. paulae* (Figure 13), *B. illuminata* differs by having a less rounded medial end of the metatarsal IV facet. It differs from both *B. nullarbora* and *B. paulae* by having a more rugose interosseous ligament attachment.

**Remarks.** Most of what we know about *B. illuminata* is as it was in 2008, but the subsequent description of *B. nullarbora*, the belated 2014 discovery of the *B. illuminata* holotype right femur, and the allocation of pedal remains to other species have allowed the diagnosis and comparisons to be refined. Our understanding of the geographic distribution of *B. illuminata* has also been augmented through the referral to this species of loose molars from Curramulka Quarry, central Yorke Peninsula (Figure 1). Ancient DNA that aligned best with that of a tree-kangaroo has been recovered from a late Pleistocene archaeological deposit in Tunnel Cave, southwestern Australia (Figure 1; Murray *et al.* 2013), and may belong to *B. illuminata* or *B. nullarbora*, but confirmation of its tree-kangaroo identity must await further molecular work.

### Bohra nullarbora Prideaux & Warburton, 2009

*Bohra* sp. nov. 2: Prideaux (2006), p. 1524. Prideaux *et al.* (2007), p. 423, table 1. *Bohra* sp. nov.: Warburton & Prideaux (2010), pp. 138–139, 143, 147, 149, figures 13.1, 13.5–13.6.

**Holotype.** WAM 05.4.70, partial adult skeleton. Craniodental elements: fragmentary cranium (preserving left P3, left and right M1–4); partial left dentary (preserving base of i1, m1–3); right dentary preserving posterior half of m2, m3–4). Postcranial elements: vertebrae including atlas, axis, cervical 3–5, thoracic 1, ?5–6, ?10, ?12, dorsal lumbar fragment, two mid-caudal and two distal-caudal elements; one mid-caudal chevron; left and right clavicles; six ribs; proximal portion of left humerus and distal fragments; partial diaphysis of right humerus; left ulna; left radius diaphysis fragment; right hamatum; left scaphoid; left metacarpal III; right metacarpal III; left metacarpals IV–V; manual phalanges, including those of digits I–IV proximal, digits III–V medial, digits III–IV distal; partial left

TABLE 6. Cheek-tooth	limensio	ns (mm) oi	f Bohra nu	llarbora.											
			dP3					P3					M1		
	L	AW	ΡW	ΗH	Hd	L	AW	ΡW	ΗH	Hd	L	AW	ΡW	ΗH	Hd
WAM 05.4.70						8.93	4.42	4.14	4.23	3.61	7.39	6.44	6.92	,	
SAMA P55204															
SAMA P55205															
SAMA P55206															
SAMA P55389											7.65	6.12	6.71	2.62	3.01
SAMA P55390											7.48	5.52	6.34	ı	ı
SAMA P55391											7.42	6.26	6.40	ı	ı
SAMA P55392											8.00	6.24	6.72	3.48	3.74
SAMA P55393											8.34	6.76	7.35	ı	ı
SAMA P55394											7.57	6.48	6.94	ı	ı
SAMA P55395											7.71	69.9	6.90	4.03	4.10
SAMA P55396											7.90	6.29	6.84	3.40	4.20
SAMA P55397											7.98	6.71	6.93	3.88	4.24
SAMA P55398															
SAMA P55400															
SAMA P55407											7.39	6.07	6.77	ı	ı
SAMA P55413	6.25	5.08	5.47	3.23	3.42										
			ml					m2							
	L	AW	ΡW	ΗH	Hd	L	AW	ΡW	ΗH	Hd					
WAM 05.4.70	6.94	4.57	4.58		1	7.90	5.44	5.47	ı						
SAMA P55411						7.65	5.03	5.27	ı	ı					
SAMA P55412						8.29	5.92	5.71	5.29	5.66					
SAMA P55417	6.14	4.33	4.36	ı	ı										
SAMA P55419						I	5.50	I	ı	ı					
													con	tinued on th	ie next page

TABLE 6 (continued).															
			M2					M3					M4		
	L	AW	ΡW	ΗH	Hd	L	AW	ΡW	ЧH	Hd	Г	AW	ΡW	ΗH	Hd
WAM 05.4.70	8.38	7.39	7.07	I		8.95	7.94	6.62	3.74	3.68	8.57	7.14	5.67	3.86	4.17
SAMA P55204	8.58	7.53	7.19	5.04	5.04										
SAMA P55205	8.68	7.22	7.00	4.09	4.74										
SAMA P55206	8.84	7.95	7.70	4.21	4.59										
SAMA P55389															
SAMA P55390															
SAMA P55391															
SAMA P55392															
SAMA P55393															
SAMA P55394															
SAMA P55395															
SAMA P55396															
SAMA P55397															
SAMA P55398	8.42	6.90	6.63	4.24	4.82										
SAMA P55400						10.31	8.01	7.57	4.89	5.01					
SAMA P55407															
SAMA P55413															
			m3					m4							
	L	AW	ΡW	ΗH	Hd	L	AW	ΡW	ΗH	Ηd					
WAM 05.4.70	9.12	6.03	6.08	3.65	4.32	8.51	6.04	5.47	3.76						
SAMA P55411															
SAMA P55412															
SAMA P55417															
SAMA P55419															

innominates; fragments of right innominate; left epipubic; proximal portion of left femur; abraded distal fragments of right femur; fragments of left distal tibia diaphysis; right tibia diaphysis; distal portion of right fibula; left calcaneus; left talus; left navicular; right entocuneiform; right metatarsals IV–V, pedal phalanges including those of digits II, IV–V proximal, digits II–V medial, digits IV–V distal.

**Type Locality.** Leaena's Breath Cave, Nullarbor Plain, southeastern Western Australia. The holotype was collected by Paul D. Devine and GJP in July 2002 from a tight space beneath an overhanging boulder atop the main boulder pile, adjacent to the 'gypsum powder floor'. Fossils from the Leaena's Breath Cave boulder floor, although previously inferred to be of early middle Pleistocene age (Prideaux *et al.* 2007), are actually undated, but are associated with remains of other species known from dated middle and late Pleistocene sites elsewhere. At this point the type locality age is best considered conservatively as Pleistocene. The precise location from which the holotype was collected is recorded with the Department of Earth and Planetary Sciences, Western Australian Museum.

**Referred specimens.** Leaena's Breath Cave (stratigraphic unit 3), Nullarbor Plain, southeastern Western Australia. WAM 2020.3.201, right cuboid.

RF95 fissure fill, Curramulka Quarry, Yorke Peninsula, South Australia. SAMA P55204, left M2; SAMA P55205, left M2; SAMA P55206, right M2; SAM P55389, right M1; SAMA P55390, right M1; SAMA P55391, right M1; SAMA P55392, right M1; SAMA P55393, left M1; SAMA P55394, left M1; SAMA P55395, left M1; SAMA P55396, left M1; SAMA P55396, left M1; SAMA P55397, right M1; SAMA P55398, left M2, right M2 (these teeth are identical in morphology, wear and preservation, so are considered to belong to the same individual); SAMA P55400, right M3; SAMA P55407, right M1; SAMA P55411, left m2; SAMA P55412, left m2; SAMA P55413, left dP3; SAMA P55417, left m1; SAMA P55419, left m2 trigonid. These specimens were picked from concentrate sieved from sediment collected in 1997 by Jim McNamara (South Australian Museum).

**Revised diagnosis.** *Bohra nullarbora* is distinguished from *B. illuminata* in the following cranial features: a shallow buccinator fossa; a supraorbital crest that is more markedly projected laterally above the posterior end of the eye orbit; a less-domed dorsal neurocranial surface; a wider ectoglenoid process; a more distally narrowed postglenoid process. The cheek teeth are smaller relative to the dimensions of the palate than in *B. illuminata*. P3 is wider anteriorly than posteriorly, but narrow overall relative to M1, and it bears a small, low posterolingual cusp and narrow lingual cingulum. The dentary is characterised by a well-developed digastric eminence and sulcus, and a distinctly hooked mesial process on the postalveolar shelf. The dorsal and ventral enamel flanges on i1 are thinner than in *B. illuminata*. The lower molars are distinguished from those of other species of *Bohra* by having a short anterior portion of the trigonid, and a very low paracristid and cristid obliqua. The m4 has a very low parametacristid, which extends to centre of trigonid basin.

*Bohra nullarbora* is distinguished from *B. illuminata* in the following postcranial features. The clavicle is more robust and less flattened, with expanded articular facets and a more laterally positioned cranial inflection. The humerus is more robust with a stronger pectoral crest, deltoid ridge, bicipital groove and spinodeltoid insertion, but with a less pronounced teres major tubercle. The distal articular surface (especially the capitulum) of the humerus is relatively narrow. The ilium is relatively broader anteroposteriorly, and with a more sinuous medial border. A marked oval fossa is contiguous with a rugose muscle scar of the m. rectus femoris dorsal to the acetabulum. The epipubic is very large. The calcaneus is larger with partial separation of posterior talar facets, a very short anteroplantar sulcus, a more strongly developed plantar tuberosity, a wider sustentaculum tali, and a relatively narrow, less mesially tapered lateral talar facet. The talus is relatively longer with a higher lateral trochlear ridge. Metatarsal IV is more robust with a larger cuboid facet, a less medially constricted facet for metatarsal V, and a less rounded, less distally orientated sesamoid facet. Metatarsal V is more robust.

*Bohra nullarbora* is distinguished from *B. paulae* in the following pedal features: smaller absolute size (Table 8); separation of the talar facets, less complete assimilation of the ventromedial cuboid facet with the dorsal cuboid facets, and very short anteroplantar sulcus on the calcaneus; higher trochlear crests (deeper trochlear groove) and a longer neck on the talus; more gracile metatarsals IV and V.

*Bohra nullarbora* is distinguished from *B. planei* by having a less laterally flared base of the greater trochanter, distinct posterior talar facets and more smoother cuboid step on the calcaneus, and higher trochlear crests on the talus, and from *B. wilkinsonorum* in its much smaller overall size and more complete assimilation of the ventromedial cuboid facet on the calcaneus.

TABLE 8. Postcranial element c	dimensions (mm)	) for representati	ve specimens o	f species of Bohi	a and Dendrold	gus. Abbreviati	on: est., estimat	ted.	
Element	Bohra paulae	Bohra illumi-	Bohra nullar-	Bohra planei	Bohra wilkin-	Bohra sp.	Bohra sp.	Dendrolagus	Dendrolagus
		<i>nata</i> WAM	<i>bora</i> WAM	UCMP 70128	sonorum	indet. l	indet. 2	bennettianus	lumholtzi
		03.5.10	05.4.70		QM F675	QM F51762	UCMP 60850a	QM IM19863	FUR 403
HUMERUS							*		
Maximum length (est.)		105	110					92.9	101
Maximum distal width		37.4	39					32.2	30.0
FEMUR									
Maximum length		145 (diaphy- sis)	150 (diaphy- sis)	204				136	137
Proximal maximum width				57.0					33.4
(est.)									
Mid-shaft height (depth) × width			$17.4 \times 18.8$	18.2 x 18.7					13.5 x 13.4
TIBIA	AM F62101								
Diaphysis length	260	183						115	125
Proximal epiphysis width × depth	45.8 x 51.3							28.9 x 24.8	27.5 x 25.4
Distal epiphysis width × depth	42.3 x 35.9 АМ ЕКЛООО		22.8 x 13.7	23.4 x 18.3				19.1 x 10.9	18.6 x 14.6
Moutiminal municipal	2 CO 20 I MIL	36.1	12 1	10.0	3 ( S	15.0		21.0	217
Maximum rengu	32.0	73.7		6.04 2.5C	0.20	70 C		6.1C	20.2 20.2
Tuber calcanei posterior width	0.70	1.07	20.8	0.07	25.4	20.0 19.6		2.1.2 11.6	20.2 11.2
Tuber calcanei depth	20.3	13.7	16.5	16.7	20.8	17.6		11.8	12.0
Talar articulation width	27.2	19.9	22	19.6	28.1	22.0		17.6	16.6
Cuboid dorsomedial facet width	13.5	10.0	10.9	8.4	10.5	9.8		5.6	7.9
Cuboid dorsolateral facet width	12.9	6.2	6.8	7.4	11.1	6.9		5.5	4.6
Cuboid ventromedial facet	8.3	8.2	8.4		8.9	7.0		6.4	7.3
width									
TALUS	AM F62100								

Maximum length	27.5	21.0	24.2	20.2	24.2	17.4	16.5
Maximum width	32.0	26.1	28.7	25.5	26.2	22.7	23.5
Trochlear width between crests	19.5	14.3	15.2	13.2	13.0	11.9	11.7
Navicular facet (head)	$14.5 \times 9.0$	$10.6 \times 9.1$	$11.0 \times 9.7$	10.6 x 6.5	11.0 x 6.5	8.5 x 6.7	8.1 x 5.9
METATARSAL IV							
Maximum length	68.6 (miss-	66.5	68.6			47.2	43.7
	ing distal						
	epiphysis)						
Proximal width	17.2	16.5	16.2			11.7	12.5
Distal epiphysis width		15.1	14.9			11.6	11.3
Mid-diaphysis width	10.7 (AM	9.6	11.4			8.1	8.9
	F104550)						
	11.3 (AM						
	F104075)						
Mid-diaphysis height	11.0 (AM	8.3	8.3			7.2	5.2
	F104550)						
	8.7 (AM						
	F104075)						
Metatarsal V facet	$11.7 \times$	$12.4 \times 4.7$	$10.4 \times 5.1$			8.0 x 4.0	8.3 x 3.8
	5.5 (AM						
	F104550)						
	$11.7 \times$						
	5.9 (AM						
	F104075)						

Sesamoid facet	× 6.9	$7.4 \times 4.6$	$7.0 \times 5.0$	4.7 x 3.6	4.4 x 3.3
	6.4 (AM				
	F104550)				
	$7.5 \times$				
	4.9 (AM				
	F104075)				
METATARSAL V					
Maximum length	77.9 (AM		60.1	43.7	43.1
	F103802)				
	69.8 (AM				
	F104092)				
Proximal width	17.7 (AM	11.6	13.9	12.0	11.8
	F103802)				
	13.3 (AM				
	F104092)				
Mid-diaphysis width	8.4 (AM	6.2	6.5		6.2
	F103802)				
	7.6 (AM				
	F104092)				
Mid-diaphysis height	10.6 (AM	7.2	8.0		5.3
	F103802)				
	9.8 (AM				
	F104092)				
Distal epiphysis width	15.1 (AM		11.6	7.8	10.2
	F103802)				
	12.1 (AM				
	F104092)				



**FIGURE 27.** Partial cranium (adult) of the holotype of *Bohra nullarbora* (WAM 05.4.70). A: dorsal view of neurocranium. B: ventral / internal view of neurocranium. C: anterior view of neurocranium. D: posterior view of neurocranium. E: stereo palatal view. F: posterior view of neurocranium.

Etymology. The species name refers to the Nullarbor Plain, the region whence the holotype was collected.

**Description and comparisons.** Cranium. Among the species of *Bohra*, only *B. nullarbora* (Figure 27) and *B. illuminata* (Figure 23) are known from parts of the cranium other than the tooth-bearing portion of the maxilla. The incisor-bearing portion of the premaxilla is slightly deeper in *B. nullarbora* than in *B. illuminata*. The buccinator fossa is shallower and less distinct than in *B. illuminata*. The supraorbital crest is markedly projected laterally above the posterior end of the eye orbit and underlain by a deep sulcus, whereas the supraorbital crest is more of a triangular swelling in *B. illuminata*. The zygomatic arch is relatively deeper in *B. nullarbora* than in *B. illuminata*, and the dorsal surface of the neurocranium is less domed. The ectoglenoid process is wider and the postglenoid process is more narrowed distally (ventrally).

Upper dentition. The upper check teeth (Figures 27E, 28A–O) are similar in size to those of *B. planei* and *B.* sp. cf. *B. bandharr*, but smaller than in *B. illuminata*, *B. bandharr* and *B. bila* (Tables 1–7). Greater width of the P3 anteriorly compared with posteriorly (Figure 27E) is a condition unique to *B. nullarbora*. P3 is narrower relative to

M1 than in any other species of *Bohra*. As in *B. illuminata*, there is no manifestation of a posterobuccal eminence on P3, whereas it is slight in *B. bandharr* and distinct in *B. wilkinsonorum*. The upper molars are most similar in morphology to those of *B. illuminata*, but differ by being slightly smaller overall and shorter relative to their width, and by having a more concave lingual margin of the crown adjacent to the interloph valley and a more protuberant lingual metaloph base. Absence of a stylar crest in the region of cusp C is a condition shared with *B. bandharr*, *B. illuminata* and *B. wilkinsonorum*, but not *B. bila* and *B. planei*, in which this crest is distinct.



**FIGURE 28.** Molars of *Bohra nullarbora*. SAMA P55395, left M1 (A–E). A: stereo occlusal view. B: lingual view. C: buccal view. D: posterior view. E: anterior view. SAMA P55204, left M2 (F–J). F: stereo occlusal view. G: lingual view. H: buccal view. I: posterior view. J: anterior view. SAMA P55400, right M3 (K–O). K: stereo occlusal view. L: lingual view. M: buccal view. N: posterior view. O: anterior view. SAMA P55417, left m1 (P–R). P: stereo occlusal view. Q: buccal view. R: lingual view. SAMA P55412, left m2 (S–W). S: stereo occlusal view. T: buccal view. U: lingual view. V: posterior view. W: anterior view.

Dentary. The well-developed digastric eminence and sulcus (Figure 29A–C), and distinctly hooked mesial process on the postalveolar shelf (Figure 29G) distinguish *B. nullarbora* from other species of *Bohra*. Although it is broken off, it is evident that the mandibular condyle was positioned at a higher level relative to the cheek teeth than in *B. illuminata*. The anterior insertion area for the internal superficial masseter muscle (Figure 29A) is larger than in *B. illuminata*, similar in proportions to *B.* sp. cf. *B. bandharr* (QM F4750), but smaller than in *B. bandharr* and *B. bila*.

Lower dentition. The il of *B. nullarbora* is similar in size to that of *B. illuminata*, but it has thinner dorsal and ventral enamel flanges. In overall size and morphology, the lower molars are most similar to those of *B.* sp. cf. *B. bandharr* (e.g., QM F4750, QM F58665), but they have a shorter anterior portion of the trigonid (precingulid + anterior portion of paracristid) than in any other species of *Bohra*, and the paracristid and cristid obliqua are also comparatively very low. The species is also distinguished by the presence, on m4, of a very low parametacristid, which extends to the centre of the trigonid basin, terminating against the paracristid (Figure 29F).

Clavicle. The clavicle is more robust and less flattened than in *B. illuminata*, with expanded articular facets and less-pronounced cranial curvature.

Humerus. The humerus is more robust than in *B. illuminata*, with a stronger pectoral crest, deltoid ridge, bicipital groove and spino-deltoid insertion. The teres major insertion is less protruding. The distal articular surface, in particular the capitulum, is relatively narrower than in *B. illuminata*.



**FIGURE 29.** Dentaries (adult) of the holotype of *Bohra nullarbora* (WAM 05.4.70). A: lateral view of left dentary. B: lateral view of partial right dentary. C: mesial view of left dentary. D: buccal view of i1. E: lingual view of i1. F: partial right dentary (partial m2, m3–4) in stereo occlusal view. G: left dentary (m1–4) in stereo occlusal view.

Innominate. The base of the ilium is relatively broader in the craniocaudal axis, and the medial border is sinuous by comparison with the straight medial border in *B. illuminata*. An oval fossa contiguous with the rugose muscle scar of m. rectus femoris dorsal to the acetabulum is distinct and unique to *B. nullarbora*.

Femur. The femur of *B. nullarbora* is distinguished from that of *B. illuminata* in its more caudally positioned scars for the mm. adductores femoris, and from *B. planei* by having a less laterally projected base of the greater trochanter.

Calcaneus. Morphologically, the calcaneus of *B. nullarbora* is distinguished from those of *B. illuminata, B. paulae* and *B. planei* by having distinctly separate medial and lateral talar facets, and from *B. wilkinsonorum* and *B.* sp. indet. 1 by having a straight lateral edge to the medial facet, which extends both cranially and caudally from the facet margins. It shares with *B. illuminata* and *B. paulae* a less acute, more smoothed cuboid step than in *B. planei, B. wilkinsonorum* and *B.* sp. indet. 1. It shares with *B. illuminata* a ventromedial cuboid facet that is confluent with

the dorsal facets, though the entire surface is not as smoothed as in *B. paulae*. The relatively very short anteroplantar sulcus between the rugose plantar surface and anterior plantar tubercle is unique to *B. nullarbora*.

Talus. The talus of *B. nullarbora* is distinguished from all other species of *Bohra* and *Dendrolagus* (e.g., Figure 9F–K) in its relatively higher trochlear crests, and thus deeper trochlear groove, and in the distinct separation between the calcaneal facets. It also has a relatively deeper malleolar fossa, more projected malleolar tubercle, and longer neck than in other species of *Bohra*.

Metatarsals. Metatarsal IV and, in particular, metatarsal V of *B. nullarbora* are more robust than in *B. illuminata*, though this might be accounted for by the ontogenetically younger age of the holotype of *B. illuminata* versus that of *B. nullarbora*. The facet for metatarsal V is relatively smaller and the gap between this and the sesamoid facet is relatively wider in *B. nullarbora* compared with the conditions of *B. illuminata* and *B. paulae*, though this may be within the normal range of intraspecific variation given their differing ontogenetic ages. Metatarsal V of *B. nullarbora* is more gracile than in *B. paulae*, with a relatively narrower facet for metatarsal IV, a more elongate proximolateral process and a more deeply flexed cuboid facet.

**Remarks.** Our understanding of *B. nullarbora* is fundamentally as it was when it was named and first described in 2009, but the broader comparisons made here mean that the species is now better circumscribed. In addition, several loose molars referable to *B. nullarbora* have been identified in a Pleistocene assemblage from Yorke Peninsula, 1,000 km southeast of the Nullarbor type locality (Figure 1). Whether the ancient DNA retrieved from Tunnel Cave in southwestern Australia (Murray *et al.* 2013) belongs to *B. nullarbora*, *B. illuminata* or neither, remains to be verified with further molecular work.

#### Bohra planei sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:47F6EBDE-2594-4710-B440-D1D940951248

cf. Dorcopsis, large form: Plane (1967): pp. 50-55, figures 11-13. Hoch & Holm (1986), p. 188.

cf. *Dendrolagus* sp.: Woodburne (1967), p. 82. *Dorcopsis* large species: Flannery *et al.* (1983b), p. 77. cf. *Dorcopsis* sp.: Flannery *et al.* (1989), pp. 151–152. "*Dorcopsis*": Menzies & Ballard (1994), p. 131. *Silvaroo* sp. indet.: Dawson (2004b), p. 284, table 1. *Silvaroo* sp. indet. 2: Dawson (2004b), pp. 286–287. ?*Dorcopsis* sp.: Dawson (2004b), p. 288. *Dorcopsis* sp. nov.: Black *et al.* (2012), p. 1050.

**Holotype.** UCMP 70128, partial right adult hindlimb, including femur, distal half of tibia, distal end of fibula, talus and calcaneus. The fibula fragment could not be located in the UCMP collection in August 2007.

**Type locality.** Watut 3 (UCMP V6356), located on the eastern bank of the Upper Watut River, downstream from Awe Fauna Type Locality (= Watut 1, V6234), Morobe Province, Papua New Guinea. Judging from the location map (figure 15 in Plane 1967), V6356 lies perhaps 500 m northeast of Awe Fauna Type Locality. UCMP 70128 was collected by Michael D. Plane in 1963 and is the only specimen recorded from Watut 3. The specimen was collected from a blue-grey claystone stratigraphically lower than Awe Fauna Type Locality.

**Referred specimens.** Charlie Lawrence Locality (V6172), Wiganda Creek, Upper Watut Valley, Morobe Province, Papua New Guinea. AM F49468, right adult maxilla (preserving M1–4). This specimen was collected in 1961 and presented to the Australian Museum by T. Brown. Before becoming submerged by a pond, the site was located "on the lower stretch of Wiganda Creek where the Gold and Power Company were working alluvial gold" (Plane 1967: 63). No stratigraphic details were recorded.

Widubosh goldmine, Upper Watut Valley. NHMD 193283 (formerly GMK 55709), partial right calcaneus. This specimen was collected by Ella Hoch on 29 August 1983.

**Etymology.** This species is named in honour of Michael D. Plane (1933–2017), who collected the holotype and first described the Awe LF and Otibanda Formation.

**Diagnosis.** *Bohra planei* most closely resembles *B. nullarbora* and *B. bila* in upper molar size and morphology. Upper molars differ from those of *B. nullarbora* by having a cusp C region of the stylar crest on M1–3, incurved postpara- and premeta-cristae, and a broader, more open posterior metaloph face on M4. Upper molars differ from

those of *B. bila* by having the bifurcation between the postparacrista and stylar cusp C region further from the paracone apex and a lingually thinner precingulum.

Femur is transversely broad and craniocaudally compressed proximally with very broad greater trochanter, broad, shallow trochlea and rugose adductor scars running along the length of the caudomedial aspect of the shaft. Distal epiphysis and talar articular facet of the tibia are relatively narrow in comparison to other *Bohra* and *Dendrolagus*. Calcaneus is transversely broad and dorsoventrally flattened, with distinct plantar epiphyseal ridge and medial crest. Medial and lateral talar facets are mesially constricted and more confluent with each other than in all other species of *Bohra*. The distal extremity is narrow relative to the talar and fibular facets, and the calcaneocuboid facets relatively deep and narrow and with a more acutely stepped articulation than in other species of *Bohra*. Talus transversely broad, dorsoventrally flattened, with broad, shallow trochlea, medially extended malleolus, broad and shallow malleolar fossa, short talar neck and smoothly contiguous calcaneal facets.

**Description and comparisons.** Maxilla and palatine. Very little is preserved of the maxilla of AM F49468, but there is sufficient to indicate that the base of the masseteric process was positioned above the anterior root of M3 in lateral view (Figure 30A, C). The shape of the fracture through the palate that represents the mesial limit of this specimen is consistent with a line of breakage along the maxilla–palatine suture (Figure 30C). This is orientated anteromesially from adjacent to the M4 protoloph. What remains of the palatal portion of the maxilla is broadest adjacent to the anterior root of M3.



FIGURE 30. Partial maxilla (right, adult) of *Bohra planei* sp. nov. (AM F49468). A: lateral view. B: mesial view. C: stereo occlusal view.

The position of the masseteric process relative to M3 in AM F49468 matches that observed in adult specimens of *B. nullarbora*, *B. bila* and *B. bandharr*. The anteromesial orientation of the inferred maxilla–palatine suture is a close match for that of *B. nullarbora* (Figure 27E), including the point at which it inflects anterolingually, as also is the relative width of the maxilla mesial to M3. By contrast, in *B. bandharr*, the maxilla–palatine suture runs anteroposteriorly for more of its length before inflecting anterolingually adjacent to M3 (Figure 14C), while it runs anteroposteriorly up to a position mesial to the M2 protoloph in *B. bila* (Figure 21B).



**FIGURE 31.** Femur (right, adult) of the holotype of *Bohra planei* **sp. nov.** (UCMP 70128). A: cranial view. B: caudal view. C: medial view. D: lateral view. E: proximal view. F: distal view.

Upper dentition. The single known maxillary specimen (AM F49468) preserves M1–4. The protoloph of M1 is marginally narrower than the metaloph, but from M2 to M4 the protoloph becomes increasingly wider than the metaloph (Figure 30C; Table 7). The molars are moderately worn, with dentine breached along the lengths of the lophs of M1–2, on the protoloph and metaconule of M3, and on the protocone of M4. Despite this, they were clearly low crowned, and it is evident from the less worn molars that the postparacrista, postprotocrista, premetacrista and postmetacrista are very fine and low (Figure 30). The postparacrista and premetacrista are distinctly incurved on all molars. On M1–3, the cusp C region of the stylar crest is evident, diverging from the postparacrista about halfway up the paracone face, such that it forms an inverted Y shape. The stylar crest remnant is projected buccally at 50° on M1 to the longitudinal axis of the crown, at 40° on M2 and at 30° on M3 (Figure 30C). The postmetaconulecrista forms a small but distinct shelf on the posterior face of M4.

The upper molars of *B. planei* are smaller than in *B. bandharr* and *B. illuminata*, and closest in size and morphology to those of *B. nullarbora* and *B. bila* (Tables 1, 4–6). By comparison, *B. nullarbora* lacks any sign of a cusp C region of the stylar crest on any molars, and has anteroposteriorly orientated postpara- and premeta-cristae, a less lingually tapered precingulum, and a narrower, deeper, more 'pocketed' M4 posterior metaloph face. In *B. bila*, a cusp C region of the stylar crest is present on M1–2, but not M3, and differs by diverging from the postparacrista closer to the paracone apex. As in *B. bila*, the postpara- and premeta-cristae are incurved, but not as well developed as in *B. wilkinsonorum*. The configuration of these crests and the stylar crest on M1–3 is very like that of the species of *Dorcopsulus*, but in the much larger *B. planei* there is no obvious cusp D region of the stylar crest. It should be noted, however, that there is a small wear facet on the metacone anterior face buccal to the premetacrista on M1–2, which, in a minimally worn specimen, may reveal that this portion of the stylar crest was indeed retained in *B. planei*. The upper molars of *B. planei* share very weakly development of the anteroposterior crests with *B. nullarbora* and *B. bandharr*.

TABLE 7.	Cheek-tooth	dimensions	(mm) o	of Bohra	planei	sp.	nov.
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			M1					M2		
	L	AW	PW	AH	PH	L	AW	PW	AH	PH
AM F49468	7.62	6.95	7.03	-	-	8.17	7.43	7.06	-	-
continued.										
			M3					M4		
	L	AW	PW	AH	PH	L	AW	PW	AH	PH
AM F49468	8.75	7.80	6.87	-	-	8.76	7.28	6.09	3.58	3.73
				U	A LINE TO A LINE AND A				20	mm
									Е	

**FIGURE 32.** Partial tibia (right, adult) of the holotype of *Bohra planei* **sp. nov.** (UCMP 70128). A: cranial view. B: lateral view. C: caudal view. D: medial view. E: distal view.

Femur. Well preserved and largely complete, the holotype femur is missing only the lateral condyle of the distal epiphysis (Figure 31). The femoral head is large and roughly hemispheric. The proximal epiphyseal margin is more distally placed than the caudal margin of the head. The greater trochanter is very rugose at its apex, particular in cranial view, and strongly laterally flared at its base (Figure 31A). The lesser trochanter is robust and long, with a distally extended ridge and distinct sulcus on its craniodistal aspect (Figure 31C). The femoral shaft is slightly compressed in the craniocaudal plane, and is cranially convex. The caudal surface of the diaphysis is marked by a rugose adductor muscle scar, which runs obliquely from below the lesser trochanter to a depression marking the insertion for the m. quadratus femoris midway along the length of the bone (Figure 31B–C). A second scar marking the more distal portions of the m. quadratus femoris is rugose and concave (Figure 31B). The caudomedial fossa for the m. gastrocnemius is shallow and the caudolateral fossa for the m. flexor digitorum superficialis is very shallow. The distal femoral condyles are relatively low and the trochlea groove relatively shallow (Figure 31A–B, F). The medial condyle is transversely quite narrow.

The femur of the *B. planei* holotype is approximately 33% larger in size than in *D. lumholtzi* and 20% larger than in *B. illuminata*. The greater trochanter is taller than in species of *Dendrolagus*, and its rugose apex is distinct. The base of the greater trochanter bears a distinct fossa on its cranial surface for the m. vastus lateralis, which is of similar depth in *B. illuminata* and *B. nullarbora*, but noticeably wider. The laterally flared distal extremity is most

like *Thylogale billardierii* (Desmarest, 1822). The thickened lateral margin or crest upon which the m. gluteus medius inserts is proportionally shorter than in most macropodines, terminating proximally to the distal margin of the lesser trochanter, as in *B. illuminata* and species of *Dendrolagus* (Figure 7A–D). The lesser trochanter is more flared proximally than in species of *Dendrolagus, Setonix* and *Thylogale*, and may have been similar in *B. illuminata* and *B. nullarbora*, though the area is abraded in the only known specimens of each species. The shaft is similar in relative robustness to *B. illuminata*, and less robust than in *B. nullarbora* and species of *Dendrolagus* (Figure 7). The adductor muscle scars are more marked than in *B. nullarbora*, while in *B. illuminata* there are narrow but relatively deep longitudinal scars for the mm. adductores femoris along the medial aspect of the femoral shaft as in *Dendrolagus* (Figure 7C; Warburton *et al.* 2012). The concave insertion of the m. quadratus femoris is unusual, in contrast to the typically raised tubercle in most macropodines. In this attribute, *B. planei* resembles *T. billardierii*. The diaphysis flares toward its distal end of shaft more than in species of *Dendrolagus* and terrestrial species but similar to *B. illuminata* and *B. nullarbora*.



**FIGURE 33.** Calcaneus and talus (right, adult) of the holotype of *Bohra planei* **sp. nov.** UCMP 70128, holotype calcaneus (A–E). A: plantar view. B: dorsal view. C: cranial view. D: medial view. E: lateral view. NHMD 193283, partial right calcaneus (F–G). F: dorsal view. G: medial view. UCMP 70128, holotype talus (J–M). H: plantar view. I: dorsal view. J: medial view. K: lateral view. L: caudal view. M: cranial view.

The shallow fossae for m. gastrocnemius and m. flexor digitorum superficialis contrast markedly with the deep fossae in ground-dwelling species of *Macropus* Shaw, 1790, *Osphranter* Gould, 1842 and *Thylogale*, but are similar to the morphology in *B. illuminata* and species of *Dendrolagus*. The craniocaudally compressed distal epiphysis is reminiscent of species of *Dendrolagus* (Figure 7F). The transversely narrow medial condyle is similar in morphology to *B. illuminata*.

Tibia. The *B. planei* holotype preserves only the distal two-thirds of the tibia, the diaphysis of which is relatively straight, being very slightly sinuous from cranial view, and similarly in the cranial face of the proximal portion from the lateral view (Figure 32B). Distally, the diaphysis is sub-rectangular in cross-section. The distal fibular facet is estimated to have extended for approximately the distal two-fifths of the tibial shaft. The interosseous border above the distal fibula facet is moderately rounded. The distal epiphysis is equal in width to the end of the diaphysis (Figure 32C). The medial malleolus is robust, moderately long and aligned in the parasagittal plane (Figure 32C). The talar articular facet is aligned square to the craniocaudal axis (Figure 32E).

In overall shape, the tibial diaphysis and proportional length of the distal fibular facet of *B. planei* is very similar to that of *B. illuminata*. The rounded interosseous border is in contrast to the sharper interosseous crest observed in *B. illuminata*, *B. nullarbora* and the species of *Dendrolagus* (Figure 8) and *Thylogale*, but it is less rounded than in *Setonix brachyurus*. The distal epiphysis and talar articular facet are relatively narrower than in *B. illuminata* and species of *Dendrolagus*, and are not as laterally flared as in *D. bennettianus*. The medial malleolar process is more distally extended than in species of *Dendrolagus*, but narrower anteroposteriorly than in species of *Thylogale* and *Setonix*. In distal view, the process of the medial malleolus is more obliquely orientated than in other species of *Bohra* and *Dendrolagus* (Figure 8F), being more similar to *Thylogale* in both this and in cranial view, in which it is relatively flat and horizontal.

Calcaneus. The calcaneus is stout, robust, broad and dorsoventrally compressed (Figure 33A–G). The tuber calcanei is expanded caudally and constricted cranially (Figure 33B). The rugose plantar surface is very broad, and is expanded along the length of the medial margin by a distinct flange (Figure 33A). The mid-lateral margin is particularly enlarged. The epiphyseal line on the rugose plantar surface is raised into a distinct, ventrally projected ridge. Paired tubercles (the lateral one much larger) on the craniolateral extremity of the plantar surface are positioned adjacent to the groove for the peroneal tendons, and are bounded on the opposite side by a projection cranial to the attachment site of the anterior calcaneofibular ligament. The transverse flexor sulcus is not well defined, being relatively shallow and with irregular margins. The sustentaculum tali is very broad, particularly caudally, extending well beyond the medial edge of the talar articular surface (Figure 33D). The ventral surface is smoothly curved and the flexor groove relatively deep, accentuated by the expanded medial margin of the plantar surface. The lateral and medial facets for the talus are very broad; the lateral facet is smaller, mesially constricted and smoothly contiguous with the oval medial facet. The fibular facet is very small, though the tubercles for the fibular ligaments, particularly the calcaneocuboid ligaments, are strongly developed. The anteromedial facet for articulation with the talar head is small and distinct. The calcaneocuboid articulation is transversely broad and dorsoventrally compressed (Figure 33C). The dorsomedial facet for the cuboid is rectangular, broader than deep, and convex in profile. The dorsolateral facet is narrower and subtriangular in shape, tapering from dorsal to ventral. The step between the two facets is distinct, only slightly smoothed and obliquely orientated in dorsal view (Figure 33A-G). The ventromedial cuboid facet is abraded on the holotype, but was apparently relatively small and smoothly continuous with the dorsolateral facet, but separate from the dorsomedial facet.

The calcaneus of *B. planei* is similar overall in morphology to *B. illuminata, B. nullarbora* and the species of *Dendrolagus* (Figure 9). The distinct ridge formed at the plantar epiphyseal line distinguishes *B. planei* from all other species, but is most similar to *D. bennettianus* (Figure 9B), and may reflect augmentation of the digital flexor muscles in the pes. The rugose tuberosities at the cranial margin of the plantar surface are similar to those observed in *B. wilkinsonorum* (Figure 20A). The flaring of the medial plantar margin of the calcaneal tuber and flexor groove are developed to a greater extent than in other *Bohra* species. The morphology of the talar facets is most similar to that of *B. paulae* (Figure 12A), but even more confluent and more dorsoventrally flattened. In all other species of *Bohra*, the margins of the medial and lateral facets are more clearly delineated, even where they abut each other. The calcaneocuboid step is deeper and more angular than in other species of *Bohra* and *Dendrolagus*, being most similar to *B. wilkinsonorum*, and also approaching the depth in species of *Setonix* and *Thylogale*. When viewed dorsally, the cranial extremity (cuboid articulation) is relatively much narrower (does not extend to the width of the fibular

facet) in comparison to other species of *Bohra*. The cuboid facets are relatively deep and narrow compared to other species of *Bohra*. The separation of the ventromedial facet appears most like *B. wilkinsonorum*.

Talus. The talus is wider than long, dorsoventrally compressed (especially in cranial view) with low trochlear crests, which are subequal in height, and a shallow trochlea groove (Figure 33H–M). The malleolar fossa is moderately wide and shallow. The talar neck is very short. The talar head is medially displaced relative to the medial trochlear crest and transversely quite broad in cranial view. The articular facet for the navicular is ovoid around an axis that is approximately 40° from a dorsoventral plane (Figure 33M). The calcaneal facets are transversely broad, moderately deep and smoothly contiguous. The posterior plantar process is bulbous, transversely broad and dorsoventrally compressed.

The trochlear groove is shallower than in *B. illuminata, B. nullarbora, D. bennettianus* (Figure 9H–I, K) and *D. lumholtzi*, but similar to that of *B.* sp. indet. 1. The medial trochlear crest is lower than in *B. paulae*, and also more similar to that of *B.* sp. indet. 1. The malleolar fossa is broad and shallower in *B. planei* than in other species of *Bohra* and species of *Dendrolagus*. The medial malleolus is broad and flattened, similar to the conditions seen in *B. paulae* and *B. sp. indet*. 1. It is relatively less projected than in *B. nullarbora* and species of *Dendrolagus, Dorcopsulus, Setonix* and *Thylogale*. The very short talar neck is similar to the morphology seen in species of *Dendrolagus* (Figure 12K). The navicular facet of the talar head is set at a less oblique angle than in other species of *Bohra*, including *B. paulae* and especially *B. illuminata* and species of *Dendrolagus*, resulting in a narrower and more elongate outline. The lateral border of the navicular facet lies outside of, rather than in line with, the cranial extremity of the medial crest, as in *B. paulae* and *D. bennettianus*, *D. lumholtzi*. The talocalcaneal facets are smoothly conjoined and relatively shallow. The posterior plantar process is short and broad, as in *B. nullarbora* and *B. illuminata*, but proportionally smaller than in species of *Dendrolagus*.

**Remarks.** Bohra planei is the only species in this genus identified from New Guinea. It is one of only three species of fossil macropodoid, along with *B. paulae* and *Rhizosthenurus flanneryi* Kear, 2002, initially described wholly or fundamentally on the basis of hindlimb elements. This reinforces past observations (Flannery & Szalay 1982; Prideaux & Warburton 2008, 2009; Warburton & Prideaux 2010; Warburton *et al.* 2011), as well as those made in this paper, that demonstrate the high taxonomic utility of hindlimb material for recognising fossil tree-kangaroo remains. Along with *Protemnodon otibandus* Plane, 1967, *'Silvaroo' buloloensis* and *Watutia novaeguineae*, *B. planei* is the fourth extinct macropodine species identified from the Otibanda Formation (Figure 1) and described primarily on the basis of material form it.

The partial maxilla, AM F49468, has had a varied taxonomic history. It was first described and referred to 'cf. *Dorcopsis*, large form' by Plane (1967) in his monograph on the Otibanda Formation and Awe LF, but in another monograph published in the same series on the same day, Woodburne (1967) considered it more likely to belong to a taxon related to *Dendrolagus*. In part, this was because Woodburne inferred that the anteromesially orientated broken edge of what remains of the palate marks the maxilla–palatine suture, and that this orientation was more like that seen in *Dendrolagus* than in any dorcopsin. To our eyes, having examined multiple species of each, there is no consistent difference between species of *Dendrolagus* and dorcopsins in the shape of this suture: it is fundamentally anteroposteriorly orientated. However, an anteromesially orientated suture very obviously *is* a feature of *Bohra nullarbora* (Figure 27E). For this reason, and given the marked similarities in molar morphology between AM F49468 and both *B. nullarbora* and *B. bila*, we confidently identify it as representing a species of *Bohra*. That Flannery *et al.* (1989) and Dawson (2004b) viewed the upper molars of AM F49468 as more like *Dorcopsis* than *Dendrolagus* is hardly surprising: it was not until 2008 that the first molars unequivocally referable to a species of *Bohra* were described and shown to resemble those of the species of *Dorcopsis* (Prideaux & Warburton 2008).

AM F49468 and the holotype partial hindlimb (UCMP 70128) come from different but nearby sites in the Otibanda Formation, yet we have chosen to allocate AM F49468 to the same species on size grounds: both AM F49468 and UCMP 70128 are a very close size match for the holotype of *B. nullarbora* (Tables 6–8). Although a second Awe LF maxilla fragment preserving M3 (UCMP 70132) might possibly belong to another species of *Bohra*, the M3 is considerably smaller than that of AM F49468 and differs from it by lacking a stylar cusp C remnant and having a precingulum that terminates abruptly, well short of lingual side of the crown. These features are more suggestive of a large species of *Dorcopsis* than of *Bohra*, which is consistent with the original tentative identification (Plane 1967).

# Bohra sp. indet. 1

Bohra sp.: Hocknull (2005a), p. 26, figure 1B,C. Hocknull (2005b), p. 86.

Bohra sp. indet.: Prideaux & Warburton (2008), pp. 463–464, figure 1; partim. Prideaux & Warburton (2009), p. 166, figure 1; partim.



**FIGURE 34.** Calcanei (adult, right) of *Bohra* sp. indet. 1. QM F49453. A: plantar view. B: dorsal view. C: medial view. D: lateral view. QM F51762. E: plantar view. F: dorsal view. G: medial view. H: lateral view. QM F58666. I: plantar view. J: dorsal view. K: lateral view. L: medial view.

**Referred specimens.** Chinchilla Rifle Range (site not specified), Queensland. QM F58666, right calcaneus; QM F49453, right calcaneus. Collected by Doris and Cecil Wilkinson.

Unit C/D, QM L1311C/D, Speaking Tube Cave, western side of Mount Etna near Rockhampton, Queensland. QM F51762, right adult calcaneus. Retrieved by S. Hocknull and others from cave fill exposed by a mining operation (Hocknull 2005b).

Description and comparisons. Calcaneus. Three calcanei very similar in absolute size and morphology are referred to Bohra sp. indet. 1, the most complete of which is QMF51762 (Figure 34E–H). The calcaneus is broad, stout and dorsoventrally flattened, with transversely broad articular surfaces and rugose ligament insertions. The tuber calcanei is broad and flared caudally, particularly on the lateral side of the epiphysis (Figure 34E-F, I-J). The broad, rugose plantar surface is laterally flared cranially, giving an impression of an oblique alignment of the long axis, although this is less pronounced in QM F49453. The anterior plantar tubercle is small and the transverse sulcus is only very slightly oblique from medial to lateral sides, and moderately wide and shallow (Figure 34E). The sustentaculum tali is extended medially, moderately long craniocaudally, and gently convex (Figure 34G, L). The flexor groove running over the sustentaculum is very shallow, particularly in QMF49453; the flexor groove is deeper and more distinct in QMF58666. The medial and lateral talar facets are conjoined, though with distinct margins. The lateral facet is tapered medially (Figure 34A-B, E-F, I-J). The caudal margin of the oval medial facet is projects dorsally, and the articular surface is slightly expanded on the dorsal surface toward the base of the calcaneal tubercle. The fibular facet is abraded to varying degrees in all specimens, but appears to be relatively small. The sulcus for the posterior calcaneofibular ligament is deep, and the tubercle and sulcus for the anterior calcaneofibular ligament are laterally expanded and rugose. The scar for the ligament of the talar head is moderately deep. The calcaneocuboid articulation is transversely broad and dorsoventrally compressed in cranial view. The step between the rather rectangular dorsomedial and dorsolateral facets is obliquely aligned and moderately smoothed (Figure 34E–F), and the ventromedial facet is reduced and smoothly continuous with the dorsal facets.

The *Bohra* sp. indet. 1 calcaneus is 15% larger in absolute size than in *B. nullarbora* and *B. planei*, but most similar in overall proportions to *B. planei* (Table 8). The rugose plantar surface most closely resembles that of *B. nullarbora*. The anterolateral tubercle is less prominent than in *B. wilkinsonorum* and *B. planei*. The transverse sulcus is most similar to that of *B. paulae*. The sustentaculum tali is longer than in *B. paulae*, but not as long or wide as in *B. wilkinsonorum* and *B. planei*. The very shallow flexor groove of QM F49453 is more similar to the conditions observed in *B. illuminata*, *B. nullarbora* and, particularly, *B. paulae*. The groove is deeper in *B. wilkinsonorum* and *B. planei*. The sustentact are conjoined, as in *B. paulae* and species of *Dendrolagus*, but are not as smoothly confluent as in *B. planei*. By contrast, the facets are distinctly separate in *B. wilkinsonorum* and *B. nullarbora*. The ventromedial cuboid facet is more confluent with the dorsomedial portion than in *B. nullarbora*, *B. wilkinsonorum* and *B. planei*. The sustent and the calcaneocuboid step is not smoothed to the extent seen in *B. paulae* and species of *Dendrolagus*.

**Remarks.** It is possible that the few slight differences in morphology between the three calcanei referred to *Bohra* sp. indet. 1 indicate that they belong to different species. Yet, they more closely resemble each other than any other species of *Bohra* in calcaneal morphology. Unfortunately, much of the taxonomically diagnostic cuboid articulation is broken off of the two Chinchilla LF specimens. Clearly, they cannot belong to *B. wilkinsonorum*, because its calcaneus is much larger and morphologically very distinct. However, teeth or tooth-bearing remains within a size range commensurate with that of these calcanei are known for *B. bila* and *B.* sp. cf. *B. bandharr* from the Chinchilla LF. In all probability, the calcanei referred to *Bohra* sp. indet. 1 belong to one or the other of them.

### Bohra sp. indet. 2

**Referred specimen.** UCMP 60850a, right talus. SAM Hill (= Lake Kanunka Site 2, UCMP V5773), Lake Kanunka, eastern Lake Eyre Basin, South Australia (Figure 1). This specimen was collected by Richard H. Tedford *et al.* on 16 August 1961.

**Description and comparisons.** In overall morphology, the talus is dorsoventrally compressed (especially in cranial view) with low trochlear crests, subequal in height and very shallow trochlea groove (Figure 35). The malleolar fossa is large, longer than wide, and moderately deep. The medial malleolus is broad and flattened. The neck of talus is intermediate in length, and extends cranially rather than craniomedially, such that lateral margin of navicular facet overlaps with medial trochlear crest from cranial view. The navicular facet of talar head is obliquely

aligned relative to the craniocaudal plane, and relatively narrow and elongate. The talocalcaneal facets are smoothly conjoined and relatively shallow. The posterior plantar process is blunt (short) and broad.

UCMP 60850a is intermediate between the holotype tali of *B. illuminata* and *B. nullarbora* in size and morphology, differing from the former by having a wider malleolar fossa and from the latter by bearing confluent calcaneal facets. The trochlear groove is more shallow than, but not as wide as, in *B. illuminata, B. nullarbora, D. bennettianus* and *D. lumholtzi*, but similar to *B. planei*. The medial trochlear crest is lower than in *B. paulae*, and is more similar to *B. planei*. The wide malleolar fossa is similar to *D. bennettianus*. The medial malleolus is relatively less projecting than in *B. nullarbora, Dendrolagus, Dorcopsulus, Setonix, Thylogale*, but similar to *B. paulae* and *B. planei*. The neck of talus is longer than in other species of *Bohra* and *Dendrolagus*, and the navicular facet of the talar head is narrower and more elongate, and less obliquely orientated than in *B. paulae* and *B. planei*, and particular *B. illuminata* and *B. nullarbora*. Although slightly water worn and abraded, the tibiotalar ligament fossa on the medial face of UCMP 60850a appears to have been very shallow and not extended above the dorsal border of the malleolus. The form of this fossa is most similar to the condition observed in *B. planei* in its medial restriction, but UCMP 60850a differs by lacking a distinct dorsal margin.



FIGURE 35. Talus (right) of *Bohra* sp. indet. 2 (UCMP 60850a). A: plantar view. B: dorsal view. C: medial view. D: cranial view. E: caudal view.

**Remarks.** UCMP 60850a has suffered some post-depositional abrasion due to the fluviatile nature of the deposit, but it is complete enough to confidently say that it belongs to a species of *Bohra*. Although its morphology is not consistent with the talus of any of the four species for which this element is known (*B. paulae, B. illuminata, B. nullarbora, B. planei*), it is too incomplete to put a species name on. Nevertheless, UCMP60850a represents a definitive record for the genus in the late Pliocene of inland Australia. This is significant, because specimens from the Tirari Formation of the Lake Eyre Basin previously identified as belonging to large tree-kangaroos can now be attributed to other taxa. A maxilla fragment from Stirton Quarry (AMNH 144684 = SIAM 70) referred to cf. *Dendrolagus* (Tedford *et al.* 1992) belongs to a sthenurine (GJP, pers. obs.), while metatarsals from the Toolapinna LF tentatively referred to *Dendrolagus* (Tedford *et al.* 1992) belong to a species of *Protemnodon* (A. B. Camens, pers. comm., 2019; NMW, pers. obs.).

### **Phylogenetic analysis**

Analysis of the 42 species and 85 characters (Appendices 1–2) produced 168 equally most parsimonious trees with a length of 251 steps, consistency index of 0.56, and retention index of 0.83. The strict consensus tree (Figure 36) collapses multiple nodes, the majority of which are within the Dendrolagina. *Bohra* is problematic due to the large proportion of missing data for most species, whereas *Dendrolagus* is challenging due to the markedly uniform osteology of its species.

Macropodinae is supported by four unique synapomorphies (Figure 36): I3 bears a distinct anterobuccal crest (character 15); i1 rests on the palate, bordered by I2–3, during cheek-tooth occlusion (character 38); the ischium and ilium are aligned in the same plane (character 77); the ulnar olecranon process is moderately proportioned (character 85). Macropodines are also united by the possession of either a slightly or markedly broadened I1 (character 14), and by shared possession of bilophodont molars that lack a urocrista, a condition convergently characteristic of the sthenurine *Hadronomas puckridgi* Kear, 2002 (character 25). Macropodinae is supported by a bootstrap value of 72.



**FIGURE 36.** Strict consensus of 168 most parsimonious trees depicting the phylogenetic position and interrelationships of treekangaroos within the Macropodidae. Unique synapomorphies (closed circles) and homoplastic traits (open circles) are indicated upon each branch. Numbers above represent characters, those below represent character states (see Appendices 1–2). *Dorcopsoides fossilis* Woodburne, 1967 is united with a *Dorcopsis–Dorcopsulus–Watutia* clade (Dorcopsini) as the basal macropodine branch in 64% of trees, where they are united by two unique synapomorphies: lateral constriction of P3 immediately anterior to the posterolingual cusp (character 21); a deep masseter muscle that extends to below the posterior cheek teeth, with the masseteric canal posteriorly confluent with the dental canal (character 35). In the strict consensus tree, *D. fossilis* forms a trichotomy with the dorcopsins and a clade giving rise to all other macropodines (Figure 36). *Dorcopsis, Dorcopsulus* and *Watutia* are united by two unique synapomorphies: the main crest of P3 is characterised by four cuspules with coarse ridgelets that extend to the crown base (character 17); the P3 crown is markedly deeper anteriorly than posteriorly (character 19).

The clade giving rise to all other macropodines is supported by one unique synapomorphy (I1 markedly broadened; character 14) and four homoplastic features (Figure 36). *Setonix brachyurus* is reconstructed as the sister taxon to Dendrolagini + Macropodini in 82% of trees, but forms a trichotomy with those two tribes in the strict consensus tree. The monophyly of a clade composed of *Wallabia* Trouessart, 1904, *Lagorchestes* Gould, 1841, *Prionotemnus* Stirton, 1955, *Kurrabi* Flannery & Archer, 1984, *Baringa* Flannery & Hann, 1984, *Onychogalea* Gould, 1841, *Osphranter* and *Macropus* (Macropodini) is solidly supported (bootstrap value 74) by three unique podial synapomorphies: relatively short articular region for the talus on the calcaneus (character 53); rounded sustentaculum tali (character 60); medial malleolus on the talus characterised by a narrow, deep fossa and a small process (character 65) (Figure 36).

*Thylogale, Petrogale, Dendrolagus* and *Bohra* (Dendrolagini) are united by two unique synapomorphies: triangular inflation of the squamosal between the occiput and zygomatic arch (character 11); relatively broad calcaneocuboid articulation (character 56). This clade is not supported in the bootstrap analysis.

*Dendrolagus* and *Bohra* (Dendrolagina) are united by three unique synapomorphies (Figure 36), each a feature of the calcaneus. These are: posteromedial expansion of the tuber calcanei (character 51); relatively broad calcaneus–talus articulation (character 57); marked medial taper of the lateral talar facet (character 59). This alliance is reinforced by several homoplastic synapomorphies (Figure 36) and supported by a bootstrap value of 70. *Bohra* is recovered as paraphyletic in all 168 trees, and all species of *Bohra* collapse to form a comb with *Dendrolagus* in the bootstrap reconstruction due to having support values <50%. However, in the strict consensus tree, *B. illuminata*, *B. nullarbora* and *B. paulae* form a clade with *Dendrolagus*, united by three unique synapomorphies: smooth calcaneocuboid articulation (character 54); ventromedial facet of cuboid articulation on calcaneus reduced and confluent with dorsomedial facet (character 55); talus with medial malleolar fossa broad and moderately deep with large malleolar process (character 65).

The species of *Dendrolagus* are united by four unique synapomorphies (Figure 36): a deep cleft on P3/p3 immediately posterior to the anterior cusp of the main crest (character 18); a relatively broad metatarsal V (character 69); a relatively long anterior crest on tibia (character 72); a short tibia relative to the femur (character 74). Two homoplastic traits may also be considered solid synapomorphies for the clade: a relatively shallow sustentaculum tali on the calcaneus otherwise only characterises the outgroup *Hypsiprymnodon moschatus* (character 62), while a short metatarsal IV relative to the length of the calcaneus is only seen elsewhere in *Setonix brachyurus* (character 66). Within *Dendrolagus*, the strict consensus tree produces a trichotomy between *D. inustus*, a *D. bennettianus–D. lumholtzi* clade and a clade composed of *D. matschiei* Förster & Rothschild, 1907, *D. dorianus* Ramsay, 1883, *D. goodfellowi* Thomas, 1908, *D. scottae* Flannery & Seri, 1990 and *D. mbaiso*. The New Guinea clade (excluding *D. inustus*) is united by two solid synapomorphies: relatively short distal fibular facet on the tibia (character 71); short pes (character 76). The latter is homoplastic, but only with the evolutionarily distant outgroup *Hypsiprymnodon moschatus*, and so is a very reliable synapomorphy.

engin, erb	, calcalleas taser aspin	, e1, <b>e</b>		maan, r c	, iemai enee	anner enree.	
Species	Registration No.	Sex	Mass (kg)	CL	CTD	CTW	FC
Dendrolagus dorianus	AM M30720	male	9	_	-	-	39
Dendrolagus dorianus	AM M30750	female	6.5	_	_	_	38
Dendrolagus dorianus	AM M30753	male	8.5	_	_	_	40
Dendrolagus goodfellowi	AM M9145	female	5.6	29.55	12.84	12.94	43

**TABLE 9.** Calcaneal and femoral dimensions (mm) of adult specimens of modern macropodines of known body mass. CL. calcaneus length: CTD, calcaneus tuber depth; CTW, calcaneus tuber width; FC, femur circumference.

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## TABLE 9. (Continued)

Species	Registration No.	Sex	Mass (kg)	CL	CTD	CTW	FC
Dendrolagus inustus	AM M21840	female	11	_	_	_	43
Dendrolagus inustus	AM M24437	female	10.6	32.51	13.76	14.45	_
Dendrolagus inustus	AM M25390	male	17	38.03	16.14	16.99	49
Dendrolagus lumholtzi	ANWC M29301	male	7.5	31.44	12.74	12.98	40
Dendrolagus lumholtzi	QM JM10086	male	4.3	24.92	10.73	9.83	37
Dendrolagus mbaiso	AM M30749	female	9	_	_	_	37
Dendrolagus mbaiso	AM M30751	female	8.5	27.31	12.87	13.51	_
Dendrolagus scottae	AM M21867	male	9.5	_	_	_	37
Dendrolagus scottae	AM M24424	male	11.5	31.69	14.00	15.70	41
Dendrolagus scottae	AM M25397	female	9.5	29.17	11.87	14.03	38
Dorcopsis atrata	AM M19461	male	7.5	27.51	11.62	10.83	39
Dorcopsis muelleri	AM M32339	female	5.9	_	_	_	38
Dorcopsis muelleri	AM M32341	male	13	36.78	12.53	13.88	46
Dorcopsulus vanheurni	AM M30727	male	2	19.34	7.25	6.74	23
Notamacropus eugenii	ANWC M11459	female	2.1	_	_	_	32
Notamacropus eugenii	ANWC M18014	male	3.5	_	_	_	32
Macropus fuliginosus	ANWC M01370	female	24.4	65.70	19.41	17.34	61
Macropus fuliginosus	ANWC M01375	female	27	61.44	19.63	17.35	67
Macropus fuliginosus	ANWC M01378	female	24.1	63.88	19.00	16.58	61
Macropus fuliginosus	ANWC M01379	female	22.9	64.81	18.79	17.51	65
Macropus fuliginosus	ANWC M01381	female	24.5	62.01	19.46	17.54	66
Macropus fuliginosus	ANWC M01384	male	55.5	81.4	24.87	24.14	70
Macropus fuliginosus	ANWC M01385	male	34	75.75	23.74	21.65	67
Macropus giganteus	ANWC M01371	female	21.6	65.41	19.02	18.38	64
Macropus giganteus	ANWC M01372	female	23.8	68.56	19.42	18.82	63
Macropus giganteus	ANWC M01376	female	21.1	66.78	18.48	18.38	58
Macropus giganteus	ANWC M01377	female	25.5	65.26	19.61	19.51	66
Macropus giganteus	SAM M22820/011	female	28	_	_	_	65
Macropus giganteus	SAM M22820/013	female	36	_	_	_	77
Macropus giganteus	SAM M22820/015	female	36	_	_	_	73
Notamacropus parma	ANWC M08979	female	4.5	_	_	_	34
Osphranter rufus	SAM M22821/001	male	55	_	_	_	78
Osphranter rufus	SAM M22821/007	male	57	_	_	_	84
Osphranter rufus	SAM M22821/008	male	64.5	_	_	_	82
Osphranter rufus	SAM M22821/010	male	47	_	_	_	76
Osphranter rufus	SAM M22821/011	male	39.5	_	_	_	78
Osphranter rufus	SAM M22821/012	male	60	_	_	_	90
Osphranter rufus	SAM M22822/005	female	18.5	_	_	_	67
Osphranter rufus	SAM M22822/008	female	35	_	_	_	73

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TABLE 9. (Continued)

Species	Registration No.	Sex	Mass (kg)	CL	CTD	CTW	FC
Osphranter rufus	SAM M22822/011	female	26.5	_	_	_	67
Osphranter rufus	SAM M22822/013	female	26.5	_	_	_	68
Osphranter rufus	SAM M22822/014	female	34.5	_	_	_	75
Petrogale assimilis	QM JM19898	?	3.7	29.75	8.88	9.53	31
Petrogale assimilis	QM JM10474	male	4.35	_	_	_	35
Petrogale brachyotis	AM M10363	male	5	27.26	9.16	9.41	32
Petrogale mareeba	AM M9187	male	2.6	26.65	9.04	8.87	31
Petrogale penicillata	AM M43676	female	4.3	_	_	_	38
Petrogale penicillata	ANWC M29544	male	5.5	32.37	11.00	10.57	39
Petrogale persephone	QM JM9750	male	8	_	_	_	44
Petrogale persephone	QM JM9782	male	6.75	_	_	_	40
Petrogale persephone	QM JM10559	male	5.3	_	_	_	42
Petrogale purpureicollis	QM JM17235	female	5.1	31.76	9.50	9.30	33
Thylogale browni	ANWC M15123	male	5.2	_	_	_	39
Thylogale stigmatica	AM M37142	male	4.5	27.68	10.16	9.78	32
Thylogale stigmatica	QM JM10562	female	3.7	_	_	_	32
Thylogale stigmatica	QM JM10563	?	6.05	_	_	_	37
Thylogale stigmatica	QM JM12560	male	6.15	29.26	9.87	10.11	38
Thylogale stigmatica	QM JM16376	?	2.55	25.50	7.95	8.44	32
Wallabia bicolor	AM M32724	female	14.6	46.75	17.06	14.78	51

TABLE 10.	Regression	equation	$(\log_{10})$	and $p$	values	for	hindlimb	dimensions,	along	with	the	corresponding	; ratio
(smearing) e	stimator use	d to correc	et for bi	asing e	effects o	f log	garithmic	transformatio	n.				

Dimension	r ²	p value	y-intercept	Regression coefficient	Ratio estimator value
Dendrolagina (n = 14)					
FC	0.31	0.06	2.40947	-2.92850	1.03862
CL	0.72	< 0.05	2.91436	-3.38573	1.01910
CTW	0.90	< 0.05	2.52102	-1.92741	1.01280
CTD	0.75	< 0.05	3.11435	-2.53849	1.01676
$CL \times CTW$	0.88	< 0.05	1.45312	-2.86921	1.01064
$CL \times CTD$	0.77	< 0.05	1.56459	-3.12961	1.01502
$\mathrm{CL}\times\mathrm{CTW}\times\mathrm{CTD}$	0.86	< 0.05	1.56459	-2.85881	1.01050
Macropodinae (n = 63)					
FC	0.91	< 0.05	-3.5557	2.7537	1.2283
CL	0.86	< 0.05	-2.0146	1.8965	1.4487
CTW	0.70	< 0.05	-0.1431	0.9890	0.9649
CTD	0.95	< 0.05	-1.7944	2.4714	0.9777
$\mathrm{CL} \times \mathrm{CTW}$	0.95	< 0.05	-2.1583	1.1635	1.1546
$CL \times CTD$	0.93	< 0.05	-2.0171	1.1089	1.2347
$\mathrm{CL}\times\mathrm{CTD}\times\mathrm{CTW}$	0.96	< 0.05	-2.0704	0.7985	1.0974
Species	Specimen	Dimension	Measurement	Body Mass (kg)	Body Mass (kg)
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			(mm)	Dendrolagina	Macropodinae
Bohra paulae	AM F 62099	CL	52.6	43.5	25.7
	AM F 62099	CTD	20.3	34.9	26.9
	AM F 62099	$CL \times CTD$	1070	41.4	27.1
Bohra	QM F675	CL	52.5	43.1	25.6
wilkinsonorum	QM F675	CTW	25.4	41.7	
	QM F675	CTD	20.8	37.4	28.4
	QM F675	$\mathrm{CL} \times \mathrm{CTW}$	1333	47.4	34.6
	QM F675	$CL \times CTD$	1091	42.6	27.7
	QM F675	$\mathrm{CL}\times\mathrm{CTW}\times\mathrm{CTD}$	27702	45.7	32.9
Bohra nullarbora	WAM 05.4.70	FC	57.0		23.4
	WAM 05.4.70	CL	43.4	24.8	17.9
	WAM 05.4.70	CTW	20.8	25.2	
	WAM 05.4.70	CTD	16.5	18.2	16.0
	WAM 05.4.70	$CL \times CTW$	903	26.9	22.0
	WAM 05.4.70	$CL \times CTD$	716	22.1	17.4
	WAM 05.4.70	$\mathrm{CL}\times\mathrm{CTW}\times\mathrm{CTD}$	14895	24.3	20.0
Bohra planei	UCMP 70128	FC	59.8		26.7
	UCMP 70128	CL	40.8	20.8	15.9
	UCMP 70128	CTD	16.7	19.0	16.6
	UCMP 70128	$CL \times CTD$	683	20.5	16.5
Bohra sp. indet. 1	QM F58666	CL	44.8	27.1	18.9
	QM F58666	CTW	17.7	22.8	
	QM F58666	CTD	18.7	19.3	19.1
	QM F58666	$\mathrm{CL} \times \mathrm{CTW}$	837	24.1	20.2
	QM F58666	$CL \times CTD$	794	25.9	19.5
	QM F58666	$\mathrm{CL}\times\mathrm{CTW}\times\mathrm{CTD}$	14840	24.3	20.0
	QM F51762	CL	46.3	29.9	20.2
	QM F51762	CTW	19.6	21.6	
	QM F51762	CTD	17.6	22.1	18.7
	QM F51762	$CL \times CTW$	906	27.1	22.1
	QM F51762	$CL \times CTD$	813	26.9	20.0
	QM F51762	$CL \times CTW \times CTD$	15917	26.0	21.1

**TABLE 11.** Calcaneal and femoral dimensions and body-mass estimates for specimens of *Bohra paulae*, *B. wilkinsonorum*, *B. nullarbora*, *B. planei* and *B.* sp. indet. 1 based on equations derived from a modern dendrolaginan-only dataset and a modern macropodine dataset. Due to specimen incompleteness, some dimensions could not be measured for some specimens. Only body-mass estimates predicted from measurements where  $r^2 > 0.70$  are presented.

### **Body-size estimation**

Calcaneal measurements and body mass are highly positively correlated (p < 0.05) within extant tree-kangaroos and macropodines as a whole (Table 10). This engenders confidence in their utility for modelling body masses of fossil kangaroos. The correlation between femur circumference and body mass is weaker than expected ( $r^2 = 0.31$ ) within tree-kangaroos and is not significant (p = 0.06), although it is significant within the larger macropodine sample ( $r^2 = 0.91$ ). Ratio estimators range from 0.9649 to 1.4487 (Table 10). Corrected body-mass predictions vary depending on the dataset used to generate them, with those estimated from the modern tree-kangaroo dataset larger than those estimated from the macropodine dataset (Table 11). Body-mass estimates predicted from measurements where  $r^2 \ge 0.70$  fall within the following ranges: 25.7–43.5 kg for *Bohra paulae*; 25.6–47.4 kg for *B. wilkinsonorum*; 16.0–26.9 kg for *B. nullarbora*; 15.9–26.7 kg for *B. planei*; and 18.7–29.9 kg for *B.* sp. indet. 1 (Table 11). No body-mass estimates were generated for *B. illuminata*, because the holotype is a young adult with unfused epiphyses, including that of the calcaneus.

#### Discussion

### Taxonomy

The subtribe Dendrolagina is solidly defined on the basis of a broad array of craniodental and postcranial attributes, many of them synapomorphies (Figure 36). The species of *Bohra* are also united by a range of features, but none are synapomorphies. This is because *Dendrolagus*, although itself monophyletic, arises from within *Bohra*, rendering it paraphyletic. In other words, *Bohra*, as currently composed, is a grade of non-*Dendrolagus* dendrolaginans. In fact, based on podial morphology, it really encompasses two grades: those that retain the ancestral, stepped calcaneocuboid articulation (*B. planei*, *B. wilkinsonorum*, *B.* sp. indet. 1), and those in which this joint is smoothed (*B. paulae*, *B. illuminata*, *B. nullarbora*), as in the species of *Dendrolagus*. A case could, therefore, be made for splitting *Bohra* into two genera on these grounds. However, one outcome of that would be that *B. bandharr*, *B.* sp. cf. *B. bandharr*, *B. bila* and *B.* sp. indet. 2 would be generically unaligned, because no calcaneus (or cuboid) has been ascribed to any of these species. For the sake of stability and simplicity, we retain a single genus for the non-*Dendrolagus* dendrolaginans, although we acknowledge the likelihood of a future division when more informative fossil material is described.

The best diagnosed species of *Bohra* are those known from unequivocally associated craniodental and postcranial remains (*B. illuminata, B. nullarbora*), followed by those known from associated hindlimb elements (*B. paulae, B. planei*). Even though its holotype is a partial juvenile maxilla, *B. wilkinsonorum* is well diagnosed, whereas the holotype partial dentaries of *B. bila* and *B. bandharr* preserve few defining traits. Nevertheless, these two clearly fall outside of the other named species. Thus, we define seven species of *Bohra*: *B. paulae, B. bandharr, B. wilkinsonorum, B. bila, B. illuminata, B. nullarbora* and *B. planei*. Although *B. bandharr* might possibly turn out to be a junior synonym of *B. paulae*, it is also likely that specimens identified as *B. sp. cf. B. bandharr* belong to at least one undescribed species currently too incomplete to sufficiently diagnose. Either way, that would still make at least seven species of *Bohra*. A minimum of three species existed on mainland Australia and one in New Guinea during the Pliocene, and a minimum of four existed on mainland Australia during the Pleistocene. The maximum number of species in any one assemblage is three in the Chinchilla LF. Today, no more than two species of *Dendrolagus* are known to coexist in any one location (Eldridge *et al.* 2018).

### Phylogeny

Our maximum parsimony analysis of skeletal attributes, which is a more refined and tree-kangaroo-focused version of that presented in Prideaux & Warburton (2010), retains tree-kangaroos and rock-wallabies in close phylogenetic proximity. The key difference is the closer association of *Thylogale*, facilitated, in part, by the presence of a triangular squamosal inflation in *T. billardierii*, which we overlooked previously. In the prior analysis, *Thylogale* formed an unresolved trichotomy with Dendrolagini and Macropodini. The current result is harmonious with phylogenies based on albumin immunology (Baverstock *et al.* 1989), DNA hybridization (Kirsch *et al.* 1995; Campeau-

Péloquin *et al.* 2001), DNA sequencing (Meredith *et al.* 2009; Mitchell *et al.* 2014; Cascini *et al.* 2019), and a total-evidence analysis (Beck *et al.* 2022). Still, osteological support for a Dendrolagini that includes non-tree-kangaroo taxa is distinctly underwhelming. The clade is not retained in the bootstrap consensus tree and only two unique synapomorphies support *Thylogale* + *Petrogale* + Dendrolagina. On the sum of molecular and osteological grounds, it appears that tree-kangaroos, rock-wallabies and pademelons are closely related. Here we retain all three clades within the Dendrolagini, but the recovery of more fossil taxa from the late Miocene and early Pliocene will be essential for improving resolution in this portion of the tree.

The hypothesis that tree-kangaroos and rock-wallabies share a common ancestor to the exclusion of other macropodines contrasts with most prior anatomy-based assessments (e.g., Bensley 1903; Raven & Gregory 1946; Archer 1981; Flannery 1989). Nevertheless, several authorities over the preceding century (DeVis 1887; Barrett 1943; Windsor & Dagg 1971; Ziegler 1977) did flag this possibility based on hunches that they developed from general behavioural similarities between tree-kangaroos and rock-wallabies. Both groups are adept in three-dimensionally heterogeneous environments (indeed, some rock-wallabies are good tree climbers; Martin 2005), both have comparatively long tails for enhanced balance, and they share some similarities in the way that they hop (Windsor & Dagg 1971). The reality, though, is that the shared skeletal features that link tree-kangaroos with rock-wallabies and pademelons that we have been able to detect thus far are very subtle and not very convincing. They are overwhelmed by both specialisations (especially for tree-kangaroos) and the homoplasy that is a well-noted nuisance to macropodine systematists (Archer 1984; Flannery 1989). In fact, the only osteological traits that we can identify that exclusively link rock-wallabies and tree-kangaroos do not even relate to anything postural or locomotory, but rather to aspects of incisor morphology.

Several molecular-clock estimates have been produced for the divergence timing of the dendrolaginan and *Petrogale* lineages: 7.5 Ma ago (Campeau-Péloquin *et al.* 2001); 10–6 Ma ago (Meredith *et al.* 2009); 11–6 Ma ago (Potter *et al.* 2012); 8–6 Ma ago (Cascini *et al.* 2019); 7–5 Ma ago (Celik *et al.* 2019); 11.7–8.0 Ma ago (Westerman *et al.* 2022). Together, these estimates span the entire late Miocene. The key fossil calibration point has been the small dendrolaginan in the 4.5-Ma-old Hamilton LF recognised from three partial premolars, originally identified as cf. *Dendrolagus* sp. (Flannery *et al.* 1992). Over time, the tentative nature of the generic attribution was dispensed with, including by us (Prideaux & Warburton 2008, 2010), but without justification. These specimens share a posterobuccal eminence on P3, which is a trait that only characterises species of *Bohra* and *Dendrolagus* within the Macropodinae. So, while there is no disputing that these specimens belong to a tree-kangaroo, they retain no attributes that allow identification below the subtribe level. To advance further in our understanding of the basal splits within Dendrolagini, the late Miocene to early Pliocene record will need to improve beyond a few tiny tooth fragments.

The common ancestry of *Bohra* and *Dendrolagus*, widely accepted since *B. paulae* was first described (Flannery & Szalay 1982), is strongly reinforced here. However, phylogenetic resolution within *Bohra* is poor (Figure 36), potentially driven by markedly inadequate elemental representation for most species. By contrast, the species of *Dendrolagus* are united as a monophyletic group in parsimony and bootstrap analyses. Emergence of *D. inustus* as an outlier to the remaining species is consistent with a phylogenetic study based on cytochrome *b* (Bowyer *et al.* 2003), but not the recent work combining nuclear and mitochondrial DNA, which reconstructs *D. inustus* as the sister to the other New Guinea species (Eldridge *et al.* 2018). Earlier morphology-based assessments (Flannery & Szalay 1982; Groves 1982; Flannery *et al.* 1996) and a second cytochrome-*b* analysis (McGreevy *et al.* 2012) grouped the two Australian species, *D. bennettianus* and *D. lumholtzi*, with *D. inustus*. This trio has been dubbed the "long-footed" group, with the remaining New Guinea species making up the "short-footed" group (Groves 1982; Flannery *et al.* 1996). Our parsimony and bootstrap analyses support the view that the short-footed species shared a common ancestor to the exclusion of all other tree-kangaroos, which is consistent with the most recent DNA-based analysis (Eldridge *et al.* 2018).

By favouring the normal prior distribution because it had the lowest mean rate of evolution, Eldridge *et al.* (2018) advocated for a mean molecular-clock estimate of 7.1 Ma ago for the split between the Australian and New Guinean clades of *Dendrolagus*. Westerman *et al.* (2022) proposed an even earlier mean estimate of 7.8 Ma ago. An obvious implication is that the *Bohra–Dendrolagus* divergence would have to have occurred even earlier. These results were likely influenced by the assumption of a slow rate of evolution and the recognition of *Dendrolagus* at 4.5 Ma ago, whereas we argue above that this is best identified as Dendrolagina gen. et. sp. indet. As things stand now, the genus *Dendrolagus* has no representation prior to the middle Pleistocene, in contrast to most other macropodine genera (Prideaux & Warburton 2010).

In an early stage of this study, we reported that we believed *Watutia novaeguineae* from the Pliocene of New Guinea was also a tree-kangaroo (Prideaux *et al.* 2015). This taxon has been largely ignored since its initial description (Flannery *et al.* 1989), wherein it was interpreted as a plesiomorphic macropodine, most closely resembling *Hadronomas puckridgi* and *Wanburoo hilarus* Cooke, 1999 (the 'undescribed Riversleigh macropodine' of Flannery *et al.* 1989). The latter two taxa were subsequently shifted to the Sthenurinae (Murray 1991; Prideaux 2004; Prideaux & Warburton 2010). We were led to our initial impression of *W. novaeguineae* by some phenetic similarities in molar morphology shared with species of *Bohra* and the unsupportable assumption that the hindlimb elements here designated as the holotype of *B. planei* may have belonged to *W. novaeguineae*. Here, *W. novaeguineae* is embedded within the Dorcopsini (Figure 36).

#### Ecomorphology

Numerous skeletal features that phylogenetically circumscribe the Dendolagina can be interpreted as adaptations to their browsing diet and arboreal (or scansorial) habits. Clearly, several are strongly linked within a functional complex (e.g., ankle attributes).

**Diet.** The cranium of tree-kangaroos is more robust than that of all other macropodids, bar the very robust sthenurines. This robustness is manifested in the depth of the rostrum and the relatively broad occiput, the latter indicating a strong, well-muscled neck. The functional significance of the enlarged palatines, which form a non-fenestrate secondary palate along with the maxillae, is unclear. The only other macropodines with non-fenestrate palates are the species of *Macropus, Osphranter, Protemnodon* and *Congruus*. Given that all extant tree-kangaroos are browsers (Arman & Prideaux 2015; Martin 2005), as almost certainly were the extinct species given their dental morphology, the parallel advent of a solid palate in these lineages was not driven by obvious dietary parallels. On the other hand, the dental attributes uniting tree-kangaroos likely do relate to diet. These include the advent of a lingual shelf on the I3, in addition to reduction of the main (lingual) crest relative to the anterobuccal crest. This resembles the morphology seen in numerous sthenurines, in which the anterolingual crest is thickened and posteriorly extended (Prideaux 2004). This may reflect similarities in incisor usage for plucking browse items. The robust, thinly flanged morphology of the i1, with which the I3 occludes during incisor occlusion, is consistent with this inference.

The reduced postprotocrista on the upper molars indicates a reduced emphasis on molar shearing. This aligns with the reduced molar crown heights of tree-kangaroos (Couzens & Prideaux 2018). Extension of the masseteric canal into the body of the dentary in tree-kangaroos is also typical of most earlier-derived macropodids. This reflects the relative development of the deep masseter muscle, which has been posited to correlate with the relative length of the third premolars and to play a role in the precise alignment of their shearing blades (Ride 1959; Sanson 1989). One point of distinction between the p3 of tree-kangaroos and that of most other macropodids with a long-bladed p3 is the presence of an inflated posterobuccal corner, which has become a distinct cusp or short crest in some species of *Dendrolagus* (Figures 3-4), and possibly was also in *B. bila* (Figure 22). A more modest version of this is observed in W. novaeguineae, but the condition is distinctly different in sthenurines, where a neomorphic eminence manifests itself on the buccal cingulum of early taxa (e.g., R. flannervi), developing into a crest in more derived forms (Prideaux 2004). Although the p3 of tree-kangaroos remains a primarily shearing tooth, the posterobuccal eminence or crest suggests enhanced crushing capability. Given that this is also an attribute of koalas, it probably correlates with a more exclusively folivorous diet than is typical of the species of *Dorcopsis* and *Dorcopsulus*, which consume significant quantities of fungi (Vernes & Lebel 2011), much like potoroines, which also have elongate, serrated, blade-like premolars (Sanson 1989). The parallel development of the posterobuccal facet on p3 in W. novaeguineae, the very robust nature of its premolars and their marked anterior depth, plus the lack of a broad cingulum on the P3, suggest a potential capacity to crack into hard fruits or seeds.

**Locomotion.** Osteologically, tree-kangaroos are most easily distinguished from all other macropodids on the basis of pedal attributes that represent key adaptations to arboreality. These include a broad, shallow calcaneus characterised by a short, posteromedially expanded tuber calcanei, which provides for greater torque over a wider range of positions than in terrestrial macropodines. Stout metatarsals that are subequal in length facilitate greater manoeuvrability and balance in a three-dimensionally heterogeneous environment (Warburton & Prideaux 2010). The stepped calcaneocuboid articulation is a quintessential macropodid attribute that functions to stabilise the pes during bipedal hopping (Szalay 1994; Bishop 1997; Warburton & Prideaux 2010). Marked smoothing of this joint, and coalescence of the ventromedial and dorsomedial facets, facilitates greater rotational and translational

movements, and characterises most, but not all, tree-kangaroos. *Bohra planei, B. wilkinsonorum* and *B.* sp. indet. 1 retain the step and distinct ventromedial facet. *Bohra paulae, B. nullarbora* and *B. illuminata* are more similar to the species of *Dendrolagus* in the morphology of the calcaneocuboid articulation, but the facets are not quite as smoothed overall. That is, a hint of the step remains, which points to slightly less translational capacity than in the species of *Dendrolagus* (Warburton & Prideaux 2010).

Modification of the upper ankle joint, whereby the trochlear crests on the talus are reduced in height, also characterises most tree-kangaroo species for which the talus is known, but not *B. nullarbora* and *B. illuminata*, which retain a well-developed medial crest. The flattening of the talus points to greater rotational ability of the upper ankle joint. Proportionally greater lateral movement at the lower ankle joint (talocalcaneal articulation) in *B. paulae* and *B. planei* is indicated by a loss of separation between the lateral and medial facets. This is a reversion to the plesiomorphic macropodid condition. All other dendrolaginan species retain distinct lateral and medial facets. Thus, although it would be true to say that, as a whole, tree-kangaroos are characterised by modifications to the pes that facilitate an expanded range of inversion/eversion and abduction/adduction movements (Warburton & Prideaux 2010), the species of *Bohra* vary in the combination of modifications that they express. This contrasts with the species of *Dendrolagus*, which are more consistent in tarsal morphology.

Species of *Dendrolagus* have extended hindlimb modifications for arboreal living beyond the tarsus. The tibia is robust and subequal in length to the femur, with the ratio of tibia-to-femur length varying slightly between species. The tibial crest is also long, i.e., it extends for more of the length of the tibia than in other macropodids. These two characters are correlated and reflect lower hindlimb gearing associated with the transition from being wholly ground-dwelling to primarily arboreal. All of the New Guinea species of *Dendrolagus* are united by having a short to non-existent distal facet between the tibia and fibula, which reflects greater rotational capacity of the lower hindlimb. With the exception of *D. inustus*, all of the New Guinea species are characterised by a relatively short pes, which is a reversion to the condition otherwise only seen among macropodoids in the quadrupedally bounding *Hypsiprymnodon moschatus*. In *H. moschatus*, a short pes is a plesiomorphy retained from the arboreal phalangeriform ancestor of macropodoids. *Dendrolagus bennettianus*, *D. lumholtzi* and *D. inustus* retain a pes of relatively intermediate length, as in *Dorcopsis, Dorcopsulus, Setonix* and *Thylogale*. A shortened and more flexible pes reflects selection for increased manoeuvrability and balance when climbing (Warburton & Prideaux 2010). In addition, features of the forelimb of tree-kangaroos, as exemplified by *D. lumholtzi* and *B. illuminata*, also reflect increased emphasis on adduction, grasping and gripping, and improved mobility (Warburton *et al.* 2011).

Extant species of *Dendrolagus* range from 7 to 17 kg in mean adult body mass, which puts them in the same size range as those larger extant placental browsers that spend the majority of their lives in trees, e.g., the Proboscis Monkey *Nasalis larvatus* (9–19 kg) and Black Colobus Monkey *Colobus satanus* (10–13 kg). Extinct dendrolaginan species that express the derived condition of a smoothed calcaneocuboid articulation probably also spent more time in the canopy than on the ground. Those species of *Bohra* retaining the stepped joint were likely more adept on the ground, potentially splitting their time between the ground and trees, as some langurs (species of *Semnopithecus*) do today (Rahman *et al.* 2015). Although such behavioural inferences will prove challenging to verify, especially in the absence of more complete skeletal material for more species, some insights may emerge from dietary investigations. It has been hypothesised, for example, that differences observed in dental microwear patterns between extant tree-kangaroos and terrestrial browsers may reflect the adherence of less dust and grit on higher versus lower browse (Arman *et al.* 2019).

Although larger arboreal Old World monkeys may be reasonable extant ecological analogues for the species of *Dendrolagus*, the species of *Bohra* were larger than any arboreal herbivores living today, with the exception of the Orang-utan *Pongo pygmaeus* (30–100 kg). For the species that may have been predominantly arboreal, our body-mass predictions range from 16–27 kg for *B. nullarbora* and 26–44 kg for *B. paulae*, with *B. illuminata* probably intermediate between them. For those species that may have divided their time more equally between ground and canopy, estimates range from 16–27 kg for *B. planei*, 19–30 kg for *B.* sp. indet. 1 and 26–47 kg for *B. wilkinsonorum*. Ecologically, the species of *Bohra* bring to mind the late Quaternary lemurs of Madagascar, particular those within the genera *Archaeolemur, Hadropithecus* and *Palaeopropithecus*, which spanned a similar size range (Jungers *et al.* 2002). Most of these lemur species were evidently adapted for tree-dwelling, and even the largest species (*Megaladapis edwardsi*, 75 kg; *Archaeoindris fontoynontii*, 160 kg) retained unequivocal arboreal adaptations (Jungers *et al.* 2002; Godfrey *et al.* 2006). The large Pleistocene macropodin, *Congruus kitcheneri*, also appears to have been scansorial (Warburton & Prideaux 2021). Although it might seem unlikely that large dendrolaginans

would have expressed anything approaching the remarkable variation in body form seen among giant lemurs, who would have foreseen the discovery that multiple species of large arboreal kangaroo once inhabited relatively open, dry habitats? We should assume that the marsupial fossil record will continue to surprise us.

# Zoogeography

The scantness of the late Miocene fossil record for Australian terrestrial vertebrates has resulted in us knowing very little about the zoogeographic machinations of this evolutionarily pivotal interval. The only described late Miocene macropodine is *Dorcopsoides fossilis* from the Alcoota LF of central Australia. Nevertheless, both molecular and osteological data (Meredith *et al.* 2009; Prideaux & Warburton 2010) have been used to posit that most major macropodine divergences occurred in the late Miocene, including that between tree-kangaroos and rock-wallabies (Campeau-Péloquin *et al.* 2001; Potter *et al.* 2012; Cascini *et al.* 2019; Celik *et al.* 2019; Westerman *et al.*, 2022). A likely centre of evolution for the Dendrolagina cannot yet be identified with any confidence. According to molecular data, two of the three earliest-derived lineages within *Petrogale* are now represented only in tropical northern Australia (Potter *et al.* 2012), which suggests that adaptation to more arid habitats in several species occurred subsequently (cf. Prideaux & Warburton 2010). With the benefit of the improving fossil record for the species of *Bohra*, and in light of our phylogenetic analysis, it has become evident that the assertion that "the common ancestor of *Dendrolagus* and *Petrogale* was probably initially distributed in the region of Cape York" (Campeau-Péloquin *et al.* 2001, pp. 481–482) was heavily influenced by the high concentration of extant species of both genera in that area.

The fossil record has provided minimal insight to date into the evolution of rock-wallabies. A lower molar from the early Pliocene Bluff Downs LF of northeastern Australia referred to *Petrogale* (Bartholomai 1978) may belong to an early member of that genus. However, given the difficulty with which numerous mixed-feeding macropodines may be distinguished on the basis of isolated lower molars, this identification should be treated as tentative. No other rock-wallaby fossils older than middle Pleistocene have yet been described. The upper premolar specimens from the early Pliocene Hamilton LF cannot currently be identified to genus level (Flannery *et al.* 1992). *Bohra* is represented by a minimum of four late Pliocene species, three in Australia and one in New Guinea, but no species of *Dendrolagus* are known from prior to the middle Pleistocene, not even in the late Pliocene Awe LF of Papua New Guinea, where *Bohra* is represented by *B. planei* (Plane 1967; Hoch 1988; Flannery *et al.* 1989).

The species of *Bohra* are less derived than those of *Dendrolagus*, and capture two stages in a transition to increasing arboreality, as demonstrated by the tarsal complex. Our parsimony analysis reconstructs *Bohra* as paraphyletic, with *Dendrolagus* arising from within it (Figure 36). The three species of *Bohra* that are closest to the base of the *Dendrolagus* clade (*B. paulae*, *B. illuminata*, *B. nullarbora*) are known only from the Pleistocene of southern and eastern Australia. Therefore, together, our osteology-based phylogeny and the current fossil record would suggest that the *Dendrolagus* lineage originated no earlier than the late Pliocene. This differs from the prevailing hypotheses of a Miocene rainforest origin for *Dendrolagus*, and a Miocene dispersal into New Guinea (e.g., Groves 1982; Flannery 1990; Martin 2005; Black *et al.* 2012; Eldridge *et al.* 2018). It is, however, consistent with conclusions drawn by Murray (1992) about the timing of diprotodontid dispersal into New Guinea. If supported by further evidence in the future, it also might help explain the purported existence of several species of *Dendrolagus* in the middle Pleistocene of eastern Australia, including at least one member of the New Guinea clade, along with other marsupial forms that are said to be more allied to modern New Guinean rather than modern Australian taxa (Hocknull *et al.* 2007). That is, the absence of certain New Guinean clades from the Australian mainland today might not necessarily reflect long-term endemism in New Guinea, but rather their extinction in Australia (Beck 2017).

Four central and eastern Australian Pliocene assemblages have yielded species of *Bohra*: the Kanunka, Big Sink, Bow and Chinchilla LFs. Palaeoenvironmental reconstructions for each suggest a mosaic of habitats, from riparian forest through sclerophyll woodland to grassland, with indications of episodic aridity (Flannery & Archer 1984; Dawson *et al.* 1999; Prideaux 2004; Montanari *et al.* 2013). There is no evidence to suggest that *B. bandharr*, *B. bila* or *B. wilkinsonorum* were restricted to rainforest, although in New Guinea, *B. planei* probably was, judging from the dental adaptations of the herbivores present in the Awe LF (Hoch 1988). The Pleistocene *B. illuminata*, *B. nullarbora* and *B. paulae* are represented in assemblages that accumulated in palaeoenvironments that were clearly not forested, but may have included woodland, semi-arid and/or seasonally dry habitats (Tedford *et al.* 1992; Prideaux *et al.* 2007; Prideaux & Warburton 2008, 2009; Sniderman *et al.* 2016). However, *B. sp.* indet. 1

persisted into the middle Pleistocene, where it is represented in cave-fill deposits at Mt Etna in coastal northeastern Queensland (Hocknull 2005a,b). The diverse Mt Etna assemblage reflects a mix of habitats, including tropical rainforest, and purportedly includes remains of up to four species of *Dendrolagus* not yet identifiable to species level (Hocknull *et al.* 2007). Until at least as recently as the middle Pleistocene, tree-kangaroos had a far broader distribution (Figure 1) through a greater array of habitats than they do now.

# Evolution

Increased aridity has been the overriding trend in Australian climate since the middle Miocene climatic optimum 14 Ma ago, with forest and closed woodland declining and retracting to the continental periphery and highlands (Martin 2006; Fujioka & Chappell 2010). Overwhelmingly, patterns in the evolution of Australia's terrestrial biota have been couched in terms of the impacts of this trend (e.g., Byrne *et al.* 2008, 2011; Kealy & Beck 2017). Indeed, significant faunal turnover characterised the early–middle and middle–late Miocene transitions, with the diversity of taxa adapted to moister habitats declining, particularly for several arboreal lineages (Black *et al.* 2012). In this light, it seems counterintuitive that a lineage of mammalian browsers would move into the trees in the midst of a period marked by diminishing arboreal niche space and diversity, yet the number of known fossil koala species was also higher in the Pliocene and Pleistocene than at any time since the early Miocene (Black *et al.* 2014).

Perhaps competition on the ground from other marsupial folivores played a role in tree-kangaroo evolution, particularly from macropodins as they diversified (Couzens & Prideaux 2018). Early tree-kangaroos may also have been advantaged by digestive differences: they are foregut fermenters, not hindgut fermenters like koalas and possums (Hume 1999). The bilophodont molars of tree-kangaroos are higher crowned and have relatively thicker, more wear-resistant enamel than in possums (Couzens 2017), which may have been an advantage as wear rates increased into the late Cenozoic (Couzens & Prideaux 2018). Alternatively, the way that macropodids move by comparison with koalas and possums might have been significant. Modern species of *Dendrolagus* are much more agile on the ground, utilising the ancestral bipedal hopping mode of locomotion. This allows more rapid movement between feeding sites, and they can also leap long distances from the canopy to the ground (Martin 2005). Such factors may have played facilitating roles, but it is difficult to envisage how any would have been a primary driver of a shift to arboreality. This leads us back to look again at the potential of environmental change.

Although the overarching climatic trend through the late Cenozoic was toward cooling and drying, this was punctuated by a return to warmer, wetter conditions in the early Pliocene (McGowran *et al.* 2004; Byrne *et al.* 2008). Semi-arid habitats were replaced by mesic forests in south-central Australia c. 5 Ma ago, before returning 1.5 Ma later (Sniderman *et al.* 2016). Similarly, the 4.5-Ma Hamilton LF of southeastern Australia, which is dominated by small to medium-sized terrestrial browsers and arboreal forms, including a small tree-kangaroo (Flannery *et al.* 1992), is associated with a pollen assemblage indicative of *Araucaria*-dominated rainforest mixed with open sclerophyll forest or woodland (Macphail 1996). Prevailing early Pliocene vegetation in central western New South Wales was similar (e.g., Martin 1987, 2006; Macphail 1997). Greenhouse conditions would have driven a diversification of arboreal habitats, in turn potentially catalysing diversification within the Dendrolagina, and possibly the radiation of macropodine lineages more broadly. As widespread aridity returned from the late Pliocene, some species of *Bohra* established themselves in drier, more open habitats, while species of *Dendrolagus* did likewise in New Guinea and the remnant tropical rainforest of northeastern Australia.

# Extinction

When and why all species of *Bohra* became extinct is a mystery. The only Pleistocene fossil associated with absolute dates (c. 300 ka) is a calcaneus of *B*. sp. indet. 1 from the Mt Etna caves (Hocknull 2005a, b; Hocknull *et al.* 2007). For the others we cannot currently do better than middle or late Pleistocene, which has long been a deficiency that has beset our understanding of change in Quaternary assemblages and extinction trajectories (Prideaux 2006). *Bohra paulae, B. illuminata* and *B. nullarbora* may have become extinct in the late Pleistocene at around the same time as numerous other larger species, soon after the arrival of humans in Australia and New Guinea (e.g., Prideaux *et al.* 2009, 2010, 2022; Johnson *et al.* 2016; Saltré *et al.* 2016), or they may have disappeared earlier due to climatic changes (e.g., Wroe *et al.* 2013). Faunal turnover at Mt Etna sometime between 280 and 205 ka ago has been interpreted as a response to increased aridity (Hocknull *et al.* 2007), and two frog species bound to free water

were lost from the Nullarbor region in the middle Pleistocene (Tyler & Prideaux 2016). Even so, several lines of evidence indicate that *B. illuminata* and *B. nullarbora* were members of a Nullarbor fauna that inhabited a region of relatively low rainfall and open vegetation (Prideaux *et al.* 2007). Remains of *B. nullarbora* and *B. illuminata* have been collected from a fissure-fill deposit on Yorke Peninsula alongside several arid-zone sthenurines (Prideaux 2004), and *B. illuminata* is also known from the Pleistocene of inland Australia. More fossil evidence, especially from well-dated contexts, is needed to clarify the potential impacts of Pleistocene environmental changes on species of *Bohra*, but it is clear that they were not all adapted to the same habitats and climatic conditions.

Indeterminate scraps of bone collected from an archaeological deposit in Tunnel Cave, southwestern Australia, from a layer that accumulated 22 ka ago, have produced ancient DNA interpreted to align most closely with *Dendrolagus* among the extant fauna (Murray *et al.* 2013). No tree-kangaroo bones have yet been recognised among the tens of thousands recovered from several Pleistocene cave deposits in the southwest (Merrilees 1984; Prideaux 2004; Prideaux *et al.* 2010; Jankowski *et al.* 2016); however, it could be worth screening the samples again now that we have partial skeletons of *B. illuminata* and *B. nullarbora* upon which to base comparisons (Prideaux & Warburton 2008, 2009). Although it remains possible that the DNA belongs to one or both species of *Bohra*, confirmation from other evidence is required before we can go out on a limb to argue that tree-kangaroos persisted in the southwest until near the end of the Pleistocene.

# Conclusions

We recognise the existence of seven species of *Bohra* in the late Cenozoic of mainland Australia, and one in New Guinea. Most are known from very few specimens. Among them, the four species (*B. paulae, B. illuminata, B. nullarbora, B. planei*) known from associated skeletal elements have been pivotal in allowing us to recognise as remnants of extinct tree-kangaroos a motley array of isolated foot bones and loose teeth that have accumulated in museum collections for the past century and a half. The current balance of evidence indicates that tree-kangaroos formerly had a wide distribution across the continent in the Pliocene and Pleistocene, occupying multiple climatic zones and habitats. So, although we now think of tree-kangaroos as among the most quintessential of rainforest denizens, this is an artefact of differential extinction that saw all species of *Bohra* and *Dendrolagus* is in the middle Pleistocene Mt Etna assemblage of eastern Queensland.

Taxonomically, the species of Bohra are united by a range of dental, pedal and other osteological features. Cladistically, Bohra is a paraphyletic grade from within which the monophyletic Dendrolagus is derived. The Dendrolagina is defined on the basis of three unique tarsal traits that would have facilitated greater pedal torque and rotation adaptive for climbing. Nested within Dendrolagina is a clade composed of the species of Dendrolagus and three species of Bohra known only from the Pleistocene of southern and eastern Australia. Together, the phylogeny and fossil record support the idea that the Dendrolagus clade may have originated much later than molecular and modern zoogeographic analyses have suggested. The species of *Dendrolagus* are characterised by further hindlimb modifications that would have promoted greater power and rotational ability. Adaptively, the changes in hindlimb morphology observed through dendrolaginan evolution represent successive steps in increasing arboreal adeptness within a group whose members, judging from their simple, low-crowned dentition, probably obtained much of their food from the canopy. A spectrum in relative time spent in the trees is seen across the species of largerbodied cercopithecid and lemuroid primates, and we infer that it was similar for the dendrolaginan radiation. The disappearance of tree-kangaroos from much of Australia, along with other large climbing kangaroos (e.g., Congruus kitcheneri), as well as exclusively ground-dwelling browsers, likely had significant flow-on effects on the ecology of communities across the continent. Determining the varying ecological roles of these herbivores will require the use of multiple lines of empirical evidence and considerable research effort for some time yet.

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# **APPENDIX 1.** Morphological characters used in the phylogenetic analysis.

Modified from Prideaux & Warburton (2010). See that work for detail on characters and states.

- 1. Rostrum depth relative to posterior (neurocranial) portion of cranium: shallow (0), intermediate (1), deep (2).
- 2. Level of basicranial plane relative to palatal plane: same plane or slightly higher (0), markedly higher (1).
- 3. Splanchnocranium anteroventral deflection: marked (0), intermediate (1), minimal (2).
- 4. Superficial masseter origin on jugal: shallow (0), deep, with distinct orbital rim (1).
- 5. Large ectoglenoid process: absent (0), present (1).
- 6. Postglenoid process: small or absent (0), large (1).
- 7. Neurocranium element contact: frontal-squamosal (0), parietal-alisphenoid (1).
- 8. Ectotympanic proportions: small (0), thick, wide, rugose, ventrally keeled (1).
- 9. Maximum occiput breadth relative to height: deeper than broad (0), broader than deep (1).
- 10. Occipital condyles markedly recessed into occiput, each bordered dorsally by distinct sulcus: absent (0), present (1).
- 11. Large triangular (V-shaped) squamosal inflation between occiput and posterior end of zygomatic arch: absent (0), present (1).
- 12. Large palatal fenestrae: present (0), absent (1).
- 13. Relative anteroposterior length of upper incisors: I2 and/or I3 not reduced relative to I1 (0), I2 distinctly shorter than I1 and I3 (1), I2 and I3 distinctly shorter than I1 (2).
- 14. Il shape: sub-cylindrical (0), slightly broadened (1), markedly broadened (2).
- 15. I3 anterobuccal crest: absent or very small, restricted to anterior end (0), distinct (1).
- 16. I3 lingual surface: no anterolingual crest or lingual shelf (0), anterolingual crest present, no lingual shelf (1), anterolingual crest and small lingual shelf present (2).
- 17. Number of cuspules/ridgelets on P3 anterior to large posterior cusp: five or more (0), four of fine to moderate coarseness (1), four coarse extending to crown base (2), three (3), less than three (4).
- 18. Deep cleft on main crest of P3 and p3 immediately posterior to anteriormost cuspule: absent (0), present (1).
- 19. Anterior relative to posterior crown depth of P3: anterior and posterior depths similar or slightly deeper anteriorly (0), markedly deeper anteriorly (1).
- 20. P3 lingual cingulum: absent or very low, fine (0), low, narrow to moderately broad, tapered anteriorly (1), broad, with no distinct crest along lingual edge (2), broad, raised into low crest along lingual edge (3), raised into high crest along lingual edge (4), broad, raised into low crest along lingual edge before tapering anteriorly (5).
- 21. P3 lateral constriction immediately anterior to posterolingual cusp: absent (0), present (1).
- 22. P3 posterobuccal eminence or accessory cusp: absent (0), present (1).

- 23. P3 length relative to molars: does not exceed combined M1-2 length (0), exceeds combined M1-2 length (1).
- 24. Molar progression: absent (0), present (1).
- 25. Molar morphology: bundont or bundlophodont (0), bilophodont, urocrista small and expressed only on anterior molars (1), bilophodont, lacking urocrista on all molars (1).
- 26. Stylar crest in region of cusp C: present, minimally on anterior upper molars (0), absent (1).
- 27. Preprotocrista development: strongly developed, confluent with precingulum (0), very small or absent (1).
- 28. Postprotocrista orientation: restricted to lingual side of tooth (0), extends into interloph valley near to tooth midline (1).
- 29. Postprotocrista development: short, thick (0), fine, low (1), intermediate (2), high, thick, strongly developed (3).
- 30. Postprotocrista division: absent (0), incipiently or completely divided into two components (1).
- 31. Postparacrista development: present (0), absent or very fine and low (1).
- 32. Postmetacrista / postmetaconulecrista development: both distinct (0), postmetaconulecrista enlarged, postmetacrista absent or very weak (1).
- 33. Morphology of symphyseal plate of dentary: shallow, smooth or very slight rugose (0), deep, rugose (1), deep, very rugose and anteriorly expanded (2).
- 34. Buccinator sulcus on dentary: absent (0), broad, deep concavity (1), narrow, shallow (2), narrow, deep (3).
- 35. Anterior extent of deep masseter muscle: to below anterior cheek teeth, masseteric canal confluent with dental canal (0), to below posterior cheek teeth, masseteric canal separate from dental canal (1), to below posterior cheek teeth, masseteric canal posteriorly confluent with dental canal (2), posterior to m4 (near vertical) (3).
- 36. Anterior insertion area for the internal superficial masseter muscle: small to moderately proportioned (0), broad and concave (1), large, terminates ventrally at distinct ridge (2).
- 37. Mandibular condyle shape: barrel shaped, not tapered medially (0), oval or circular (1), barrel shaped, tapered medially (2).
- 38. Position of i1 occlusal surface during incisor occlusion: i1 rests on crowns of I2 and I3 and posterior facet on I1 (0), i1 rests on palate, bordered by I2 and I3 (1).
- 39. i1 morphology: procumbent, thin and elongate (0), procumbent blade with thick enamel flanges (1), slightly robust with thin enamel flanges (2), markedly upturned and robust (3).
- 40. Enamel distribution on i1: principally buccal side (0), buccal enamel layer extended to completely encircle crown (1), separate lingual enamel layer present (2).
- 41. Morphology of p3: blade with many fine serrations along length of crown (0), crown markedly curved in lingually at posterior end, forming rounded L-shape (1), straight or slightly curved blade with fewer coarser serrations (2), base of crown markedly broadened relative to length (3).
- 42. Buccal side of p3: lacks eminence, cingulid or crest (0), bears posterobuccal eminence (1), bears well-developed buccal cingulid or crest (2).
- 43. Cheek tooth row shape in dorsoventral plane: flat or very slightly convex (0), markedly convex dorsally (1).
- 44. Parametacristid: absent (0), present (1).
- 45. Slight postmetacristid: present (0), absent (1).
- 46. Postprotocristid development: distinct (0), slight or absent (1).
- 47. Cristid obliqua form: restricted to buccal side of tooth (1), straight or slightly curved, terminates near tooth midline low on posterior face of protolophid (2), distinctly kinked, terminates near tooth midline low on posterior face of protolophid (3).
- 48. Paracristid and cristid obliqua division: absent (0), present (1).
- 49. Development of postentocristid and posthypocristid: postentocristid distinct, meets large posthypocristid (0), both crests fine or absent (1), posthypocristid present, adjacent to distinct central groove (2).
- 50. Lophid enamel crenulations: absent (0), present (1).
- 51. Tuber calcanei posteromedial expansion: absent (0), present (1).
- 52. Calcaneus plantar surface shape: tapered anteriorly (0), not tapered anteriorly (1).
- 53. Relative length of talus articular region on calcaneus: long (>0.43) (0), intermediate (0.43–0.35) (1), short (<0.35) (2).
- 54. Step of calcaneocuboid articulation: incipient (0), stepped (1), smoothed (2).
- 55. Ventromedial facet of cuboid articulation on calcaneus: absent (0), continuous with dorsolateral facet (1), separate, distinct, well-developed (2), reduced, confluent with dorsomedial facet (3).
- 56. Relative breath of calcaneocuboid articulation: narrow (<1.3)(0), broad (>1.3)(1).
- 57. Relative breadth of calcaneus-talus articulation: intermediate (0.3–0.5) (0), narrow (<0.3) (1), broad (>0.5) (2).
- 58. Distinctness of medial and lateral talar facets on calcaneus: confluent, smoothly continuous anteriorly (0), continuous anteriorly but facet contours distinct (1), distinct, separate facets (2).
- 59. Shape of lateral talar facet on calcaneus: untapered or slightly tapered medially (0), markedly tapered medially (1).
- 60. Shape of sustentaculum tali of calcaneus: straight (anteroventrally orientated) or very slightly curved (0), rounded (1), squared (2).
- 61. Posterior extent of sustentaculum tali of calcaneus: roughly in line with fibular facet (0), intermediate (1), significantly posteriorly placed from fibular facet (2).
- 62. Relative depth of sustentaculum tali of calcaneus: shallow (<0.5) (0), intermediate (0.5–0.8) (1), deep (>0.8) (2).
- 63. Orientation of trochlear crests of talus: oblique (anterolaterally orientated) (0), anteroposteriorly orientated (1).
- 64. Trochlear groove on talus: shallow with medial and lateral crests subequal in height (0), intermediate (1), deep with very high medial crest (2).
- 65. Morphology of medial malleolus on talus: fossa breadth/depth intermediate, process small or indistinct (0), fossa narrow/

deep, process small (1), fossa broad/shallow, process large (2), fossa broad/moderately deep, process large (3).

- 66. Metatarsal IV length relative to calcaneus length: long (>1.5) (0), short (<1.5) (1).
- 67. Metatarsal IV relative breadth: narrow (<0.12) (0), intermediate (0.12–0.15) (1), broad (>0.15) (2).
- 68. Metatarsal IV distal epiphysis breadth: narrow relative to ligament attachments (0), distinctly broad relative to shaft width, minimum development of ligament attachments (1).
- 69. Metatarsal V relative breadth: intermediate (0.07–0.13) (0), narrow (<0.07) (1), broad (>0.13) (2), highly to extremely reduced (3).
- 70. Metatarsal V plantar ridge: small, posteriorly restricted (0), absent (1), elongate, well developed (2).
- 71. Relative length of distal fibular facet on tibia: intermediate (0.2–0.5) (0), long (>0.5) (1), short (<0.2) or absent (2).
- 72. Relative length of cranial crest of tibia: intermediate (0.24–0.27) (0), long (>0.27) (1), short (<0.24) (2).
- 73. Shape of cranial tibial crest: stepped in distally (0), not stepped distally, curves smoothly into diaphysis (1).
- 74. Length of tibia relative to that of femur: intermediate (1.1-1.5)(0), short (<1.1)(1), long (>1.5)(2).
- 75. Development of greater trochanter crest of femur: distally flared or intermediate (0) distally narrowed (1), distally flared and markedly broadened (2).
- 76. Pes length relative to femur length: short (<0.65) (0), intermediate (>0.65–0.8) (1), long (>0.8) (2).
- 77. Angle of ilium to ischium: slight angle (0), aligned in same plane (1), large angle (2).
- 78. Position of rectus femoris origin on ilium: distinctly separate from acetabular rim (0), intermediate (1), immediately adjacent to acetabular rim (2).
- 79. Iliopubic process at junction of ilium and pubis: very small, pointed (0), long, well-developed, square in outline (1), short, broad (2), very large (3).
- 80. Area of supraspinous fossa relative to infraspinous fossa of scapula: supraspinous fossa roughly half area or less (0), supraspinous fossa roughly one-third area (1), supraspinous fossa much smaller than infraspinous (2).
- 81. Scapula acromion shape: anterodorsally curved (0), straight (1).
- 82. Displacement of acromion relative to glenoid fossa on scapula: not cranially displaced (0), cranially displaced (1).
- Bevelopment of deltoid tuberosity versus pectoral crests on humerus: deltoid insertion poorly developed (0), intermediate, small deltoid tuberosity connected by oblique ridge (1), large deltoid tuberosity separated from pectoral crest by sulcus (2).
- 84. Relative width of trochlear notch posterior margin on ulna: wide (0), narrow (1).
- 85. Olecranon length/shape relative to length of ulna: long, deep (0), intermediate (1), reduced (2).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Hypsiprymnodon moschatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bettongia penicillata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lagostrophus fasciatus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	3	0	0	5	0	0
Troposodon minor	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	0	3	0	0	5	0	0
Bulungamaya delicata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0
Ganguroo robustiter	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Wanburoo hilarus	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	0	2	0	0
Hadronomas puckridgi	2	0	2	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	2	0	0
Simosthenurus occidentalis	2	1	2	0	1	1	1	1	1	0	0	0	1	0	0	1	1	0	0	4	0	1
Procoptodon goliah	2	1	2	0	1	1	1	1	1	0	0	0	1	0	0	1	1	0	0	4	0	1
Bohra illuminata	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	2	3	0	0	0	0	0
Bohra nullarbora	1	?	0	?	0	1	1	0	?	0	?	1	?	?	?	?	3	0	0	2	0	0
Bohra paulae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra bila	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	3	0	?	3	0	?
Bohra wilkinsonorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	3	0	1
Bohra sp. indet. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watutia novaeguineae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	0	1	0
Bohra planei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Dendrolagus bennettianus	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	2	4	1	0	2	0	1
Dendrolagus notatus	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	2	3	1	0	2	0	1
Dendrolagus inustus	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	2	3	1	0	2	0	1
Dendrolagus lumholtzi	1	0	0	0	0	1	1	0	1	0	1	1	0	1	1	2	4	1	0	2	0	1

#### **APPENDIX 2.** Morphological character matrix for phylogenetic analysis.

Dendrolagus matschiei	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	2	3	1	0	2	0	1
Dendrolagus goodfellowi	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	2	3	1	0	2	0	1
Dendrolagus mbaiso	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	2	3	1	0	2	0	1
Dendrolagus scottae	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	2	3	1	0	2	0	1
Petrogale brachyotis	0	0	0	0	0	1	1	0	1	1	1	0	0	2	1	2	3	0	0	1	0	0
Petrogale rothschildi	0	0	0	0	0	1	1	0	0	1	1	0	0	2	1	0	3	0	0	1	0	0
Petrogale xanthopus	0	0	0	0	0	1	1	0	0	1	1	0	0	2	1	2	3	0	0	1	0	0
Thylogale billardierii	0	0	0	0	0	1	1	0	0	0	1	0	0	2	1	0	3	0	0	0	0	0
Dorcopsis luctuosa	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	2	0	1	0	1	0
Dorcopsoides fossilis	0	0	0	0	0	0	1	0	0	0	0	0	?	1	1	0	1	0	0	0	1	0
Dorcopsulus vanheurni	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	2	0	1	0	1	0
Lagorchestes conspicillatus	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	0	3	0	0	1	0	0
Macropus fuliginosus	0	0	0	0	0	1	1	0	0	0	0	1	0	2	1	0	4	0	0	0	0	0
Macropus robustus	0	0	0	0	0	1	1	0	0	0	0	1	0	2	1	0	4	0	0	1	0	0
Onychogalea unguifera	0	0	0	1	0	1	1	0	0	0	0	0	2	2	1	0	4	0	0	0	0	0
Baringa nelsonensis	?	?	?	1	?	?	?	?	?	?	?	?	2	2	?	?	3	0	0	0	0	0
Kurrabi mahoneyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	0	0	1	0	0
Setonix brachyurus	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	?	1	0	0	2	0	0
Wallabia bicolor	0	0	0	0	0	1	1	0	0	0	0	0	0	2	1	0	3	0	0	3	0	0
Prionotemnus palankarinnicus	?	?	?	0	?	?	?	?	?	?	?	?	?	2	1	0	3	0	0	1	0	0

# **APPENDIX 2. (Continued)**

Species	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Hypsiprymnodon moschatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bettongia penicillata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lagostrophus fasciatus	0	0	1	1	0	1	2	0	0	0	1	1	3	1	1	0	0	1	1	0
Troposodon minor	0	0	1	1	0	1	2	0	0	0	1	1	1	1	1	0	0	1	1	0
Bulungamaya delicata	0	0	0	0	0	0	0	0	0	0	0	2	1	0	?	?	0	0	2	0
Ganguroo robustiter	0	0	1	0	0	1	1	0	0	0	0	2	1	0	1	?	0	0	2	0
Wanburoo hilarus	0	0	1	0	1	1	1	0	0	0	0	3	1	0	1	?	1	0	2	1
Hadronomas puckridgi	0	0	2	1	1	1	1	0	0	0	0	3	1	0	1	0	1	2	3	2
Simosthenurus occidentalis	0	0	1	1	1	1	1	1	0	0	2	3	3	0	2	0	3	2	3	2
Procoptodon goliah	0	0	1	1	1	1	1	1	0	0	2	3	3	0	2	0	3	2	3	2
Bohra illuminata	0	0	2	1	1	1	1	0	0	0	0	2	1	0	?	1	2	0	2	1
Bohra nullarbora	0	0	2	1	1	1	1	0	0	0	0	2	1	0	?	?	2	0	?	?
Bohra paulae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra bila	0	0	2	0	1	1	1	0	0	0	?	2	1	0	?	?	?	?	2	1
Bohra wilkinsonorum	0	0	2	0	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Bohra sp. indet. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watutia novaeguineae	0	0	2	0	1	1	1	0	0	0	0	2	?	?	?	?	?	?	2	1
Bohra planei	?	0	2	0	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Dendrolagus bennettianus	0	0	2	0	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus notatus	0	0	2	1	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus inustus	0	0	2	1	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus lumholtzi	0	0	2	0	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus matschiei	0	0	2	0	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus goodfellowi	0	0	2	1	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1

Dendrolagus mbaiso	0	0	2	1	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Dendrolagus scottae	0	0	2	1	1	1	1	0	0	0	0	2	1	0	1	1	2	0	2	1
Petrogale brachyotis	0	0	2	0	1	1	2	0	0	0	0	2	3	0	1	1	2	0	2	0
Petrogale rothschildi	0	0	2	1	1	1	2	0	0	0	0	2	3	0	1	1	2	0	2	0
Petrogale xanthopus	0	0	2	0	1	1	2	0	0	0	0	2	3	0	1	1	2	0	2	0
Thylogale billardierii	0	0	2	0	1	1	2	0	0	0	0	2	3	0	1	1	1	0	2	0
Dorcopsis luctuosa	1	0	2	0	1	1	1	0	0	0	0	2	2	0	1	1	0	0	2	0
Dorcopsoides fossilis	0	0	2	0	1	1	1	0	0	0	0	2	2	0	?	1	1	2	2	0
Dorcopsulus vanheurni	1	0	2	0	1	1	1	0	0	0	0	2	2	0	1	1	0	0	2	0
Lagorchestes conspicillatus	0	0	2	1	1	1	2	0	0	0	0	2	3	0	1	1	0	0	2	0
Macropus fuliginosus	0	1	2	1	1	1	3	0	1	1	0	2	3	0	1	1	1	0	2	0
Macropus robustus	0	1	2	1	1	1	3	0	1	1	0	2	3	0	1	1	1	0	2	0
Onychogalea unguifera	0	0	2	1	1	1	3	0	0	0	0	2	3	2	1	1	0	0	2	0
Baringa nelsonensis	0	0	2	1	1	1	3	0	1	1	0	2	3	2	?	1	1	0	2	0
Kurrabi mahoneyi	0	0	2	1	1	1	3	0	1	1	0	2	3	0	?	?	1	0	2	0
Setonix brachyurus	0	0	2	1	1	1	2	0	0	0	0	2	1	0	1	1	1	0	2	0
Wallabia bicolor	0	0	2	1	1	1	2	0	0	0	0	2	3	0	1	1	1	0	2	0
Prionotemnus palankarinnicus	0	0	2	1	1	1	3	0	1	0	0	2	3	0	?	1	1	0	2	0

# **APPENDIX 2. (Continued)**

Species	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Hypsiprymnodon moschatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bettongia penicillata	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	2	0	0
Lagostrophus fasciatus	0	0	1	1	0	1	0	0	0	1	1	1	0	0	1	0	2	1	2	0	1
Troposodon minor	1	1	1	2	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bulungamaya delicata	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ganguroo robustiter	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wanburoo hilarus	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hadronomas puckridgi	0	1	1	1	0	1	0	0	0	1	1	2	0	0	1	0	0	1	2	1	1
Simosthenurus occidentalis	0	1	1	1	1	1	1	0	0	1	1	2	0	0	1	0	2	2	2	1	2
Procoptodon goliah	0	1	1	1	1	0	1	0	0	1	1	2	0	0	1	0	2	2	2	1	2
Bohra illuminata	0	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	1	0	1
Bohra nullarbora	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	1	0	1
Bohra paulae	?	?	?	?	?	?	0	1	0	0	2	3	1	2	1	1	0	0	1	0	0
Bohra bila	?	1	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra wilkinsonorum	?	?	?	?	?	?	?	1	0	0	1	1	1	2	2	1	0	0	1	?	?
Bohra sp. indet. 1	?	?	?	?	?	?	?	?	1	0	0	1	1	1	2	2	1	0	0	1	?
Watutia novaeguineae	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra planei	?	?	?	?	?	?	?	1	0	0	1	1	1	2	1	1	0	0	1	0	0
Dendrolagus bennettianus	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus notatus	1	1	1	1	0	1	0	1	0	1	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus inustus	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus lumholtzi	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus matschiei	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus goodfellowi	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus mbaiso	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0
Dendrolagus scottae	1	1	1	1	0	1	0	1	0	0	2	3	1	2	2	1	0	0	0	0	0

Petrogale brachyotis	1	0	1	1	0	1	0	0	1	1	1	2	0	0	2	0	0	0	1	0	1
Petrogale rothschildi	1	0	1	1	0	1	0	0	1	1	1	2	0	0	2	0	0	0	1	0	1
Petrogale xanthopus	0	0	1	1	0	1	0	0	1	1	1	2	1	0	2	0	0	0	1	0	1
Thylogale billardierii	0	1	1	1	0	1	0	0	0	1	1	1	1	0	2	0	0	0	1	0	1
Dorcopsis luctuosa	0	1	1	1	0	1	0	0	0	1	1	2	0	0	2	0	0	0	1	0	1
Dorcopsoides fossilis	0	1	1	1	0	1	0	0	0	1	1	2	0	0	1	0	0	1	2	0	1
Dorcopsulus vanheurni	0	1	1	1	0	1	0	0	0	1	1	2	0	0	2	0	0	0	2	0	1
Lagorchestes conspicillatus	0	1	1	1	0	1	0	0	0	2	1	2	0	0	2	0	1	0	2	0	1
Macropus fuliginosus	0	1	1	2	0	2	0	0	0	2	1	2	0	1	2	0	0	2	2	0	1
Macropus robustus	0	1	1	2	0	2	0	0	0	2	1	2	0	1	2	0	0	2	2	0	1
Onychogalea unguifera	0	1	1	2	0	1	0	0	0	2	1	2	0	0	2	0	1	2	2	0	1
Baringa nelsonensis	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kurrabi mahoneyi	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Setonix brachyurus	0	1	1	1	0	1	0	0	0	1	1	1	0	0	2	0	0	0	1	0	1
Wallabia bicolor	0	1	1	1	0	1	0	0	0	2	1	2	0	0	2	0	1	2	1	0	1
Prionotemnus palankarinnicus	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

# **APPENDIX 2. (Continued)**

Species	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Hypsiprymnodon moschatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bettongia penicillata	0	0	0	0	1	1	1	2	0	0	0	2	0	0	1	0	0	0	0	0	0
Lagostrophus fasciatus	0	0	1	0	0	2	1	2	0	0	0	2	0	0	1	0	0	0	1	0	0
Troposodon minor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bulungamaya delicata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ganguroo robustiter	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	1	1	0	0	0	2
Wanburoo hilarus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hadronomas puckridgi	0	0	1	1	0	2	1	0	1	?	1	?	0	1	3	1	1	0	?	1	2
Simosthenurus occidentalis	0	0	1	1	3	1	1	0	1	0	1	1	2	1	3	2	1	1	2	1	2
Procoptodon goliah	0	0	1	1	3	1	1	0	1	2	1	?	2	1	3	2	1	1	2	1	2
Bohra illuminata	3	0	2	0	?	0	1	2	0	0	0	1	1	1	2	?	1	0	1	0	?
Bohra nullarbora	3	0	2	0	0	0	?	?	?	?	0	1	1	1	?	?	?	?	1	0	1
Bohra paulae	3	?	2	?	0	?	1	2	0	?	?	?	?	?	?	?	?	?	?	?	?
Bohra bila	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra wilkinsonorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra sp. indet. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watutia novaeguineae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bohra planei	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Dendrolagus bennettianus	3	1	2	0	2	0	1	1	0	1	0	1	1	2	2	1	1	0	1	0	1
Dendrolagus notatus	0	1	2	0	2	0	2	1	0	1	0	0	1	2	2	1	1	0	1	0	1
Dendrolagus inustus	3	1	2	0	2	0	0	1	0	1	0	1	1	1	2	1	1	0	1	0	1
Dendrolagus lumholtzi	3	1	2	0	2	0	0	1	0	1	0	1	1	2	2	1	1	0	1	0	1
Dendrolagus matschiei	3	1	2	0	2	0	2	1	0	1	0	0	1	2	2	1	1	0	1	0	1
Dendrolagus goodfellowi	3	1	2	0	2	0	2	1	0	1	0	0	1	2	2	1	1	0	1	1	1
Dendrolagus mbaiso	0	1	2	0	2	0	2	1	0	1	0	?	1	2	2	1	1	0	1	1	1
Dendrolagus scottae	3	1	2	0	2	0	2	1	0	1	0	0	1	2	2	1	1	0	1	1	1
Petrogale brachyotis	0	0	1	0	0	0	1	2	0	0	0	1	1	0	1	1	1	0	1	0	1
Petrogale rothschildi	0	0	1	0	0	0	1	2	0	0	0	1	1	0	1	1	1	0	1	1	1

Petrogale xanthopus	0	0	1	0	0	0	1	2	0	0	0	2	1	0	1	1	1	0	1	0	1
Thylogale billardierii	0	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	1	0	1	0	1
Dorcopsis luctuosa	0	0	1	0	0	2	1	2	0	0	0	1	1	1	1	1	1	0	0	0	1
Dorcopsoides fossilis	0	0	1	0	0	2	0	2	0	2	0	?	1	0	1	?	?	0	0	0	1
Dorcopsulus vanheurni	0	0	1	0	0	2	1	2	0	0	0	1	1	1	1	1	1	0	0	0	1
Lagorchestes conspicillatus	1	0	0	0	1	2	1	2	0	0	0	2	1	0	1	1	1	0	1	0	0
Macropus fuliginosus	2	0	0	0	1	2	1	2	0	2	0	2	0	0	1	0	1	0	1	0	1
Macropus robustus	2	0	1	0	1	2	1	2	0	2	0	2	0	0	1	0	1	1	1	0	1
Onychogalea unguifera	1	0	0	0	1	2	1	2	0	2	0	2	0	0	1	0	1	0	1	0	0
Baringa nelsonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kurrabi mahoneyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Setonix brachyurus	0	1	1	0	0	0	1	2	0	0	0	1	1	0	2	1	1	0	0	0	1
Wallabia bicolor	1	0	1	0	0	2	1	2	0	0	0	2	1	0	1	1	1	0	2	0	1
Prionotemnus palankarinnicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?