

Contributions to the Mammalogy of New Guinea

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Tim F. Flannery and Kristofer M. Helgen

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The Last Land. A History of Mammalogy in New Guinea

TIM F. FLANNERY  AND STEPHEN M. JACKSON 

Australian Museum Research Institute
1 William Street, Sydney NSW 2010, Australia

After Greenland, New Guinea is the second largest island on Earth. It is a region of exceptional biodiversity, as its eastern part alone—the independent nation of Papua New Guinea, ranks twelfth among nations for biodiversity (Williams, 2001). New Guinea’s indigenous mammalian fauna consists of four major clades: monotremes (Tachyglossidae), marsupials (Australidelphia), murids (Muridae), and bats (Microchiroptera), each of which has a differing zoogeographic history in the New Guinean region (Flannery, 1995a). New Guinea lies east of Wallace’s Line, and its northwestern and southern parts form the northern margin of the Australian Plate, while the rest of the island is largely made up of rocks of oceanic crust and island arc origin (Baldwin *et al.*, 2012). Unlike Australia, which is dry and flat, New Guinea is rain-soaked and mountainous, creating a perfect natural laboratory to investigate how faunas with a common ancestry evolve under different conditions.

To the west of New Guinea lies the geographic region known as Wallacea, which has its own distinctive fauna (Flannery, 1995b). Composed of many islands, Wallacea is varied, with some island groups, such as the Spice Islands, sharing mammal lineages with New Guinea, while others are dominated by mammalian lineages originating in Asia (see Helgen & Jones, 2023). The mammalian fauna of the Spice Islands (modern Maluku Utara, Indonesia) was first documented by Europeans as early as the mid-sixteenth century (Calaby, 1984), yet it was not until the end of the nineteenth century that a sense of the composition of the mammalian fauna of New Guinea itself was established. Indeed, the island was such a terra incognita that as late as 1875 a fictitious account of a purported expedition to New Guinea could be published and read by a credulous public, which reported encounters with man-like apes, tigers, and enormous herds of buffalo (Lawson, 1875).

The earliest account of a mammal that was clearly collected on the island of New Guinea appears to be René-Primevère Lesson’s and Prosper Garnot’s observations of *Dorcopsis veterum* Lesson & Garnot, 1826 (synonym of *Dorcopsis mülleri* (Schlegel, 1866)) made at Dorei (present day Manokwari) on Vogelkop. The two were surgeons who also worked as zoologists aboard the French vessel *Coquille*, under the command of Louis Isodore Duperrey, during its circumnavigation of the globe from 1822 to 1825. The *Coquille* reached ‘*le harvre du Dorery*’ on 26 July 1824, and the encounter with the wallaby must have occurred shortly thereafter (Duperrey, 1826).

Opportunistic and sporadic records of mammal specimens from the lowlands of New Guinea continued to be made throughout the nineteenth century. Among the most significant were those of Salomon Müller, a zoologist and botanist at the short-lived settlement of Fort Du Bus (in Triton Bay, now in Kaimana Regency, Indonesia), where in 1828 he collected specimens of *Dendrolagus inustus* and *D. ursinus*. In 1840, Müller published accounts of both species, making them the first tree-kangaroos known to western science (Müller, 1840). Other important collections, principally from the lowlands, made during the nineteenth century were those of the Russian Nicholas Mikluho Maclay in southeastern New Guinea between 1871–1880 (e.g., Miklouho-Maclay, 1884), various German collectors working in German New Guinea (e.g., Matschie, 1912), and Sir William Macleay’s 1875 Chevert Expedition to the Gulf of Papua (Macleay, 1875; Fulton, 2018).

The New Guinea highlands (areas above 1000 m) with their rich endemic mammal fauna, were not visited by a European zoologist until the Italian naturalist Luigi Maria D’Albertis reached the Arfak Mountains on Vogelkop. Singing arias from popular Italian operas to fortify himself as

ORCID ID: Flannery 0000-0002-3005-8305, Jackson 0000-0002-7252-0799

Corresponding author: Tim Flannery tim.fridtjof.flannery@gmail.com

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he scaled the steep lower slopes and reached an elevation of around 1000 m on 7 September 1872. There he based himself in the village of Hatam, where he raised the Italian flag and began collecting. Birds of paradise were his principal focus, but he did collect a few mammals, most if not all of which were purchased from villagers. With a tribal war threatening, D'Albertis departed the Arfaks on 29 September (D'Albertis, 1881), but in his three short weeks there he collected a diversity of montane endemic mammals, including *Phascolosorex dorsalis*, *Microperoryctes longicauda* (to this day the only record from Vogelkop) and *Pseudocheirops albertisii*, which were entirely unknown to the outside world.

Other collectors, principally Dutch and French (e.g., Milne-Edwards, 1880; Raffray, 1879), followed D'Albertis into the mountains of Vogelkop, but soon other more distant regions of New Guinea began to open up to collectors, and organized collecting activity on Vogelkop tapered off. From the 1880s onwards, the establishment of mission and colonial government outposts in British New Guinea facilitated the exploration of the mammals of the eastern end of the island. By the mid-1890s the Italian anthropologist Dr Lamberto Loria was collecting mammals at 1300 m elevation in the Astrolabe Range near Port Moresby (Thomas, 1898; Dimpflemeier *et al.*, 2018). By the early years of the 20th century, other collectors, including Antwerp Edgar Pratt and sons (e.g., Pratt, 1906), Walter Goodeflow (e.g., Thomas, 1908) and Albert Meek, a collector for Lord Walter Rothschild who reached an elevation of 1220 m asl on the Aroa River area in 1903 (see Tennent, 2021), all primarily interested in birds and insects, were making incidental collections of mammals at high elevations in southeastern New Guinea. The highest mountains in New Guinea lie in the Maokop Range where, until the early twenty-first century, two glaciers occurred. Mammals were first collected at high elevation there during the 1909–1910 Lorentz Expedition (Lorentz, 1913), and the 1910–1911 British Ornithologists Union expedition led by Alexander Frederick Richmond Wollaston (e.g., Thomas, 1914), but the remoteness of the region prevented large-scale collecting until the advent of aviation.

The motive forces behind much early twentieth century collecting were Lord Walter Rothschild (whose primary interest was ornithology, but whose collectors also brought back mammals) and Oldfield Thomas. Thomas worked on mammalian systematics at the British Museum, as a paid employee or in retirement, between 1876 and 1929. He named around 2,000 new mammalian species and subspecies, and his most productive period coincided with the opening up of much of New Guinea to biological collectors. He hired his own fieldworkers, but many colonial-era adventurers and administrators with an interest in natural history also sent specimens to him (Hill, 1990). Collectors, working alone in New Guinea during the mid-twentieth century, included Evelyn Cheeseman (e.g., Cheeseman, 1948), Fred Shaw-Mayer (e.g., Laurie, 1952), Ernst Mayr (e.g., Stein, 1932), and Alan Jock Marshall (e.g., Marshall, 1938). Ellis LeGeyt Troughton, mammalogist at the Australian Museum Sydney (1908–1954) described several species (e.g., Troughton 1937), collected in New Guinea, and was active in encouraging donations.

From the 1930s onwards, a huge burst of mammalogical research, powered largely by the American Museum of Natural History's Archbold Expeditions, took place. Five

of the Archbold Expeditions, all focussed explicitly on mammalogy, explored New Guinea between 1934 and 1964. The expeditions were the first to use aircraft to reach remote areas, spent up to 18 months in the field amassing the enormous collections of mammals (Archbold & Rand, 1935, 1940; Archbold *et al.*, 1942; Brass, 1956; Van Deusen, 1978). The published mammalogical research, primarily by George H. H. Tate, covered every aspect of New Guinean mammalogy. By 1954 enough was known that a checklist of New Guinean mammals could be compiled (Laurie & Hill, 1954).

By the 1970s systematic mammalogy was finally being undertaken by researchers living in New Guinea, with James Menzies of the University of Papua New Guinea (e.g., Menzies, 1991) and Frank Bonaccorso of the PNG National Museum (e.g., Bonaccorso, 1998) playing leading roles. Collectors working for institutions outside New Guinea also continued. Abid Beg Mirza, for example, contributed substantial collections to the Bernice Pauahi Bishop Museum, Hawai'i (e.g., Ziegler, 1981). The number of species described was expedited by Australian Museum Scott Expeditions (1985–1992), led by TF who undertook surveys across New Guinea and surrounding islands (e.g., Flannery, 1995a, 1995b). In addition other survey work was completed by Ken Aplin (e.g., Helgen *et al.*, 2020) and others, who sampled hitherto poorly-known regions of the island. In December 2007 Kris Helgen surveyed the Foja Mountains, the last entirely unsurveyed mountain range in New Guinea, for mammals (*National Geographic*, 2009).

Importantly, by the 1980s frozen tissues of a diversity of New Guinean mammals were being collected, and the first genetic data on New Guinean mammals were being published (e.g., Aplin *et al.*, 1993 and references therein). By 1990 sufficient data had been accumulated to allow for the publication of the first account of the mammals of the island (Flannery, 1990).

As a result of the various expeditions by researchers the number of species described from New Guinea rapidly grew, with over 60 species having been described, or recognized, since 1980. These include some highly unusual species including Attenborough's Long-beaked Echidna (*Zaglossus attenboroughi*) and the alpine woolly rat (*Mallomys gunung*), which were described in 1989. The dingiso (*Dendrolagus mbaiso*), described in 1995, appears to be largely terrestrial, which is unlike other tree-kangaroos. It is astonishing that some of New Guinea's largest and most distinctive mammals, including *D. mbaiso*, *D. scottae* Flannery & Seri 1990 and *D. puicherrimus* Flannery, 1993 had escaped detection by European scientists until the 1990s. Earlier collectors may have been reluctant to trek into the remote regions where these species linger, and to spend weeks camping with local landowners in order to detect such elusive and rare species. Large areas of New Guinea are still poorly studied, so it is likely that many more mammals remain to be discovered and described.

Any review of New Guinean mammalogy must acknowledge indigenous expertise. Because traditional lifestyles continue in many areas, the average New Guinean is highly knowledgeable about their mammal fauna, partially depending upon it for sustenance. Moreover, many native mammals are deeply significant in traditional belief systems. The only comprehensive account of mammals written by an indigenous hunter is Iain Saem Majnep's *Animals*

the ancestors hunted: an account of the wild mammals of the Kalam area, Papua New Guinea (Majnep & Bulmer, 2006). It is a truly scholarly work, filled with ecological and reproductive detail, much observed at first hand.

Hopefully, the future of New Guinean mammalogy will increasingly lie with in-country researchers, both in Papua New Guinea and Indonesian Papua. But if this is to occur, in-country universities and museums must be provided with the resources required.

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A New Species of Bandicoot in the Genus *Peroryctes* (Marsupialia: Peramelemorphia) from Kwiyawagi, West Baliem Valley of Papua Province, Indonesia

KENNY J. TRAVOUILLO¹ , TERRY BERTOZZI^{2,3} , ANNA J. MACDONALD⁴ ,
STEVEN J. B. COOPER^{2,3} , TIM F. FLANNERY⁵ , AND KRISTOFER M. HELGEN⁶ 

¹ Western Australian Museum, Locked Bag 49, Welshpool DC WA 6986, Australia

² South Australian Museum, North Terrace, Adelaide SA 5000, Australia

³ Environment Institute and School of Biological Sciences, The University of Adelaide SA 5005, Australia

⁴ The John Curtin School of Medical Research/Research School of Biology,
The Australian National University, Acton ACT 2601, Australia

⁵ Australian Museum Research Institute,
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

⁶ Bernice Pauahi Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i 96817, United States of America

ABSTRACT. Many bandicoot species occur in New Guinea and surrounding islands. Here, a new species of *Peroryctes* is described from the West Baliem River Valley, western New Guinea (Papua Province, Indonesia). Morphometric analyses, qualitative morphological examination, and formal morphological phylogenetic assessment clearly distinguish this new taxon from the two currently recognized species of *Peroryctes*, *P. raffrayanus* and *P. broadbentii*. Our attempt to recover molecular data for this new taxon recovered poor quality sequences insufficient for analysis. Little is yet known about the basic biology of this new species, but it is rare and may be threatened.

Introduction

New Guinea and its surrounding islands are home to two families (Peroryctidae and Peramelidae) and five genera of peramelemorphians. These include the peroryctid genera *Echymipera* (5 species), *Rhynchoemeles* (1 species), *Microperoryctes* (5 species), *Peroryctes* (2 species) and the peramelid genus *Isoodon* (1 species; Warburton &

Travouillon, 2016; Travouillon & Phillips, 2018). The taxonomy of many New Guinean taxa remains unresolved, with more species expected to be discovered in ongoing fieldwork, studies of museum material, and through taxonomic revision (Helgen, 2007; Westerman *et al.*, 2012; Warburton & Travouillon, 2016; Travouillon & Phillips, 2018).

Keywords: Bandicoot; Indonesia; New Guinea; morphological systematics; taxonomy; new species

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ORCID iD: Travouillon, 0000-0003-1734-4742; Bertozzi, 0000-0001-6665-3395; MacDonald, 0000-0003-2972-200X; Cooper, 0000-0002-7843-8438; Flannery, 0000-0002-3005-8305; Helgen, 0000-0002-8776-4040

Corresponding author: Kenny Travouillon kenny.travouillon@museum.wa.gov.au

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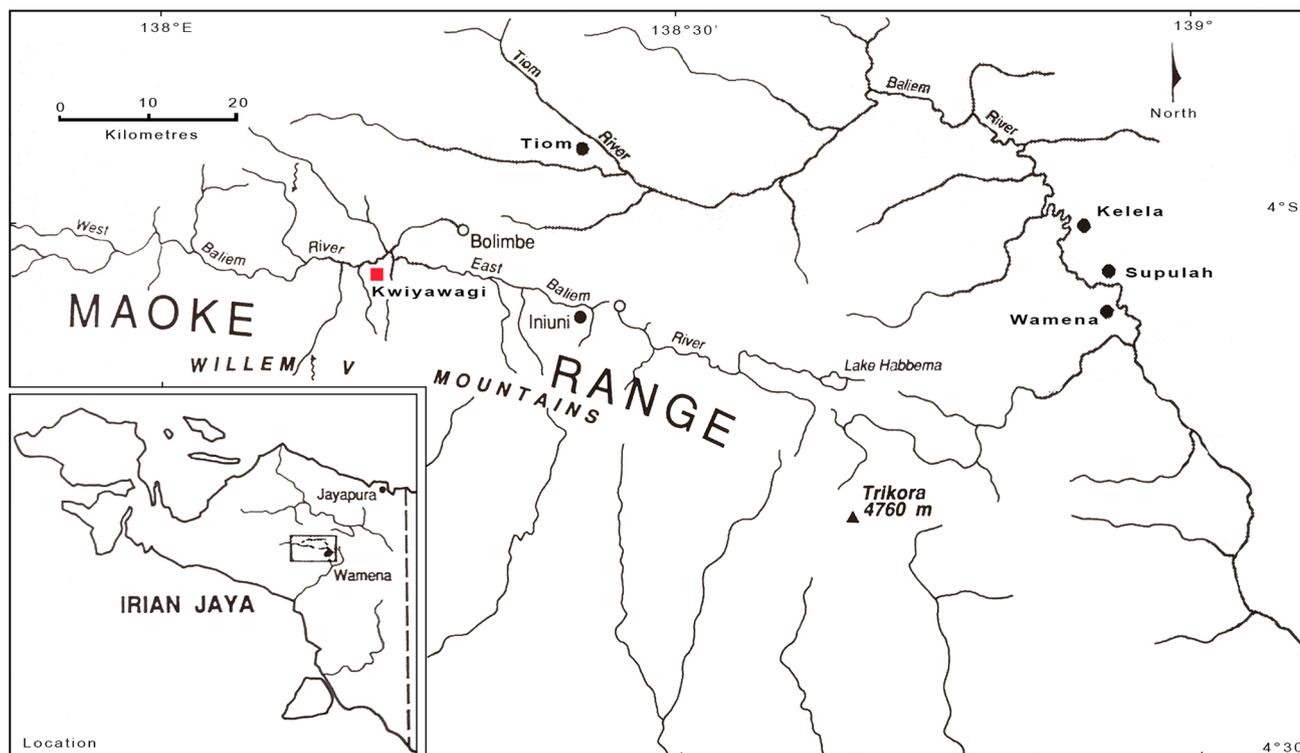


Figure 1. Map of New Guinea showing the location of the Kwiyawagi (red), in the West Baliem Valley in the Central Cordillera of western New Guinea, type locality of *Peroryctes trigonodon* sp. nov. Modified from Hope *et al.* (1993).

In the 1990s, Kwiyawagi (Fig. 1) was the largest human settlement in the West Baliem Valley, Papua Province, Indonesia, comprising around 1,000 Western Dani (Lani) inhabitants. Before TFF's visits (1991–1996), it had been a station for American evangelical missionaries. Located at an elevation of 2,950 m, it lay on a meander of the West Baliem River where the river is crossed by a suspension bridge, one of the only crossing points on the West Baliem River. A search on Google Earth in 2022 revealed that Kwiyawagi had completely transformed. The original mission buildings and the dense settlement of round, thatched hongis of the Western Dani that surrounded them had been replaced by newly constructed buildings, and the grass mission airstrip had been upgraded and enlarged.

The Kwiyawagi area receives an estimated 2,900 mm rainfall per year (Hope *et al.*, 1993). After meandering across the largely flat valley floor for around 50 km, the West Baliem River flows into the East Baliem River just east of Kwiyawagi, the conjoined streams entering Bolimbe (the Baliem Swallet) and flowing underground for several kilometres before re-emerging and joining the Baliem River in the Baliem Valley. We present here the discovery of a new species of *Peroryctes*, collected in 1994 by one of us (TF), during a field trip to the Kwiyawagi area of western New Guinea. We became aware of this new taxon because two of us (KJT and KMH) independently noticed distinctive dental traits that set this species apart from samples of *Peroryctes raffrayanus*, with which this new taxon has heretofore been confused (e.g., Flannery, 1999). The new species of *Peroryctes* we describe here has not yet been found outside the West Baliem Valley.

Materials and methods

Material

The specimens of the new taxon are stored in the mammal collections of the Australian Museum (AMS M), Sydney, Australia, and the Museum Zoologicum Bogoriensis (MZB), Cibinong, Indonesia. They were collected by one of us (TFF), during fieldwork in the Kwiyawagi area (Fig. 1). Logfall traps of local manufacture were the main method of obtaining game in the forest remnants in the area (Flannery, 1997: plate 22, for an example).

Comparative specimens of *Peroryctes broadbentii* and *Peroryctes raffrayanus* were examined from the Australian Museum, Sydney (AMS) (including the type specimen of *P. broadbentii*, AMS A.3238); the American Museum of Natural History (AMNH), New York, USA; Museum national d'Histoire naturelle (MNHN, including the type specimens of *P. raffrayanus*, MNHN ZM MO-1877-2026 to MO-1877-2030), Paris, France; the Natural History Museum (NHMUK), London, United Kingdom; the Australian National Wildlife Collection (ANWC), Canberra, Australia; and the Western Australian Museum (WAM), Perth, Australia.

Morphometric analysis

Specimens of the new taxon were assessed with detailed morphological study, both qualitative and quantitative. The qualitative assessment included a complete description of the skin, skull, and teeth, with comparison with both the type specimens of *Peroryctes broadbentii* and *Peroryctes raffrayanus*, and additional specimens of these taxa. Cranio-

dental terminology follows Travouillon *et al.* (2010, 2013a, 2013b, 2014, 2015, 2018, 2019) and Gurovich *et al.* (2014). The quantitative assessment included cranial and dental measurement (left and right sides), taken using digital callipers, on each adult specimen examined ($n = 58$). All analyses were done in the software PAST 4.08. Skulls used were mostly intact, but if a measurement couldn't be taken due to damage, missing values were estimated by the software. Cranial and dental measurements follow Aplin *et al.* (2010), Travouillon (2016), and Travouillon *et al.* (2018, 2019). Cranial and dental measurements were summarized using univariate statistics, and then analysed using a Principal Component Analysis (PCA). For the cranial PCA, males and females were indicated by different symbols, but in the dental PCA, sexes were not differentiated. A MANOVA could not be performed due to the low sample size ($n = 2$) for the new taxon.

Abbreviations

The following abbreviations are used in tables: **aIL**, length of anterior upper incisor series (I1–4), measured at crown bases; **apl**, length of incisive (anterior palatal) foramen; **anw**, combined anterior width of the nasal bones; **apw**, combined width across the paired anterior palatal foramina; **bh**, height of bullae; **bl**, length of bullae; **bw**, width of bullae; **bcl**, condylobasal length; **bol**, length of basioccipital bone; **bsl**, length of basisphenoid bone; **ctl**, length of cheektooth series (premolars + molars); **CV**, Coefficient of variation; **cw**, combined width of occipital condyles; **fs**, length of midline suture of frontal; **IL**, length of entire upper incisor series (I1–5), measured at crown bases; **iow**, width of greatest constriction of orbitotemporal fossa; **jh**, height of jaw measured between m2 and m3; **jl**, length of jaw, from anterior most point of dentary (excluding incisors) to condyle; **lmr**, combined length of lower molar series (m1–4), measured at crowns; **lpl**, combined length of upper premolar series (P1–3), measured at crowns; **lpr**, combined length of lower premolar series (p1–3), measured at crowns; **m1–4L**, length of m1–4, measured at crown; **m1–4AW**, width of m1–4, measured at crown across trigonid; **m1–4PW**, width of m1–4, measured at crown across talonid; **M1–4L**, length of M1–4, measured at crown; **M1–4W**, width of M1–4, measured at crown; **mw**, maximum width across braincase; **nl**, maximum length of nasal bone; **nps**, length of sutural contact between nasal bone and premaxilla; **onl**, greatest length of skull (occipitonasal length or occipitopremaxillary length); **oP3**, palatal width, measured across posterobuccal corner of each P3; **p1–3L**, length of p1–3, measured at crown; **p1–3W**, width of p1–3, measured at crown; **P1–3L**, length of P1–3, measured at crown; **P1–3W**, width of P1–3, measured at crown; **pnw**, combined posterior width of the nasal bones, measured at intersection with maxillofrontal suture; **pow**, width across outside of paroccipital process; **ppl**, length of maxillopalatine fenestra; **ppw**, maximum width across postorbital ridge; **rwc**, anterior rostral width, measured across outer surface of each canine; **rwi**, posterior rostral width, measured across medial surface of each infraorbital foramen; **SD**, standard deviation; **SE**, standard error; **uML**, combined length of M1–3, measured at crowns; **uMR**, combined length of M1–4, measured at crowns; **uPR**, combined length of upper premolar series (P1–3), measured at crowns; **Var**, variance; **zw**, maximum width of cranium, measured across zygomatic arches.

Morphological phylogeny

The morphological matrix from Travouillon *et al.* (2019) was used to assess the morphological relationship of the new taxon. Characters were scored and added to the matrix. Using the software PAUP* 4.0b10 (Swofford, 2002), a maximum parsimony analysis of the matrix was performed. Following Travouillon *et al.* (2019), a 'molecular scaffold' was used as a backbone 'constraint', based on the phylogeny of Westerman *et al.* (2012). A two-step heuristic search was performed comprising of 1,000 replicates, saving ten trees per replicates. The most parsimonious trees were summarized in a strict consensus tree, with bootstrap values calculated using 1,000 replicates, with ten random addition sequence replicates each.

Molecular phylogeny

DNA was extracted from a skin sample taken from the belly of specimen AMS M.30856 (the holotype), to compare with sequences from other peramelemorphians as part of an Oz Mammals Genomics Initiative (Eldridge *et al.*, 2020) phylogenomics project. All samples included in this project were analysed as follows. DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen), with modifications based on Joseph *et al.* (2016). Dried skin samples were rehydrated overnight in 300 μ l PBS (pH 7.4, Thermo Fisher), before transfer to lysis buffer. Samples were digested for 2–6 hours at 56°C with shaking at 800 rpm, in a lysis buffer mix containing 320 μ l buffer ATL, 40 μ l proteinase K, and 40 μ l 1M DTT (Thermo Fisher). Following lysis, 400 μ l buffer AL and 3.25 μ g carrier RNA (Sigma Aldrich) were added before incubation at room temperature for 30 minutes. 400 μ l of ethanol was added to each sample preparation and immediately mixed. Samples were then transferred to DNeasy spin columns in 650 μ l aliquots, with each centrifuged for 1 minute at 8000 rpm and supernatant discarded. Ethanol wash steps followed the manufacturer's protocol. DNA was eluted in 200 μ l of buffer AE containing 0.05% Tween 20 (Sigma). DNA extraction success was evaluated with the Qubit High Sensitivity DNA kit (Thermo Fisher). To mitigate contamination risks, DNA from historical museum specimens was extracted in a dedicated, physically separated, Trace DNA facility at the Australian National University's Ecogenomics and Bioinformatics Laboratory. Extraction negative controls were included to monitor for contamination.

An exon capture target enrichment library was prepared for each sample, including the AMS M.30856 DNA extraction, using the Meyer and Kircher (2010) protocol, with modifications based on Bi *et al.* (2013) and Roycroft *et al.* (2022). We used a set of custom marsupial exon capture probes (SeqCap EZ Developer Library; Roche NimbleGen) as outlined in Bragg *et al.* (2017). Pooled exon capture libraries were sequenced on an Illumina NovaSeq SP 200 cycle paired end run at the ACRF Biomolecular Resource Facility, Australian National University.

The paired end reads were processed using a containerized workflow (<https://hub.docker.com/r/hoohaah/ubuntu>) implemented through a virtual machine in the ARDC NeCTAR research cloud running Ubuntu 20.04 LTS (Turakulov, 2001). Locus alignment and subsequent processing steps were modified from the original workflow according to details and scripts provided at <https://bitbucket.org/samebu/tccp/src/master> (Bertozzi, 2001).

Results

Morphometric analysis

The results of the Principal Component Analysis (PCA), show clear distinctions between the three taxa examined, both in the cranial dataset (Fig. 2A), and the dental dataset (Fig. 2B). In the cranial PCA (Fig. 2A), PC1 accounts for 94.5% of variance and PC2 for 1.3% of variance. In the dental PCA (Fig. 2B), PC1 account for 74.7% of variance, and PC2 for 10.9% of variance. The new taxon is clearly separated from *P. broadbentii* and is closest to *Peroryctes raffrayanus* in size and shape, but is clearly distinguishable in morphometric terms both cranially and dentally.

A similar result is seen in univariate statistics (Tables 1–2, Travouillon *et al.*, 2025a, 2025b), where the mean measurements of the new taxon are closer to *P. raffrayanus*, but are generally smaller in the cranial (Table 1) dataset. The exceptions are skull width (zw), basicranial (bsl, bol, cw, pow, mw), bullae (BH, BL), and upper and lower premolars (ipr, lpr). All measurements are, on average, smaller for the new taxon compared to *P. raffrayanus* in the dental dataset (Table 2).

Morphological phylogeny

In the maximum parsimony analysis (Fig. 3), *Peroryctes*, including the new taxon, is recovered as a well-supported monophyletic clade (bootstrap = 85%). *Peroryctes raffrayanus* is sister to a moderately supported clade containing the new taxon and *P. broadbentii* (bootstrap = 73%).

Molecular phylogeny

The number of on-target reads recovered for AMS M.30856 was very low, resulting in the assembly of less than 7% of the 2168 target loci. The coverage of the assembled loci was also extremely sparse, with no locus recovered fully and only 18 loci with greater than 50% coverage. Further, the analysis workflow did not identify any mitochondrial reads in the captured sequences. Thus this sample was removed from further molecular analyses due to data deficiency. This is likely because the specimen was stored in formalin for a long period of time during transport from Indonesia to Australia, resulting in DNA fragmentation.

Systematics

Order Peramelemorphia Ameghino, 1889
(sensu Kirsch, 1968 and Aplin & Archer, 1987)

Superfamily Perameloidea Gray, 1825

Family Peroryctidae Groves & Flannery, 1990
(sensu Travouillon & Phillips, 2018)

Genus *Peroryctes* Thomas, 1906

Synonym: *Lemdubuoryctes* Kear, Aplin, & Westerman, 2016

Content of the genus *Peroryctes* was formally reviewed most recently by Aplin *et al.* (2010), who recognized two living New Guinea species, by Travouillon *et al.* (2017), who removed the Pliocene Australian species '*Peroryctes tedfordi* Turnbull *et al.*, 2003 to the newly established genus *Silvicultor*, and by Travouillon and Phillips (2018), who showed that the fossil genus *Lemdubuoryctes*, erected by Kear *et al.* (2016) from the Aru Islands, is a synonym of *Peroryctes*.

Two species of *Peroryctes* are extant and endemic to New Guinea: *P. raffrayanus* (Milne-Edwards, 1878), which is widespread and often common in montane habitats across New Guinea (the nominal forms *rothschildi* Förster, 1913 and *mainois* Förster, 1913, are regarded as synonyms), and *P. broadbentii* (Ramsay, 1879), a rare species from lowland habitats in the south-eastern peninsula of New Guinea (Aplin *et al.*, 2010). Travouillon and Phillips (2018) assigned the Late Quaternary taxon *aruensis* Kear, Aplin, & Westerman (originally named in the genus *Lemdubuoryctes*) to *Peroryctes* and noted its very strong similarities to *Peroryctes broadbentii*. Here we consider *aruensis* to be a subspecies of *Peroryctes broadbentii* as it is only differentiated by the size of the M4 and slightly longer P2 and p1. Thus, in total we recognize two previously described species of *Peroryctes*, to which we now add a third.

Peroryctes trigonodon sp. nov. Travouillon, Flannery, & Helgen

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Figs 4–6

Holotype. AMS M.30856 (Field No. FU132), adult female, study skin and extracted skull. Collected in traditional deadfall trap on 11 June 1994 by a Dani local. Young (AMS M.30233, Field No. FU133—a paratype) in pouch. Field measurements: head and body length 330 mm, tail length 148 mm, hind foot length 71.7 mm, ear length 31.2 mm, weight 900 g.

Type locality. Ubimu (elevation 2,950 m), Kwiyawagi area (4°01'S 138°07'E) in the West Baliem Valley, in the Central Cordillera of western New Guinea (Papua Province, Indonesia).

Paratypes. AMS M.30817 (Field No. FU116), adult male, skull and skeleton, Kelangurr (elevation 2,950 m), Kwiyawagi area. Caught in traditional snare, on 9 June 1994, rotten when retrieved. Measurements: scrotal width 25.7 mm, head and body 355 mm, tail 151 mm, hind foot 74.5 mm, ear 28 mm, weight 700 g. AMS M.30233 (Field No. FU133), female pouch young. Measurements: head and body 118 mm, tail 63.5 mm, hind foot 36.2 mm, ear 17.9 mm, weight 44 g.

Referred specimen. Field No. FU84, registration number unknown (specimen was assigned to be sent to Museum Zoologi Bogor when the collection was divided in 1994 but this specimen has not been located in a recent search of the collection), subadult male, Kwiyawagi area near Ndangkwilim (elevation 2,712 m). Collected by hand by

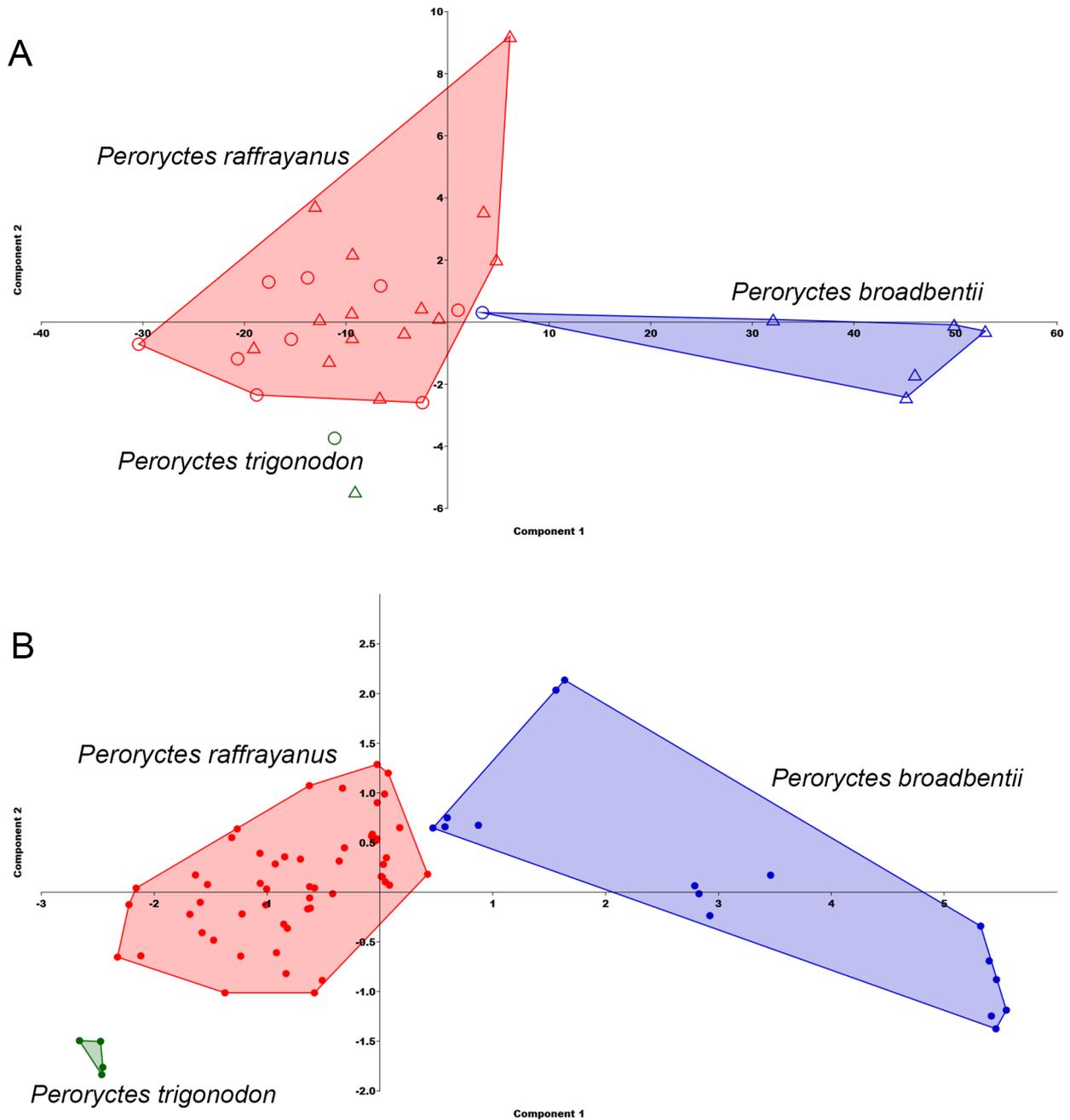


Figure 2. Principal Component Analysis (PCA) of the cranial (A) and dental (B) measurements, comparing *Peroryctes trigonodon* sp. nov. (dark green), *Peroryctes raffrayanus* (red) and *Peroryctes broadbentii* (dark blue). Open circles are females, open triangles are males.

Dinius on 3 June 1994. Measurements: head and body 263 mm, tail 123.2 mm, hind foot 61.6 mm, ear 30.7 mm, weight 342 g.

Diagnosis. *Peroryctes trigonodon* differs from *P. raffrayanus* in having a shorter infraorbital canal; a larger orbitosphenoid; the primary foramen ovale is not entirely in the alisphenoid, but bordered also by the petrosal; a smaller lingual shelf on P3; StD on M1 is not connected to the styler crest nor to StB (styler cusp B); preparacrista on M1 does not connect with the postparacrista; postprotocrista ends on the lingual flank of metacone on M1–3 with no shelf between metaconule and the base of the metacone;

StD1 absent on M1–2; styler crest not present on M2; StB conical on M3; StC and StD1 absent on M3; no anterior cingulum on M4; StB absent on M4; metacone present on M4; diastemata between canine and p1, and p1 and p2 are longer than p1; p1 and p2 having a tall anterior cusp; paraconid-metaconid distance is longer than metaconid-protoconid distance on m2; posthypocristid oblique to tooth row on m3; smaller entoconid on m4; hypoconulid present on m4.

Peroryctes trigonodon differs from *P. broadbentii* in being much smaller, and in having longer and darker pelage. Compared to *P. broadbentii* in craniodental anatomy,

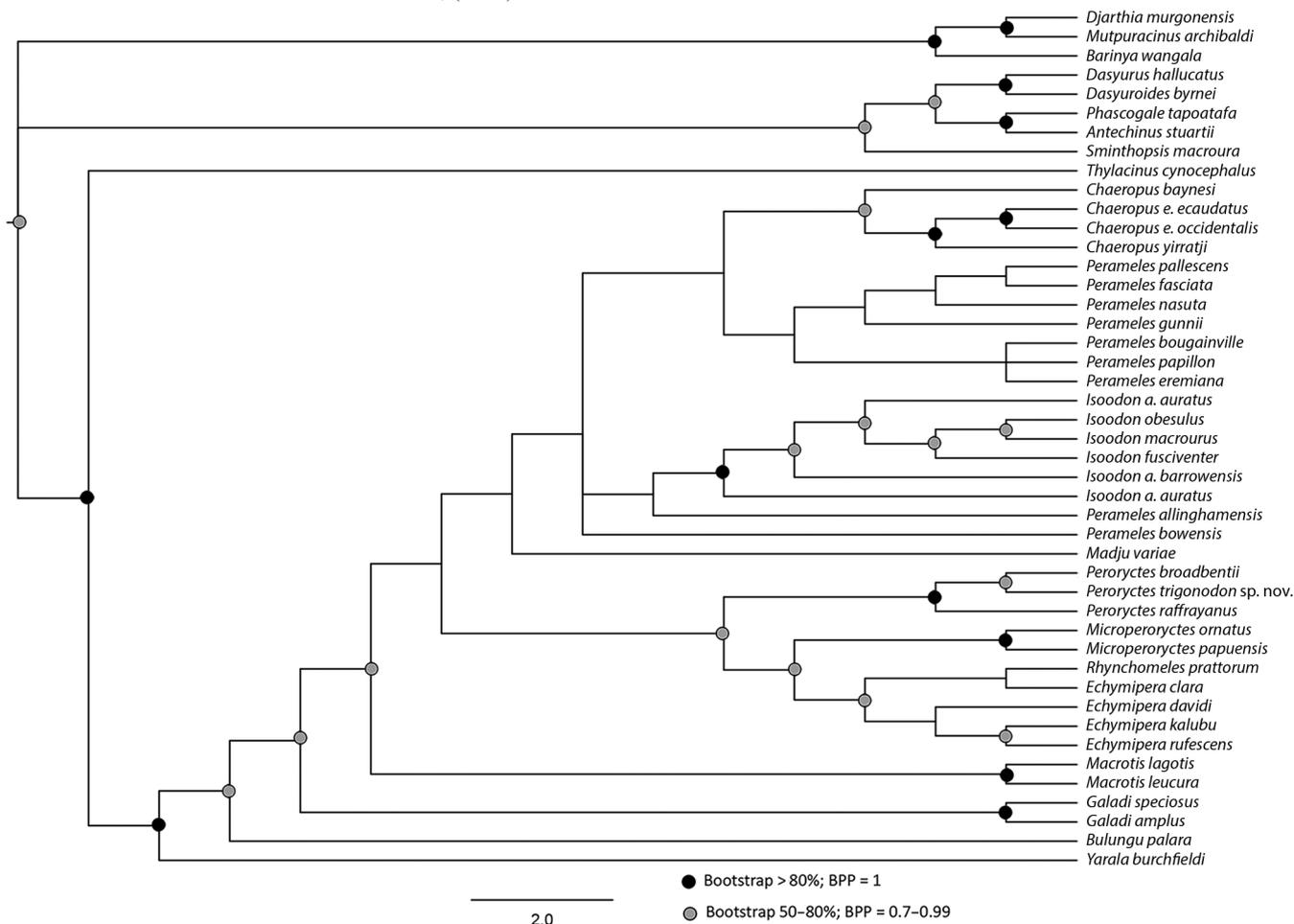


Figure 3. Consensus tree of the constraint Maximum Parsimony analysis of peramelemorphians, including *Peroryctes trigonodon* sp. nov., using morphological data.

P. trigonodon has: a weaker antorbital fossa; a larger orbitosphenoid; a smaller rostral tympanic process; the supraoccipital contributing to the upper margin of foramen magnum; a diastema longer than P1 between P1 and P2; P2 and p2 only just shorter than P3 and p3; P3 not taller than P2 but subequal in height; a smaller major cusp on P3; no shelf between metaconule and the base of the metacone on M1; StD1 absent on M1–2; preparacrista connects to StA on M2; StE smaller on M2; anterior cingulum on M2–3 is not connected to the talon; postparacrista on M3 does not connect to the premetacrista; no anterior cingulum on M4; postparacrista is straight on M4; postprotocrista ends anterior to the most posterior end of the tooth on M4; smaller metacone on M4; diastemata between canine and p1, and p1 and p2 are longer than p1; p2 and p3 having a tall anterior cusp; paraconid directly anterior to metaconid on m1; paraconid-metaconid distance is shorter than metaconid- protoconid distance on m3; smaller entoconid on m4; hypoconulid present on m4.

Etymology. Combination of ‘trigon’ and ‘odon’ meaning triangular tooth in ancient Greek, due to its molars being more triangular than other species of *Peroryctes*.

Common name. *Wablo* (Lani language).

Distribution. Found only in the Kwiyawagi area, in the West Baliem Valley, in the Central Cordillera of western New Guinea (Papua Province, Indonesia), where it has been located at elevations from 2,712 to 2,950 m.

Habitat. The West Baliem Valley has a microclimate that allows particular vegetation communities to survive at a much higher elevation than they do elsewhere in New Guinea. Completely surrounded by high limestone ranges and hills, with the West Baliem River exiting the valley via an enormous sinkhole that permits the river to flow under a range of hills, the valley is very isolated. This isolation is likely of long standing and might have been important to the speciation of *P. trigonodon*. Close to Kwiyawagi the original vegetation has been substantially disturbed by human activity, with *Deschampsia klossii* grasslands, *Cyathea* tree ferns and *Rhododendron* bushes dominating in old gardens and elsewhere where forest has been removed. The valley floor nonetheless supports significant remnants of both upper montane and swamp forest. Stands of *Nothofagus brassii* (which reaches its altitudinal limit at Kwiyawagi) dominate on better soils, while elsewhere species of *Evodiella*, *Syzygium*, *Dacrycarpus* and *Phyllocladus* occur. In areas of impeded drainage, open swamp forests dominated by *Libocedrus papuana* are found. Areas of forest cover remained substantial at the time of TFF’s last visit in 1996. Ubimu (the type locality) was a large patch of remnant upper montane forest. The trees were tall given the elevation (2,950 m), and the forest floor was mossy.

Description. The description is based on the holotype AMS M.30856, an adult female with the skin and skull preserved, and the paratype AMS M.30817, an adult male with the skull preserved.

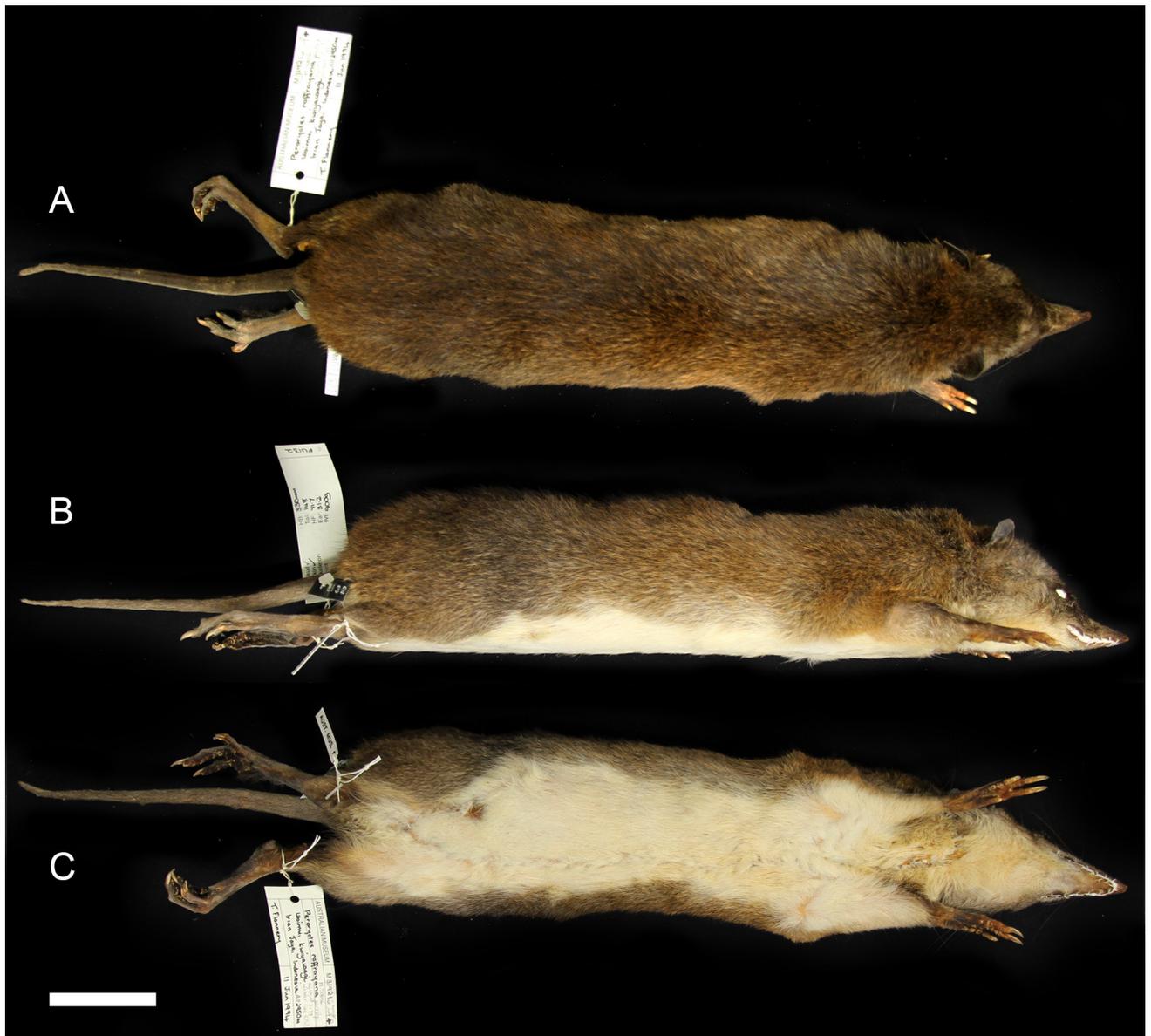


Figure 4. *Peroryctes trigonodon* sp. nov., holotype, AMS M.30856, adult female, study skin in (A) dorsal, (B) lateral, and (C) ventral views. Scale bar = 5 cm.

The pelage of *P. trigonodon* is similar to that of *P. raffrayanus* (Fig. 4). The principal differences are that the hairs extend a few millimetres beyond the tail tip in *P. trigonodon*, not projecting beyond the tail tip in *P. raffrayanus*. Further, scalation on tail appears to be less distinct, and the hairs around the margins of the pedal pads are denser, in *P. trigonodon* compared to *P. raffrayanus*.

The holotype skull is 77.84 mm long and 29.48 mm wide (Fig. 5). The paratype skull is 78.7 mm long and 31.51 mm wide. In dorsal view, the nasals are long and narrow, as in other species of *Peroryctes*, increasing in width posteriorly, before tapering. The frontals are generally flat. The parietals are fused as in all peramelemorphians, but there is no sagittal crest in the male (paratype AMS M.30817), similar to *Peroryctes raffrayanus* but unlike *P. broadbentii*. The lacrimals are smooth, with no evidence of crest development, as in other *Peroryctes* (unlike Australian peramelemorphians). In lateral view, the narial flange of the premaxilla are straight as in other species of *Peroryctes*

(wing-like in shape in all other modern peramelemorphians). The infraorbital foramen is located about M2 (above M1 in *P. raffrayanus*), reducing the length of the infraorbital canal. The antorbital fossa is deeper in the paratype than in the holotype, similar in depth to *P. raffrayanus*, but shallower than in *P. broadbentii*. The lacrimal foramen is bordered anteriorly by the maxilla as in all species of *Peroryctes* and *Macrotis* (unlike all other peramelemorphians, contained entirely by the lacrimal). The orbitosphenoid is visible as a large ossification, larger than in other species of *Peroryctes*. In posterior view, the supraoccipital contributes to the dorsal margin of the foramen magnum, unlike in *P. broadbentii*. In ventral view, the palate has two sets of foramina, which are similar to those of the other species of *Peroryctes*, and the maxillopalatine fenestrae, which are larger than other species of *Peroryctes*, extending anteriorly to the P3 (to M1 in *P. raffrayanus* and M2 in *P. broadbentii*). The basicranium is, in general, flatter than in other *Peroryctes*. The petrosal is similar in morphology to *P. raffrayanus*, with

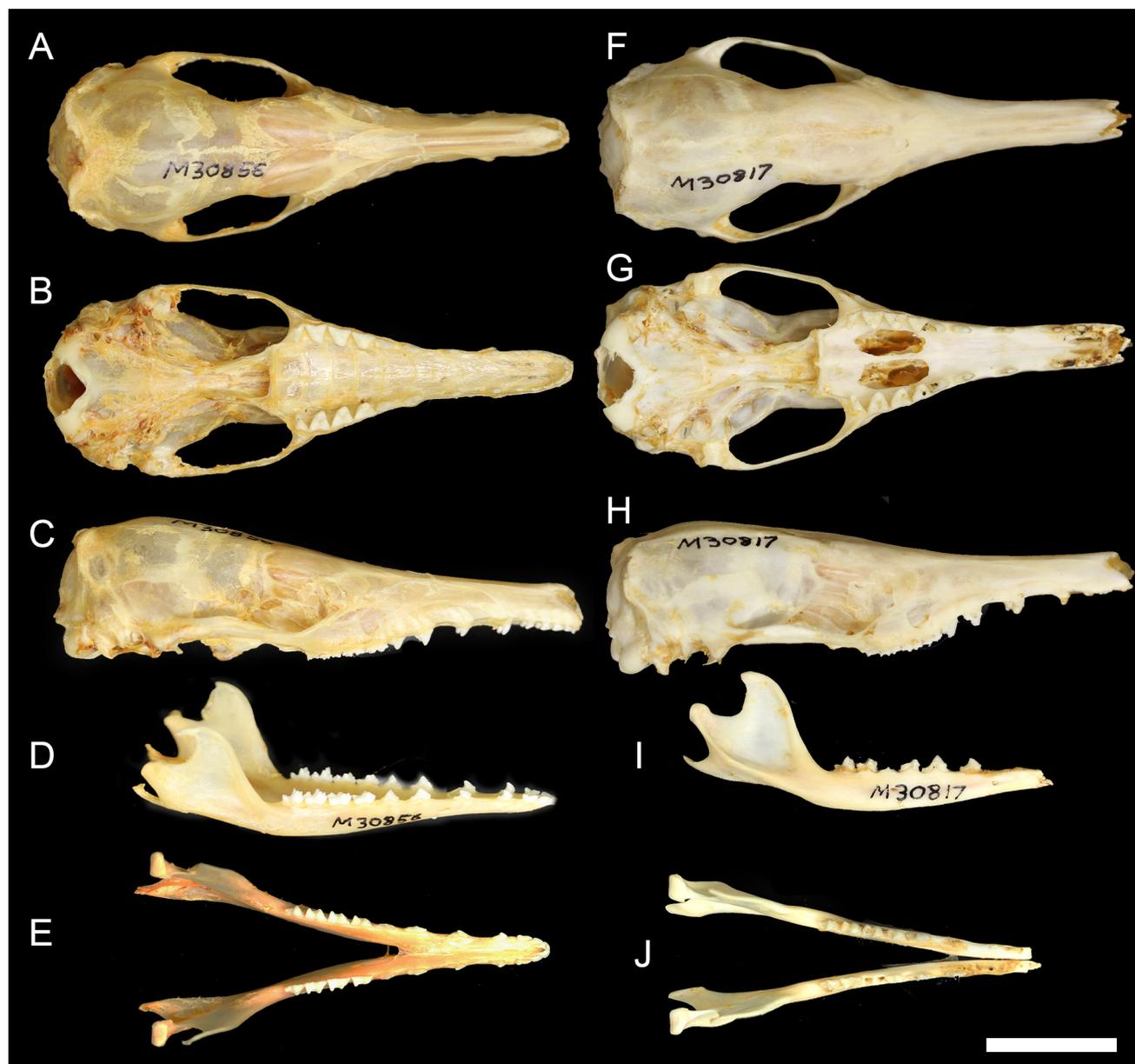


Figure 5. *Peroryctes trigonodon* sp. nov., holotype, AMS M.30856 (A–E), adult female, skull in (A) dorsal, (B) ventral, and (C) lateral views, dentary in (D) lateral, and (E) occlusal views. Paratype, AMS M.30817 (F–J), adult male, skull in (F) dorsal, (G) ventral, and (H) lateral views, dentary in (I) lateral, and (J) occlusal views. Scale bar = 2 cm.

a smaller rostral tympanic process than in *P. broadbentii*. The alisphenoid tympanic process (bullae), is flat and short as in *P. broadbentii*, with no tube-like protrusion above the secondary foramen ovale, as in *P. raffrayanus*. The primary foramen ovale is not entirely in the alisphenoid but bordered also by the petrosal as in *P. broadbentii* (entirely within the alisphenoid in *P. raffrayanus*). The dentary is slender and morphologically closer to *P. raffrayanus* than *P. broadbentii*, which is more robust. There are no other distinguishing features on the dentary.

The following description of the teeth is based principally on the holotype, as the paratype is an older individual with very worn teeth, unless stated otherwise (Fig. 6). There are five upper incisors, rhomboidal in shape, except for I5, which is more pointed and more canine-like. I1–3 increase in size posteriorly, and then I4–5 decrease in size posteriorly. There is a short diastema between I4 and I5, and a larger one

between I5 and C1. The C1 is recurved and unirooted. There are no accessory cusps on the C1. In both the holotype and paratype, the C1 is shorter than the P1, with no evident sexual dimorphism (males of *Isoodon* and *Macrotis* have an enlarged C1). A large diastema, longer than P1, separates C1 and P1, and then P1 and P2. P1–3 are similar in shape, with a tall main cusp, a small posterior cusp, and a smaller anterior cusp. P1–3 increase in length and height posteriorly, except P3 is subequal in height to P2. P3 has a small lingual shelf, similar in size to that of *P. broadbentii*, but smaller than that of *P. raffrayanus*. The P3 in both the holotype and paratype are similar in size, unlike *P. broadbentii*, in which the males have a significantly longer and taller P3. The M1 is the longer molar on the tooth row, but the least wide. StA is the most anterior cusp on the crown, with a short anterior cingulum lingually. The paracone is quite worn, but the preparacrista connects to StB/StC. This crest ends in the interloph valley, and does not connect to StD,

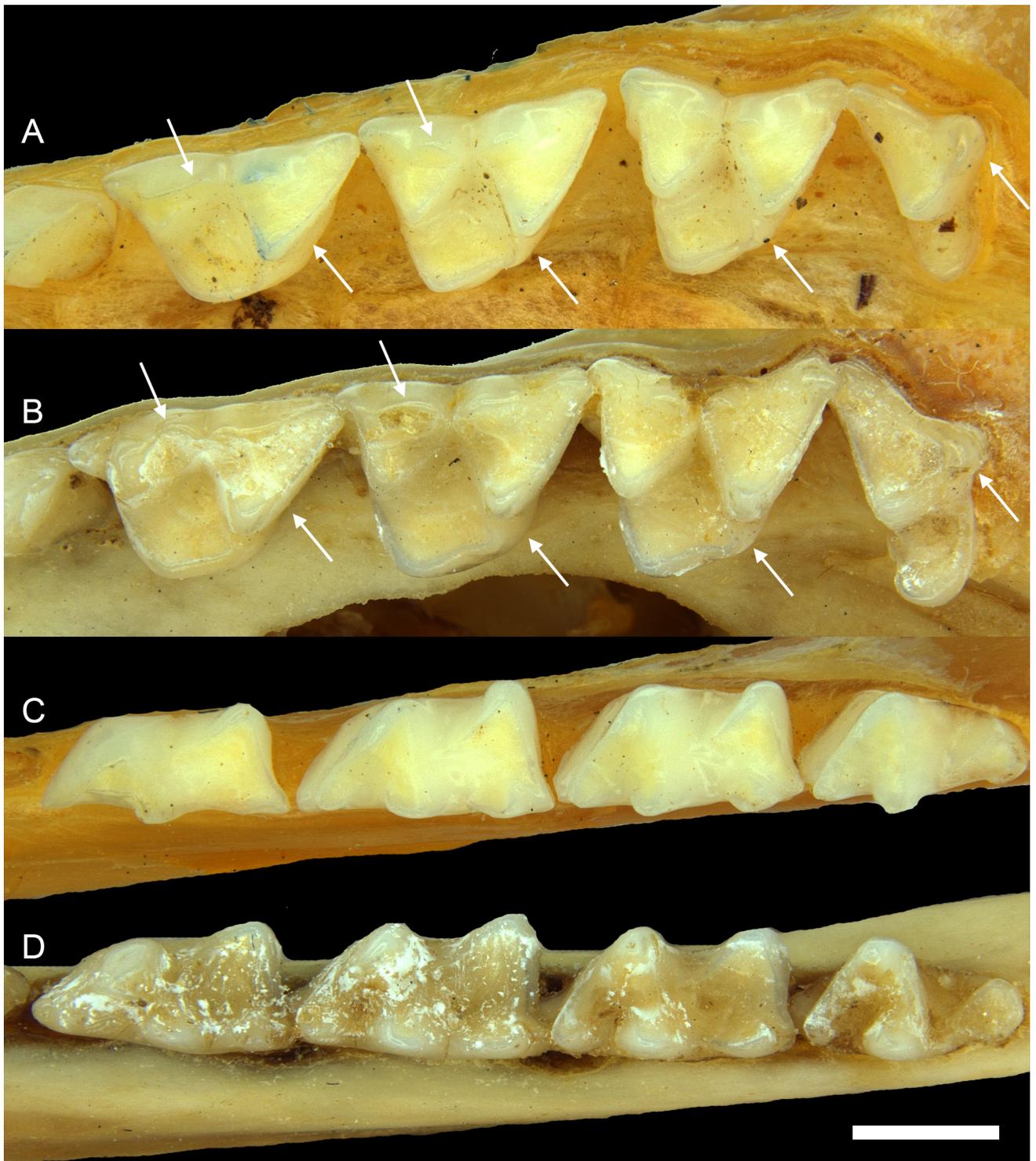


Figure 6. *Peroryctes trigonodon* sp. nov., holotype, AMS M.30856, adult female; (A) upper molars, (C) lower molars, in occlusal views. *Peroryctes raffrayanus*, WAM M23091, adult female; (B) upper molars, (D) lower molars, in occlusal views. Arrows point to diagnostic features. Scale bar = 2 mm.

nor to the postparacrista. StD1 is absent. StD is conical, tall and bladed, but it is not connected by a stylar crest posteriorly. StE is small, barely visible just anterior to the metastylar tip. The premetacrista ends at the anterior of StD. The preprotocrista ends at the lingual flank of the paracone, and the postprotocrista ends at the metaconule, at the lingual flank of the metacone. No shelf separates the metaconule from the lingual flank of the metacone. The M2 is similar in morphology to the M1 except

that the tooth is shorter but wider. The protocone, paracone, and metacone are larger and more lingual. The parastylar shelf is larger, but StC is absent. StA is taller, and connected to StB by a crest. The anterior cingulum is wider but does not connect to the talon. The stylar crest is absent, and StE is smaller. The M3 is similar to the M2 in morphology but it is shorter in length but wider. StB is conical and does not connect to StA. The preparacrista is more anteriorly directed and

connects to StA. The protocone is smaller and more lingual, elongating the preprotocrista and postprotocrista, which are both more buccally orientated. The M4 is very reduced in size, with only the parastylar shelf and talon present. The anterior cingulum, StB, StD, StE, and metaconule are absent. The postparacrista is straight and ends at a remnant of a metacone. The preprotocrista and postprotocrista are short and end on the anterior and posterior flanks of the paracone respectively.

The three lower incisors are flat and bladed, with i3 being bilobed. A short diastema separates i3 to c1. The c1 is strongly recurved, with a small posterior cuspid. The c1 is as tall as the p1. Large diastemata, longer than the length of p1, separate c1 and p1 and p1 and p2. The p1–3 are similar in morphology, with tall anterior and posterior cuspids. The p1–3 gets progressively taller and longer posteriorly, but less recurved. The m1 has a long but narrow trigonid, with no anterior cingulid. The paraconid-metaconid distance is longer than metaconid-protoconid distance. The paraconid is directly anterior to the metaconid as in *P. raffrayanus* (more buccally positioned in *P. broadbentii*). The talonid is wider than the trigonid, but as long. Cristid obliqua is parallel to the paracristid and the posthypocristid is parallel to the metacristid. The entoconid is small, ovoid, with anteriorly directed preentocristid. The smaller hypoconulid is directly posterior to the entoconid. The m2 is similar in morphology to the m1 except it is both longer and wider. An anterior cingulid is present. All cuspids are taller and crests elongated. The m3 is similar to the m2 in morphology, except the paraconid-metaconid distance is shorter than the metaconid-protoconid distance. The protoconid is taller, and the talonid is less wide, with all cuspids on the talonid reduced in size. The m4 is similar to the m3 in morphology except the talonid is further reduced, with much smaller hypoconid, entoconid, and hypoconulid present.

Discussion

Peroryctes trigonodon sp. nov. is a distinctive bandicoot, easily distinguished from its congeners by qualitative and morphometric craniodental comparisons. Despite our thorough search through museum collections, we have not found any further specimens of this taxon—all other *Peroryctes* specimens we have encountered in world museum collections represent either *P. raffrayanus* or *P. broadbentii* (Aplin *et al.*, 2010). This indicates that *P. trigonodon* is a rare component of the New Guinean fauna and may be much restricted to the high elevation West Baliem Valley. We note that Flannery (1999) reported on a Pleistocene assemblage of small mammal bones from Kelangurr Cave in the Kwiawagi area, and *Peroryctes trigonodon* is absent from this Late Glacial Maximum assemblage, potentially indicating its rarity; the only peroryctid recorded from the assemblage is a species of *Microperoryctes*, which likely awaits formal description (Helgen, 2007). Insufficient information is yet available for a more formal conservation assessment, but *Peroryctes trigonodon* may be very rare and possibly threatened. Being likely forest dependent, it may be at risk of extinction if clearance of native vegetation is ongoing in the Kwiawagi area.

The range of *P. trigonodon*, which is restricted to the West Baliem River Valley on the basis of current knowledge, contrasts with the wide geographic range of its highland congener, *P. raffrayanus*, which occurs both to the east and

west of the Baliem Valley. *Peroryctes raffrayanus* is most common in eastern New Guinea, where it occurs along the Central Cordillera from the mountains of Milne Bay Province in the far south-east to the Star Mountains in the centre of New Guinea. Records of *P. raffrayanus* are rarer in the western part of the Cordillera, but it is represented in the Idenburg River transect sampled by the Archbold Expeditions (specimens at AMNH) and is known from specimens from the Weyland Range at the western margin of the Cordillera. *Peroryctes raffrayanus* also occurs in most of the well-sampled outlying mountain ranges of New Guinea, including in the Huon Peninsula, North Coast Ranges (Torricelli Mountains), Cyclops Mountains, and the Tamrau and Arfak Mountains in the far west. Though usually found above 500 m, *P. raffrayanus* can be found in some circumstances down to less than 100 m above sea level (Flannery, 1995).

Western New Guinea is a zone of remarkable mammalian endemism (Helgen, 2007). *Peroryctes trigonodon* joins a substantive list of mammal species that are known only from quite small, circumscribed high elevation areas of the western part of the Central Cordillera of New Guinea, including one other bandicoot species, *Microperoryctes murinus* Stein, 1932, known only from the Weyland Range, and the tree-kangaroo *Dendrolagus mbaiso* Flannery, Boeadi, & Szalay, 1995, of the Sudirman Range and vicinity (Flannery, 1995; Flannery *et al.*, 1995, 1996; Helgen & Flannery, 2004; Wild & Balke, 2018). This list also includes the rodents *Brassomys albidens* (Tate, 1951), *Pseudohydromys patriciae* Helgen & Helgen, 2009, and *Mallomys gunung* Flannery, Aplin, & Groves, 1989, each known only from the vicinity of Lake Habbema and Mount Trikora (Wilhelmina); *Hydromys hussoni* Musser & Piik, 1982, known only from the Paniai Lakes; and *Macruromys elegans* Stein, 1933 and *Paramelomys steini* (Rümmeler, 1935), known only from the Weyland Range (Flannery *et al.* 1989; Menzies, 1996; Musser & Carleton, 2005; Helgen, 2005; Helgen & Helgen, 2009; Musser & Lunde, 2009). Many additional mammal species endemic to western New Guinea uplands are known from mountain ranges outlying the Central Cordillera, including the mountains of Vogelkop and northern ranges such as the Fojas and Cyclops (Helgen, 2007). Continued advances in illumination of mammalian taxonomic patterns and endemism, including new species descriptions, are of potential utility in efforts to delimit important areas for conservation in western New Guinea (Diamond, 1986; Petocz, 1989; Schipper *et al.*, 2008) and remind us of the importance of describing new species to more effectively enable their preservation (Liu *et al.*, 2022).

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Found Alive After 6,000 Years: Modern Records of an ‘Extinct’ Papuan Marsupial, *Dactylonax kambuayai* (Marsupialia: Petauridae), with a Revision of the Systematics and Zoogeography of the Genus *Dactylonax*

TIM F. FLANNERY¹ , KENNETH P. APLIN¹† , CARLOS BOCOS²,
LOUKAS G. KOUNGOULOS¹ , AND KRISTOFER M. HELGEN³ 

¹ Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

² Independent researcher, mammalwatching.com, cnbocos@gmail.com

³ Bernice Pauahi Bishop Museum, 1525 Bernice Street, Honolulu, Hawai‘i 96817, United States of America

† Kenneth P. Aplin 1958–2019, deceased.

ABSTRACT. The Pygmy long-fingered possum, *Dactylonax kambuayai*, is the smallest of the striped possums (the petaurid subfamily Dactylopsilinae). It is a ‘Lazarus species’, found living when previously known only from fossils. Recently collected museum specimens, and observations and photographs of living individuals, correspond taxonomically to the only previously reported specimens of *D. kambuayai*, which are fossil remains from a nearby Holocene location, all occurring in low- to mid-elevation rainforests on the Vogelkop Peninsula of New Guinea. Together with the recent discovery of another Lazarus possum, ‘*Petauroides ayamaruensis*’, they represent the only marsupials known as modern animals only from low elevations (below 1000 m) on the Vogelkop Peninsula. Both of these species are diminutive species with enigmatic natural histories. In reviewing the systematics of this species, we demonstrate the distinctness of *Dactylonax* as a genus-level taxon, and clarify species boundaries in this genus. *Dactylonax palpator*, the type species of *Dactylonax*, was previously considered to be a widespread montane taxon, but is recognized here as two separate species: *D. palpator* is restricted to the Arfak Mountains of the Vogelkop, while *D. ernstmayri* is widely distributed on the New Guinean Central Cordillera and the Huon Peninsula at elevations above 800 m. *Dactylonax palpator* replaces, or co-occurs with, *D. kambuayai* at elevations between around 900 m and 1,400 m on the Vogelkop. We hypothesize that colonization of montane habitats on the Vogelkop by a *D. kambuayai*-like ancestor gave rise to the larger bodied *D. palpator*, and dispersal of this lineage to montane habitats in the Central Cordillera gave rise to the highly specialized *D. ernstmayri*. The fact that the montane taxon of the Vogelkop *Dactylonax* species couplet was able to migrate eastwards, while the lowland taxon was not, suggests that an unusual elevational zoogeographic filter was in play. We observe that *D. kambuayai* is thus far recorded from sites where the other small petaurid of New Guinea, *Petaurus papuanus*, is not recorded or is uncommon.

Keywords: Marsupialia; Petauridae; *Dactylonax*; *kambuayai*; *palpator*; *ernstmayri*; Lazarus taxon; Vogelkop; New Guinea; systematic review
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ORCID iD: Flannery, 0000-0002-3005-8305; Aplin, 0000-0003-0403-8690; Koungoulos, 0000-0002-5148-0142; Helgen, 0000-0002-8776-4040
Corresponding authors: Tim F. Flannery tim.fridtjof.flannery@gmail.com and Kristofer M. Helgen kris.helgen@bishopmuseum.org
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ABSTRAK. [Bahasa Indonesia]. Posum jari-panjang kerdil (*Dactylonax kambuayai*) merupakan anggota terkecil dari kelompok posum belang (subfamili petaurid Dactylopsilinae). Spesies ini termasuk ‘spesies Lazarus’, yakni ditemukan masih hidup setelah sebelumnya hanya dikenal dari catatan fosil. Spesimen museum yang dikoleksi baru-baru ini, serta pengamatan dan dokumentasi fotografi individu hidup, secara taksonomis sesuai dengan satu-satunya spesimen yang sebelumnya pernah dilaporkan untuk *D. kambuayai*, yaitu sisa-sisa fosil dari lokasi Holosen terdekat, seluruhnya berasal dari hutan hujan dataran rendah hingga menengah di Semenanjung Vogelkop, Papua Barat.

Bersama dengan penemuan terkini spesies Lazarus lainnya, ‘*Petauroides ayamaruensis*’, kedua spesies ini merupakan satu-satunya marsupial yang diketahui sebagai hewan modern yang terbatas pada elevasi rendah (di bawah 1.000 m) di Vogelkop. Keduanya merupakan spesies berukuran kecil dengan riwayat alami yang masih enigmatik.

Dalam tinjauan sistematika spesies ini, kami menunjukkan bahwa *Dactylonax* merupakan takson yang berbeda pada tingkat genus, serta memperjelas batas-batas spesies di dalam genus tersebut. *Dactylonax palpator*, sebagai spesies tipe genus *Dactylonax*, sebelumnya dianggap sebagai takson pegunungan yang tersebar luas, namun di sini diakui terdiri atas dua spesies terpisah: *D. palpator* terbatas pada Pegunungan Arfak di Vogelkop, sedangkan *D. ernstmayri* tersebar luas di Pegunungan Tengah Nugini (Central Cordillera) dan Semenanjung Huon pada elevasi di atas 800 m.

Dactylonax palpator menggantikan, atau hidup simpatrik dengan, *D. kambuayai* pada elevasi sekitar 900 m hingga 1.400 m di Vogelkop. Kami mengajukan hipotesis bahwa kolonisasi habitat pegunungan di Vogelkop oleh leluhur yang menyerupai *D. kambuayai* menghasilkan bentuk berukuran tubuh lebih besar, yaitu *D. palpator*, dan bahwa penyebaran garis keturunan ini ke habitat pegunungan di Pegunungan Tengah menghasilkan spesies yang sangat terspesialisasi, *D. ernstmayri*. Fakta bahwa takson pegunungan dari pasangan spesies *Dactylonax* di Vogelkop mampu bermigrasi ke arah timur, sementara takson dataran rendah tidak, menunjukkan adanya suatu penyaring zoogeografis elevasional yang tidak lazim.

Kami mencatat bahwa *D. kambuayai* sejauh ini hanya tercatat dari lokasi-lokasi di mana petaurid kecil lainnya dari Nugini, *Petaurus papuanus*, tidak ditemukan atau jarang dijumpai.

Introduction

A relatively small number of animal species hold the distinction of having been described initially from fossil remains, then subsequently discovered as a living animal. In palaeontology, lineages that drop out of the fossil record and then re-emerge after long periods are termed ‘Lazarus taxa’ (Flessa & Jablonski, 1983; Jablonski, 1986; Fara, 2001) and this term may be usefully extended to cover this special class of modern species. The Australo-New Guinea region hosts four previous examples of ‘Lazarus’ mammal species. The Mountain Pygmy Possum, *Burramys parvus* was described from cave deposits of late ‘Pleistocene’ age southeastern Australia, (Broom, 1895) before being found as a living animal almost 60 years later in Australian alpine habitats (Calaby *et al.*, 1971). The northern hairy-nosed wombat *Lasiorninus krefftii*, of eastern Australia, was first named from a Pleistocene cave deposit (Owen, 1872), then renamed several times from extant populations (de Vis, 1900; Longman, 1939). Bulmer’s Fruit Bat, *Aproteles bulmerae*, a large bat endemic to the highlands of New Guinea, was first recognized in an archaeological assemblage of late Pleistocene to early Holocene age (Menzies, 1977) and a few years later was found as a living animal in a remote location (Hyndman & Menzies, 1980; Flannery & Seri, 1993). Most recently the pseudocheirid possum ‘*Petauroides ayamaruensis*’ (Aplin, 1999), of western New Guinea, was discovered as a living taxon after being previously known only from Holocene (*ca.* 6,000–7,500-year-old) fossils (Flannery *et al.*, 2026).

These most recent examples (*Aproteles bulmerae*, *Dactylonax kambuayai*, and ‘*Petauroides ayamaruensis*’) originate from the large tropical island of New Guinea. Another relatively recent example from the region comes from the Wallacean island of Flores, where the murid rodent *Paulamys naso*, originally described as a fossil (Musser,

1981; Musser *et al.*, 1986), was documented as a living animal by Kitchener *et al.* (1991, 1998). Other surprises may await, given that on some other islands in the region, the mammal subfossil fauna is as yet better studied than the modern fauna. Possibilities include a variety of other rodents known to date only in the Holocene fossil records of the Wallacean islands of Flores (Musser, 1981; Veatch *et al.*, 2023), Timor (Aplin & Helgen, 2010), and Morotai (Aplin *et al.*, 2023) to the west of New Guinea, and in New Ireland in the Bismarck Archipelago (Flannery & White, 1991) and Buka in the Solomon Islands (Flannery & Wickler, 1990) to the east of New Guinea. Lazarus may yet awake in these islands.

Dactylonax kambuayai was described as *Dactylopsila kambuayai* Aplin, 1999, from craniodontal remains within an archaeological excavation of mid Holocene age from the Ayamaru Plateau of the Vogelkop Peninsula (Cenderawasih Peninsula) of Indonesian West Papua (Aplin *et al.*, 1999) (Fig. 1). Though listed as extinct in subsequent compendia (Turvey, 2009; Turvey & Fritz, 2011), Helgen (2007) suggested that the species was likely to be found extant when the mammal fauna of western New Guinea was better surveyed. One of us (KPA) uncovered two previously overlooked modern specimens referable to *D. kambuayai* among specimens stored in fluid jars at the University of Papua New Guinea, where they had been misidentified as *D. palpator*. Based on this information, Jackson (2015: 558–559) provided the first published notice of this modern survival of *D. kambuayai*, provided the first illustration of its external appearance, and discussed its biology. Here we expand on that preliminary account to describe these modern specimens of *D. kambuayai* in more detail, and discuss additional records of *D. kambuayai* based on field observations and photographs of living animals documented since 2023.

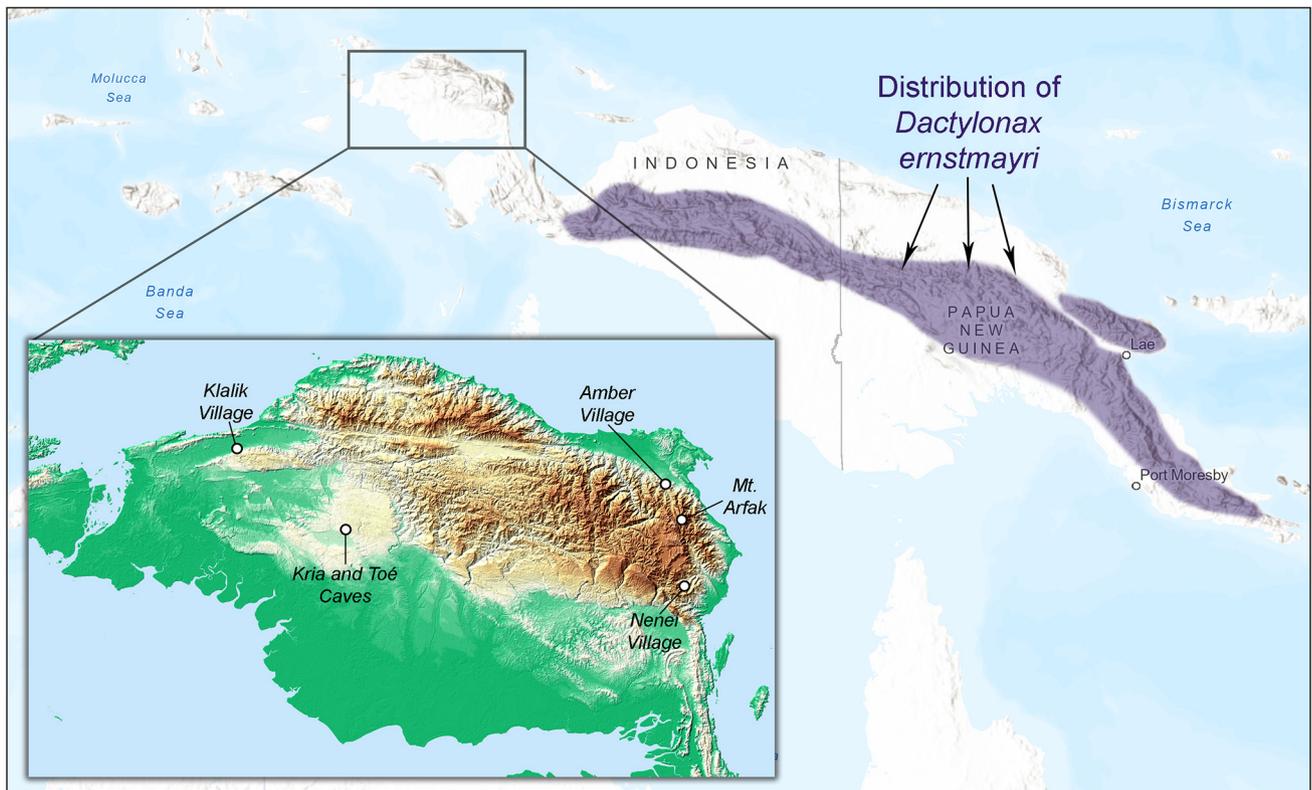


Figure 1. Map of New Guinea with distributional range of *Dactylonax ernstmayri* (shaded), and inset showing locations of *D. kambuayai* (Kria Cave, Klalilik Village, and Nenei Village) and *D. palpator* (Mount Arfak, Toé Cave and Amber Village) referred to in main text.

Though originally described within the genus *Dactylopsila* (Aplin *et al.*, 1999), here we allocate *D. kambuayai* to another, related genus, *Dactylonax*—*Dactylonax kambuayai* **n. comb.**

The genus *Dactylonax* was erected by Thomas (1910) for the broad-headed, long fingered (see Fig. 2b) striped possum *Dactylopsila palpator* Milne-Edwards, 1888 (Fig. 3). *Dactylonax* was subsequently synonymized with *Dactylopsila* by Ramme (1914), though Cabrera (1920) restored it to generic status, which was followed by Tate & Archbold (1937), Tate (1945), and Laurie & Hill (1954). Flannery (1990, 1994), however, followed Ramme in synonymizing with *Dactylopsila*, and most authors have followed this convention since (e.g., Groves, 2005; Jackson, 2015). We document below our reasons for using *Dactylonax* as a genus-level name, and for including *D. kambuayai* within the genus.

The only previously described fossil taxon in the subfamily Dactylopsilinae is *D. kambuayai*. The fossil record of dactylopsilines is fragmentary, with undescribed taxa from Oligo-Miocene Riversleigh (Archer *et al.*, 1999) and Middle Pleistocene Mt Etna Caves, Queensland (Hocknull, 2005, 2009; Hocknull *et al.*, 2007). The Middle Pleistocene dactylopsilines represent a lowland fauna and include a diminutive taxon of similar size and morphology to *D. kambuayai* (Hocknull, 2005, 2009). The Pleistocene occurrence of *D. kambuayai*, or a closely related species, on mainland coastal lowland eastern Australia demonstrates that this lineage of very small striped possum was, until relatively recently, more widespread, and suggests that entry of *Dactylonax* into New Guinea likely occurred in the Pliocene or early Pleistocene, possibly through the Vogelkop lowlands.

Here we review the rediscovery of *D. kambuayai* as

a living animal and establish its taxonomic identity with respect to its closest living relatives. The aims of this study were to: (1) establish that the modern specimens of small striped possums from western New Guinea identified by us did indeed represent *Dactylonax kambuayai* (Aplin, 1999) (Fig. 2); (2) establish the taxonomic status of the other named forms of *Dactylonax*, *D. palpator* Milne-Edwards, 1888, and *D. ernstmayri* Stein, 1932; and (3) cement the generic standing of *Dactylonax* as a lineage distinct from its sister genus *Dactylopsila* Gray, 1858. We cover these aims below in reverse order, from the generic level to the specific.

Materials and methods

All morphological measurements were made with electronic calipers. Cranial and dental measurements are all listed in Tables 1 and 2. All cranial and dental measurements were rounded to the nearest 0.1 mm. All external body measurements were taken by the original collectors of the specimens in the field, apart from any exceptions mentioned below.

Museum abbreviations: AM M = Mammal collection, Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; BMNH = Natural History Museum, London; BPBM = Bernice Pauahi Bishop Museum, Honolulu; MNHN = Muséum national d'Histoire naturelle, Paris; MZB = Museum Zoologicum Bogoriensis, Cibinong, Indonesia; NMS = Swedish Museum of Natural History, Stockholm; PNGM = Papua New Guinea Museum and Art Gallery, Port Moresby; UPNG = University of Papua New Guinea, Port Moresby; WAM = Western Australian Museum, Perth; ZMB = Museum für Naturkunde, Berlin.

Systematics

Order Diprotodontia Owen, 1877

Family Petauridae Bonaparte, 1832

Subfamily Dactylopsilinae Kirsch, 1977

Content: There are two described genera in the subfamily, *Dactylopsila* Gray, 1858 (the ‘striped possums’) and *Dactylonax* Thomas, 1910 (the ‘long-fingered possums’), both of which comprise possums with unmistakable markings consisting of bold black-and-white striping patterns on the dorsal surface of the body.

The evidence for generic separation of *Dactylonax* from *Dactylopsila* is strong. Their morphological distinction is trenchant. Specializations in skull shape (shortened rostrum, broader skull, enlarged incisors), the basicranium (Fig. 5), and fourth digit of the manus (Fig. 6) are part of a functional-adaptive complex that enables species of *Dactylonax* to specialize-feed on wood-boring insect larvae (Flannery, 1995), similar to the remarkable ecomorphology of the lemur *Daubentonia* (Szalay & Lucas, 1996; Rasmussen & Sussman, 2007). In addition to its uniquely derived hand morphology, *Dactylonax* is also easily distinguished externally by its short tail, which ranges from much shorter than, to subequal to, head-body length, as compared with the tail in species of *Dactylopsila*, which is much longer than the head and body. This difference denotes the largely terrestrial habits of *Dactylonax* compared to the arboreal *Dactylopsila*.

Molecular data demonstrate that the evolutionary divergence between *Dactylopsila* and *Dactylonax* dates to about 10 million years ago (Osborne & Christidis, 2001), a level of genetic difference and time-depth that approximates extant macropodid subfamily distinctions and is equivalent to the divergences between various well-recognized marsupial sister genera such as the Australo-Papuan cuscuses *Phalanger-Spilocuscus*, the Sulawesi cuscuses *Strigocuscus-Ailurops*, or the Australian wombats *Lasiiorhinus-Vombatus* (Mitchell *et al.*, 2014).

The sister lineage of the dactylopsilines is not yet clear. Some molecular studies (Osborne & Christidis, 2001; Meredith *et al.*, 2009) and the total evidence (molecular and morphological data) study compiled by Beck *et al.* (2022) have recovered a sister relationship between the monotypic genus *Gymnobelideus* (with sole known species *G. leadbeateri* McCoy, 1867, the Wollert or Leadbeater’s Possum) and dactylopsilines. The more recent and comprehensive molecular study of Mitchell *et al.* (2014) recovered *Gymnobelideus* as sister to the genus *Petaurus* (the gliders, sole genus of Petaurinae).

Difficulty in allocating *Gymnobelideus* to either modern petaurid subfamily demonstrates the depth of the tripartite division within the family Petauridae, with *Gymnobelideus* representing a deep evolutionary lineage dissimilar to either subfamily and with unclear immediate affinity. As a better reflection of its distinction, we allocate this genus to a newly-designated subfamily, *Gymnobelideinae* Helgen & Flannery, subfam. nov., with similar level of antiquity and morphological distinction as the other petaurid subfamilies, Petauridae and Dactylopsilinae. *Gymnobelideinae* is thus

far monotypic and can be diagnosed as for the type genus, *Gymnobelideus*. *Gymnobelideus* is morphologically isolated, distinguishable from other petaurids by a large number of anatomical character states (Beck *et al.*, 2022), and recognizable by its vestigial gliding membrane (absent in dactylopsilines, well developed in *Petaurus*), club-shaped tail, and minuscule claws, among many other distinctions (Fig. 2c). Incidentally, Leadbeater’s Possum is a Lazarus species of another kind—first described as a living animal in 1867, then undocumented between 1909 and 1961 and widely feared extinct (Flannery, 1994) before being rediscovered in Victoria in 1961 (Wilkinson, 1961) and more recently discovered extant in New South Wales for the first time (New South Wales Government, 2025). Subfamily-level standing for *Gymnobelideus* helps to demonstrate the fundamentally tripartite taxonomic distinction of living deep petaurid lineages and also helps to highlight the evolutionary distinctness of this critically endangered species that is reliant on mature mountain ash forests (Lindenmayer, 1996).

Genus *Dactylopsila* Gray, 1858

Included species: Three species are recognized, all extant—*Dactylopsila megalura* Rothschild and Dollman, 1932 (montane central and western New Guinea); *D. tatei* Laurie, 1952 (mountains of Fergusson Island off southeastern New Guinea); and *D. trivirgata* Gray, 1858 (widespread in New Guinea and extending to a number of Melanesian land-bridge islands including Aru and to Cape York Peninsula in northern Australia).

Diagnosis. Skull relatively narrow and elongate, as in petaurines. Fourth digit of manus only slightly elongated (Fig. 2a). Maxilla does not contact nasal bones, anterior incisors (upper and lower) large relative to other teeth, upper incisors strongly procumbent.

Genus *Dactylonax* Thomas, 1910

Type species: *Dactylopsila palpator* Milne-Edwards, 1888, by original designation (Thomas, 1910).

Included species: Three species are recognized, all extant—*D. palpator* (Milne-Edwards, 1888); *D. ernstmayri* (Stein, 1932); and *D. kambuayai* (Aplin, 1999), as discussed below. Until now, the similarly-sized *D. palpator* and *D. ernstmayri* have been treated as conspecific, often as separate subspecies, but we argue that these are allopatric species that differ substantively in morphology of the manus and in basicranial anatomy, as we discuss below.

Diagnosis. Skull short and extremely broad, fourth digit of manus greatly elongated (Fig. 2b). Zygomatic arches strongly convex, cranial vault high and rounded, facial region short. P¹ anteroposteriorly broad and angular, lanceolate in form, and flattened mediolaterally. P⁴ longer relative to M¹ compared to *Dactylopsila*. I₁ alveolus posteriorly recessed relative to P₁. Lower premolar row (P₁–P₄) short and ascending steeply between I₁ and M₁. Molar gradient steeper than in *Dactylopsila*. Masseteric fossa massive.

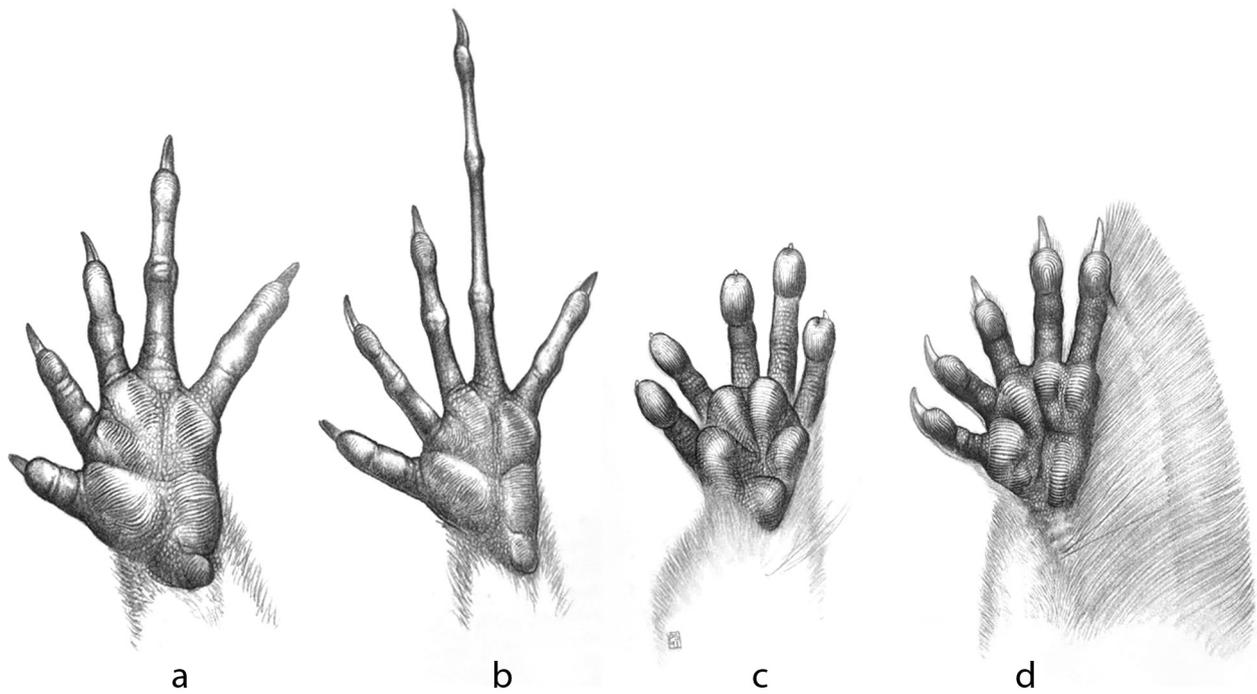


Figure 2. Hands of the four extant genera (and three subfamilies) of family Petauridae. Palmar surfaces of the manus, showing key differences in phalangeal proportions, claws, palmar pads, furring, and patagial development in (a) *Dactylopsila*, subfamily Dactylopsilinae (represented by *Dactylopsila trivirgata*); (b) *Dactylonax*, subfamily Dactylopsilinae (represented by *Dactylonax palpator*); (c) *Gymnobelideus*, represented by *G. leadbeateri* (*Gymnobelideus* McCoy, 1867 is type genus of the new subfamily proposed here: Gymnobelideinae Helgen & Flannery, **subfam. nov.**—urn:lsid:zoobank.org:act:286C8D5D-FB21-4AB7-B0C0-7BC8EEFEC7CD, *Gymnobelideus leadbeateri* McCoy, 1867 is type species of *Gymnobelideus*, the new subfamily and its type genus are both monotypic); (d) *Petaurus*, subfamily Petaurinae (represented by *P. norfolcensis*). Modified from Flannery (1994:61–65). Drawings by Peter Schouten.

Table 1. Craniodental measurements for selected specimens of *Dactylonax* (adult specimens at AM, plus the holotype of *D. palpator* at MNHN) in mm. CBL = condylobasal length, BZW = bizygomatic width, IOW = interorbital width, RW = rostrum width at I1 alveolus, LMRL = lower molar row length, M1w = lower first molar width. Additional cranial measurements for *Dactylonax* were reported by Tate and Archbold (1937) and Laurie (1952).

	CBL	BZW	IOW	RW	LMRL	M1w
<i>Dactylonax kambuayai</i>						
AM M.56796 ♀	45.0	34.1	12.5	6.3	8.5	1.7
<i>Dactylonax palpator</i>						
AM M.29254 ♀	54.3	42.0	14.5	17.6	11.0	2.3
AM M.38069	—	—	—	—	10.7	2.3
MNHM 1886-1224 ♂	60*	42.4	—	—	—	—
<i>Dactylonax ernstmayri</i>						
AM M.37997 ♀	54.9	42.5	16.2	18.5	10.4	2.3
AM M.7323 ♂	55.0	44.3	16.3	18.9	10.6	2.2
AM M.13587 ♂	—	—	20.8	19.6	—	—
AM M.15615 ♂	55.6	41.5	15.4	17.9	—	2.3
AM M.15614 ♂	58.0	46.0	15.4	18.5	10.3	2.1
AM M.15580 ♂	—	—	17.2	19.4	11.1	2.2
AM M.27312 ♂	57.8	45.5	18.8	19.5	10.4	2.2
AM M.30729 ♂	58.8	44.8	17.2	18.9	10.0	2.1
AM M.30735 ♂	57.8	43.3	16.8	18.4	10.5	2.2

* The skull is broken in the holotype, such that an accurate CBL cannot be measured. Milne-Edwards' (1888) measurement of 60 mm (larger than for other known *Dactylonax* specimens) is likely an estimate of the length of the skull including the forward-jutting incisor, rather than CBL per se, and is probably an overestimate.

Centenaire de la Société Philomathique.



Noël del.

Edwards direx.

Louveau lith.

Dactylopsila palpator.

Figure 3. The original figure of the holotype of *Dactylopsila palpator* (Milne-Edwards, 1888) published in *Mémoires publiés par la Société Philomathique à l'occasion du Centenaire de sa Fondation 1788–1888*.



Figure 4. *Dactylonax kambuayai* (Aplin, 1999)—a painting by Peter Schouten. This artwork is based on the two modern specimens in the Australian Museum (M.56796 adult female and pouch young M.56797).

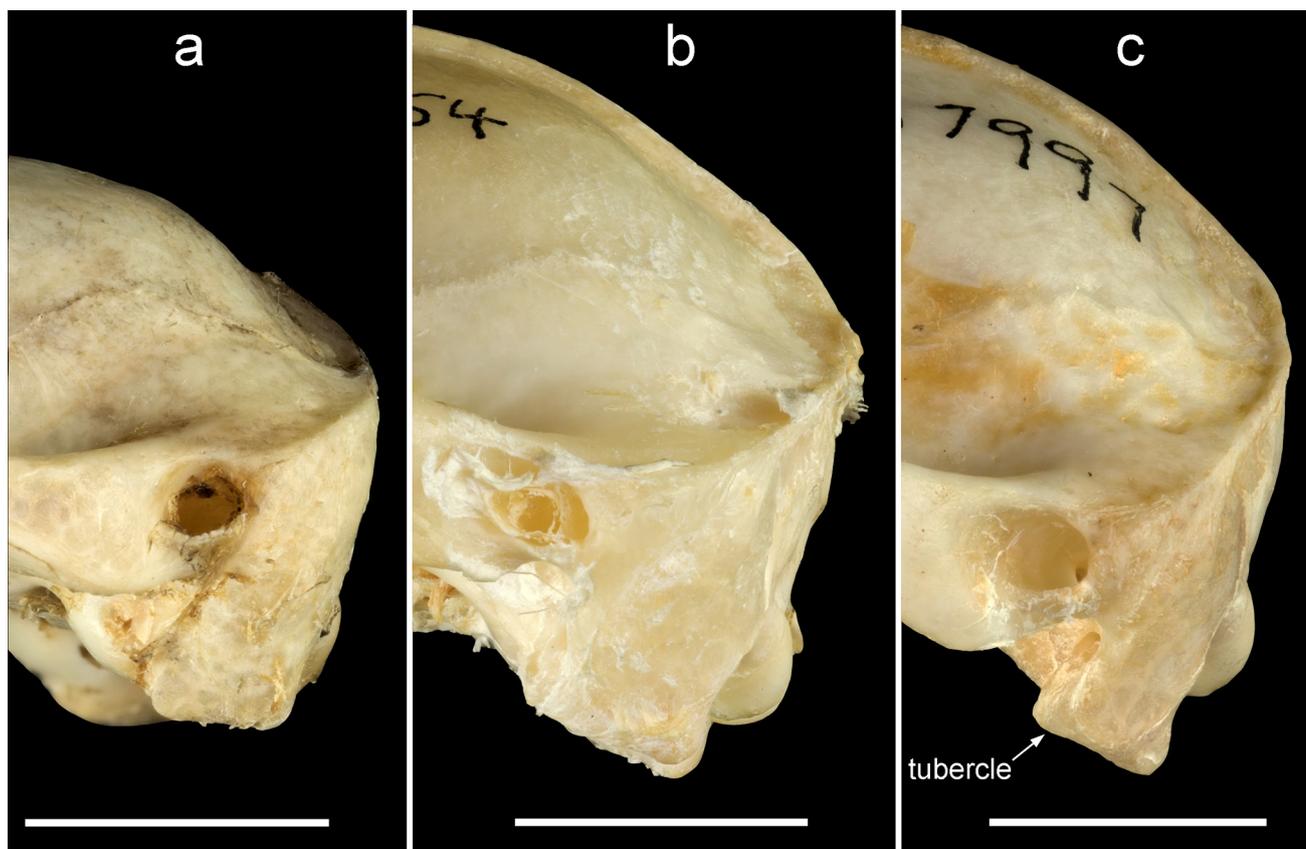


Figure 5. Lateral view of left auditory region of: (a) AM M.56796 (*Dactylonax kambuayai*); (b) AM M.29254 (*D. palpator*); and (c) AM M.37997 (*D. ernstmayri*). Tubercle = petrosal tubercle. All scale bars = 10 mm. Photo credit Emily Cave.

Dactylonax palpator (Milne-Edwards, 1888)

Western Long-fingered Possum

Diagnosis. A larger-bodied species (Tables 1–2) than *Dactylonax kambuayai*, *D. palpator* differs from *D. ernstmayri* in that the ectotympanic is large and slopes anterodorsally from the hyoid tubercle of the petrosal (homology as per Tate & Archbold, 1937) (Fig. 5a–c), in that the fourth digit of the manus is more elongate (Figs 3, 6, Table 3), and possesses a claw that is less reduced in size and less acutely hooked (Fig. 6a–c; Table 3). It may have a narrower rostrum than *D. ernstmayri* (Table 1). It is distinguished from *D. kambuayai* in lacking an ectotympanic bulla (Fig. 7), possessing a sagittal crest, in being much larger in body mass, yet with a relatively shorter ear (Table 2) and a proportionally shorter fourth digit of the manus which bears a claw that is less reduced in size relative to the other claws of the hand (Fig. 6).

Notes. Milne-Edwards (1888) received the type specimen of *palpator* from the collector Leon Laglaize in 1886, and gave the type locality as the ‘côte sud de la Nouvelle-Guinée’ (south coast of New Guinea), but this has always seemed unlikely, given that all subsequent specimens of larger *Dactylonax* (*D. palpator* and *D. ernstmayri*) originate from montane contexts above 800 m (Flannery, 1995; Helgen, 2007). Likely on the basis of this uncertainty, Beaufort (1966) stated the type locality simply as ‘Nouvelle Guinée’. However, the plaque

on the base of the holotype mount (MNHN 1886-1224) and the museum’s General Catalogue state that the specimen was from Mount Arfak (Julien-Laferrière, 1994). Given this information, and the fact that the species is known in modern contexts otherwise only from the Arfak Mountains, we here restrict the type locality to Mount Arfak.

Dactylonax palpator is poorly represented in museum collections. An edentulous dentary of probable late Pleistocene age (WAM 98.7.32) is recorded from the lower level in Toé Cave, Ayamaru Lakes area (Jelsma, 1998), Vogelkop, by Aplin *et al.* (1999) (Fig. 1). Toé Cave lies at around 400 m elevation, and a number of mammalian taxa that today are restricted to higher elevations are recorded from its late Pleistocene levels in the cave (Aplin, 1998; Pasveer & Aplin, 1998; Aplin *et al.*, 1999; Pasveer, 2004). (Elevational zonation was depressed during the last glacial maximum; for example the tree line in the Central Cordillera of New Guinea, which today occurs at 3,900 m, was then located at 2,100–2,300 m; Hope & Hope, 1976). Apart from the holotype of *palpator* from Mount Arfak, only two additional modern specimens are known: AM M.29254, an adult female skin and skull from Amber Village, Mokwam area, Vogelkop, collected on 10 October 1992; and AM M.38069, a pair of trophy mandibles from Pin-nai Village, Arfak Mountains. Amber village lies just east of Mokwam in the Menyambouw area (Fig. 1). The elevation of the region surrounding Amber village is from around 600 m to around 1,400 m. It is likely that AM M.29254 came from the higher elevation part of that range. The Hatam name given for *D.*



Figure 6. Manus of (a) *Dactylonax kambuayai* (AM M.56796), (b) *D. palpator* (AM M.29254), and (c) AM M.27312 (*D. ernstmayri*), showing phalanx proportions and unguis claw shape on elongate fourth digit. Photographs not to scale. Photo credit Emily Cave.

palpator is ‘Doncheu’. AM M.29254 was located and caught by dogs while it was sheltering in a hole in the ground. A female, it was not lactating or carrying a pouch young when captured. It had no noticeable odour when fresh (TFF *pers. obs.*) and its preserved skin lacks the odour that is so pungent on skins of *D. ernstmayri*.

Dactylonax ernstmayri (Stein, 1932)

Eastern Long-fingered Possum

Diagnosis. A larger bodied member of the genus (Tables 1–2), with a relatively shorter second phalanx on the fourth digit (Table 3) and with the claw on the fourth digit of the manus reduced in size and more acutely curved than in other species (Fig. 6). The basicranium is unique in having a prominent petrosal tubercle for the hyoid (terminology follows Tate & Archbold, 1937). This results from an extreme reduction of the ectotympanic. It differs from the much smaller *D. kambuayai* in lacking an inflated ectotympanic bulla (Fig. 5) and possessing a sagittal crest and in possessing

a modal number of four unicuspid in the lower jaw (three in *D. kambuayai*) (Fig. 7a–c).

Morphology. Stein (1932) originally described *ernstmayri*, based on a skin without skull, as a subspecies endemic to the outlying mountains of the Huon Peninsula (type locality Junzaing in the Saruwaged Range). He diagnosed *ernstmayri* as differing from *palpator* in possessing a band of yellowish-white fur around the wrist. Tate (1945) observed that this pelage character was of no systematic value, and varied in Huon Peninsula samples of *D. ernstmayri*. We conclude the same, from our larger sample of more than 80 specimens examined from throughout the broader range of this species. For example, the dorsal surface of the wrist is dark brown in AM M.37997 (Enga Prov.), while in AM M.15862 (Telefomin) it is pale brown, in AM M.7323 (Mt Hagen) it is grey, and in AM M.15880 (Telefomin), AM M.30729 and AM M.30735 (both from Kwiyawagi) it is whitish. (In AM M.29254 (the female skin of *D. palpator* available to us) the dorsal surface of the wrist is covered in extremely fine, pale (almost white) fur, but is somewhat darker colored in the male holotype (Fig. 3)).

Table 2. Body measurements of species of *Dactylonax*. HB = head-body length (mm); TV = tail-vent length (mm); TV/HB = ratio of TV to HB expressed as a percentage; HF = hindfoot length (mm); E = ear length (mm); WT = weight (grams). Table based on all adult specimens with field measurements at AM, AMNH, BMNH, BPBM, MZB, NMS, PNGNM, UPNG, ZMB.

	HB	TV	TV/HB	HF	E	WT (g)
♂ <i>Dactylonax palpator</i>	270* n = 1	200 n = 1	74%* n = 1	— —	— —	— —
♂♂ <i>Dactylonax ernstmayri</i>	236 ± 13.7 207–263 n = 42	203 ± 17.7 176–236 n = 41	87% 69–105% n = 41	46.0 ± 3.87 35–51 n = 34	26.9 ± 1.87 22–30 n = 34	453 ± 60.2 280–550 n = 19
♀ <i>Dactylonax kambuayai</i>	176 n = 1	180 n = 1	102% n = 1	42 n = 1	30 n = 1	216 n = 1
♀ <i>Dactylonax palpator</i>	195 n = 1	160 n = 1	82% n = 1	38.2 n = 1	24.4 n = 1	300 n = 1
♀♀ <i>Dactylonax ernstmayri</i>	215 ± 10.4 191–235 n = 31	186 ± 19.8 135–216 n = 30	87% 61–106% n = 30	44.1 ± 3.65 37–51 n = 26	26.8 ± 1.80 24–30 n = 28	344 ± 43.5 280–420 n = 11

* Tate & Archbold (1937:476) regarded the rather large value for HB given by Milne-Edwards for the holotype of *D. palpator* (270 mm) to be ‘probably stretched’, and we agree. It is presumably estimated from the mounted skin (Fig. 3), and may more likely approximate the average HB of male *D. ernstmayri* (i.e., ca. 236 mm), as the species seem to be similar in overall body size. If so, this would yield a TV/HB percentage of 85%.

The basicranium is highly distinctive in *D. ernstmayri*, having a reduced ectotympanic bulla, and a prominent tubercle on the petrosal for attachment of the hyoid (Fig. 5). Individuals can be highly vocal, emitting a loud snarling growl when alarmed. Both males and females possess a distinctive, pungent odour which is noticeable on museum specimens even after years of storage. In its strong odour and its boldly striped pelage, *D. ernstmayri* offers a striking parallel with skunks and stink badgers of the carnivoran family Mephitidae.

Notes. The holotype of *Dactylonax ernstmayri* (Stein, 1932) (ZMB 42418) is from the Saruwaged Range on the Huon Peninsula, and previous assessments of this taxon have recognized it in a restricted sense as a Huon endemic subspecies of *D. palpator*. In our revised assessment, *D. ernstmayri* is instead widely distributed, generally at elevations above 1,400 m along the Central Cordillera, from the Weyland Range in the west to the Mt Dayman area in the east, and in the offlying Huon ranges (as ‘*D. palpator*’ in Flannery, 1995). The vouchered elevational range of *D. ernstmayri* is from 850 m (AMNH 151964, from the Idenburg River transect on the northern face of the western Cordillera) to 2,950 m (AM M.30735, from Kwiwawagi in the Snow Mountains). The mean elevation of 38 vouchered sites of capture (specimens with elevational data at AM, AMNH, BMNH, BPBM, UPNG, ZMB) is 2,037 m (standard deviation 545 m). Helgen (2007b) noted a field observation at 3,000–3,100 m in the Kaijende Highlands near Porgera, Enga Province, and suggested this to be the upper limit of the species’ elevational occurrence.

Dactylonax ernstmayri is markedly sexually dimorphic,

males being around one third heavier than females (Table 2). There are indications that it is primarily terrestrial, living in underground burrows and fallen logs, though it has been observed climbing large diameter dead trees in search of the wood-boring beetle larvae that it feeds on and may also nest in tree hollows (Hide *et al.*, 1984). Its ecology and distribution are summarized under *D. palpator* in Flannery (1995), where all ecological records and all distributional records (except for the type locality) in fact refer to *D. ernstmayri*. Females have two teats in the pouch but only one young at a time (Helgen, 2007b).

Ecotypic and geographic variation are both evident in this widespread montane species. Specimens from lower elevation localities (850–1,800 m), such as from the Weylands (ZMB specimens, 1,400–1,800 m) have less bushy tails than specimens from higher elevations, and have smaller skulls and teeth. At present we consider this likely to reflect local ecotypic response to different habitats across New Guinea montane gradients. On top of this kind of variation within local elevational gradients, other patterns of variation are associated with broader geographic occurrence. Body size is largest in populations from the Huon Peninsula, and from the southeast Peninsula of New Guinea, extending as far to the north and west as the Wau area and the Kratke Mountains. Specimens from further west, across much of the Central Highlands, Star and Snow Mountains regions, and the Weyland Range, average smaller. Huon specimens may generally have a darker grey venter with less cream-colored fur along the ventral midline, but this requires more comprehensive review. In past reviews, Tate & Archbold (1937) and other authors (e.g., Groves, 2005) have considered the isolated Cordilleran and Huon

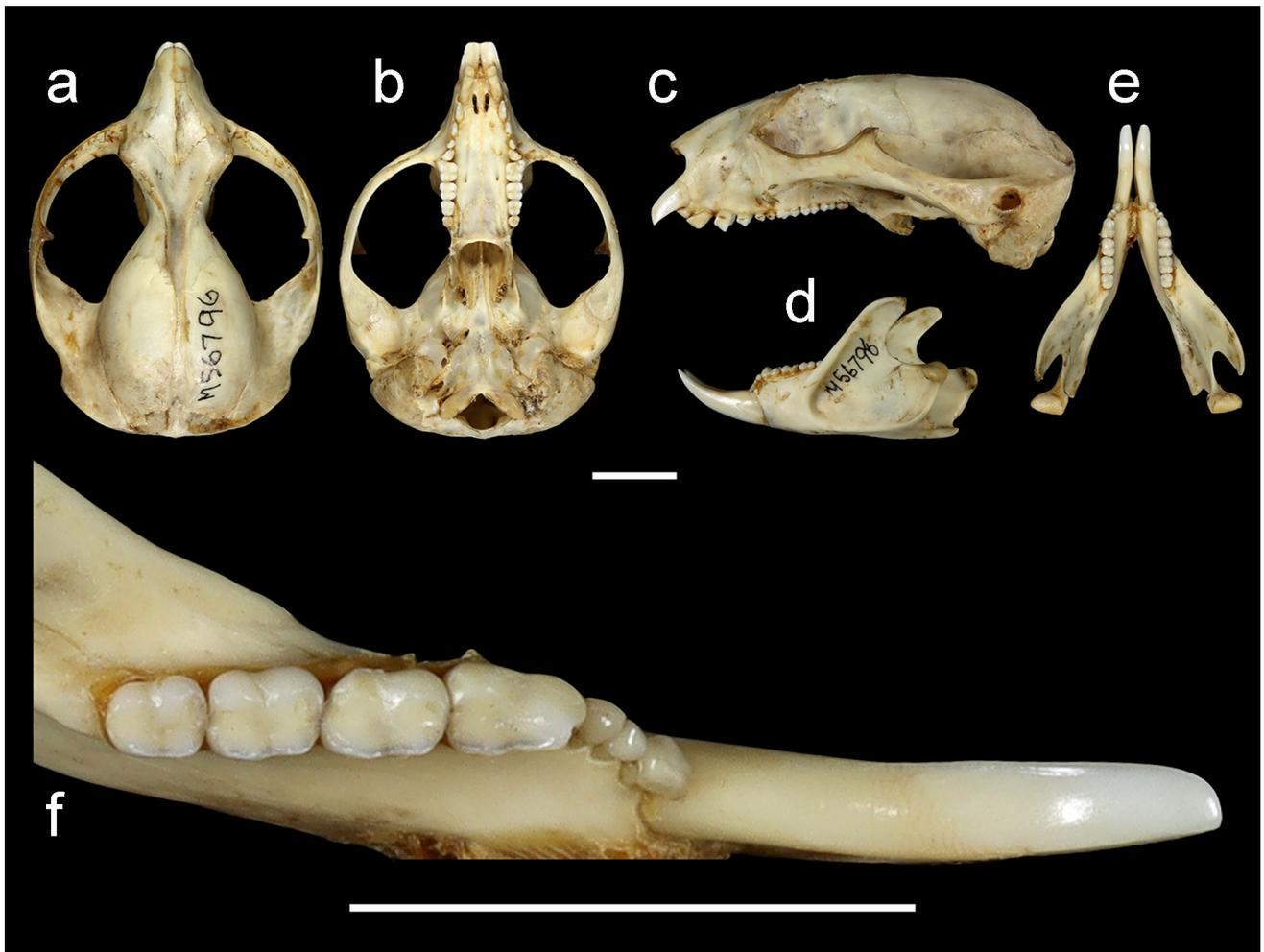


Figure 7. Skull of *Dactylonax kambuayai* AM M.56796 in dorsal (a), ventral (b), and lateral (c) views. Left mandible in lateral view (d) and occlusal tooth row (e–f) views. Scale bars equal 10 mm. Photo credit Emily Cave.

samples that we refer here to *D. ernstmayri*, to be separate subspecies (at that time with ‘*D. p. palpator*’ used for all non-Huon populations of *Dactylonax*, and ‘*D. p. ernstmayri*’ for Huon specimens). Whether our concept of *D. ernstmayri* as a species distributed across the entire Cordillera and Huon comprises additional taxonomic complexity, such as subspecies or cryptic species boundaries, awaits more detailed integrative systematic studies drawing on wide geographic sampling.

Dactylonax kambuayai (Aplin, 1999)

Pygmy Long-fingered Possum

Diagnosis. The smallest member of the genus (and of Dactylopsilinae). Despite its smaller body size, the fourth digit on the manus is as long as in other species of *Dactylonax* (and therefore proportionately longer). The claw on the fourth digit of the manus is not as reduced in size as in the other members of the genus, and not as recurved (Figs 4, 6a–c). The ears are markedly longer than in other species (30 mm vs 24–27 mm). A band of white fur extends from the upper lip to the lower margin of the eye, and the rostrum is foreshortened. The sagittal crest is absent, the bulla modestly inflated (as in species

of *Dactylopsila*) (Fig. 7). The ventral projection of the basioccipital is reduced relative to other members of the genus. The available modern specimen shows that there are three unicuspid in the lower jaw (modally 4 in other *Dactylonax*, rarely any other number).

Description. The type material of *Dactylonax kambuayai* comprises a series of partial dentaries (WAM 98.7.40, 98.7.50–54), the holotype (WAM 98.7.40) being the most complete. All are of Holocene age (7,500–6,000 ybp) from Kria Cave, 3 km East of Suiwam/Mapura Village, Ayamaru Lakes region (Fig. 1). These specimens are not only smaller than all previously named dactylopsilines, but differ in important details of molar morphology (Aplin *et al.*, 1999). The extracted and cleaned skull of the adult from Nenei (Fig. 7a–f) displays all of the diagnostic features of the type material of *D. kambuayai*, and its measurements agree with those of the holotype and referred specimens (Table 1).

Specific differences between *Dactylonax kambuayai* and *D. palpator* (including both *D. palpator* and *D. ernstmayri*) were originally argued on the basis of features observable in fragmentary dental remains; specifically, overall size and differences in molar morphology (Aplin *et al.*, 1999). Specific differentiation is amply supported by examination of the complete specimens now available, with contrasts in

Table 3. Selected phalangeal measurements for species of *Dactylonax*. The first (P1) phalanx was measured from the rear of knuckle joint to the proximal end of the second phalanx (P2) and the second phalanx was measured from the knuckle joint to the ventral base of the claw.

	P1, Digit IV	PII, Digit IV	PII, Digit V	Ratio PII Digit IV: PII Digit V
<i>Dactylonax kambuayai</i>				
AM M.56796 ♀	18.4	12.6	6.6	0.52
<i>Dactylonax palpator</i>				
AM M.29254 ♀	17.3	14.8	6.3	0.43
<i>Dactylonax ernstmayri</i>				
AM M.5089 ♂	21.5	13.5	6.8	0.50
AM M.15997 ♀	17.6	11.5	—	—
AM M.17136 ♀	19.3	10.1	—	—
AM M.12877 ♂	18.1	12.2	7.3	0.60
AM M.37997 ♀	18.7	13.8	6.4	0.46
AM M.7323 ♂	17.5	13.5	6.7	0.49
AM M.18421 ♀	18.3	12.0	7.5	0.63
AM M.27312 ♂	19.3	12.5	7.2	0.58
AM M.30729 ♂	20.5	13.2	7.9	0.60
AM M.30735 ♂	17.6	11.6	7.3	0.63
AM M.15862 ♂	17.2	10.5	6.4	0.61
AM M.15880 ♂	21.6	13.9	6.4	0.46
mean	18.9	12.3	7.0	0.56
range	17.1–21.6	10.1–13.9	6.4–7.9	0.46–0.63
sample size	n = 12	n = 12	n = 10	n = 10

both external and cranial morphology. Striking differences between it and the other two species of *Dactylonax*, noted in the original description, include the greatly foreshortened rostrum and the proportionally much smaller cheek teeth of *D. kambuayai* (Fig. 7). Although the temporal lines coalesce to the centre of the skull in the adult specimen available, *D. kambuayai* is the only member of the genus *Dactylonax* that lacks development of a sagittal crest, and it is further distinguished by possessing inflated bullae (Fig. 5). *Dactylonax kambuayai* can be distinguished from *D. palpator* by external features including its smaller adult body size (Table 1), larger ears (30 mm vs 22–30 mm in the other, larger species), more subdued overall colouration (Figs 6–7), the broad dark furring of the fore- and hind-limbs, the poorly defined nature of the off-white upper lateral stripe, and the predominantly black-furred tail, with white fur restricted to the tail base and the tip. A further striking feature of *D. kambuayai* is the band of white fur that extends from the upper lip to the lower border of the eye (Figs 6–7); in all other dactylopsilines the cheek is black, part of a broad ‘mask’ that completely surrounds the eye. Many features of the pelage are seen more clearly in the short-furred pouch young (Fig. 9) than in the adult, where they are obscured by thick fur. External measurements of the adult female are listed in Table 2 (measurements for the pouch young are HB 98 mm, TV 100 mm, HF 26 mm, Ear 12 mm, weight 49 g). The fourth digit of the manus is exceptionally long relative to body size (Figs 6, 8; Table 3), being equal in length to the digits of its much larger congeners. In particular, the 2nd phalanx of the fourth digit is elongate (Table 3). The claw on the fourth digit is short and less strongly curved relative to that of other species. These modern preserved specimens of the

Pygmy Long-fingered Possum were located in the teaching collection of the Biology Department of the University of Papua New Guinea. The alcohol preserved adult female (AM M.56796, now with skull extracted and cleaned) and an associated, well-furred immature female weighing (AM M.56797) are recorded in the university collection register as coming from ‘Nenei, Arfak Mountains’ and collected by Dr P. A. Woolley (formerly of La Trobe University, Victoria, Australia). Attached to both specimens are field tags labelled ‘PAWN/20’. The date of collection is recorded as 1992. Nenei is a small village in the Arfak Mountains and is located at 1.4921°S 133.9973°E (Fig. 1). The village and airstrip lie at an elevation of 867 m but forested ranges rise to the summit of Mt Arfak (2,955m) in the east. Woolley visited Nenei in the hope of locating a population of another poorly known marsupial, Doria’s Phascosorex (*Phascosorex doriae*; Dasyuridae) but made incidental collections of other species caught by traditional hunters (Woolley, *pers. comm.*, 18 June 2013). This included the female and pouch young, which Woolley took to be examples of the long-fingered striped possum (*D. palpator*), and several specimens of the Torresian Striped Possum (*Dactylopsila trivirgata*). Both specimens of *D. kambuayai* were subsequently transferred by KPA to the Australian Museum as a longterm loan under permission from staff at UPNG.

Six other photographic records of living individuals of *D. kambuayai* come from three localities, all clustered around Klalik village in Sorong Regency, Vogelkop Peninsula (https://www.inaturalist.org/observations?subview=map&taxon_id=1575630). Klalik village lies along the main Sorong Road, and is located at (0.8175°S 131.8084°E) at approximately 50–100 m asl.



Figure 8. Photograph of a living female *Dactylonax kambuayai*, Klalík area, Vogelkop. Photo credit Carlos Bocos.

Klalík is situated 65 km north-west of Kria Cave (Pasveer, 1998, 2004), where the holotype and paratypical fossil material was found (Aplin *et al.*, 1999). The area around Klalík is primary lowland forest characterized by low trees with some evidence of tree felling for local use. An individual was photographed on 11 June 2023 by a mammal-watching tour group led by CB and Jon Hall (Fig. 8). Mammal-watching, is a rapidly growing sector of wildlife tourism which is analogous to bird-watching but where participants focus on viewing mammals (Dinets & Hall, 2018). At 10 pm a villager approached the mammal-watchers, holding a live *Dactylonax* in his hand. No detailed measurements were taken as but it was comprehensively documented with photographs and videos before being released onto the trunk of a tree.

Notes. Ecology. Direct observation by CB reveals that *D. kambuayai* moves about close to the ground, jumping from one tree-base to another, rather like African galagos. Their reluctance to climb high allows hunters to catch them by switching off their torch, creeping up on them and pouncing on them. The fact that the specialized fourth digit of the hand is as long in the diminutive *D. kambuayai* as in the much larger *D. ernstmayri*, suggests that there is a functional significance to digit length, perhaps related to the length or diameter of the burrows made in wood by their invertebrate prey, or perhaps the digit length is relative to the body length of the wood-boring invertebrate prey itself.

Discussion

Diversification in *Dactylonax*. The recognition of three species within the genus *Dactylonax*, two of which are restricted to the Vogelkop Peninsula, allows for a more nuanced assessment of the evolutionary history of the genus. The most morphologically divergent species is the lowland-dwelling *D. kambuayai*, which retains several plesiomorphic features, including the presence of an inflated ectotympanic bulla, not otherwise seen in the genus, but shared with the outgroup *Dactylopsila*. It seems likely that a *D. kambuayai*-like ancestor gave rise to *D. palpator* when a montane adapted population became genetically separate. This montane population in turn gave rise, following an eastwards migration, to the most specialized member of the genus, *D. ernstmayri*. This pattern of dispersal represents a conundrum, for it suggests that *D. palpator*, the montane member of the Vogelkop *Dactylonax* species pair, was able to disperse eastwards, while the lowlands species (*D. kambuayai*) was not. Some as yet unknown barrier to the dispersal of lowlands species must have existed. Apart from ‘*Petauroides*’ *ayamaruensis* (Flannery *et al.*, 2026), *Dactylonax kambuayai* is the only marsupial species whose known current range is restricted to lowland forests on the Vogelkop Peninsula, a general region it shares with *D. palpator*.

These two species (*D. kambuayai* and *D. palpator*) are different enough in body mass for them to co-occur, at least



Figure 9. Pouch young *Dactylonax kambuayai*, AM M.56797. Lateral view. Photo credit Emily Cave.

on a regional scale. We predict that they will prove to be altitudinally segregated, with a zone of parapatry or sympatry occurring between 867 and 1,200 m in the Arfak Mountains. Interestingly, the Middle Pleistocene Mt Etna Caves fauna from Queensland, possess one diminutive and one larger-bodied species of dactylopsilinae (Hocknull, 2005, 2009), suggesting that this lowland co-occurrence of body-size disparity may be a long-held one for dactylopsilinae. There are indications that a dispersion event involving *Dactylonax* and other taxa, such as monotremes, occurred between New Guinea and Australia during the Pliocene to early Pleistocene (Flannery *et al.*, 2022, 2026).

Distribution of the larger montane species. The genus *Dactylonax* is now known to comprise at least three species, two of which are montane, and one lowland.

The montane species are the two larger *Dactylonax*. They are found in most high-elevation areas of New Guinea, including in the mountains of the Vogelkop Peninsula (*D. palpator*) and throughout the Central Cordillera of New Guinea, from the Weyland Range and Snow Mountains in the west, to the mountains of the Maneau Range (southeastern peninsula of New Guinea) and the outlying mountains of the Huon Peninsula (northeastern New Guinea) in the east (*D. ernstmayri*). The only significant large montane area where a larger *Dactylonax* does not occur is the North Coast Ranges, where the rare and evolutionarily distinctive large glider, *Petaurus abidi*, known to date at and above 800 m in the Torricelli Mountains, occurs. *Petaurus abidi* is less robust than, but of roughly equivalent size to, larger *Dactylonax*

(ca. 300 g, condylobasal ≥ 52 mm: Ziegler, 1981; cf. Table 1 in this paper), and both kinds of animals have large front incisors capable of gouging bark to obtain invertebrates and tree exudates, and to enlarge hollows in trees or logs. Perhaps these two lineages of petaurids represent ecological vicars of a sort, and it is the success of larger *Dactylonax* across most of New Guinea's mountains, including on the Vogelkop and Huon Peninsulas, that has left *P. abidi* as an ancient large glider lineage confined to the smaller North Coast Range. *Dactylonax palpator*, but not *P. abidi*, is recorded in the Ayamaru Lakes subfossil record on the Vogelkop, a strong suggestion that the absence of *P. abidi* from the Vogelkop is real (Aplin *et al.*, 1999). It is not yet known whether a larger species of *Dactylonax* or *Petaurus* occurs in the large but little-known north-coast Foja Range.

Distribution of the smaller lowland species. If there is a possibility that larger species of *Dactylonax* have excluded the modern distribution of larger *Petaurus* in the mountains of New Guinea, the reverse may be true for their smaller congeners in the lowlands. *Dactylonax kambuayai*, known only from the lowlands of the Vogelkop mainland, may represent a relict geographic population of a small *Dactylonax* lineage that was more widespread, including in the Middle Pleistocene fossil record of eastern Australia (Hocknull, 2005, 2009), in the past. It is the smallest petaurid in New Guinea apart from the small 'sugar gliders', which constitute a species-complex currently referred to as *Petaurus cf. papuanus* (Malekian *et al.*, 2010; Powley & Mikac, 2024). Could the distribution of this other small

New Guinea help explain the restricted distribution of *D. kambuayai*? While sugar gliders are by far the most abundant petaurid in both montane and lowland contexts across eastern New Guinea, they may be uniquely patchy in occurrence across in western New Guinea, especially in the Vogelkop. Perhaps local absence or rarity of sugar gliders in western New Guinea provides an available ecological niche otherwise not available to this small petaurid lineage elsewhere in New Guinea.

In the Vogelkop region (Bird's Head and Bird's Neck) itself, most records of sugar gliders are from land-bridge and other offshore islands, including Salawati, Misool, and Waigeo, and they have probably been introduced to islands farther afield where they occur (including Halmahera, Bacan, Kayoa, Ternate, Kofiau: Flannery, 1994; Wiantoro *et al.*, 2023). On the mainland Vogelkop itself, however, very few museum specimens are known, such that Thomas (1888), Tate & Archbold (1937), Tate (1945), and Ziegler (1981) did not have access to specimens of *Petaurus* from the Bird's Head region in their reviews of petaurid systematics, and Aplin *et al.* (1999) did not have access to modern specimens of *Petaurus* from the Vogelkop for morphological comparisons. Jentink (1887, 1888) recorded a single specimen of *Petaurus* cf. *papuanus* (as *Belideus ariel*) specimen from Lobo Bay on the Bird's Neck, and three specimens from Doreh in the northeastern Bird's Head; Flannery (1995a:207) mapped one additional record from Sorong, and has observed sugar gliders at Fef, in the northcentral Vogelkop. This dearth of *Petaurus* records in the Vogelkop may be the result, in part, of a history of relatively incomplete sampling of mammal biodiversity in the region. However, remains of *Petaurus* are apparently less common than those of *D. kambuayai* in the Ayamaru Lakes mammal subfossil assemblage reported by Aplin *et al.* (1999), a possible indication of real rarity of sugar gliders in the Vogelkop fauna, at least in that area.

Does the distribution or abundance of sugar gliders impact the occurrence of *D. kambuayai*, or vice versa, for example via ecological competition between these smaller-bodied petaurid lineages? Examination of local distributional data might point to this kind of relationship. In reviewing photo-vouchered records on the *iNaturalist* platform in February 2025, we counted 6 records of *D. kambuayai* and 8 records of *Petaurus* cf. *papuanus* from the Vogelkop, with no overlap in these recorded areas of occurrence. Combining the *iNaturalist* data with all known museum specimens demonstrates a recorded distribution for *D. kambuayai* that spans the north-central part of the Vogelkop, from sea level in the vicinity of Klalik in the west, to Nenei at 900 m in the southern body of the Arfaks in the east. For *Petaurus* cf. *papuanus*, combining Vogelkop *iNaturalist* records with museum records demonstrates sugar glider occurrence in the northeastern corner of the Vogelkop around Manokwari, in the northwestern corner of the Vogelkop west of Klalik, and in the Bird's Neck—areas to the west, north, and south, respectively, of the recorded north-central distribution of *D. kambuayai*. Perhaps *D. kambuayai* occurs especially in areas where *Petaurus* cf. *papuanus* is absent, rare, or at least relatively less dominant in the local fauna. To date, the only place where both species are documented is in the subfossil record of Kria Cave, Ayamaru Lakes (Aplin *et al.*, 1999), which may speak to an area of overlap or parapatry of these two species, whether in the present or in the past, or both.

Conservation of *Dactylonax kambuayai*. Since 1992, when Woolley collected these modern specimens of *D. kambuayai*, the Arfak Mountains Nature Reserve, an area of 63,000 ha, was gazetted by the Government of Indonesia. This area includes small sections of low-elevation forest, along with large tracts of relatively undisturbed montane forest. The nature reserve is growing in popularity as an ecotourism destination. The records from the Klalik area suggests that the species may occur more broadly in the northern Vogelkop Peninsula, assuming its distribution is contiguous. Klalik is located 250 km (150 miles) west of Nenei in the Arfak Mountains, where the only other recent record comes from. The presence of *D. kambuayai* in lightly disturbed lowland forest indicates that there is suitable habitat for the species across much of the Vogelkop, and lack of records may well be due to limited surveying of nocturnal mammals across the West Papuan lowlands.

The lowland forests of the Vogelkop Peninsula are threatened by increasing commercial interests, including forestry, oil palm plantations, and ranching, as well as rapid population growth for people in the region. As one of the most range limited mammals in New Guinea, this combination of factors may threaten its survival. Adequate reservation of lowland rainforest in the Arfak region needs to be made if the future of the Pygmy Long-Fingered Possum is to be secured there. The increasing popularity of ecotourism in the area driven mainly by birdwatching and mammalwatching tours, offers a potentially sustainable form of income generation for local communities living on the Peninsula and provides an incentive for wildlife and habitat protection on community lands.

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A New Genus of Hemibelideine Possum (Marsupialia: Pseudocheiridae) from New Guinea and Australia, Including a Lazarus Taxon from the Vogelkop Peninsula

TIM F. FLANNERY¹ , LOUKAS G. KOUNGOULOS¹ , ERIK MEIJAARD² ,
AKSAMINA M. YOHANITA³ , ARMAN MUHARMANSYAH⁴, ICHLAS ALZAQIE⁵, KENNETH P. APLIN^{1†} ,
FREDERIKA KORAIN⁶, MARNEKS MJAM⁷, and KRISTOFER M. HELGEN⁸ 

¹ Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

² Borneo Futures, Brunei Darussalam Unit503-505, 5th floor, Teck Guan Plaza,
Bandar Seri Begawan BS8811, Negara Brunei Darussalam

³ University of Papua, Jalan Gunung Salju, Amban, Manokwari Baru, Papua Barat, 98314 Indonesia

⁴ Goodhope, Indonesia

⁵ Yayasan Orangutan Indonesia /Orangutan Foundation Indonesia (YAYORIN). Yayorin.com Jl. Bhayangkara No. Km 1,
Pasir Panjang Kec. Arut Selatan, Kabupaten Kotawaringin Barat, Central Kalimantan 74112, Indonesia

⁶ Jayapura, Papua, Indonesia

⁷ Tomolol Village, Misool, Indonesia

⁸ Bernice Pauahi Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i 96817, United States of America

† Kenneth P. Aplin 1958–2019, deceased.

ABSTRACT. A new genus of gliding marsupial (Hemibelideinae; Pseudocheiridae) is proposed for several possums previously known only as fossils: *Petauroides ayamaruensis* Aplin, 1999 (Quaternary of the Vogelkop Peninsula of western New Guinea), *Pseudocheirus stirtoni* Turnbull and Lundelius, 1970 (Pliocene of Victoria and New South Wales), and an unallocated species from the Middle Pleistocene of Queensland. The type species (*ayamaruensis*) is based on early Holocene archaeological material from the Vogelkop, mainly lower jaws and teeth, and was presumed to have been extinct for around 6,000 years. However, here we describe living individuals of *ayamaruensis*, thus a ‘Lazarus species’ (‘rediscovered’ after considered to be extinct), from several locations in the West Papuan region, as well as abundant archaeological material from ca. 1,000 km to the east in Sandaun Province, Papua New Guinea. The Sandaun material provides the first upper dentition known for this species. *Petauroides ayamaruensis* is restricted to the Vogelkop and North Coast Ranges, and is the only hemibelideine known from New Guinea. Observations of modern animals representing *ayamaruensis* help to cement its status as an extremely distinctive marsupial, and

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ORCID iD: Flannery, 0000-0002-3005-8305; Koungoulos, 0000-0002-5148-0142; Meijaard, 0000-0001-8685-3685;
Yohanita, 0000-0003-4724-1648; Aplin, 0000-0003-0403-8690; Helgen, 0000-0002-8776-4040

Corresponding authors: Tim F. Flannery tim.fridtjof.flannery@gmail.com and Kristofer M. Helgen kris.helgen@bishopmuseum.org

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access to its full dentition clarifies its relationship to fossil and living Australian possums. This newly described genus is present in the Australian Pliocene and Pleistocene fossil record, and its living relatives are the Greater gliders (*Petauroides* spp.) and the Lemuroid ringtail (*Hemibelideus lemuroides*) of eastern Australia. Traditional landowners from Maybrat Regency in the Vogelkop are familiar with *ayamaruensis* and relate that it roosts in tree hollows in the tallest and most commercially valuable timber trees of the lowland rainforest, and that a pair produces only a single young per year. It may also still survive in the Mamberamo Basin of western New Guinea and the Torricelli Mountains of Papua New Guinea. It is gravely threatened by logging and forest conversion, both of which continue to expand in West Papua and Papua New Guinea.

ABSTRAK. [Bahasa Indonesia] Sebuah genus baru marsupial melayang (Hemibelideinae; Pseudocheiridae) diusulkan untuk beberapa posum yang sebelumnya hanya dikenal dari catatan fosil: '*Petauroides ayamaruensis* Aplin, 1999 (Kwartir di Vogelkop, Papua Barat, Nugini Barat), *Pseudocheirus stirtoni* Turnbull dan Lundelius, 1970 (Pliosen di Victoria dan New South Wales), serta satu spesies yang belum dialokasikan dari Pleistosen Tengah Queensland. Spesies tipe dari genus baru ini (*ayamaruensis*) didasarkan pada material arkeologis Holosen awal dari Vogelkop, terutama rahang bawah dan gigi, dan sebelumnya diduga telah punah selama sekitar 6.000 tahun. Namun, di sini kami mendeskripsikan individu hidup *ayamaruensis*, sehingga merupakan 'spesies Lazarus' (yakni kembali dari kepunahan), dari beberapa lokasi di wilayah Papua Barat, serta material arkeologis yang melimpah dari sekitar 1.000 km ke arah barat di Provinsi Sandaun, Papua Nugini. Material dari Sandaun menyediakan catatan pertama dentisi atas yang diketahui untuk spesies ini. '*Petauroides ayamaruensis* terbatas pada Pegunungan Vogelkop dan Pegunungan Pantai Utara, dan merupakan satu-satunya hemibelideina yang diketahui dari Nugini. Pengamatan terhadap individu modern yang merepresentasikan *ayamaruensis* membantu menegaskan statusnya sebagai marsupial yang sangat khas, dan akses terhadap dentisi lengkapnya memperjelas hubungan filogenetiknya dengan posum Australia, baik yang fosil maupun yang masih hidup. Genus yang baru dideskripsikan ini hadir dalam catatan fosil Pliosen dan Pleistosen Australia, dan kerabat hidupnya adalah glider besar (*Petauroides* spp.) serta posum ekor cincin lemuroid (*Hemibelideus lemuroides*) dari Australia timur. Pemilik tanah adat dari Kabupaten Maybrat di Vogelkop mengenal *ayamaruensis* dan menyatakan bahwa spesies ini beristirahat di lubang-lubang pohon pada pohon kayu tertinggi dan bernilai komersial tinggi di hutan hujan dataran rendah, serta bahwa sepasang individu hanya menghasilkan satu anak per tahun. Spesies ini juga mungkin masih bertahan di Pegunungan Foja, dan Pegunungan Torricelli, Papua Nugini. *Ayamaruensis* menghadapi ancaman serius akibat penebangan dan konversi hutan, yang keduanya terus meluas di Papua Barat dan Papua Nugini.

Introduction

Two genera of pseudocheirid are currently placed in the subfamily Hemibelideinae; *Hemibelideus* Collett, 1884, and *Petauroides* Thomas, 1888. *Hemibelideus* is monotypic, comprising the Lemuroid ring-tailed possum, *Hemibelideus lemuroides* (Collett, 1884), restricted to high elevation rainforests in the Wet Tropics of northeast Queensland. It lacks a patagium (though it has a narrow proto-patagium) and so does not glide. Instead, it possesses a strongly prehensile tail and leaps through the rainforest canopy. It forms pair bonds and has a single young with a long period of dependency (Wilson, Marsh, & Winter, 2007). *Petauroides* has usually been regarded as represented by a single living species, *P. volans* (Kerr, 1792), widespread in eastern Australia; however, recent work has suggested that as many as three species-level taxa should be recognized: *Petauroides volans* (Kerr, 1792), *P. minor* Collett, 1887, and *P. armillatus* Thomas, 1923 (KPA, *pers. obs.*; McGregor *et al.*, 2020). The three proposed species of *Petauroides* are allopatrically/parapatrically distributed folivores that inhabit tall sclerophyll forests in eastern Australia, from Victoria to north Queensland. The tail is not prehensile, though bears a naked ventral tip, but they have a large patagium which extends from elbow to ankle, making them prodigious gliders. They den in tree-hollows and are facultatively

polygynous, only rarely being seen in family groups. The single young has a long period of dependency on the female, but there is no paternal care (Henry, 1984).

The subfossil taxon '*Petauroides ayamaruensis* Aplin, 1999 is the only member of the subfamily reported from Melanesia. In the original description, Aplin was uncertain as to its generic classification, and we use apostrophes to emphasize the provisional nature of his decision. '*Petauroides ayamaruensis* was known to Aplin from six subfossil fragments (Aplin *et al.*, 1999). The holotype (WAM 98/7/39) is a fragmentary right dentary from early Holocene (7,500–6,000 BP) sediments in Kria Cave (Pasveer 1998, 2004; Pasveer *et al.*, 2002), northeast of the Ayamaru Lakes on the Ayamaru Plateau, Vogelkop, West Papua, Indonesia (Fig. 1). A fragmentary left dentary (WAM 98.7.45) from Kria Cave, three femur fragments and a single tibia fragment (WAM 98.7.46–9) from late Pleistocene sediments in Toé Cave, on the southwest margin on the Ayamaru Lakes (Jelsma, 1998) were also referred to the taxon (Aplin *et al.*, 1999). Until this publication, the species was known only from these occurrences, and has been considered to be extinct (Turvey, 2009), although Helgen (2007) suggested it was likely to be extant in western New Guinea.

In 2015, one of us (AM), while working in the south Sorong area (Fig. 1), took three photographs of an unknown marsupial (including Fig. 2b). The images were passed on

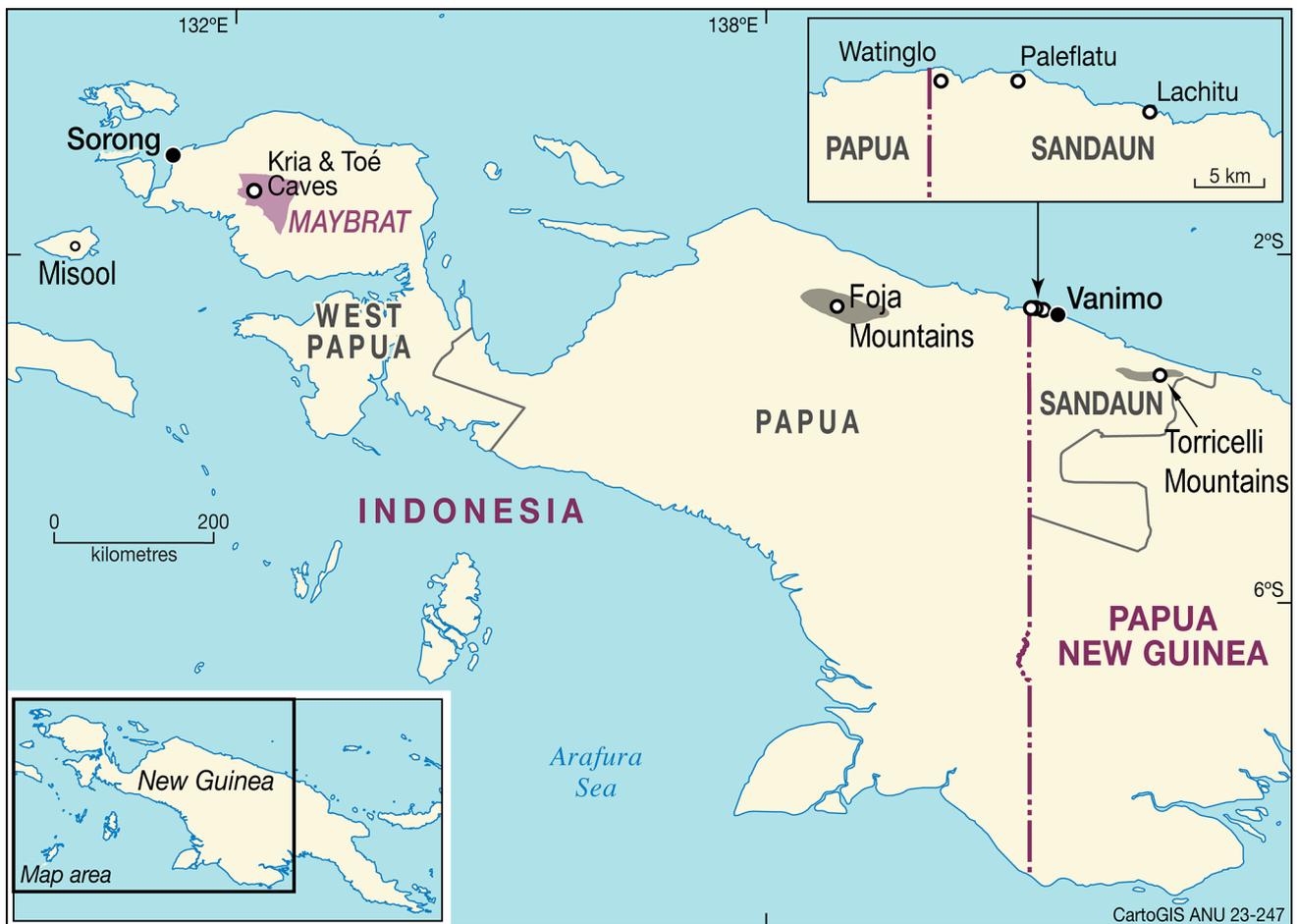


Figure 1. A map of western New Guinea showing localities mentioned, including the Maybrat language region on the Vogelkop Peninsula.

to coauthors IA and then to EM, who, in 2019, sent them to KMH, who identified the marsupial as representing a living '*Petauroides*' *ayamaruensis*. Between 2022 and 2023 TFF, LK, and KMH located additional subfossil material of *ayamaruensis* from Lachitu Cave and three nearby archaeological sites located near Vanimo, Papua New Guinea, which are under study at the Australian Museum and the Australian National University (Figs 4–6). These specimens had been attributed to *ayamaruensis* by KPA, but they had been misplaced and disassociated from their documentation. A numbering system used by KPA allowed us to re-associate the specimens with their archaeological contexts. Most recently, in 2023, another living animal was photographed on Misool Island, and in 2024 a hunted individual was photographed on the island (Figs 3a–b, 2b).

Here, we describe subfossil material attributed to '*Petauroides*' *ayamaruensis* by KPA, and determine that the subfossils represent the same taxon as that represented in photographs of living individuals, making the taxon a Lazarus species for the West Papuan mammal fauna, along with *Dactylonax kambuayai* (Flannery *et al.*, 2026). This new material makes it clear that '*Petauroides*' *ayamaruensis* possesses a unique combination of features very different from either *Petauroides* or *Hemibelideus* (Fig. 2, Table 1). In some important features it more closely resembles

Hemibelideus, including in its strongly prehensile tail, shorter pelage, and more foreshortened face with more crowded tooththrows, while in others, including its extensive gliding membrane and deep, sickle-shaped claws, it is more like *Petauroides*. While *Hemibelideus* is a leaping possum with a prehensile tail and without a developed patagium, and *Petauroides* is a glider without a fully prehensile tail and with an extensive patagium, *Tous* combines features of both, with both a strongly prehensile tail and an extensive gliding membrane. Its small size is unique in Hemibelideinae, as are its tapering, non-bushy tail, naked ears, eye ring, ear patch/flash, and the very distinct parastyle on M1.

The distinctive combination of features of *ayamaruensis* lead us to recognize a new and distinct genus to accommodate the Papuan subfossil and modern records of this species. In undertaking this taxonomic assessment, we realised that this genus is represented by both taxonomically described and undescribed species in the Australian fossil record that share similarly derived dental anatomies. Thus the Pliocene species '*Pseudocheirus*' *stirtoni* from Victoria (Turnbull & Lundelius, 1970; Turnbull *et al.*, 1987) and New South Wales (Dawson *et al.*, 1999), and an unnamed species previously attributed to '*Petauroides*' from the Middle Pleistocene of Queensland (Hocknull, 2005, 2009; Hocknull *et al.*, 2007) are both allocated to the new genus.

Table 1. Comparative external features of the three genera of Hemibelideinae.

	<i>Tous</i> gen. nov.	<i>Petauroides</i>	<i>Hemibelideus</i>
Patagium (gliding membrane)	extensive	extensive	rudimentary
Prehensile tail	present	vestigial (short naked surface ventrally)	present
Furring of tail	not bushy, tapered	bushy, untapered	bushy, untapered
Ears	small, unfurred	large, heavily furred	small, furred at base
Eye ring	black	absent	absent
Ear patch	black above*	absent	absent
Size	ca. 300 g	ca. 1–2 kg	ca. 1 kg
Distinct colour phase variants	yes	yes	yes
Colour	brown and grey variants	dark brown, grey, or cream variants	dark brown or cream variants
Pelage length	shorter	longer	shorter
Claws (hands and feet)	deep and sickle-shaped	deep and sickle-shaped	long and slender

* ... and white below, perhaps only when immature.

Materials and methods

Collection of material

No modern specimens of *'Petauroides' ayamaruensis* exist in museum collections, as the species is thus far known from subfossil remains and photographs and descriptions of living animals. In addition to the type and referred material by Aplin *et al.* (1999) from Kria and Toé Caves, newly referable specimens to *'Petauroides' ayamaruensis* have been recovered from four archaeological sites in the Vanimo region, on the north coast of Sandaun Province, Papua New Guinea (PNG). The sites, known as Lachitu (RIQ), Watinglo (WAT) and Paleflatu 1 and 2 (PF1/PF2) were excavated from 2004 to 2005. Details on their stratigraphy, antiquity of human occupation, and occupational sequence were provided by O'Connor *et al.* (2011) and Beaumont *et al.* (2018). Excavation units averaged between 2 and 5 cm in depth and all excavated deposit was sieved through a 1 mm mesh. This in combination with flotation to the <0.25 mm level ensured maximum recovery of small faunal remains. Each of these sites contains known or at least suspected owl-roost deposits, and it is likely that many of the smaller murid and marsupial remains (including those of *'P. ayamaruensis'*) are the result of owl-roosting activity within the caves rather than human hunting and discard.

Museum material

Abbreviations: PNGNM, Papua New Guinea National Museum and Art Gallery, Port Moresby, Papua New Guinea; WAM, Western Australian Museum, Perth, Australia.

The subfossils from the Vanimo region bear registration numbers PNGNM 26592–26646. Contextual and registration information is provided below for the specimens which are treated in the following text, these being diagnostic specimens or ones which otherwise record the presence of the species at a particular site: PNGNM 26597 (Fig. 4a), left dentary with i1, m1, and anterior half of m2, Paleflatu 2 Cave, no further contextual information. PNGNM 26603, right maxilla with M1–3, Paleflatu 1 Cave, Square A, Spit 20. PNGNM 26604 (Fig. 4b), left dentary with p3, m1–3, Watinglo Cave, Square A, Spit 58. PNGNM 26619 (Figs 5b, 5d), right maxilla with P2, P3, M1–4, Lachitu Cave, Square A, Spit 30. PNGNM 26640 (Fig. 6a), left P3, Lachitu Cave,

no further contextual information. PNGNM 26641 (Fig. 6b), right P3, Lachitu Cave, no further contextual information. PNGNM 26642 (Fig. 6c), left P3, Lachitu Cave, no further contextual information. PNGNM 26644, left premaxilla with I1, I3, Paleflatu 2 Cave, Square C. PNGNM 26646, left dentary, edentulous, Paleflatu 2 Cave, Square C. All morphological measurements (Table 2) were made with electronic calipers.

Systematics

Order Diprotodontia Owen, 1877

Family Pseudocheiridae Winge, 1893

Subfamily Hemibelideinae

Kirsch, Lapointe, and Springer, 1997

Content. In the past, the two described genera in this subfamily, *Hemibelideus* and *Petauroides*, were often classified as subgenera of a much more expansive generic concept of *Pseudocheirus* Ogilby, 1837 (e.g., Tate, 1945), though Thomas (1888) much earlier distinguished the generic status of *Petauroides*. Modern integrative studies of pseudocheirid evolution drawing on craniodental, cytogenetic, and molecular genetic datasets (e.g., McQuade, 1984; Archer, 1984; McKay, 1984; Baverstock *et al.*, 1990; Springer, 1988, 1993; Springer *et al.*, 1992) cemented the generic status of *Hemibelideus* and *Petauroides* (McKay, 1989) and established their sister relationship, with Kirsch *et al.* (1997) formalizing the concept by erecting the subfamily Hemibelideinae for these taxa. Subsequent morphological and molecular studies have confirmed that the Hemibelideinae is a deeply divergent and distinctive lineage within the Pseudocheiridae (Aplin *et al.*, 1999; Meredith *et al.*, 2009, 2010; Mitchell *et al.*, 2014; Beck *et al.*, 2022). Here we add a third and newly named genus to the subfamily.

Diagnosis. Hemibelideines share the following combination of characteristics, which are unique within the family Pseudocheiridae: molar cusps/cuspids strongly buttressed with anteroposteriorly oriented ridges; supplementary postparacrista and postmetacrista sharp and flexed back to run almost parallel with the actual postparacrista and

Table 2. Dental measurements of the species of *Tous* gen. nov.. All measurements in mm. L = length, W = maximum width. Data for Lachitu Cave material is original to this work; other data from Aplin *et al.* (1999) (*Tous ayamaruensis* holotype WAM 98/7/9); Dawson *et al.* (1999) (*Tous* cf. *stirtoni* from Big Sink, Wellington Caves); and Turnbull *et al.* (1987) (*T. stirtoni* from Hamilton Local Fauna).

	<i>T. ayamaruensis</i> holotype WAM 98/7/39	<i>T. ayamaruensis</i> Lachitu Cave, Papua New Guinea	<i>T. stirtoni</i> Hamilton Local Fauna	<i>T. cf. stirtoni</i> Big Sink, Wellington Caves
P2 L	—	$n = 2, r = 1.6\text{--}1.8, \bar{x} = 1.7$	$n = 6, r = 1.3\text{--}1.5, \bar{x} = 1.4$	—
P2 W	—	$n = 2, r = 1.6\text{--}1.8, \bar{x} = 1.7$	$n = 6, r = 1.3\text{--}1.5, \bar{x} = 1.4$	—
P3 L	—	$n = 3, r = 2.0\text{--}2.2, \bar{x} = 2.1$	$n = 11, r = 2.0\text{--}2.2, \bar{x} = 2.1$	—
P3 W	—	$n = 3, r = 1.7\text{--}2.0, \bar{x} = 1.8$	$n = 9, r = 1.5\text{--}1.7, \bar{x} = 1.6$	—
M1 L	—	$n = 4, r = 2.8\text{--}3.2, \bar{x} = 3.0$	$n = 23, r = 3.1\text{--}3.3, \bar{x} = 3.2$	$n = 2, r = 2.7\text{--}2.9, \bar{x} = 2.8$
M1 W	—	$n = 4, r = 2.2\text{--}2.6, \bar{x} = 2.4$	$n = 24, r = 2.4\text{--}2.8, \bar{x} = 2.6$	$n = 2, r = 2.4\text{--}2.8, \bar{x} = 2.6$
M2 L	—	$n = 10, r = 2.6\text{--}3.1, \bar{x} = 2.8$	$n = 27, r = 2.8\text{--}3.1, \bar{x} = 3.0$	$n = 2, r = 2.6\text{--}2.8, \bar{x} = 2.7$
M2 W	—	$n = 9, r = 1.9\text{--}2.6, \bar{x} = 2.5$	$n = 28, r = 2.2\text{--}2.7, \bar{x} = 2.5$	$n = 2, r = 2.3\text{--}2.4, \bar{x} = 2.4$
M3 L	—	$n = 9, r = 2.5\text{--}3.0, \bar{x} = 2.7$	$n = 13, r = 2.8\text{--}3.1, \bar{x} = 2.9$	—
M3 W	—	$n = 8, r = 2.5\text{--}3.0, \bar{x} = 2.3$	$n = 13, r = 2.8\text{--}3.1, \bar{x} = 2.9$	—
M4 L	—	$n = 9, r = 2.1\text{--}2.2, \bar{x} = 2.1$	$n = 3, r = 2.2\text{--}2.5, \bar{x} = 2.4$	—
M4 W	—	$n = 4, r = 1.7\text{--}2.1, \bar{x} = 1.9$	$n = 3, r = 1.4\text{--}1.7, \bar{x} = 1.6$	—
p3 L	—	$n = 2, r = 2.2\text{--}2.4, \bar{x} = 2.0$	$n = 14, r = 1.8\text{--}2.2, \bar{x} = 2.0$	—
p3 W	—	$n = 2, r = 1.4\text{--}1.6, \bar{x} = 1.5$	$n = 14, r = 1.1\text{--}1.3, \bar{x} = 1.2$	—
p3 alveolar L	2.1			
m1 L	3.1	$n = 3, r = 2.0\text{--}3.3, \bar{x} = 3.1$	$n = 18, r = 2.8\text{--}3.4, \bar{x} = 3.2$	—
m1 W	1.5	$n = 3, r = 1.6\text{--}1.9, \bar{x} = 1.8$	$n = 18, r = 1.5\text{--}1.8, \bar{x} = 1.7$	—
m2 L	2.7	$n = 6, r = 2.5\text{--}3.1, \bar{x} = 2.9$	$n = 17, r = 2.9\text{--}3.3, \bar{x} = 3.1$	—
m2 W	1.7	$n = 6, r = 1.6\text{--}1.8, \bar{x} = 1.7$	$n = 17, r = 1.6\text{--}2.0, \bar{x} = 1.8$	—
m3 L	—	$n = 4, r = 2.5\text{--}3.1, \bar{x} = 2.9$	$n = 9, r = 2.9\text{--}3.2, \bar{x} = 3.0$	—
m3 W	1.7	$n = 6, r = 1.7\text{--}1.9, \bar{x} = 1.8$	$n = 9, r = 1.7\text{--}1.9, \bar{x} = 1.8$	—
m4 L	2.7	$n = 5, r = 2.6\text{--}3.3, \bar{x} = 2.8$	$n = 3, r = 3.1\text{--}2.5, \bar{x} = 3.2$	—
m4 W	1.5	$n = 4, r = 1.5\text{--}1.9, \bar{x} = 1.7$	$n = 5, r = 1.4\text{--}1.6, \bar{x} = 1.5$	—

postmetacrista; reduced or absent anterior lower premolars.

Hemibelideines also share a body adapted to leaping or gliding, large and forward-facing eyes, a short rostrum, and they roost primarily in tree hollows and raise a single young per year.

Tous gen. nov. Flannery & Helgen

urn:lsid:zoobank.org:act:C5029EE0-E28B-4998-AB20-B8D3AD39F894

Diagnosis. Smallest living hemibelideine, differing from all other hemibelideines in having naked ears and a combination of a prehensile tail and a patagium (Figs 2b, 3a,b); and in possessing a very distinct parastyle on M1 (Fig. 5).

Type species. *Petauroides ayamaruensis* Aplin, 1999 (Figs 2b, 3–6). This species is now known from western New Guinea (as a living animal: from the Sorong area and from the land-bridge island of Misool; and subfossil: Ayamaru Lakes area) and northern New Guinea (subfossil: Oenake portion of the North Coast Ranges).

Included species. *Pseudocheirus stirtoni* Turnbull & Lundelius, 1970, from the Pliocene of Victoria and New South Wales. A third, undescribed species of *Tous* is known from the Middle Pleistocene of Queensland.

Etymology. From the Maybrat language-group name for the living species, ‘tous.’

Suggested common name. Ring-tailed Glider.

Description. A very small hemibelideine (probably *ca.* 300–400 g, similar in size but more robust than the other larger New Guinea gliding possum, *Petaurus abidi* Ziegler, 1981) with naked ears (the outside of the ear is densely furred in *Petauroides*, while the basal half is densely furred in *Hemibelideus*), patagium extending to elbow on forelimb, and ankle on hindlimb (as in *Petauroides*). Tail furred to the tip, except for a naked area on the ventral side. A similar naked area is present in species of *Petauroides* (though the naked area is more extensive in *Tous*), while in *Hemibelideus* the entire tip of the tail is naked (McKay, 1989). The tail is strongly prehensile (as in *Hemibelideus*, but not *Petauroides*). The claws on the hands and feet are thick and sickle-shaped, similar to *Petauroides* (longer and more slender in *Hemibelideus*). The fur on the dorsum is brownish with silver tipping (more prominent in juveniles), with pelage not as long and thick compared to *Petauroides*, and the venter is white. There is no dorsal stripe, contrasting with gliders of the genus *Petaurus* (Flannery, 1994, 1995). A patch behind the ear is black, with a white patch below the ear in one immature animal photographed (Fig. 2b). The eyes are prominent and forward-facing and surrounded by rings of dark fur (eye rings). Both grey and brown colour variants occur on Misool. Tapetum lucidum highly reflective, iris orange, muzzle narrow and short, rhinarium naked (Fig. 2b).

Dentition (Figs 4–6). The dentary and the lower molars have been described in detail by Aplin *et al.* (1999), but the antemolar lower dentition is described here for the first time. The

i1, which is represented in PNGNM 26597 (Fig. 4a), has the tip broken away. It is a robust tooth, its root being about as broad as it is deep. It is similar in morphology to the i1 in species of *Petauroides*. The only known p3, represented in PNGNM 26604 (Fig. 4b), is fragile, its enamel being pitted and discoloured. The partial dentary it is rooted in is broken into four crumbling fragments. The crown consists of a tall principal cusp, a lower anterior cuspule, and an even lower, posterior cusp with twin posteriorly-directed ridges. The enamel in the region of the posterior cusp is discoloured: it may have been affected by wear and/or breakage. A well-developed basal cingulum is present buccally and lingually. Overall, the structure of p3 is similar to that of species of *Petauroides* and *Hemibelideus*. It differs from the p3 of *Tous stirtoni* in that the principal and posterior cusps are not closely adpressed. The articular facet of the dentary (preserved in PNGNM 26646) is transversely narrower than in other hemibelideines (Fig. 5a).

The upper dentition is described here for the first time based on the Vanimo-area material, as premaxillary and maxillary elements were not available to Aplin *et al.* (1999) in the original Vogelkop material. PNGNM 26644 (Paleflatu 2 site, Square C) is a left premaxilla preserving I1 and I3, with alveoli for I2. As in other hemibelideines I1 is markedly robust, its diameter exceeding that of the other upper incisors. It is more robust than the I1 of species of *Pseudochirulus* (*P. canescens* being the only similar-sized pseudocheirid occurring in the Vanimo deposits). The crown is petiolate-shaped and barely worn (Fig. 5c). The alveolus for I2 suggests that this tooth was relatively small, possibly smaller than I3, and likely smaller than in other hemibelideines. I3 is anteroposteriorly elongate and blade-shaped (Fig. 5b–d).

PNGNM 26619 (Lachitu site, square A) is a maxillary fragment, preserved from the premaxillary suture posterior to the posterior root of M4, including part of the palate and the root of the zygomatic process, with a near-complete cheektooth row (P2–3, M1–4), with an alveolus for P1 (Fig. 5b). The alveolus indicates that P1 was single rooted, the root was ovoid in cross section, and much smaller than P2. It seems likely that a short diastema existed between P1 and the canine (of which no evidence remains, even though parts of the premaxillary-maxillary suture is preserved).

The crown of P2 is triangular in occlusal view, dominated by a single central cusp with a crista running posteriorly from it. The rear moiety of the tooth consists of a broad lingual and buccal basin separated by this crista. P3 is substantially larger than P2. It consists of a sharply defined anterior cusp with a crista running posteriorly from its apex and terminating against the base of a prominent central cusp. PNGNM 26640, 26641 and 26642 are almost unworn P3s (Fig. 6a–c). PNGNM 26642 is more elongate than the others, but is within the observed variability of *Hemibelideus*. A crista runs buccally from the apex of the central cusp, dividing the buccal basin into two moieties. A second crista runs posteriorly to terminate against the parastyle of M1. Another crista runs buccally and anteriorly from this juncture to partially enclose the posterior moiety of the buccal basin. On PNGNM 26619 the posterolingual surface of the tooth is heavily worn, while the other teeth in the maxilla are barely worn (Fig. 5b, d). Remnants of a posterolingual basin can be seen in the worn surface, along with a posterolingual cingulum (Fig. 5d).

The M1 is subrectangular in shape, the four principal cusps being strongly buttressed by antero-posteriorly oriented cristae, and the parastyle is prominent. A small buccal cingulum is present at the base of the paracone. The tooth is strongly selenodont, with supplementary cristae running almost parallel to the post and pre-paracrista and post and pre-metacrista. The protocone and hypocone are strongly crested, the cristae forming selenes that define the buccal margin of the tooth. M2 differs from M1 principally in that the parastyle is reduced. M3 differs from M2 in that the parastyle is further reduced, the selenes in the median valley are reduced in length, and in that posterior moiety of the tooth is markedly narrower. M4 differs from M3 in being markedly smaller, in lacking a parastyle, and on the posterior moiety in lacking a selene in the median valley. There is no posteriorly directed crista on the metacone, and the hypocone is rudimentary, the posterior moiety of the tooth being markedly reduced (Fig. 5b).

Differences from congeners. *Tous stirtoni* from the early Pliocene type locality on Grange Burn, Victoria, Australia, is the only other described species referred to *Tous*. It differs from *T. ayamaruensis* (to which it is very similar in size, see Table 1), in that the pre-entocristid and metastylid do not contact on lower molars, p3 has two distinctive and closely spaced cusps, and in having a remarkably short P3.

The original hypodigm of *stirtoni* including the associated tooth crowns of m1–4 (the holotype), a p3, an isolated P3 and some isolated upper molars (Turnbull & Lundelius, 1970). Turnbull *et al.* (1987) attributed nearly 200 additional specimens to the taxon, including a partial dentary, all from the Grange Burn Local Fauna, Western Victoria. Turnbull & Lundelius (1970) noted similarities between *P. stirtoni* and *Pseudocheirus* (*Petauroides*) *volans*, and Archer (1984) formally transferred the species to the subgenus (later genus) *Petauroides*, a designation adopted by Turnbull *et al.* (1987). Aplin *et al.* (1999) provided further evidence for the relationship between *stirtoni* and *Petauroides volans*, arguing that the premolars and upper molars share detailed similarities. We concur that species of *Petauroides* share similarities with *stirtoni*, but the similarities with *T. ayamaruensis* are even more compelling, leading us to place *stirtoni* in the genus *Tous*.

Differences in the dentitions of *T. stirtoni* and *T. ayamaruensis* are concentrated in the premolars. The P2 and P3 of *T. stirtoni* consists of two prominent cusps and a lingual cingulum (a structure similar to that seen in the P2 of species of *Pseudochirops* but not in other pseudocheirids), while in *T. ayamaruensis* it consists of a single, prominent central cusp with posterior-buccal and postero-lingual basins (Fig. 5b, d). The P3 of *T. stirtoni* differs from that of *T. ayamaruensis* in being foreshortened, and in having a very shallow basin on its buccal side (in *T. ayamaruensis* the buccal basin is in contrast expansive, and its posterobuccal margin is enclosed by a unique, well-developed cristid; Fig. 5d). In *T. stirtoni* the anterior moiety of P3 is unique in consisting of a single prominent cusp with no anteroposterior linking. In *T. ayamaruensis* this cusp is less prominent, and a cristid runs posteriorly from it towards the principal cuspid. The M1, M2, and M3 of *T. stirtoni* are strikingly similar to those of *T. ayamaruensis*, the molar cusps being strongly buttressed with anterior-posteriorly oriented cristae (Fig. 5b).

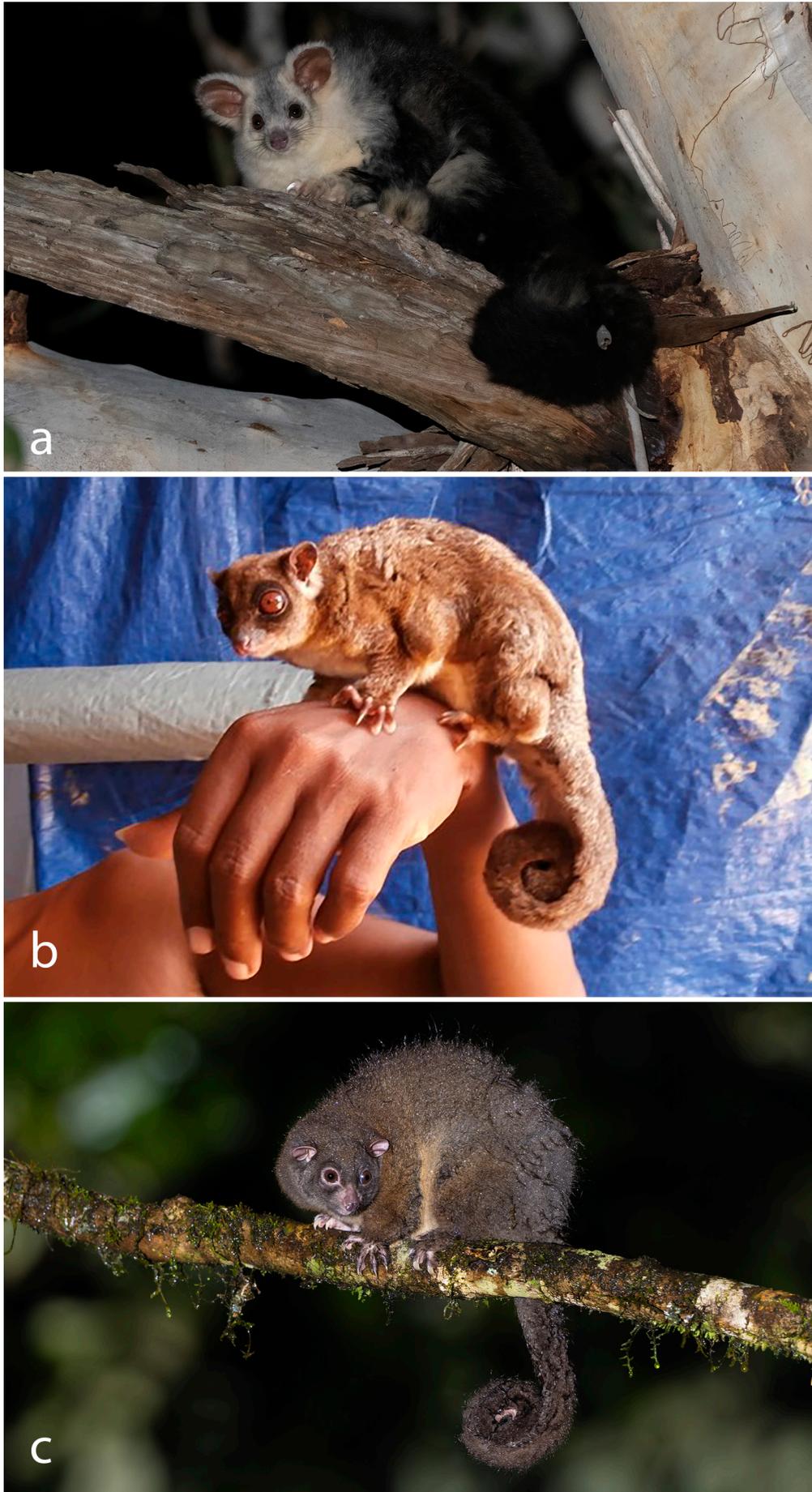


Figure 2. The three genera of subfamily Hemibelideinae: (a) *Petauroides*, © David Sinnott CC BY-NC 4.0; (b) *Tous*, subadult, South Sorong area, Vogelkop Peninsula (photo credit Arman Muharmansyah); and (c) *Hemibelideus*, © Jono Dashper CC BY-NC 4.0. Images not to scale.

Discussion

Association of modern observations and subfossils of *Tous*

With no modern museum voucher specimens currently available, our association of the subfossil remains from archaeological deposits (including the holotype of *ayamaruensis*) with images of modern animals and observations by traditional owners who are familiar with this possum, requires justification.

The initial description of *T. ayamaruensis* by Aplin *et al.* (1999) clearly established that:

- (1) it is a small marsupial known from Holocene archaeological context in the Vogelkop Peninsula of western New Guinea,
- (2) it is a hemibelideine pseudocheirid, sharing a variety of derived traits, such as premolar and molar cristae arrangement, otherwise found only in the living hemibelideines *Hemibelideus* and *Petauroides*,
- (3) its closest dental resemblance is to *Petauroides*, though it is much smaller than extant species of both hemibelideine genera (Aplin *et al.*, 1999).

Because the mammal fauna of western New Guinea, particularly the Vogelkop, remains relatively little-studied in general, Helgen (2007:732) suggested that *ayamaruensis* was ‘likely to survive undiscovered today in the Vogelkop’ and ‘should be especially sought in future biological surveys in the region.’ Thus, KMH was on the lookout for evidence for extant occurrence of this species. When KMH first saw photos of the living animal from the Sorong area of the Vogelkop (Fig. 2b), he immediately realized that the animal had external features of a small gliding pseudocheirid marsupial, and the only previously known candidate for such an animal could be *ayamaruensis*, which was described from nearby on the Vogelkop in an archaeological context. He could tell from the body form and tail morphology that the species was a pseudocheirid, but that it differed profoundly from all other pseudocheirids in being small, having small ears, having a prehensile tail thickly furred dorsally to its distal tip, and in having a gliding membrane (NB in the particular picture in Fig. 2b, the patagium is bunched up against the body of the animal). The only other gliding Pseudocheiridae are species of the Australian genus *Petauroides*, which are much larger, have large furred ears, long pelage, and a bushy, non-prehensile tail, ruling out that possibility of identification (Fig. 2).

Additional subfossil remains of *ayamaruensis* from the Vanimo area demonstrate that the features of the upper jaw suggest that *ayamaruensis* is a small possum that has a short-snouted, rounded face, probably similar in overall shape to *Hemibelideus lemuroides*. This too, corresponds in size and appearance with the modern animals we associate with *Tous ayamaruensis* (Fig. 2).

Finally, in showing the photographs of the living ringtail in question to local landowners, alongside extensive contextual discussion, we found that knowledgeable people in lowland areas of the Vogelkop are familiar with this species, and discriminate it in various ways from other small possums, such as *Petaurus papuanus*, *Dactylopsila trivirgata*, and *Pseudochirulus canescens*. Landowner knowledge describes

the species as having a suite of characteristics typical of hemibelideines, including strongly forward-facing eyes, distinctive locomotor behaviour and morphology of leaping and gliding, and nesting and reproductive strategies such as monogamy and hollow nesting. Combined, the fossils, images and traditional knowledge we attribute to *Tous* are all consistent with the characteristics of the Hemibelideinae. Moreover, the fossils are from a creature the size of the photographed individuals, and traditional knowledge relates to a possum of similar size to both fossils and photographed animals.

Rediscovery of *T. ayamaruensis*, and documentation to date of its biology as a living animal, points to the fundamentally important approach of integrating both indigenous ways of knowing and understanding the world, and scientific approaches (in this case from both zoology and palaeontology) to illuminate New Guinea’s remarkable mammal fauna (Majnep & Bulmer, 2006; Morib *et al.*, 2025), which remains poorly understood in global context (Flannery, 1995; Helgen, 2007). This is the future of New Guinea biodiversity study.

Tous ayamaruensis in the New Guinea archaeological record

Tous ayamaruensis is now known from five archaeological deposits (two in the Ayamaru Lakes region of West Papua, and three from Sandaun Province, Papua New Guinea), ranging in age from late Pleistocene to mid Holocene. The holotype (WAM 98/7/39) is a fragmentary right dentary with m1–4 and roots of i1 and p3 from Kria Cave, 3 km east of the village Suwiam/ Mapura, northeast of the Ayamaru Lakes. It was excavated from Unit V (135–140 cm depth) of Kria Cave square IN1E, dated to *ca.* 7,500–6,000 BP (Pasveer, 1998). An edentulous left dentary from the same unit is referred to the species. Fragmentary femur and tibial fragments from late Pleistocene sediments in Toé Cave on the southwestern margin of the Ayamaru lakes are also referred to it (Aplin *et al.*, 1999).

Numerous upper and lower dentitions were recovered from Lachitu Cave (2.6339°S 141.1364°E), which lies at approximately 25 m elevation and 150 m inland from the coast about midway between the town of Vanimo and the Indonesian border, in northwestern PNG. The sediments in Lachitu Cave are mostly late Pleistocene to mid-Holocene in age, with surface layers dating to the last few hundred years (O’Connor *et al.*, 2011), there being a hiatus in sediments between about 7,600 BP and 300 BP (Beaumont *et al.*, 2018). The majority of the Lachitu specimens show evidence of acid etching, possibly as a result of fossil preparation by Aplin and/or because the specimens derive from owl-roost deposits and were partially digested prior to deposition. Nearly all Lachitu specimens of *T. ayamaruensis* appear to have been recovered from layers dating to the late Pleistocene to early Holocene, although a few come from mid-Holocene strata. None were found in the upper layers, which date to the last few centuries, suggesting local extinction, or absence of the predator accumulator from the cave chamber.

A single specimen of *Tous ayamaruensis* (PNGNM 26604) is recorded from Watinglo Cave. It derives from Square A, Spit 58, and is dated to between 7,559–7,314 cal BP and 11,707–11,261 cal BP. Watinglo Cave is located a few hundred metres from the Indonesian border in Sandaun Province, less than 1 km inland and at an elevation of *ca.*

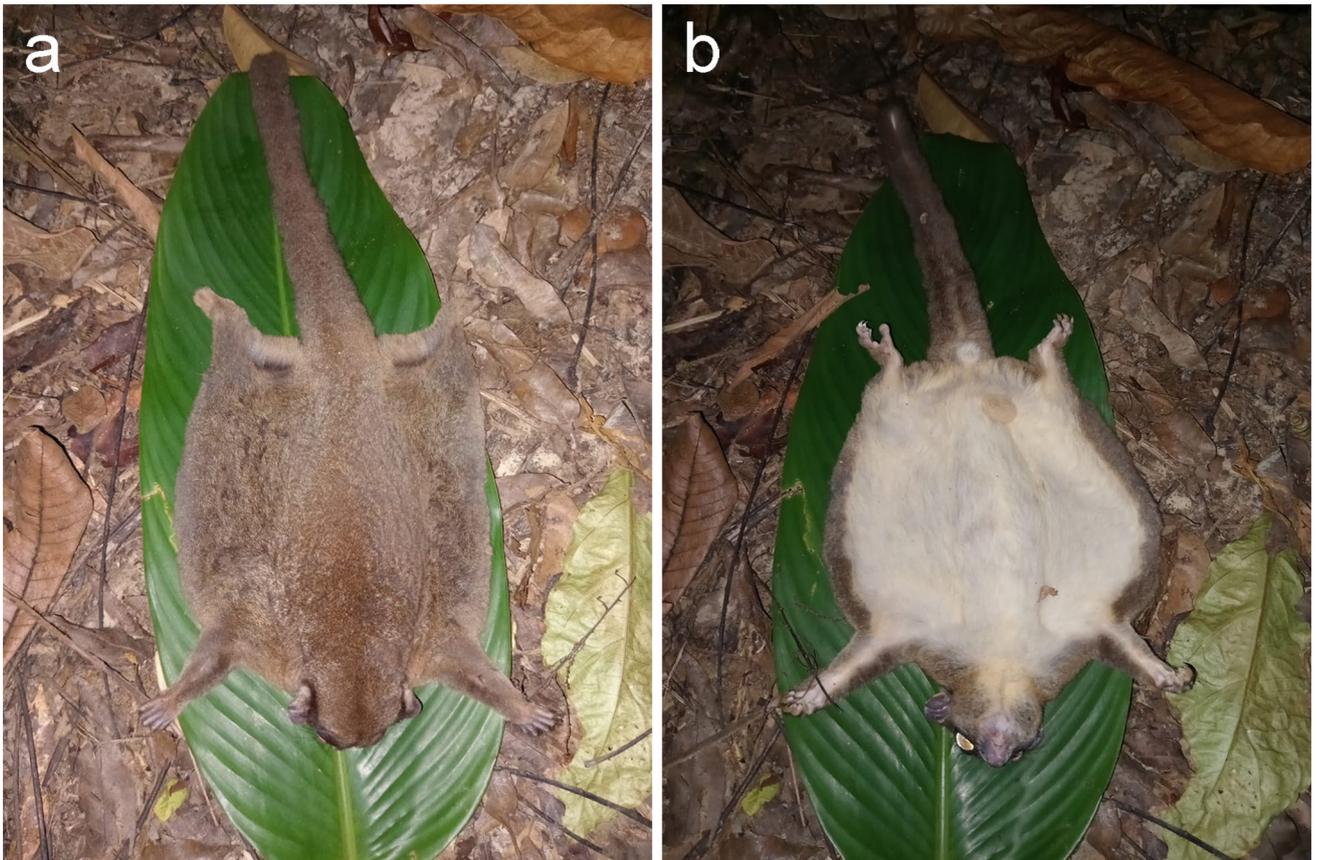


Figure 3. Photos of *Tous ayamaruensis*, adult male, Batkaji forest, Misool Island in (a) dorsal and (b) ventral views (photo credit Marneks Mjam).

100 m above sea level. The deposit has a stratigraphic hiatus between 5,500 and 2,000 ybp (O'Connor *et al.*, 2011). Paleflatu 1 cave is located approximately 5 km east of Watinglo and is 20 m above sea level. It also has yielded a single specimen (PNGNM 26603) with a date of 7,744–7,460 cal BP from the same context. A number of specimens are recorded from an adjacent cave known as Paleflatu 2, for which only square, but no spit information, was recorded. It seems likely that the sample was excavated in bulk as an owl roost deposit. Paleflatu, like Watinglo and Lachitu, appears to have a stratigraphic hiatus between around 5,000 and 2,500 BP (Beaumont *et al.*, 2018).

The absence of *T. ayamaruensis* in latest Holocene and recent deposits in PNG may be evidence for its decline, and possible local disappearance from the area, sometime after the mid-Holocene (O'Connor *et al.*, 2011). It is also possible, however, that changing human hunting preferences, or the absence of owls from the caves, accounts for the absence of *Tous* in these more recent sediments. The region remains thinly populated, and its forests appeared to be largely undisturbed as of late 2023, suggesting that a search for living specimens might be fruitful (TFF *pers. obs.*).

We present one other observation gleaned from the study of the Vanimo-area subfossils of *T. ayamaruensis*. The P3 in hemibelideines, with its two postero-lingual basins separated by a ridge, is distinctive among pseudocheirids. Functionally, the complex ridge and basin structure serves to resist wear. Despite this wear-resistance, in *T. ayamaruensis* the lingual region of P3 becomes heavily worn long before wear is evident on other parts of the upper dentition (e.g., see Figs 5b, 5d, 6). This differential wear pattern is not present, at least

to the same extent, in other pseudocheirids, including species of *Petauroides* and *Hemibelideus*. A possible clue about this feature comes from another group of gliding mammals in Africa, where species of the rodent family Anomaluridae are rainforest-dwellers that, like *T. ayamaruensis*, roosts in tree hollows and glide to other trees to forage. Several species of anomalures, including *Anomalurus derbianus*, are known to prune seedlings growing in the vicinity of their feed trees, in order to maintain access to food supplies and to keep flight paths open (Kingdon, 2013, 2023). One possible explanation for the distinctive wear pattern seen in the only known complete upper cheektooth row of *T. ayamaruensis* is that it, like anomalures, prunes twigs.

***Tous ayamaruensis* as a living species in the Vogelkop region**

A living individual was photographed by IA in 2015. Based on its relatively large hands, placid disposition, and small overall size (Fig. 2b), we suspect it was a juvenile. The animal had been caught by AM, by the side of a river in a High Conservation Value forest set-aside belonging to a palm oil company. He saw the animal on a branch and simply grabbed it, believing it to be a slow loris (*Nycticebus*) (which do not occur in New Guinea) or cuscus (Phalangeridae). When he asked local Papuans whether they knew the species, they said that they had no special name for it (or did not recognize it), but mentioned that they hunted and ate it. It is not clear whether they were referring specifically to *Tous* or to arboreal marsupials more generally. The images were passed on to KMH for identification (reaching him around a

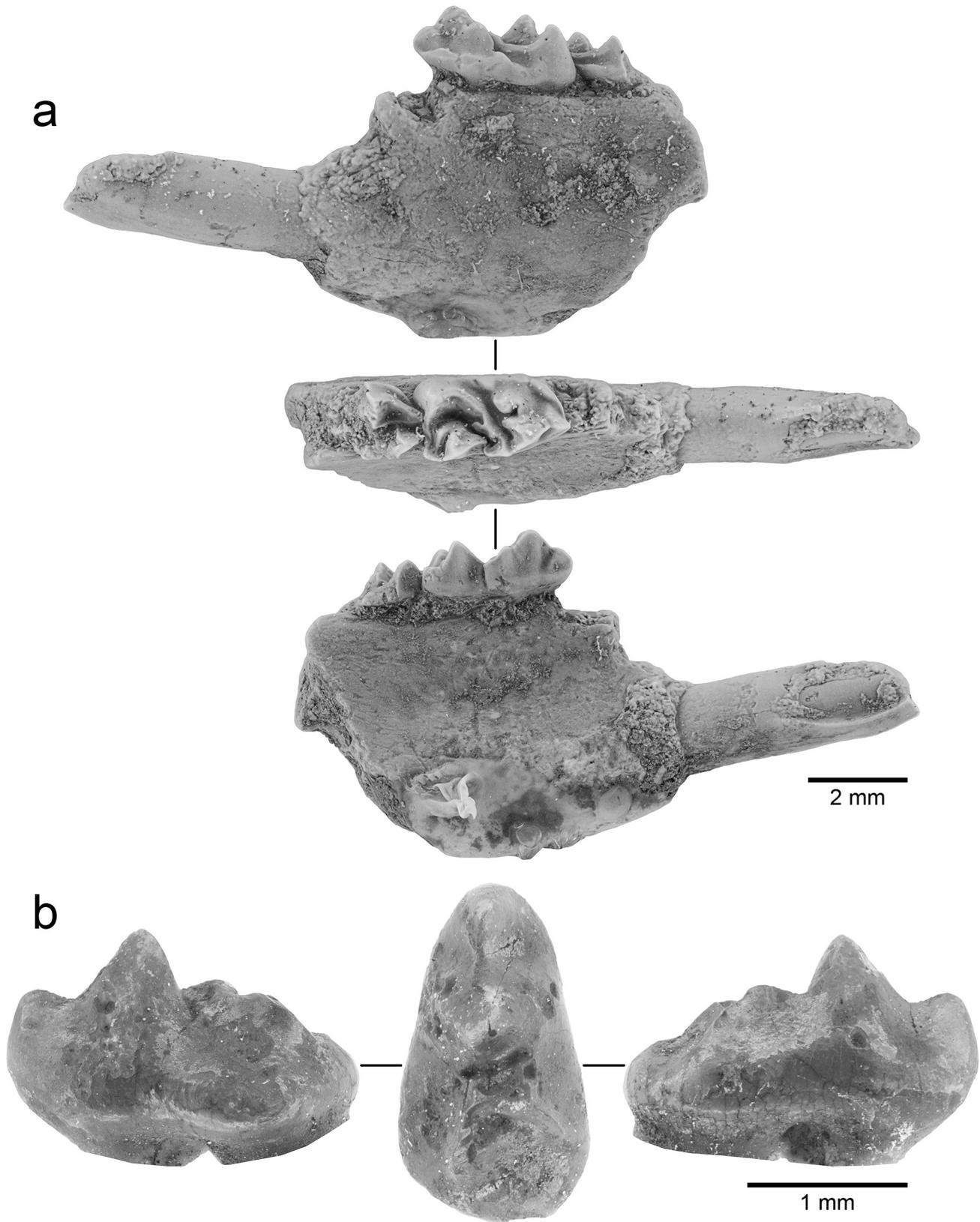


Figure 4. Lower dental material of subfossil *Tous ayamaruensis* from Vanimo sites. (a) PM 25697, left dentary preserving i1, m1, and anterior half of m2 in buccal, occlusal, and lingual views; (b) isolated view of p3 from PM 26604 in buccal, occlusal, and lingual views.

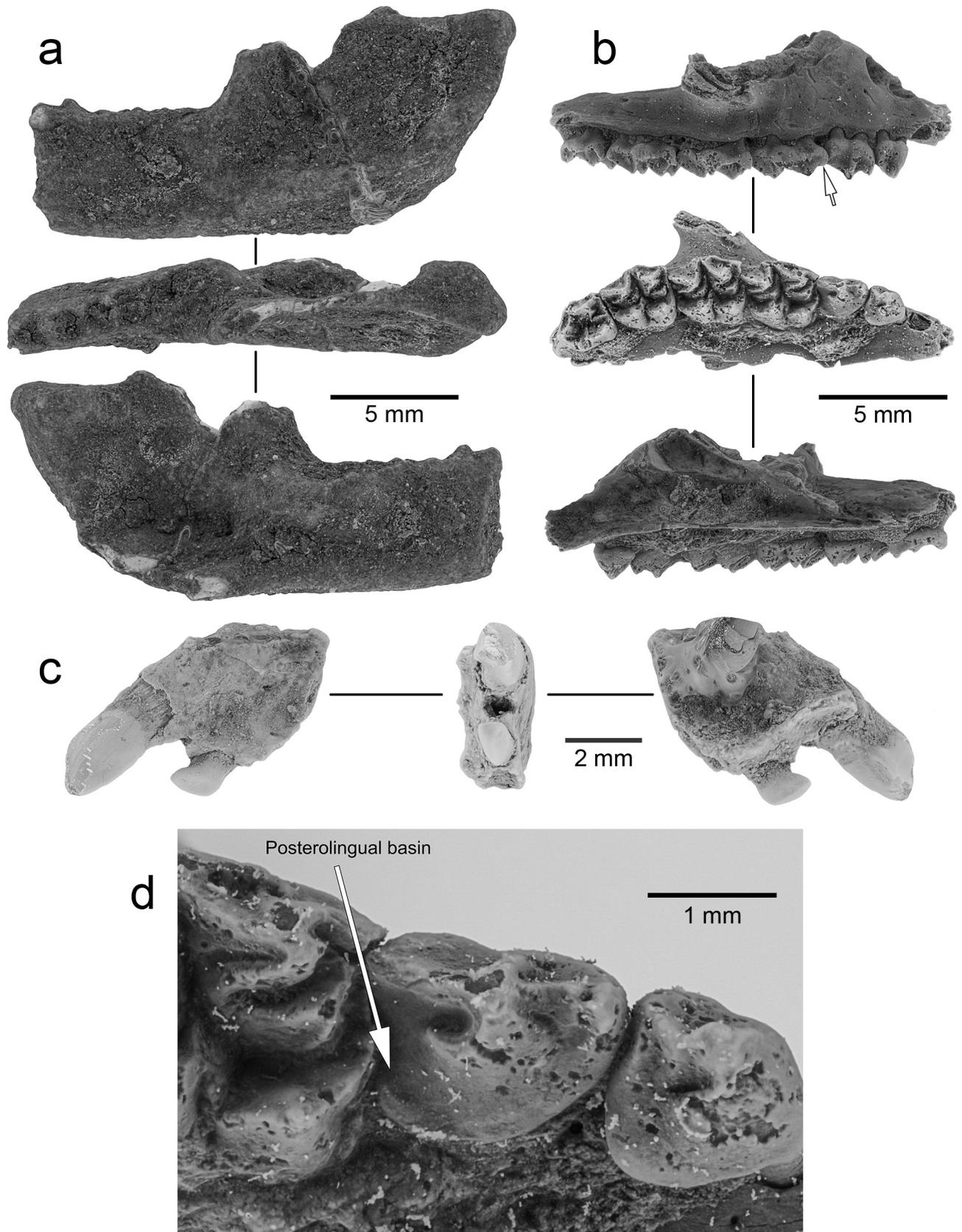


Figure 5. Lower and upper dental material of subfossil *Tous ayamaruensis* from Vanimo sites. (a) PM 26646, edentulous left dentary preserving articular facet in buccal, occlusal, and lingual views; (b) PM 26619, right maxilla with P2, P3, and M1–4 in buccal, occlusal, and lingual views, parastyle indicated by arrow; (c) PM 26644, left premaxilla with I1, I3, and alveoli for I2 in buccal, occlusal, and lingual views; and (d) detail of P3 posterolingual basin in PM 26619.

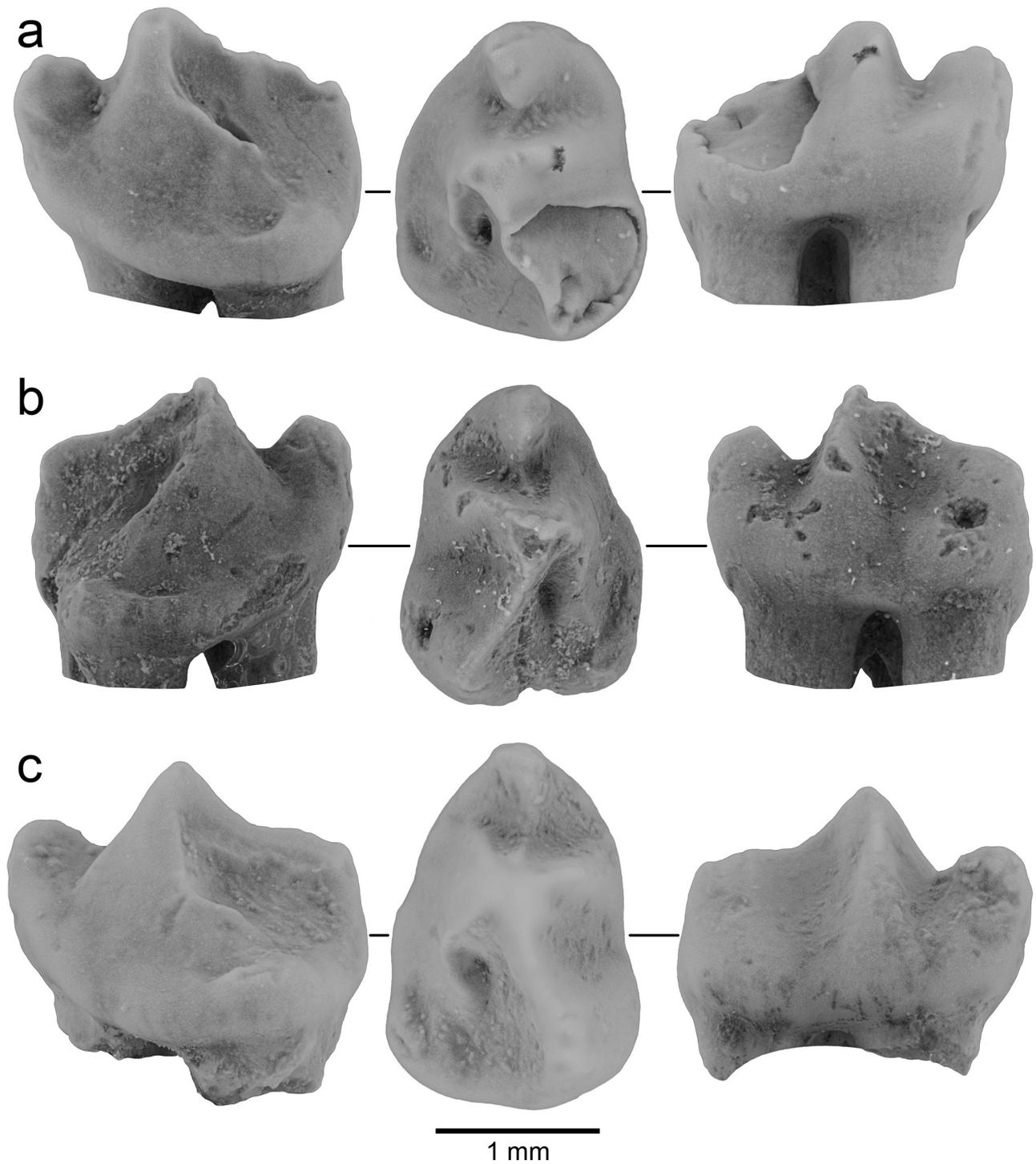


Figure 6. Subfossil *Tous ayamaruensis* isolated P3s from Vanimo sites in lingual, occlusal, and buccal views. (a) PM 26640 (left); (b) PM 26641 (right); (c) PM 26642 (left).

week after the death of KPA), who recognized the potential link with the subfossil *ayamaruensis*. Following this, IA and EM conducted community interviews in April 2019 to verify that community members were aware of the species, whether they knew its local name, and whether they knew anything about its ecology. We do not reveal the location of these interview surveys to avoid negative impacts on remaining populations (Meijaard & Nijman, 2014). The community interviews indicated that local villagers claimed familiarity with the species. They recounted that it was restricted to coastal areas, where it was not uncommon, was sometimes seen in coconut palms, and was known to use tree hollows for nesting. These data are consistent with the known habits of *Petaurus papuanus*, and we suspect that some, if not the majority, of these observations relate instead to this ‘sugar glider’ species (Flannery *et al.*, 2026).

In 2022 FK, who is a Maybrat and Tambrau speaker, showed a photograph of *T. ayamaruensis* to tribal elders Barnabas Baru and Carlos Yesnat of the Tambrau and Maybrat language group area, Tambrau Regency, West Papua (Fig. 1). In October 2023 TFF and RK jointly questioned Yesnat and Baru about the taxon. These discussions revealed the following: Both tribal elders recognized the animal depicted as a species that had, prior to logging, occurred in the Sorong area, and which still existed in the unlogged forests of Tambrau Regency, West Papua. Both identified the photograph of *Tous* shown to them as depicting the animal known in their local language as ‘Tous wan.’ *Petaurus papuanus* is also known to Maybrat speakers as ‘Tous wan’, but the two species are distinguished by Maybrat speakers by their reproductive biology and size. The lowland ringtail *Pseudochirulus canescens* is known as ‘Tifam’. The striped possum *Dactylopsila trivirgata* is also referred to as ‘Tous.’

Baru and Yesnat provided the following information about the larger form of ‘Tous wan’ (our *Tous ayamaruensis*). The creature has a body about the length of two open palms (hands). It is a skillful leaper, able to cover great distances with a single leap. It can use its tail to give power to its leaps by grasping a branch or vine, creating tension which, when released, propels it forwards. Its tail can be arched over its body, and is used to arrest the animal at the end of a leap. Its ability to grasp with its tail tip is so powerful that the Maybrat say that it is almost as if it has glue at the tail tip.

The species is nocturnal, and its diet consists of tree sap, leaves, and possibly some fruit and invertebrates. The tree sap is obtained from scratches made in the bark of the feeding tree with the animal’s sharp claws. The sap is left to congeal, and later is removed from the trunk with the sharp claws or teeth, and consumed. It has large, forward-facing eyes and lives in hollows in the tallest and oldest forest trees, particularly the species known in Indonesian as ‘merbau’ (*Intsia bijuga*) and ‘kayu besi’ (ironwood). The larger ‘Tous wan’ is nocturnal and monogamous, raising a single young per year. This is contrasted with the smaller form of ‘tous wan’ (i.e. *Petaurus papuanus*) which is characterized as having larger litters and practicing ‘kawin lepas’ (short-term pair-bonding). The larger tous wan is considered sacred by the people of the Maybrat region, and is protected by tradition. Its lifestyle, including its monogamy and limited number of young, are taught as an ideal arrangement to which young men should aspire. When discussing *Tous* with village leaders, the men used a low tone of voice which FK recognized as a form of speaking deployed

when discussing sacred subjects. The women in the group did not use the name ‘Tous wan’, instead referring to it in Indonesian as ‘that animal’.

In 2023 TFF visited Tomolol Village on Misool Island and showed local hunters photographs of *Tous ayamaruensis*, but did not encounter the species. In June 2024 AMY conducted a mammal survey of Misool, but did not encounter the species. On 24 September 2024 MM sent AMY four images of an animal he had encountered (Fig. 3a–b). The animal was crossing through the canopy in Batkaji forest (which AMY visited in June 2024) when it was shot and killed by air rifle. The body was photographed and then buried, but the next day, when checked, its carcass was no longer there, and probably eaten by dogs, so no specimen was retained. There have been no reported sightings since. Pak Marnik referred to the animal as ‘Ha’keo’, a name which is also applied in the language of Misool to *Dactylopsila trivirgata*. Local hunters report that the species is common on Misool.

Misool is a low-elevation, land-bridge island that was connected to the New Guinea mainland during the Last Glacial Maximum, which suggests that *T. ayamaruensis* has survived on the island since that time. Misool has deeper geological connection and similarity to the Bomberai Peninsula, on the ‘Bird’s Neck’ of New Guinea (Decker *et al.*, 2009), another area poorly surveyed for mammals where living populations of *T. ayamaruensis* might be sought. Its presence on Misool also indicates the possibility that it may still occur in relevant habitats on the other major land-bridge islands in the vicinity of north-western New Guinea, Yapen and Salawati. The mammal faunas of these islands remain little known today (Lavery & Flannery, 2023).

The subfossil record indicates that large owls are major predators on the species. In New Guinea, the principal predator accumulator of rodents and small marsupials, including gliders and ringtails, in cave deposits is generally considered to be the Sooty Owl (*Tyto tenebricosa*), which hunts mammals up to 2 kg in weight, and roosts in caves (Pratt & Beehler, 2014). The larger Rufous owl (*Ninox rufa*), which roosts in trees, is also widespread in New Guinea (Pratt & Beehler, 2014) and probably also an important predator of *T. ayamaruensis*. Neither of these large owl species are known from Misool. The only species of owl present on Misool is the Papuan boobook (*Ninox theomacha*) which is too small to predate *T. ayamaruensis* (Avibase, 2025: <https://avibase.bsc-eoc.org/checklist.jsp?region=IDijmi>). The absence of large owls from Misool may help account for the persistence and/or detectability of *T. ayamaruensis* on this relatively small island.

Based on the limited archaeological material available, particularly from a few fragmentary postcranial remains, Aplin *et al.* (1999) originally predicted that *T. ayamaruensis* was a leaper rather than a glider, although his allocation of *ayamaruensis* to the genus *Petauroides* at that time (rather than to *Hemibelideus* or a new genus) indicates that KPA realised that it might also, or instead, be a glider. Traditional knowledge now reveals that it is, in fact, both—an adept leaper, but also a glider with a fully developed patagium. Aplin *et al.* (1999) suspected that *T. ayamaruensis* was a montane forest animal, based on the mixed assemblage of montane and lowland species present in the Ayamaru Caves deposits (Aplin, 1998; Pasveer & Aplin, 1998). However, all records to date indicate that it in fact inhabits tall lowland forests, an increasingly endangered habitat in New Guinea.

Possible survival of *Tous ayamaruensis* in offlying northern areas of New Guinea

The Vanimbo-area cave remains, documented above, demonstrate that *T. ayamaruensis* occurred in the recent past in northern New Guinea, and it may still persist in some areas in northern New Guinea. We have spoken with local landowners who may be familiar with living *T. ayamaruensis* in two areas of northern New Guinea—in the Torricelli Mountains and in the vicinity of the Foja Mountains (Fig. 1).

The Olo speakers of the Lumi area of the Torricelli Mountains, PNG (which lies around 150 km east of the archaeological sites that have yielded *T. ayamaruensis*) may have knowledge of living *T. ayamaruensis*. In September 1991, one of us (TFF) asked Kaspar Seiko, the oldest resident of Wilbeite Village who was born in the 1920s, whether we had missed any mammal species during our 6-year survey of the Torricelli Mountains. After some thought he mentioned just one—a creature about the size of 2 fists, with large, forward-pointing eyes, that lives in tree hollows. Known in the Olo language as ‘Engolben’, he had seen the species in his youth, but not since. TFF was ill at the time, and did not question Mr Seiko further. But the few details he provided are consistent with what is known of *T. ayamaruensis*. This account suggests a relatively recent presence of *T. ayamaruensis* in the Torricelli Mountains, which would be expected based on its occurrence in the nearby, lower-altitude Oenake Range.

In 2005 and 2008, two of us (KMH and AMY) undertook mammal surveys in and near the Foja Mountains of Papua Province, Indonesia. Hunters in the village of Kwerba, located on the Mamberamo River in the foothills of the Fojas, expressed familiarity with two kinds of lowland gliding possums. One of the species was said to be smaller and to have grey-based fur on its back and on its belly, corresponding well to the sugar glider *Petaurus breviceps*. The other was said to be larger and to have darker fur on the dorsum and pure white on its underside. This latter animal could be the darker brown phase of *T. ayamaruensis*, the only other lowland gliding possum known from New Guinea. Neither species is eaten by people according to Kwerba villagers. The extensive and sparsely populated Mamberamo Basin of north-western New Guinea, including the Foja and Van Rees Ranges, is an expansive area that has received very little mammalogical study but is an important area of occurrence for a variety of rare or endangered mammals including *Dendrolagus inustus*, *Dendrolagus pulcherrimus*, *Spilocuscus rufoniger*, and others—possibly including *T. ayamaruensis* (Helgen, 2007).

Tous in the Australian fossil record

Tous stirtoni (Turnbull & Lundelius, 1970), originally described as *Pseudocheirus stirtoni* by Turnbull & Lundelius (1970), is from the early Pliocene Grange Burn Local Fauna, western Victoria (37°43'58"S 141°57'14"E), which is dated to 4.46 ± 0.1 ma (Turnbull & Lundelius, 1970; Turnbull *et al.*, 1987). All fossils from the locality were recovered from a paleosol underlying a basalt flow, which included the charred stumps of *Phyllocladus* trees intruding into the basalt. The environment has been interpreted to represent a littoral rainforest, the paleosol including pollen of *Nothofagus* and the gymnosperms *Podocarpus*, *Phyllocladus*, and *Dacrydium* (Flannery *et al.*, 1992).

The latter two gymnosperms no longer occur naturally on mainland Australia. The associated mammalian fauna at this site is diverse, and includes a number of rainforest-dwelling taxa, such as species of *Dendrolagus* and *Dorcopsis*, which today are restricted to northeastern Australia and/or New Guinea (Flannery *et al.*, 1992; Eldridge *et al.*, 2006).

Dawson *et al.* (1999) allocated a series of isolated molars from the Big Sink, Wellington Caves, to *Pseudocheirus* sp. cf. *P. stirtoni*, which we recognize as *Tous* cf. *stirtoni*. On the basis of biochronology, the Big Sink fauna is considered to be late early Pliocene in age—greater than 3.5 ma (Dawson *et al.*, 1999). The presence of murids in the Big Sink fauna suggests that it is probably younger than the Hamilton Local Fauna, which lacks murids. The teeth referred to *T. cf. stirtoni* from the Big Sink differ from those of the type locality in being somewhat smaller, in having lower, less prominent parastyles, and in that the anterior crest of the paracone on M2 is larger and with a more definite connection to the anterior cingulum. They also possess an uninterrupted entostylid ridge on m1–3 and a small anterobuccal cingula on all lower molars. In their smaller molar size and paracone structure, the Big Sink specimens are similar to *T. ayamaruensis*.

Hocknull (2005, 2009; Hocknull *et al.*, 2007) identified ‘*Petauroides*’ from the Mt Etna Caves of central eastern Queensland and remarked on the close morphology of the fossils to *ayamaruensis*. Hocknull (2005) and (2009) briefly described and provided measurements but did not fully treat these forms, because by this time KPA and Hocknull had discussed the similarities of the Middle Pleistocene Mt Etna Caves ‘*Petauroides*’ with ‘*P.* *ayamaruensis*’ and that additional Holocene specimens had been collected from PNG that would be described to complement the original type material of ‘*P.* *ayamaruensis*’, ultimately assisting in the identification of the Middle Pleistocene species at Mt Etna as very close to, if not conspecific with ‘*P.* *ayamaruensis*’ (KPA and Hocknull, 2008/2009; Hocknull, *pers. comm.*, 2025). Most specimens are considered closest in morphology among named forms to *T. ayamaruensis* and comparison between the measurements provided in Hocknull (2009) with those of *T. ayamaruensis* provided here for M1, demonstrates that the smallest Mt Etna Caves ‘*Petauroides*’ sp. is well within the variation of the M1s of *T. ayamaruensis*. Although none of this material has been formally described, it provides support for diminutive rainforest-dwelling hemibelideines existing in eastern Australia during the Middle Pleistocene. The formal description of *Tous* now allows a fuller taxonomic appraisal of these Pleistocene Australian members of *Tous*, which is underway (Hocknull, *pers. comm.*, 2025).

One final taxon from the Australian fossil record requires comment. *Pseudocheirus marshalli* Turnbull & Lundelius, 1970, from the Grange Burn locality in eastern Australia, is based on a left M1. Referred material includes one complete and six partial upper molars, four complete and seven partial lower molars, and a p3, all of which are isolated tooth crowns (Turnbull & Lundelius, 1970). Turnbull & Lundelius (1970) allied the taxon with *Petauroides* on the basis that they regard these taxa as sharing ‘a rounded anterior edge to the paracone of M1’ and ‘the interruption of the entostylid ridge in m1–2, and its absence in m4’. Turnbull *et al.* (1987) assigned an additional 66 specimens from the type locality to *Pseudocheirus marshalli*. This larger sample allowed them to characterize the species as possessing

‘very simple, uncomplicated teeth’ (p. 712). Turnbull *et al.* (2003) referred a further eight teeth from the type locality to the taxon. They do not support the earlier association of *P. marshalli* with hemibelideines, instead retaining it in the genus *Pseudocheirus*, a decision with which we concur.

Phylogeny

All three extant genera of hemibelideine possums are extremely distinctive lineages, and the relationships between these genera are not yet firmly established. A lack of modern tissue samples for *Tous* thus far has prevented us from conducting a molecular genetic assessment of its relationships, but this can be a priority for future work. A phylogeny for all three living hemibelideine genera, placed in the increasingly comprehensive molecular phylogenomic contexts available (e.g., Mitchell *et al.*, 2014; Eldridge *et al.*, 2019; Álvarez-Carretaro *et al.*, 2021; Beck *et al.*, 2022), will help to better illuminate patterns of biogeography, divergence times, and relationships in this subfamily. It will also allow better understanding of the evolution of adaptations in the family and subfamily, which is of particular interest in terms of understanding the evolution of gliding in *Tous* and *Petauroides*. The strongly prehensile tail of *Tous*, shared with *Hemibelideus*, is presumably a plesiomorphic character given the ubiquity of tail prehensility across Pseudocheiridae (Flannery, 1994), and certain other external similarities (Table 1) may also reflect a relatively conserved ringtail morphology. Aplin *et al.* (1999) made a strong case for the closest relationship of *Tous* to *Petauroides* on the basis of shared derived dental traits, an assessment with which we generally concur. The shared-derived extensive gliding membrane of *Tous* and *Petauroides* presents another compelling trait pointing to this possible sister relationship. However, *Hemibelideus* also possesses a very rudimentary patagium (Johnson-Murray, 1987), which may be evolutionarily incipient or vestigial. Open questions regarding whether the functional patagium in hemibelideines has evolved more than once, or if the functional patagium *Hemibelideus* has been lost since it shared a gliding common ancestor with other hemibelideines, mirror similar uncertainties posed by current understanding of phylogenetic relationships and morphological character states in other gliding mammal groups, including in the marsupial family Petauridae (Beck *et al.*, 2022) and the rodent family Anomaluridae (Fabre *et al.*, 2018).

Conservation

Little is yet known of *T. ayamaruensis*, including its current conservation status. The present-day restricted distribution of *T. ayamaruensis*, its dependence on the tallest and most valuable rainforest trees for roosting, and upon other (as yet unidentified) tree species for food, suggest that it is vulnerable to forest clearance and unsustainable offtake levels. Its low reproductive rate also makes it vulnerable to unsustainable hunting. Papuan informants report its local

extinction in the Sorong area over the past decade as a result of logging. Logging and forest conversion are expanding in West Papua and Papua New Guinea (Gaveau *et al.*, 2021) presenting a clear and present danger to this Lazarus species. Logging and conversion of lowland rainforest to oil palm plantations are already widespread in the Vogelkop, while satellite imagery reveals accelerated forest loss in the Torricelli Mountains (Canon, 2023). Here we do not report the exact location on the Vogelkop (which is easily accessible to wildlife traffickers) where live specimens have recently been photographed because Indonesia’s conservation authorities are struggling to control nation-wide animal trade, driven by demand through social media that is decimating forest species (Nijman *et al.*, 2024). Thus, urgent and secret survey work is required to identify areas where the species remains in sustainable numbers, so that the forest vital to its existence can be preserved and its populations protected from wildlife traders.

Tous as a Lazarus species

Tous ayamaruensis can be labelled a ‘Lazarus species’, a designation sometimes applied to species, or higher taxa, once considered to be extinct but subsequently found as living animals (Wignall & Benton, 1999; Dawson *et al.*, 2008). Flannery *et al.* (2026) reviewed the history of mammals in the Australia-New Guinea region that fall into this category in terms of being initially named as a fossil taxon and later discovered to be extant, including *Dactylonax kambuayai* Aplin, 1999, another species that, like *T. ayamaruensis*, was originally named from Quaternary deposits in the Vogelkop region before its ‘rediscovery’ as a living animal (Flannery *et al.*, 2026).

Perhaps the most famous examples of modern Lazarus taxa are the coelacanths (*Latimeria* spp.), which represent an ancient lineage of large lobe-finned fishes thought to be extinct since the Late Cretaceous before being ‘rediscovered’ as living species in the 20th and 21st centuries (Bruton, 2018). Famous mammalian examples of Lazarus higher-taxa are the modern Australidelphian marsupial order Microbiotheriidae, originally described from Miocene deposits in South America, but later found as a living species, *Dromiciops gliroides*, and the rodent family Diatomyidae, originally described from the Oligo-Miocene but represented by the living species *Laonastes aenigmaticus* (Dawson *et al.*, 2006). Other mammalian examples are considered notable because they involve large extant mammals, such as the False killer whale (*Pseudorca crassidens*), which is globally distributed in the world’s oceans, the Northern hairy-nosed wombat (*Lasiorhinus krefftii*) of Australia, and the Chacoan peccary (*Catagonus wagneri*) and Bush dog (*Speothos venaticus*) of South America. Each of these species was originally described from Quaternary fossils before being ‘discovered’ by scientists as living animals. Happily, the ring-tailed glider joins their ranks, as a species whose extinction can yet be averted.

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Phylogenetic Analysis Reveals Additional Diversity within the *Dendrolagus dorianus* (Marsupialia: Macropodidae) Group from New Guinea

MARK D. B. ELDRIDGE¹ , RENAE C. PRATT¹ , REBECCA N. JOHNSON^{1,2} ,
ROBERTO PORTELA MIGUEZ³ , TIM F. FLANNERY^{1,4} ,
KRISTOFER M. HELGEN^{1,5} , AND SALLY POTTER^{1,6} 

¹ Australian Museum Research Institute,
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

² Current address: National Museum of Natural History, District of Columbia,
Washington, 20560 United States of America

³ The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

⁴ Melbourne Sustainable Society Institute, Melbourne University, Parkville Vic. 3010, Australia

⁵ Current address: Bernice Pauahi Bishop Museum,
1525 Bernice Street, Honolulu, Hawai'i 96817, United States of America

⁶ School of Natural Sciences, Macquarie University NSW 2109, Australia

ABSTRACT. The tree-kangaroos (genus *Dendrolagus*) are specialized arboreal macropodids now confined to the rainforests of New Guinea and northeastern Queensland, Australia. Within New Guinean *Dendrolagus*, a distinct Doria's group has been recognized since 1936. However, establishing the species limits and inter-relationships within the group has long been hampered by limited sampling. In this study we supplement published genetic data from high quality tissue samples with molecular data generated from museum specimens to improve taxon sampling and geographic coverage within the Doria's group to enhance our understanding of their evolutionary history. This included the addition of the previously unsampled *D. mayri* (holotype and only known specimen) and additional specimens of *D. dorianus* and *D. notatus*. DNA sequence data were generated from three mitochondrial loci and six distinct Doria's group lineages were identified: *D. dorianus*, *D. notatus*, *D. stellarum*, *D. scottae*, *D. cf. stellarum* and *D. mayri*. Phylogenetic analysis improved the resolution of relationships within the Doria's group, with *D. dorianus* being recovered as the sister to all other taxa. Surprisingly, *D. mayri* and *D. cf. stellarum* were monophyletic and formed a sister group to the three other species (*D. notatus*, *D. stellarum* and *D. scottae*). This indicates that the molecular affinities of *D. cf. stellarum*, from the Sudirman Range, Central Cordillera, lie with *D. mayri* (isolated on the Wondiwoi Peninsula to the west) rather than true *D. stellarum* from the Star Mountains further east along the Central Cordillera. The molecular divergence

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ORCID iD: Eldridge, 0000-0002-7109-0600; Pratt, 0009-0004-1248-7351; Johnson, 0000-0003-3035-2827; Portela Miguez, 0000-0003-3094-9949; Flannery, 0000-0002-3005-8305; Helgen, 0000-0002-8776-4040; Potter, 0000-0002-5150-7501

Corresponding author: Mark Eldridge mark.eldridge@australian.museum

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between *D. cf. stellarum* and *D. mayri* (3.8% sequence divergence) is less than that reported between other *Dendrolagus* species ($\geq 4.7\%$). Therefore, *D. cf. stellarum* is best regarded as a differentiated population of *D. mayri* and should be referred to as *D. cf. mayri* pending further studies. This finding means that *D. stellarum* (*sensu stricto*) does not occur on the Maokop (Central Cordillera mountains east of the Baliem Valley, West Papua).

Introduction

Tree-kangaroos (*Dendrolagus*) are a group of specialized arboreal macropodids (kangaroos and wallabies) that originated in Australia, but have undergone several secondary radiations in the tropical forests of New Guinea (Flannery *et al.*, 1996; Martin, 2005; Eldridge *et al.*, 2018). Despite their biological interest, tree-kangaroos are poorly studied (Dabek *et al.*, 2021), and many taxa are only known from a handful of specimens (Flannery *et al.*, 1996; Eldridge & Coulson, 2015). The limited number of specimens available for study, lack of comprehensive geographic coverage and morphological variability has led to considerable taxonomic uncertainty (Groves, 1982; Flannery *et al.*, 1996). In 1996, 10 tree-kangaroo species were recognized, two in Australia and eight in New Guinea (Flannery *et al.*, 1996), although several authors suggested that additional species could be recognized within New Guinea (Groves, 2005; Helgen, 2007; Eldridge *et al.*, 2018).

A distinct Doria's group within *Dendrolagus* was first proposed in 1936 (Rothschild & Dollman, 1936) and has subsequently been supported by most authors (Flannery *et al.*, 1996; Groves, 1982; Eldridge *et al.*, 2018). The Doria's group comprises a monophyletic lineage of medium/large (6–14.5 kg; Table 1), dark brown to black tree-kangaroos,

with short, well-furred ears, short, broad feet, short tails (less than the head/body length), a variably positioned dorsal hair-whorl (often poorly expressed), significant sexual dimorphism and associated higher sociality (Table 1) (Rothschild & Dollman, 1936; Groves, 1982; Flannery, 1995; Flannery *et al.*, 1996). Doria's group species are considered the most derived tree-kangaroos, with the most highly modified feet and shortest tails (Flannery *et al.*, 1996; Eldridge *et al.*, 2018). Members of the Doria's group are widely distributed through the mountainous areas of New Guinea (except for the Vogelkop Peninsula; Fig. 1) and show considerable individual and geographic morphological variability (Groves, 1982; Flannery & Seri, 1990a; Flannery *et al.*, 1996). This has resulted in eight taxa attributable to this group being described, with the number of species recognized by various authors ranging from one to five (Table 2). This ongoing taxonomic instability continues to hamper research and effective conservation of this group, with all currently recognized taxa listed as threatened by the IUCN (Eldridge & Coulson, 2015). In New Guinea, most tree-kangaroo species are threatened by increased subsistence hunting, as well as by habitat loss and degradation associated with human population growth, as well as expanding agriculture, mining and petroleum exploration and exploitation (Eldridge & Coulson, 2015; Dabek *et al.*, 2021).

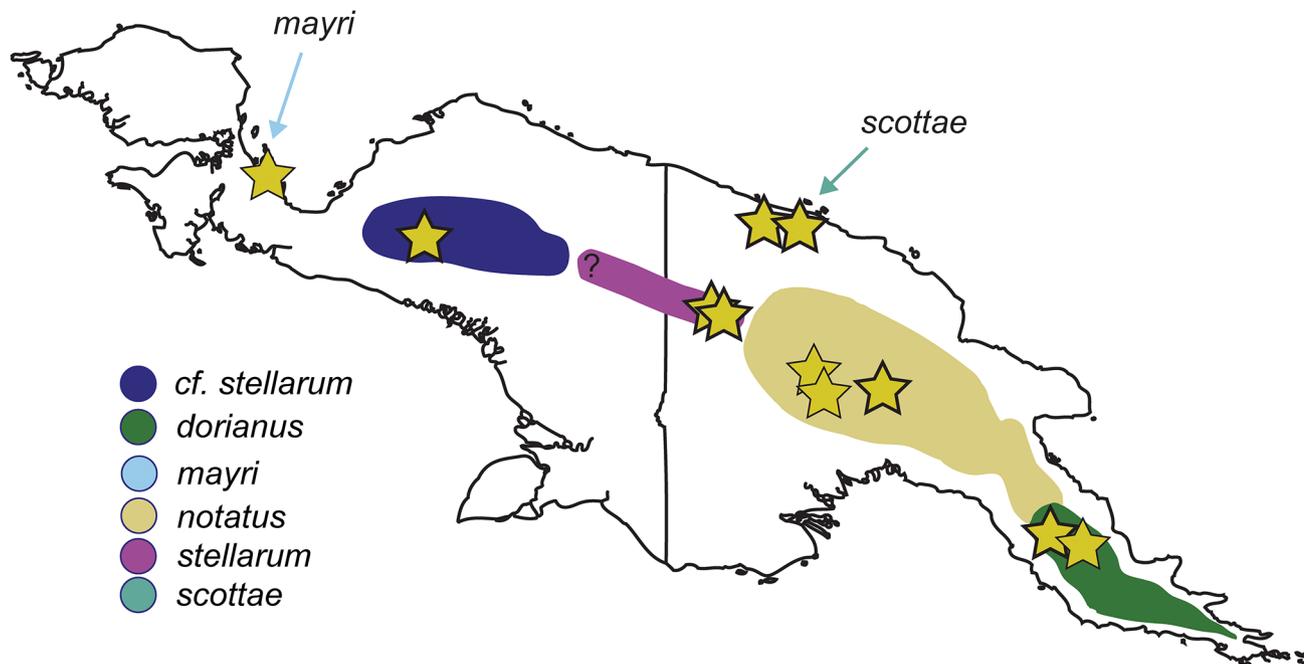


Figure 1. Distribution of *Dendrolagus* taxa of the Doria's group in New Guinea, with sampling sites indicated. Symbols for high quality tissue samples have bold outline, museum samples have normal outline. Note: *D. cf. stellarum* = *D. cf. mayri*.

The first Doria's group species to be scientifically described was *D. dorianus* in 1883 based on specimens from near Mt Astrolabe, south-eastern Papua New Guinea (Ramsay, 1883), followed in 1916 by *D. notatus* from the Schrader Mountains, Central Highlands, Papua New Guinea (Matschie, 1916). In 1933, a further species *D. mayri* was described from a single specimen (Fig. 2) collected in 1928 far to the west on the isolated Wondiwoi Peninsula on the northern coast of West Papua (Rothschild & Dollman, 1933) (Fig. 1). In the first comprehensive review of *Dendrolagus* taxonomy Rothschild & Dollman (1936) recognized, within the Doria's group, a single polytypic species; *D. dorianus* containing three subspecies; *D. d. dorianus* from the eastern Central Cordillera, *D. d. notatus* from the Central Highlands and *D. d. mayri* from the Wondiwoi Peninsula. They also described a local colour variant (*D. d. aureus*) from the Aroa River, southeastern Papua New Guinea (Rothschild & Dollman, 1936). In 1936, another two Doria's group taxa were described (Troughton & Le Souef, 1936); *D. d. profugus* and *D. d. palliceus*, another local colour variant, both from south-eastern Papua New Guinea. In 1954, Laurie and Hill recognized a single species, *D. dorianus* containing five subspecies (*dorianus*, *aureus*, *profugus*, *notatus*, *mayri*) (Table 2).

The next comprehensive revision of *Dendrolagus* taxonomy was conducted using morphology by Groves in 1982. Within the Doria's group a single polytypic species *D. dorianus* was recognized, containing three subspecies (Groves, 1982); *D. d. dorianus* (including *aureus*, *palliceus* and *profugus* as synonyms), *D. d. notatus* and *D. d. mayri*. In 1990, two new Doria's group taxa were described based on divergent morphology; *D. d. stellarum* from the Star Mountains and Telefomin area, western Papua New Guinea (Flannery & Seri, 1990a) and *D. scottae* from Mt Somoro, Torricelli Mountains in northern coastal Papua New Guinea (Flannery & Seri, 1990b) (Fig. 1). Subsequently, specimens attributable to *D. scottae* were also collected on nearby Mt Menawa and appearing morphologically and behaviourally distinct were thought to represent an undescribed subspecies (Flannery *et al.*, 1996). Finally, in 1995, another new tree-kangaroo species *D. mbaiso*, was described from the Tembapapura area in the Sudirman Range (Snow Mountains) from the western Central Cordillera, West Papua (Flannery *et al.*, 1995). This new species was also placed in the Doria's group on the basis of multiple shared features, although many differences were also noted (Flannery *et al.*, 1995; Flannery *et al.*, 1996). Additional specimens referred to *D. d. stellarum* were also collected from the Tembapapura area in the early 1990s, which significantly extended the range of this taxon 300 km westwards along the Central Cordillera into West Papua (Flannery *et al.*, 1996) (Fig. 1). This range extension went some way in closing the anomalous ca. 600 km gap that had previously existed within the distribution of *D. dorianus* between western Papua New Guinea (Star Mountains) and the Wondiwoi Peninsula in north-western West Papua (Fig. 1).

Thus, by the end of the 20th century, three species were recognized within the Doria's group: *D. mbaiso* and *D. scottae*, as well as polytypic *D. dorianus* (containing four subspecies *dorianus*, *notatus*, *stellarum* and *mayri*) (Flannery *et al.*, 1996). However, some authors subsequently suggested that some *D. dorianus* subspecies were sufficiently distinct to be considered separate species (Groves, 2005; Helgen, 2007; IUCN, 2008) and some limited mitochondrial DNA sequence

Table 1. Morphological measurements (range and average) for adult *Dendrolagus* from the Doria's group.

Taxon	Sex	Head-body (mm)	n	Tail (mm)	n	Hindfoot (mm)	n	Ear (mm)	n	Weight (kg)	n
<i>D. dorianus</i>	M	550–780 (672.8)	9	497–600 (552.6)	9	107–125 (116.3)	7	38–60 (52.9)	6	9.1–14.5 (11.8)	3
<i>D. dorianus</i>	F	596–770 (650.1)	13	450–662 (547.3)	13	100–120 (107.4)	9	45–58 (51.7)	11	8.2–11.8 (10.1)	10
<i>D. notatus</i>	M	580–690 (628.9)	9	435–565 (496.6)	9	100–115 (108.1)	8	45–58 (51.4)	8	7.0–9.1 (8.2)	3
<i>D. notatus</i>	F	515–630 (590.3)	9	430–540 (472.2)	9	90–109 (103.0)	8	45–59 (51.3)	8	6.0–6.5 (6.3)	2
<i>D. stellarum</i>	M	634–700 (667)	2	520–529 (524.5)	2	104–120 (112)	2	47–50 (48.5)	2	7.5–9.5 (8.5)	2
<i>D. stellarum</i>	F	610	1	490	1	100	1	50	1	6.75	1
<i>D. cf. stellarum</i>	M	645–673 (659)	2	510–570 (540)	2	100–112 (106)	2	52	1	8.5–9.0 (8.8)	2
<i>D. cf. stellarum</i>	F	626	1	585	1	98	1	50	1	6.5	1
<i>D. mayri</i>	M	635	1	570	1	112	1	53	1	9.3	1
<i>D. scottae</i>	M	720–750 (735.0)	2	520–590 (555)	2	108–119 (113.5)	2	50–55 (52.5)	2	9.5–11.5 (10.5)	2
<i>D. scottae</i>	F	565–725 (625.0)	4	520–540 (531.3)	4	104–115 (108)	4	45–55 (49.5)	4	6.8–9.5 (8.4)	3

Data from Flannery *et al.* (1996) and AM database.



Figure 2. Painting by Frederick William Frohawk [1861–1946] of *Dendrolagus mayri* holotype (NHMUK ZD 1939.2931) and only known specimen from Rothschild & Dollman (1936, plate XLII, pp. 518–519).

Table 2. Described *Dendrolagus* taxa in the Doria's group and their changing recognition by various authorities from 1936 to 2018.

Described Taxon	Rothschild & Dollman, 1936	Laurie & Hill, 1954	Groves, 1982	Flannery, 1995; Flannery <i>et al.</i> , 1996	Groves, 2005	Helgen, 2007; IUCN, 2008	Eldridge & Coulson, 2015	Eldridge <i>et al.</i> , 2018
<i>D. dorianus</i> Ramsay, 1883	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>
<i>D. dorianus aureus</i> Rothschild & Dollman, 1936	<i>D. d. aureus</i>	<i>D. d. aureus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>
<i>D. dorianus palliceps</i> Troughton & Le Souef, 1936	—	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>
<i>D. dorianus profugus</i> Troughton & Le Souef, 1936	—	<i>D. d. profugus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>	<i>D. d. dorianus</i>	<i>D. dorianus</i>
<i>D. notatus</i> Matschie, 1916	<i>D. d. notatus</i>	<i>D. d. notatus</i>	<i>D. d. notatus</i>	<i>D. d. notatus</i>	<i>D. d. notatus</i>	<i>D. notatus</i>	<i>D. d. notatus</i>	<i>D. notatus</i>
<i>D. mayri</i> Rothschild & Dollman, 1933	<i>D. d. mayri</i>	<i>D. d. mayri</i>	<i>D. d. mayri</i>	<i>D. d. mayri</i>	<i>D. d. mayri</i>	<i>D. mayri</i>	<i>D. d. mayri</i>	<i>D. mayri</i>
<i>D. dorianus stellarum</i> Flannery & Seri, 1990b	—	—	—	<i>D. d. stellarum</i>	<i>D. stellarum</i>	<i>D. stellarum</i>	<i>D. d. stellarum</i>	<i>D. stellarum</i>
<i>D. scottae</i> Flannery & Seri, 1990a	—	—	—	<i>D. scottae</i>	<i>D. scottae</i>	<i>D. scottae</i>	<i>D. scottae</i>	<i>D. scottae</i>

data showed large divergences between (and within) some *D. dorianus* subspecies (Bowyer *et al.*, 2003).

More recently, a multi-locus (mitochondrial and nuclear) molecular analysis demonstrated that *D. mbaiso* represented a distinct evolutionary lineage with *Dendrolagus*, that was the sister to the Doria's group (Eldridge *et al.*, 2018), diverging from the group's common ancestor almost 5 mya. This study also provided some greater taxonomic clarity, within the Doria's group, supporting the specific distinction of *D. notatus* and *D. stellarum* from *D. dorianus*, but indicating that little genetic divergence was present between the Mt Somoro and Mt Menawa populations of *D. scottae* (Eldridge *et al.*, 2018). However, species level genetic divergence in both mitochondrial and nuclear DNA was also detected within *D. stellarum* between the type series from the Star Mountains, Papua New Guinea and the population sampled in the Tembagapura area of the Sudirman Range, West Papua, 300 km to the west (referred to as *D. cf. stellarum* hereafter) (Eldridge *et al.*, 2018). Although data from *D. d. mayri* was not included in this analysis, the pattern of divergence detected in the other Doria's group taxa suggested that it too is likely to represent a distinct species, (*D. mayri* hereafter) rather than a subspecies of *D. dorianus* (*sensu stricto*) which under these taxonomic changes is now a species restricted to the far east of New Guinea (Fig. 1). However, without data from *D. mayri* it could not be concluded if the Tembagapura specimens represent an additional new taxon or are an eastern population of *D. mayri* which occurs a further 300 km to the west on the Wondiwoi Peninsula. Since the type (and only known) specimen of *D. mayri* was collected in 1928 (Flannery *et al.*, 1996), this taxon had not been relocated until 2018 when an individual consistent with *D. mayri* was sighted and photographed on the Wondiwoi Peninsula (Dabek *et al.*, 2021).

Although greatly improving our understanding of *Dendrolagus* evolution, phylogenetic relationships and taxonomy, recent molecular analyses, utilizing high quality DNA, suffered from unavoidable sample size and geographic coverage limitations for most taxa. For example, within the Doria's group only 1–3 samples were available for most taxa, while a sample from *D. mayri* was not available (Eldridge *et al.*, 2018). Therefore, in the current study we have sought to extend the analysis of Eldridge *et al.* (2018) by utilizing museum specimens (both study skins and skeletal material) as an additional source of DNA for sequence analysis. This study increases geographic coverage for two taxa and also adds data for *D. mayri* to improve our understanding of taxon boundaries and inter-relationships within the Doria's group.

Materials and methods

Available sequence data

Published DNA sequence data, from high quality tissue samples, from 14 individuals of five Doria's group taxa (*D. dorianus* n = 1; *D. notatus* n = 3; *D. stellarum* n = 3; *D. cf. stellarum* n = 3; *D. scottae* n = 4) were included (Eldridge *et al.*, 2018) (Table 3). This included data from the holotype and/or paratypes of *D. scottae*, and *D. stellarum* (Table 3). Individuals of *D. bennettianus*, *Petrogale xanthopus*, *Petrogale concinna* and *Thylogale stigmatica* were included as out-groups. See Appendix 1 for GenBank numbers.

Table 3. Details of the *Dendrolagus* specimens used in this study.

Taxon	Specimen Voucher	Lab ID	Sample ID	Locality	DNA Source
<i>D. dorianus</i>	AM M.12854	—	ABTC42523	Kosipe, Mt Albert Edward, CP, PNG 1981	Eldridge <i>et al.</i> , 2018
<i>D. dorianus</i>	AM M.32134	—	—	Lake Trist, MP, PNG 1995	Limb bones, skin
<i>D. mayri</i>	NHMUK ZD 1939.2931 Holotype	—	—	Wondiwoi Peninsula, West Papua, 1928	Dried tissue on skull
<i>D. notatus</i>	AM M.17374	S1618	ABTC46285	Mt Sisa, Bobole, HP, PNG 1985	Eldridge <i>et al.</i> , 2018
<i>D. notatus</i>	AM M.17746	S1617	ABTC46283	Mt Sisa, Bobole, HP, PNG 1985	Eldridge <i>et al.</i> , 2018
<i>D. notatus</i>	AM M.17153	S1613	ABTC46292	Bobole (Waro), HP, PNG 1985	Eldridge <i>et al.</i> , 2018
<i>D. notatus</i>	AM M.7273	—	—	Mt Rentoul, SHP, PNG 1947	Skin
<i>D. notatus</i>	AM M.46213	S2873	—	Hegigio River, HP, PNG, 2013	Dried tissue on limb bone
<i>D. stellarum</i>	AM M.16699 Paratype	S1614	ABTC47179	Sol River Basin, WSP, PNG 1986	Eldridge <i>et al.</i> , 2018
<i>D. stellarum</i>	AM M.17789 Holotype	—	EBU23021	Dokfuma Basin, Star Mts, WP, PNG 1987	Eldridge <i>et al.</i> , 2018
<i>D. stellarum</i>	AM M.19463 Paratype	—	EBU23048	Dokfuma Basin, Star Mts, WP, PNG 1987	Eldridge <i>et al.</i> , 2018
<i>D. cf. stellarum</i>	AM M.30720	S1607	EBU8059	Tempagapura area, West Papua 1994	Eldridge <i>et al.</i> , 2018
<i>D. cf. stellarum</i>	AM M.30750	S1609	EBU8056	Tempagapura area, West Papua 1994	Eldridge <i>et al.</i> , 2018
<i>D. cf. stellarum</i>	AM M.30753	S1608	EBU8052	Tempagapura area, West Papua 1994	Eldridge <i>et al.</i> , 2018
<i>D. scottae</i>	AM M.19481 Holotype	S2087	EBU23412	Sweipini, Torricelli Mts, WSP, PNG 1988	Eldridge <i>et al.</i> , 2018
<i>D. scottae</i>	AM M.21867	S2088	EBU25197	Mt Menawa, WSP, PNG 1990	Eldridge <i>et al.</i> , 2018
<i>D. scottae</i>	AM M.22257	S2089	EBU25161	Mt Menawa, WSP, PNG 1990	Eldridge <i>et al.</i> , 2018
<i>D. scottae</i>	AM M.23044	S2090	EBU25183	Mt Menawa, WSP, PNG 1990	Eldridge <i>et al.</i> , 2018

CP = Central Province, HP = Hela Province, MP = Morobe Province, PNG = Papua New Guinea, SHP = Southern Highland Province, WP = Western Province, WSP = West Sepik Province.

Tissue sampling and DNA extraction from museum specimens

Samples were collected from four museum specimens, including fragments of dried soft tissue remaining on prepared skeletal material or study skins, including from the holotype and only known specimen of *D. mayri*, as well as additional specimens of *D. dorianus* ($n = 1$) and *D. notatus* ($n = 2$) (Table 3). The following abbreviations are used: AM = Australian Museum, Sydney; NHMUK = Natural History Museum, London; EBU = Australian Museum tissue collection; ABTC = South Australian Museum tissue collection.

Subsequent DNA extraction and PCR amplification was undertaken in a designated ultraclean low-template DNA extraction laboratory (with positive air pressure and HEPA filtered air handling system) at the Centre for Wildlife Genomics, Australian Museum Research Institute. Neither *Dendrolagus* DNA nor tissue samples had previously been handled in this laboratory facility. Reagent blank controls and no-template PCR controls were routinely included for each round of DNA extractions to detect reagent contamination. Dried tissue samples were initially hydrated in sterile phosphate buffered saline (PBS) solution at 37°C for 24–30 hours. We then aspirated the PBS and DNA extracted from both the supernatant and tissue with a QIAamp Micro Extraction kit (QIAGEN) following the 'Isolation of total DNA from chewing gum' protocol.

PCR and sequencing

Three mitochondrial gene segments, cytochrome oxidase c subunit 1 (*COI*), cytochrome *b* (*Cytb*) and NADH dehydrogenase subunit 2 (*ND2*), were PCR amplified using a series of short (*ca.* 100–200 bp) overlapping fragments (*COI*, 12 fragments; *Cytb*, 7 fragments; *ND2*, 4 fragments). For primer details see Appendix 2. These genes were chosen due to their proven utility in resolving relationships within marsupials (Osborne & Christidis, 2001; Meredith *et al.*, 2008; Malekian *et al.*, 2010; Potter *et al.*, 2012) including *Dendrolagus* (Eldridge *et al.*, 2018; Eldridge *et al.*, 2024).

PCR-amplifications were carried out in 25 μ L reactions with 100–400 ng genomic DNA, 1 \times PCR Buffer II (Applied Biosystems), 0.2 mM each dNTP, 1.5–3.0 mM MgCl₂, 0.2 μ mol each primer (Appendix 2) and 1.0U AmpliTaq Gold™ polymerase (Applied Biosystems). A negative control was included for each batch of amplifications and for each primer set. PCR conditions were: initial denaturation at 95°C for 9 min, then 40–50 cycles of 94°C for 1 min, annealing for 1 min at 45–50°C and extension at 60°C for 1 min, and a final extension at 60°C for 10 min. PCR products were purified using ExoSap-IT© (USB Corporation) and directly sequenced on a AB 3730xl at the Australian Genome Research Facility (AGRF), Sydney. Forward and reverse strands were combined and sequences checked for errors with SEQUENCHER (version 5.2.4) (Genecodes). Only samples that provided clear and unambiguous sequence were subject to further analysis. See Appendix 1 for GenBank accession number of new sequences.

Sequence divergence and phylogenetic analysis

Uncorrected pairwise sequence divergence was estimated on aligned genes in MEGA v5 (Tamura *et al.*, 2011) between individuals and species. In addition, nucleotide diversity,

polymorphic sites and parsimony informative sites were estimated in DnaSP v5.10 (Librado & Rozas, 2009).

A maximum likelihood analysis was performed on individual genes and the concatenated alignment of all three genes in RAxML v8.2.4 (Stamatakis, 2014). The nucleotide substitution model for each gene and the concatenated mitochondrial dataset was estimated using PartitionFinder (Lanfear *et al.*, 2012) based on the full search scheme allowing for all partitioning schemes. The raxml model of evolution was used and model selection was based on the BIC. Analysis was performed on individual genes as well as the concatenated mitochondrial dataset. For the concatenated dataset, data was partitioned by codon, with all codon 1 positions grouped together for the first partition (*ND2 + COI + Cytb*), and similarly for codon 2, and two partitions for the third codon (*ND2 + COI*) and *Cytb* separately (individual gene partitions available in supplementary results). Analysis was performed using the rapid bootstrap algorithm, the GTRGAMMA model, 100 bootstrap replicates and a random starting seed.

Results

Genetic Diversity

In total, 3116 bp of sequenced DNA was aligned from representative of all species currently recognized in the Doria's group: *D. dorianus*, *D. notatus*, *D. stellarum*, *D. scottae* and *D. mayri*—651 bp *ND2*, 1323 bp *COI* and 1142 bp *Cytb*. For the museum samples, 1.3–42.6% of the data were missing. There were 164 variable sites amongst the Doria's group taxa, 130 of which were parsimony informative (78–125 variable sites per gene; 62–99 parsimony informative). When including outgroup species, this increased to 263 variable sites and 172 parsimony informative sites with the highest variance for *COI*. Nucleotide diversity ranged from 0.049–0.061 for individual genes and was 0.059 for the concatenated data (0.081 with outgroups).

The average uncorrected pairwise sequence divergence (sd) amongst identified lineages within the Doria's group ranged from 3.8% between *D. mayri* and *D. cf. stellarum* to 7.9% between *D. stellarum* and *D. dorianus* (Table 4). Average sd between *D. stellarum* and *D. cf. stellarum* was 6.5% (Table 4). The largest divergences were for *Cytb* (4.1–9.0%) and the lowest were for *ND2* (3.5–7.4%) (Appendix 3). Within putative taxa, average divergence ranged from 0.0% within *D. cf. stellarum* to 1.4% within *D. dorianus* (Table 4). Average divergence comparisons with the outgroups (*D. bennettianus*, *P. concinna*, *P. xanthopus* and *T. stigmatica*) ranged from 10.5–14.8% (Table 4).

Phylogenetic analysis

The maximum likelihood analysis of the concatenated mitochondrial data resolved six lineages within the Doria's group: *D. cf. stellarum*, *D. mayri*, *D. notatus*, *D. stellarum*, *D. scottae* and *D. dorianus* (Fig. 3). The additional museum specimens of *D. notatus* (AM M.7273, M.46213) grouped tightly with their congeners, as did an additional museum specimen of *D. dorianus* (AM M.32134). The inclusion of *D. mayri* identified a well-supported relationship between this species and *D. cf. stellarum* separate from the remaining Doria's group taxa (Fig. 3). Aside from *D. mayri*,

Table 4. Average uncorrected pairwise sequence divergence [and range] across three concatenated mtDNA loci between *Dendrolagus* taxa examined in this study, including within taxon divergences on the diagonal.

	<i>dorianus</i>	<i>notatus</i>	<i>stellarum</i>	<i>cf. stellarum</i>	<i>scottae</i>	<i>mayri</i>	<i>bennettianus</i>	<i>P. concinna</i>	<i>P. xanthopus</i>
<i>D. dorianus</i>	0.014								
<i>D. notatus</i>	0.075 [0.069–0.080]	0.008 [0.000–0.019]							
<i>D. stellarum</i>	0.079 [0.075–0.087]	0.063 [0.057–0.075]	0.011 [0.000–0.017]						
<i>D. cf. stellarum</i>	0.072 [0.071–0.073]	0.069 [0.067–0.074]	0.065 [0.063–0.069]	0.000					
<i>D. scottae</i>	0.070 [0.067–0.071]	0.070 [0.067–0.073]	0.047 [0.043–0.050]	0.061 [0.058–0.062]	0.004 [0.000–0.008]				
<i>D. mayri</i>	0.075 [0.074–0.075]	0.071 [0.069–0.076]	0.065 [0.063–0.069]	0.038	0.063 [0.061–0.064]	—			
<i>D. bennettianus</i>	0.124 [0.122–0.126]	0.125 [0.125–0.126]	0.131 [0.130–0.133]	0.117	0.120 [0.120–0.121]	0.125	—		
<i>P. concinna</i>	0.129 [0.126–0.131]	0.132 [0.132–0.134]	0.130 [0.130–0.131]	0.133	0.120 [0.120–0.121]	0.126	0.118	—	
<i>P. xanthopus</i>	0.127 [0.125–0.128]	0.127 [0.126–0.130]	0.109	0.131	0.105 [0.103–0.105]	0.121	0.118	0.102	—
<i>T. stigmatica</i>	0.135 [0.132–0.137]	0.148 [0.147–0.150]	0.142 [0.140–0.147]	0.145 [0.138–0.141]	0.140	0.145	0.125	0.113	0.125

the phylogeny supported similar relationships amongst Doria's group lineages as previously reported (Eldridge *et al.*, 2018), with *D. stellarum* and *D. scottae* forming sister clades, followed by *D. notatus* (Fig. 3). However, the node connecting *D. dorianus* as sister to a clade of the five remaining Doria's group lineages showed only moderate support (70% bootstrap), which is consistent with varied results from previous mtDNA and nDNA+mtDNA analyses (Eldridge *et al.*, 2018). The bootstrap support at all remaining major nodes across the tree was strong (100%) (Fig. 3).

Discussion

The inclusion of genetic data in this study, obtained from museum specimens, has improved taxon and geographic sampling within the Doria's group. Six distinct Doria's group lineages were identified, enabling clarification of several long-standing phylogenetic and evolutionary questions within the group. Five of these lineages correspond to the currently recognized species within the group: *D. dorianus*, *D. notatus*, *D. stellarum*, *D. scottae* and *D. mayri*. An additional identified lineage represented sampled individuals of *D. cf. stellarum*.

Differentiation within the Doria's group

The first molecular data generated from the poorly known *D. mayri* has convincingly placed it within the Doria's group. Phylogenetically, *D. mayri* forms a strongly supported monophyletic lineage with the nearest sampled Doria's group population (*D. cf. stellarum*) from the Tembapapura area ca. 300 km to the east. Together, they form a sister group to three other species (*D. notatus*, *D. stellarum* and *D. scottae*). The *mayri*- *cf. stellarum* lineage is highly differentiated from all other Doria's group species, differing by 6.1–7.5% sd (Table 4). This demonstrates that the molecular affinities of *D. cf. stellarum* lie with *D. mayri* (isolated on the Wondiwoi Peninsula to the west) rather than true *D. stellarum* from the Star Mountains ca. 300 km to the east along the Central Cordillera.

The mtDNA sequence divergence detected between *D. mayri* and *D. cf. stellarum* (3.8%) is below the level of divergence detected between other closely related but clearly differentiated *Dendrolagus* species pairs, for example *D. scottae* and *D. stellarum* differ by 4.7% (Table 4), while *D. spadix* and *D. matschiei* differ by 5.1% (Eldridge *et al.*, 2024). However, divergences between two morphologically similar subspecies of Goodfellow's tree-kangaroo (*Dendrolagus goodfellowi*) are 7% (Eldridge *et al.*, 2024), while intra-taxon divergences reach a maximum of 1.4% in the Doria's group (Table 4) and 1.6% within Goodfellow's group (Eldridge *et al.*, 2024). Thus, the divergence detected between *D. mayri* and *D. cf. stellarum* sits in a grey-zone between reported intra- and inter-species divergences for this genus.

The high molecular divergence detected between *D. stellarum* and *D. cf. stellarum* is concordant with marked differences in pelage colouration and markings between these two populations (Fig. 4). In contrast, the pelage of *D. cf. stellarum* is most similar to that of the holotype of *D. mayri* (Fig. 4), although there are also some differences in colouration and markings (Fig. 4). The concordant moderate divergence between *D. mayri* and *D. cf. stellarum*

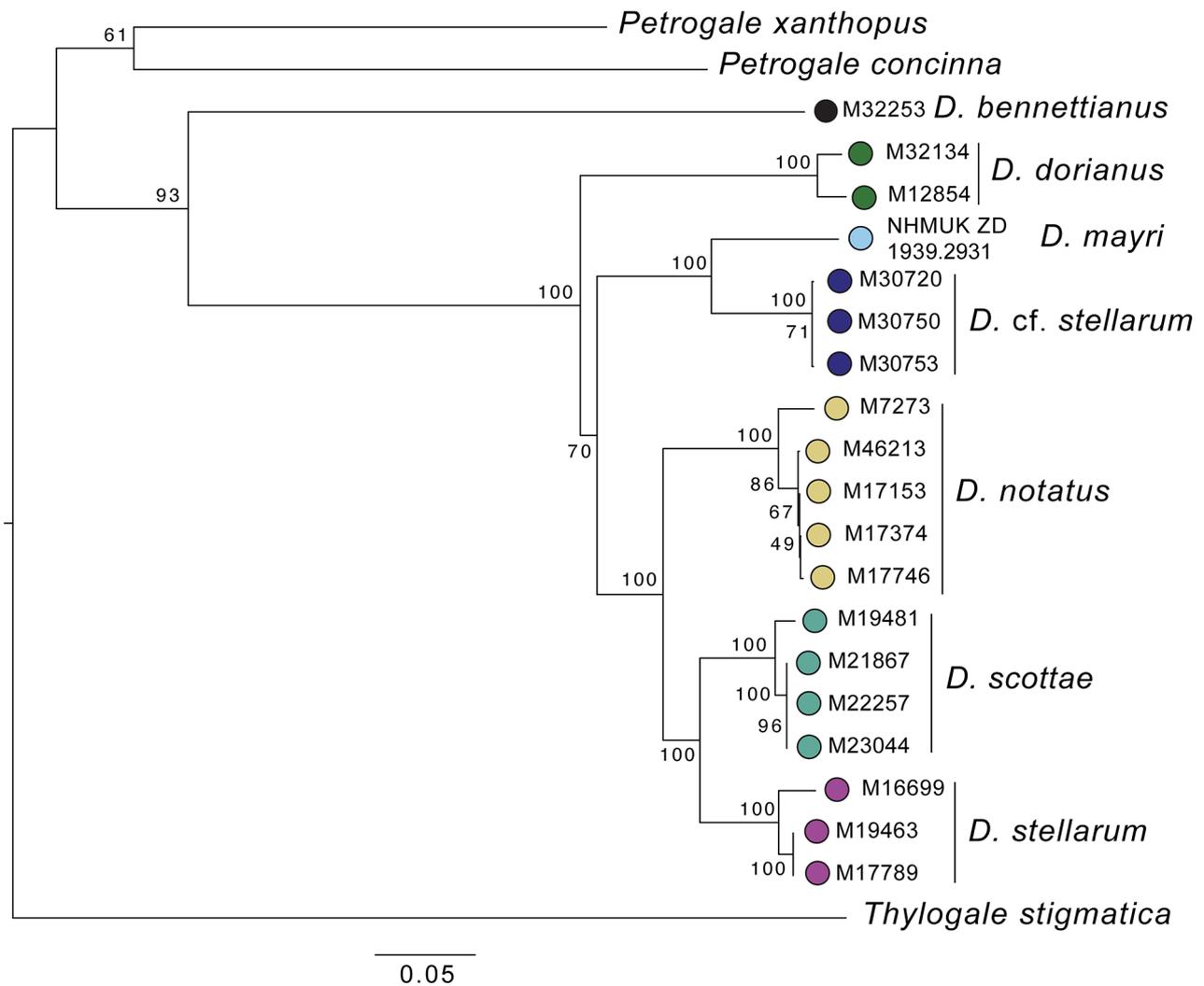


Figure 3. Phylogenetic relationships (ML) amongst mtDNA sequences from six sampled Doria's group taxa. Percentage bootstrap support is indicated.

in pelage morphology and genetics therefore suggests they are currently best regarded as differentiated subpopulations of *D. mayri*. However, mtDNA data can be misleading, as the increasing recognition of mito-nuclear discordance demonstrates (Firneno Jr *et al.*, 2020; Potter *et al.*, 2024). Therefore, this hypothesis requires testing with improved sampling, comparative nuclear DNA data and an analysis of skull morphology.

Phylogeography

Previous ancestral state reconstruction analysis (Eldridge *et al.*, 2018) revealed that the ancestral lineage leading to the Doria's group and its sister taxon, *D. mbaiso*, was already associated with high elevation environments. The divergence of *D. mbaiso* from the Doria's group occurring almost 5 mya (Eldridge *et al.*, 2018) when mountain building in New Guinea was well underway (van Ufford & Cloos, 2005). Subsequent diversification within the Doria's group occurred along the Central Cordillera 2–3 mya (late Pliocene, early Pleistocene) (Eldridge *et al.*, 2018), a period associated within ongoing mountain building of the Central Ranges (van Ufford & Cloos, 2005) and intensified climatic

cycling (Byrne *et al.*, 2011). During these climatic cycles, the periodic expansion to lower altitudes and then contraction of mid-high elevation habitats would have facilitated the dispersal and differentiation of Doria's group species along the Central Cordillera. Currently the distribution of Doria's group species/lineages along the Central Cordillera appears associated with major high elevation mountain systems (southeast Peninsula, Central Highlands, Star Mountains, Snow Mountains) which are separated by lower elevation zones including major river valleys. These low elevation areas appear to form contemporary barriers to gene flow in the Doria's group and other groups of specialist mid-high elevation taxa including birds (Irestedt *et al.*, 2015), other mammals (Helgen & Helgen, 2009; Westerman *et al.*, 2012), and insects (Janda *et al.*, 2016).

Dendrolagus scottae appears to be a more recently derived species originating via a dispersal event (from the ancestral *D. stellarum* population) from the Central Cordillera to the Northern Coastal Ranges about 1.3 mya (Eldridge *et al.*, 2018). Given that *D. mayri* and *D. cf. stellarum* show less genetic divergence than *D. scottae* and *D. stellarum* (Table 4), we hypothesize that a more recent dispersal event from the western end of the Central



Figure 4. Comparison of pelage variation across Doria's group taxa. Top to bottom: *D. mayri* (NHMUK ZD 1939.2931, holotype), *D. cf. stellarum* (AM M.30720 = *D. cf. mayri*), *D. scottae* (AM M.24424), *D. stellarum* (AM M.16699, paratype), and *D. notatus* (AM M.16419). Photography of AM specimens by Ron Lovatt (AM DigiVol). Photography of specimen from the collections of the Natural History Museum, London by Phaedra Kokkini.

Cordillera to the Wondiwoi Peninsula resulted in the differentiation of *D. mayri* on the Wondiwoi Peninsula from the ancestral Sudirman Range population. However, a better understanding of the distribution and evolution of *Dendrolagus* taxa in western New Guinea requires improved sampling and additional nuclear DNA data to test this assumption.

Conservation implications

Populations attributable to *D. cf. stellarum* are reported to be widespread in the western Central Cordillera (Sudirman Range), West Papua, Indonesia, being known from the Tembagapura and Kwiyaugai areas (Australian Museum specimens), Kamu Valley (Peabody Museum, Yale specimens) and Mt Mbinggela/Mt Dugudok area (Wild & Balke, 2018). They are therefore likely to be distributed from the Baliem Valley west to the Paniai Lakes near Pogapa. Further west, in the Weyland Mountains, tree-kangaroos appear to be absent (Flannery *et al.*, 1996).

Populations of *D. cf. stellarum* have previously been included within *D. stellarum* for description of biological attributes and conservation assessments (Flannery *et al.*, 1996; Helgen, 2007; Eldridge & Coulson, 2015; Leary *et al.*, 2016a). Since we have now shown that populations of *D. cf. stellarum* in the western Central Cordillera are more appropriately classified as a differentiated subpopulation of *D. mayri*, some reassessment will be required. These changes significantly reduce the known distribution of true *D. stellarum*, which is now restricted from the Telefomin area, through the Star Mountains and possibly west to the Baliem Valley. With this smaller distribution, *D. stellarum* may be more threatened than previously thought. *Dendrolagus stellarum* (*sensu lato*) is currently classified as Vulnerable by the IUCN (Leary *et al.*, 2016a). Conversely, these data significantly expand the known distribution of populations attributable to *D. mayri*, although there remains a major, but puzzling, gap in the distribution between the Wondiwoi Peninsula and western Central Cordillera subpopulations. Any reassessment of conservation status should take into account the differentiation apparent between the Sudirman Range and Wondiwoi Peninsula subpopulations of *D. mayri*, as well as their geographic isolation and large differences in distribution area / population size. *Dendrolagus mayri* (*sensu lato*) is currently classified as Critically Endangered by the IUCN (Leary *et al.*, 2016b).

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Appendix 1. GenBank accession numbers for *Dendrolagus* mtDNA data used in the analysis of Doria's group taxa.

Taxon	Specimen ID	<i>Cytb</i>	<i>ND2</i>	<i>COI</i>
<i>D. dorianus</i>	AM M.12854	MH197953	MH197919	MH197986
<i>D. dorianus</i>	AM M.32134	PX418938	PX418942	PX372088
<i>D. mayri</i>	NHMUK ZD 1939.2931 holotype	PX418939	PX418943	PX372089
<i>D. notatus</i>	AM M.17374	MH197954	MH197920	MH197987
<i>D. notatus</i>	AM M.17746	MH197955	MH197921	MH197988
<i>D. notatus</i>	AM M.17153	MH197956	MH197922	MH197989
<i>D. notatus</i>	AM M.7273	PX418936	PX418940	PX372086
<i>D. notatus</i>	AM M.46213	PX418937	PX418941	PX372087
<i>D. stellarum</i>	AM M.16699 paratype	MH197957	MH197923	MH197990
<i>D. stellarum</i>	AM M.17789 holotype	MH197958	MH197924	MH197991
<i>D. stellarum</i>	AM M.19463 paratype	MH197959	MH197925	MH197992
<i>D. cf. stellarum</i>	AM M.30720	MH197960	MH197926	MH197993
<i>D. cf. stellarum</i>	AM M.30750	MH197961	MH197927	MH197994
<i>D. cf. stellarum</i>	AM M.30753	MH197962	MH197928	MH197995
<i>D. scottae</i>	AM M.19481 holotype	MH197979	MH197945	MH198012
<i>D. scottae</i>	AM M.21867	MH197980	MH197946	MH198013
<i>D. scottae</i>	AM M.22257	MH197981	MH197947	MH198014
<i>D. scottae</i>	AM M.23044	MH197982	MH197948	MH198015
<i>D. bennettianus</i>	AM M.32253	MH197950	MH197916	MH197984
<i>P. concinna</i>	S-315	JQ042124	JQ042147	JQ042170
<i>P. xanthopus</i>	S-359	JQ042136	JQ042159	JQ042181
<i>T. stigmatica</i>	S-1101	JN202479	JQ042163	JQ042186

Appendix 2. Primers used to amplify segments of the *COI*, *Cytb* and *ND2* genes from *Dendrolagus* taxa.

Gene	Primer		Reference
<i>COI</i>	M134	GTATTTATCCTGCTTACTCTTAGTTAACAGC	KN Armstrong, unpubl. data
	Den_CO1_R1	CCTACTATTCCTGCTCARGCRCCGAATAG	Eldridge <i>et al.</i> , 2024
	Den_CO1_F1	TCAATGCTTKCCTCAGC	Eldridge <i>et al.</i> , 2024
	Den_CO1_R2	ATAACATTATAAAATCTG	Eldridge <i>et al.</i> , 2024
	Den_CO1_F2	CTTATTCGCGCAGAGCTCGG	Eldridge <i>et al.</i> , 2024
	Den_CO1_R3	TCGGGTGCGCCGATCATTAG	Eldridge <i>et al.</i> , 2024
	Den_CO1_F3	ATAATGTTATTGTRACRGC	Eldridge <i>et al.</i> , 2024
	Den_CO1_R4	GTTCTGCTCCYGCTTCTAC	Eldridge <i>et al.</i> , 2024
	Den_CO1_F4	CCTCCTTCTATTRGCATC	Eldridge <i>et al.</i> , 2024
	Den_CO1_R5	GTGATRAAGTTGATAGCTCC	Eldridge <i>et al.</i> , 2024
	Den_CO1_F5	CACGCTGGGGCTTCTGTAG	Eldridge <i>et al.</i> , 2024
	Den_CO1_R6	AAGGAGGAGAAGRACTGCTGT	Eldridge <i>et al.</i> , 2024
	Den_CO1_F6	ACCACCCGCTATCTCAATATC	Eldridge <i>et al.</i> , 2024
	Den_CO1_R7	CTTCTGGATGTCCRAAGAATCA	Eldridge <i>et al.</i> , 2024
	Den_CO1_F7	ACAATACTTTTAACAGACCG	Eldridge <i>et al.</i> , 2024
	Den_CO1_R8	TTACCAGAATAGTAGGTTAC	Eldridge <i>et al.</i> , 2024
	Den_CO1_F8	TGATTCTTYGGACATCCAGAAG	Eldridge <i>et al.</i> , 2024
	Den_CO1_R9	TAAGCTCGAGTGTGACGTC	Eldridge <i>et al.</i> , 2024
	Den_CO1_F9	TTACACAGTCGGATTAGACG	Eldridge <i>et al.</i> , 2024
	Den_CO1_R10	ATAAATCCGAGAGCTCATAG	Eldridge <i>et al.</i> , 2024
	Den_CO1_F10	GTATTTAGTTGACTAGCAAC	Eldridge <i>et al.</i> , 2024
Den_CO1_R11	CCTATRGTAGGACRTAGTGGAAGTG	Eldridge <i>et al.</i> , 2024	
Den_CO1_F11	CATGACACTTACTATGTA	Eldridge <i>et al.</i> , 2024	
<i>Cytb</i>	M31(COA)	AGTATAAGCGTCTGGGTAGTC	Palumbi <i>et al.</i> , 1991
	L14724	CGAAGCTTGATATGAAAAACCATCGTTG	Pääbo, 1990
	Den_CB_R1	GCAGGCTCCTAGTAGTGA	Eldridge <i>et al.</i> , 2024
	Den_CB_F1	CACCCACTAATTAAAAAT	Eldridge <i>et al.</i> , 2024
	Den_CB_R2	ATGAAGAATATGGATGCTC	Eldridge <i>et al.</i> , 2024
	Den_CB_F2	CCCACATCTGCCGAGAYGT	Eldridge <i>et al.</i> , 2024
	Den_CB_R3	CGATATAAGGAATAGCGGA	Eldridge <i>et al.</i> , 2024
	Den_CB_F3	GACAAATATCRTTCTGAGG	Eldridge <i>et al.</i> , 2024
	Den_CB_R4	GTATAGTACGGGTGGAATGG	Eldridge <i>et al.</i> , 2024
	Den_CB_F4	CTATTYCTACAYGAAAC	Eldridge <i>et al.</i> , 2024
	Den_CB_R5	CGGAGAATRGCATATGCAAA	Eldridge <i>et al.</i> , 2024
	Den_CB_F5	TTGCATAYGCYATYCTCCGATC	Eldridge <i>et al.</i> , 2024
	Den_CB_R6	AAGTATGAGATTGATGCT	Eldridge <i>et al.</i> , 2024
	Den_CB_F6	TGAATCGGAGGCCAACCAGTAG	Eldridge <i>et al.</i> , 2024
<i>ND2</i>	Mr2	AGGGTGTTATACCTTCATTTTTGG	Bulazel <i>et al.</i> , 2007
	mmND2.1	GCACCATTCCACTTYTGAGT	Osborne & Christidis, 2001
	Den_ND2_R1	GTTRAGTATGAGRAATAGGGTTAG	Eldridge <i>et al.</i> , 2024
	Den_ND2_F1	TCCTAGCCTACTCCTCTAT	Eldridge <i>et al.</i> , 2024
	Den_ND2_R2	CCTCCAAGRGATANAAGTGTGAG	Eldridge <i>et al.</i> , 2024
	Den_ND2_F2	AAATCACTRACAAACCTATG	Eldridge <i>et al.</i> , 2024
	Den_ND2_R3	GGAAATATAGTAAGTGTGAG	Eldridge <i>et al.</i> , 2024
	Den_ND2_F3	GCCACCCTAATAGCACTYTC	Eldridge <i>et al.</i> , 2024
	mrND2c	GATTTGCGTTCGAATGTAGCAAG	Osborne & Christidis, 2001

Appendix 3. Average uncorrected pairwise sequence divergence [and range] across the three mtDNA loci for *Dendrolagus* taxa examined in this study, including within taxon divergences on the diagonal.

COI	<i>dorianus</i>	<i>notatus</i>	<i>stellarum</i>	<i>cf. stellarum</i>	<i>scottae</i>	<i>mayri</i>	<i>bennettianus</i>	<i>P. concinna</i>	<i>P. xanthopus</i>
<i>dorianus</i>	0.010								
<i>notatus</i>	0.076 [0.072–0.078]	0.005 [0.000–0.009]							
<i>stellarum</i>	0.084 [0.081–0.087]	0.042 [0.040–0.045]	0.005 [0.000–0.008]						
<i>cf. stellarum</i>	0.076 [0.056–0.058]	0.057 [0.062–0.067]	0.064	0.000					
<i>scottae</i>	0.075 [0.073–0.077]	0.036 [0.035–0.039]	0.030 [0.028–0.033]	0.054 [0.000–0.005]	0.003				
<i>mayri</i>	0.086	0.073	0.071 [0.069–0.074]	0.037	0.062	—			
<i>bennettianus</i>	0.122 [0.121–0.123]	0.124 [0.123–0.125]	0.127	0.121	0.121	0.132	—		
<i>P. concinna</i>	0.136 [0.135–0.137]	0.127 [0.127–0.128]	0.130 [0.128–0.131]	0.126	0.120 [0.116–0.121]	0.131	0.126	—	
<i>P. xanthopus</i>	0.114	0.120 [0.119–0.121]	0.120 [0.118–0.121]	0.114	0.107	0.125	0.117	0.105	—
<i>T. stigmatica</i>	0.128 [0.126–0.130]	0.120 [0.119–0.122]	0.141	0.130	0.123	0.131	0.132	0.141	0.112
Cytb	<i>dorianus</i>	<i>notatus</i>	<i>stellarum</i>	<i>cf. stellarum</i>	<i>scottae</i>	<i>mayri</i>	<i>bennettianus</i>	<i>P. concinna</i>	<i>P. xanthopus</i>
<i>dorianus</i>	0.012								
<i>notatus</i>	0.084 [0.070–0.092]	0.011 [0.000–0.024]							
<i>stellarum</i>	0.090 [0.087–0.096]	0.075 [0.070–0.084]	0.013 [0.000–0.019]						
<i>cf. stellarum</i>	0.075 [0.072–0.077]	0.080 [0.080–0.082]	0.081 [0.080–0.084]	0.000					
<i>scottae</i>	0.067 [0.063–0.070]	0.066 [0.060–0.070]	0.047 [0.043–0.051]	0.065 [0.060–0.067]	0.004 [0.000–0.007]				
<i>mayri</i>	0.073 [0.070–0.075]	0.078 [0.077–0.080]	0.079 [0.077–0.082]	0.041	0.060 [0.058–0.060]	—			
<i>bennettianus</i>	0.130	0.144 [0.137–0.147]	0.149 [0.147–0.152]	0.130	0.130 [0.128–0.130]	0.130	—		
<i>P. concinna</i>	0.107 [0.106–0.108]	0.122 [0.118–0.125]	0.122 [0.120–0.125]	0.128	0.113 [0.111–0.113]	0.111	0.125	—	
<i>P. xanthopus</i>	0.106 [0.104–0.108]	0.110 [0.104–0.113]	0.097 [0.096–0.099]	0.113	0.086 [0.084–0.087]	0.101	0.108	0.089	—
<i>T. stigmatica</i>	0.134 [0.133–0.135]	0.147 [0.145–0.149]	0.150 [0.147–0.157]	0.142	0.140 [0.135–0.142]	0.130	0.125	0.096	0.113
ND2	<i>dorianus</i>	<i>notatus</i>	<i>stellarum</i>	<i>cf. stellarum</i>	<i>scottae</i>	<i>mayri</i>	<i>bennettianus</i>	<i>P. concinna</i>	<i>P. xanthopus</i>
<i>dorianus</i>	0.016								
<i>notatus</i>	0.066 [0.063–0.070]	0.006 [0.000–0.014]							
<i>stellarum</i>	0.068 [0.063–0.077]	0.051 [0.045–0.066]	0.009 [0.000–0.014]						
<i>cf. stellarum</i>	0.069 [0.068–0.070]	0.057 [0.054–0.068]	0.049 [0.047–0.054]	0.000					
<i>scottae</i>	0.073 [0.070–0.075]	0.074 [0.068–0.082]	0.047 [0.042–0.049]	0.056	0.005 [0.000–0.009]				
<i>mayri</i>	0.076 [0.075–0.077]	0.064 [0.061–0.075]	0.051 [0.049–0.056]	0.035	0.067 [0.063–0.068]	—			
<i>bennettianus</i>	0.119 [0.115–0.122]	0.107 [0.103–0.115]	0.114 [0.113–0.115]	0.103	0.111 [0.110–0.115]	0.120	—		
<i>P. concinna</i>	0.150 [0.146–0.153]	0.142 [0.141–0.146]	0.137 [0.136–0.138]	0.138	0.128 [0.127–0.131]	0.141	0.110	—	
<i>P. xanthopus</i>	0.147 [0.146–0.148]	0.145 [0.143–0.148]	0.121 [0.120–0.122]	0.148	0.122	0.141	0.127	0.115	—
<i>T. stigmatica</i>	0.135 [0.129–0.141]	0.149 [0.148–0.153]	0.135 [0.134–0.138]	0.148	0.141	0.160	0.124	0.129	0.136

A Range Extension and First Voucher Echolocation Call for the New Guinea Big-eared Bat, *Pharotis imogene* (Chiroptera: Vespertilionidae)

IAIN A. WOXLVOLD¹ , KYLE N. ARMSTRONG² , ELYSSA M. MCLEOD³ ,
MELLIE S. MUSONERA⁴ , ANTHONY C. SIMMS⁵ , AND STEPHEN J. RICHARDS⁶ 

¹ Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

² School of Biological Sciences, University of Adelaide, Adelaide SA 5005, Australia; and
South Australian Museum, North Terrace, Adelaide SA 5000, Australia

³ Level 5, 348 Edward Street, Brisbane Qld 4000, Australia

⁴ Unit 4, Doc Street, West Goroka, Eastern Highlands Province, PNG; formerly TotalEnergies EP PNG Limited

⁵ PO Box 1860, Coolalinga NT 0839, Australia; formerly TotalEnergies EP PNG Limited

⁶ Herpetology Department, South Australian Museum, North Terrace, Adelaide SA 5000, Australia; and
Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

ABSTRACT. The New Guinea Big-eared Bat *Pharotis imogene* is one of the region's least known mammals, with prior confirmed records from only two localities, both in Central Province, Papua New Guinea. We report the recent capture of a *Pharotis imogene* from Kuriva Forestry Station, approximately 50 km north of Port Moresby, extending the species' known range more than 130 km northwest of its previous limit. We describe and illustrate the new specimen and its habitat and provide the first description of this species' echolocation call.

Introduction

The monotypic genus *Pharotis* (Chiroptera: Vespertilionidae) is known only from Central Province in southeast mainland Papua New Guinea (PNG) (Armstrong *et al.*, 2021). Its sole member, the New Guinea Big-eared Bat *Pharotis imogene* Thomas, 1914, is among the most poorly known of all New Guinean mammals. It is known from just two localities southeast of Port Moresby.

The discovery, description, and recent rediscovery of *Pharotis* are described in Hughes *et al.* (2014). Briefly, in

1890, Dr Lamberto Loria collected 45 vespertilionids from near the coastal village of Kamali in Rigo District (Fig. 1) that were initially lodged in the Museo di Storia Naturale in Genoa and assigned by Thomas (1897) to *Nyctophilus timoriensis* (Geoffroy, 1806). The collection was later distributed among several institutions, and only six of these specimens have been relocated (Flannery, 1995; Armstrong *et al.*, 2021). The original description of *Pharotis* (Thomas, 1914) refers only to the type, one of three specimens from the Kamali collection reportedly held at the Natural History

Keywords: *Pharotis*; Vespertilionidae; New Guinea; range extension; echolocation call; habitat use

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ORCID iD: Woxvold, 0009-0005-3258-7592; Armstrong, 0000-0002-3228-9182; McLeod, 0009-0003-5641-6523; Musonera, 0000-0002-2596-4055; Simms, 0009-0004-6413-8196; Richards, 0000-0002-0251-3884

Corresponding author: Iain A. Woxvold iainwoxvold@gmail.com

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Museum in London (Flannery, 1995), and provides no insight as to the missing Kamali vouchers. Following its discovery, *P. imogene* was not seen again for more than 120 years and was considered possibly extinct (Flannery, 1995; Bonaccorso *et al.*, 2008) until a single individual was captured in 2012 in a logging concession near Oio village in Abau District, 120 km east of Kamali (Hughes *et al.*, 2014). That specimen is lodged at the PNG National Museum & Art Gallery (PNGNM 27464) (Hughes *et al.*, 2014).

Almost nothing is known of the ecology of *P. imogene* (Hughes *et al.*, 2014; Moratelli & Burgin, 2019; Armstrong *et al.*, 2021). The exact location and habitat at the Kamali type locality were not described (Thomas, 1897, 1914). The Oio individual was captured at the boundary of logged rainforest and an extensive clearing. Its foraging habits are assumed to be similar to those of the closely related long-eared bats (*Nyctophilus* spp.) due to their similar morphologies, but its roosting and foraging habitats are still unknown. All known adult specimens of *P. imogene* are female and the only subadult is male ($n = 7$; Flannery, 1995; Hughes *et al.*, 2014).

Pharotis imogene is listed as Critically Endangered on *The IUCN Red List of Threatened Species* (Armstrong *et al.*, 2021). It was recently included among the global top ten research-priority island endemic bat species (IEBs) based on a combination of extinction risk, taxonomic distinctiveness and data availability (Conenna *et al.*, 2017).

In this paper we aim to: (1) report a range extension for *P. imogene* based on the capture of a single animal at Kuriva Forestry Station, located in the Kairuku-Hiri District of Central Province approximately 50 km north of Port Moresby; (2) describe its echolocation call, and; (3) discuss available data on habitat use.

Materials and methods

Kuriva Forestry Station is managed by the PNG Forest Authority (PNGFA). Covering more than 9,460 ha, it is centred on the Veimauri and Veiya River catchments immediately north of the Hiritano Highway and includes a wide range of habitats with a complex pattern of historical land use. Native forest covers more than 70% of the area, particularly on higher ground in the north and east. Most of this forest has been logged in recent decades. In the south, there are large areas of teak (*Tectona grandis*) plantation of varying age and *kunai* grassland with patches of regenerating scrub.

In 2024, TotalEnergies E&P PNG Limited commissioned a series of multi-disciplinary biodiversity surveys of Kuriva Forestry Station. Fauna surveys were conducted from 30 April to 10 May 2024. The survey team (EM, MM, SJR, AS, IW) was based at the Kuriva Station base, located next to the Veimauri River and the 'Kuriva Teak Plantation Picnic Park' in the station's south. Harp traps were set to

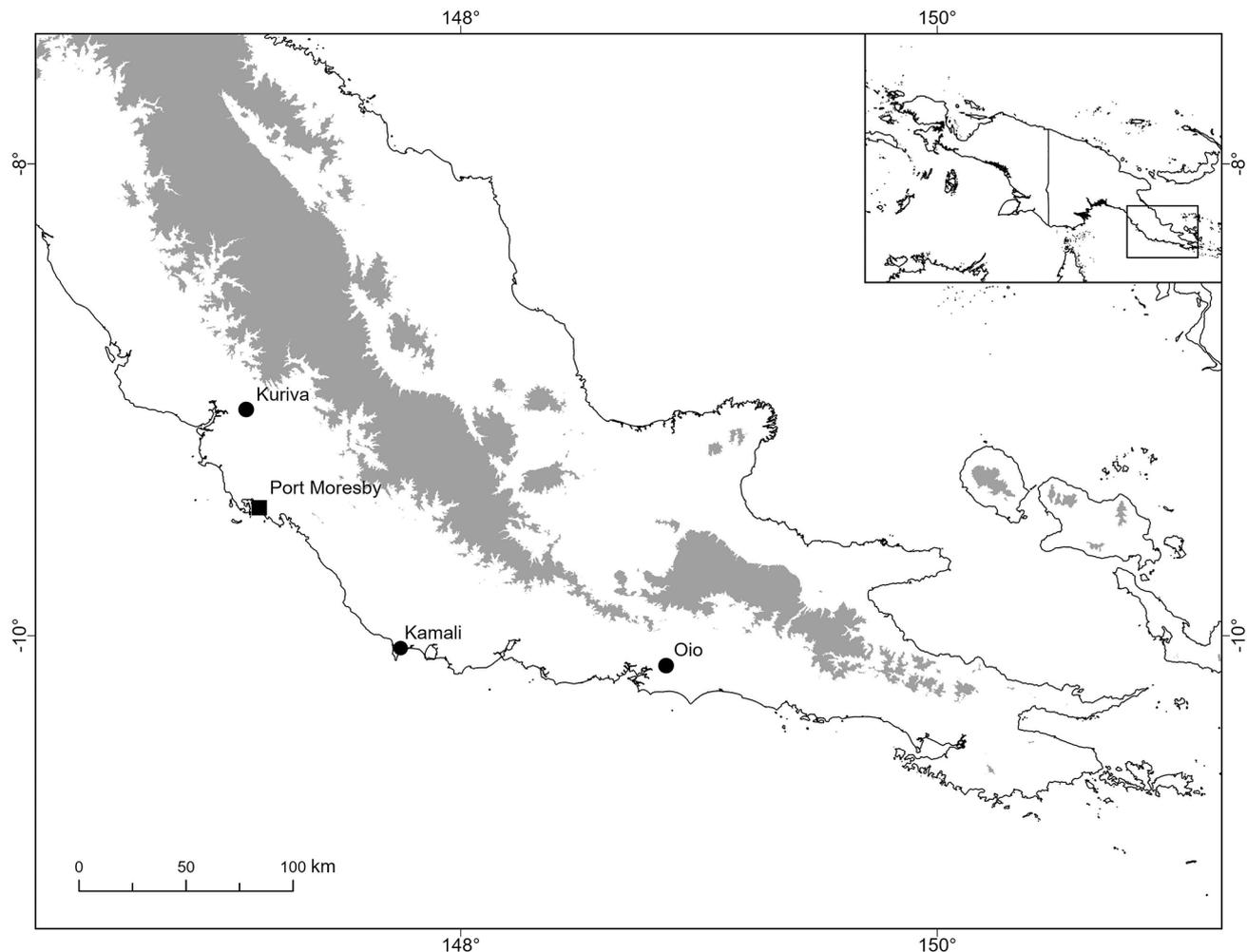


Figure 1. Map showing *Pharotis imogene* localities and the national capital Port Moresby. Shading indicates land above 1,000 m.

capture echolocating bats across an elevational gradient of more than 800 m, from *ca.* 40 m above sea level (asl) near the southern lease boundary to more than 850 m asl in the northeast. However, for logistical reasons, most harp traps were set below 70 m asl near the station base (4/6 positions, 5/8 trap nights).

Voucher echolocation calls were recorded indoors using a 'zip-line' method (Parson & Szewczak, 2009). A small gauge fishing line tied to the animal's lower leg was fixed with a loop at the other end to a horizontal line stretched taut across the room. In this way, flight calls were recorded while preventing possible escape from the poorly sealed building. Terminology of measured call parameters follows Binary Acoustic Technology (2014). Pulse characteristics of *P. imogene* echolocation calls were compared against those of two sympatric species with similar call structure, the Maluku myotis *Myotis moluccarum* Thomas, 1915, and Papuan Long-eared Bat *Nyctophilus microtis* Thomas, 1888, using measurements extracted from a limited sample of quality recordings with SCAN'R software (version 1.8.3, Binary Acoustic Technology, USA).

The specimen was fixed in a 10% formalin solution for two days prior to preservation in 70% ethanol. Tissues (liver) were extracted prior to fixation and preserved in 95% ETOH. Body mass was measured in the field to the nearest 0.1 g using a 10 g Pesola scale. Other measurements were taken from the preserved specimen to the nearest 0.1 mm using digital callipers.

Area estimates were calculated using the area measurement tool in ArcGIS Pro with LiDAR Digital Elevation Model (DEM) data and recent publicly available satellite imagery.

Results

On the night of 3–4 May 2024, an adult female *P. imogene* (Fig. 2a–c) was captured in a harp trap set at the Kuriva Station base (at 9°02'25"S 147°05'59"E) (Fig. 3). The specimen is lodged at the Australian Museum, Sydney (M.56355). The measurements are: head-body (snout–vent)—41.5 mm; ear (from notch)—24.4 mm; forearm—38.8 mm; tibia—18.6 mm; hindfoot (without claw)—9.5 mm; weight—7.2 g.

The trap was located about 60 m from the Veimauri River at the edge of the Kuriva Picnic Park area at 45 m asl. It was positioned in a break along a fence planted with a narrow strip of vegetation separating two lawn areas that serve as a car park and a recreation area (Fig. 3). Surrounding habitats (within *ca.* 1 km) include clearings with buildings and nursery infrastructure, extensive teak plantations east of the Veimauri River, *kunai* grassland and remnant logged forest west of the river, and remnant disturbed riparian forest (Fig. 4).

The voucher echolocation call of *P. imogene* is shown in Fig. 5, alongside representative (non-voucher) call sequences of similar structure from two sympatric species that were also present at the site—*Myotis moluccarum* and *Nyctophilus microtis*. Table 1 presents measurement data on 13 pulse characteristic variables for each species. The echolocation pulses of *P. imogene* are longer in duration than those of the *N. microtis* example, and they occupy a lower frequency band and are somewhat straighter (less curvilinear) than pulses of both *M. moluccarum* and *N. microtis* (Fig. 5; Table 1).

Discussion

The Kuriva record extends the known range of *P. imogene* some 132 km northwest of the Kamali type locality (Fig. 1). Kuriva lies about 250 km northwest of the easternmost site at Oio. Considering all habitats below 100 m asl, the reported upper limit for *P. imogene* (Moratelli & Burgin, 2019; Armstrong *et al.*, 2021), the species' potential range between Kuriva and Oio is about 4,700 km². However, some of these habitats may be unsuitable for *P. imogene*.

Habitat requirements of *P. imogene* remain largely unknown. It is often stated that *P. imogene* occupies savanna woodland or rainforest patches in savanna (Bonaccorso, 1998; Bonaccorso *et al.*, 2008; Moratelli & Burgin, 2019). This is due to Kamali's position, and that of an unconfirmed record from nearby Kapa Kapa village, near the eastern limit of the Central Province savannas in one of the country's driest areas (McAlpine *et al.*, 1983; Bryan & Shearman, 2008). However, the Kapa Kapa specimen (now lost) was never identified as *P. imogene* (see Hughes *et al.*, 2014), and the exact location and habitat at the Kamali capture site were not reported (Thomas, 1897, 1914). In fact, Kamali is surrounded by a complex array of habitats, with vegetation mapping (Hammermaster & Saunders, 1995) and recent satellite imagery showing eucalypt savanna, mangroves, low swamp vegetation, remnant or regenerating alluvial forest, coconut plantation, gardens, and extensive areas of open habitat all present within 3 km of the village. Moreover, both the Kuriva and Oio sites receive substantially higher rainfall than Kamali (McAlpine *et al.*, 1983; Bryan & Shearman, 2008) and lie outside of the savanna zone; the closest mapped occurrences of savanna (or denser monsoon forest/scrub with *Eucalyptus*) south of the cordillera are more than 12 km from Kuriva and 50 km from Oio (Hammermaster & Saunders, 1995).

Both the Oio and Kuriva specimens were captured in open sites. Natural vegetation within 5 km of the Oio and Kuriva capture sites is predominantly rainforest with some areas of freshwater swamp vegetation (Hammermaster & Saunders, 1995); however, much of this habitat has been removed or heavily disturbed through logging, and there are no records of *P. imogene* from the forest interior. The Oio site is surrounded by a large expanse of logged rainforest, but the specimen was captured in a narrow strip of open habitat along a logging skid trail that opened out to an approximately 100 ha area of grassland and former coconut plantation (Hughes *et al.*, 2014). The Kuriva specimen was captured in an approximately 7 ha area of continuous open habitat (grassland with scattered trees, buildings and plant nursery infrastructure) within a broader modified landscape dominated by teak plantation and grassland with patches of riparian forest and logged foothill forest. It is not possible to determine if captured individuals were foraging at the trap sites or if they were travelling between foraging and roosting sites. There is currently no information on *P. imogene* foraging or roosting habitat.

Considering all available evidence: (1) *P. imogene*'s use of savanna is unconfirmed—if it does occupy savanna, then recent data indicate that the species does not rely on savanna as some authors have previously suggested; (2) the Oio specimen shows that *Pharotis* may be found in areas dominated by rainforest, but it remains unknown whether the species utilizes the forest interior or is reliant on open



Figure 2. Live adult female *Pharotis imogene* captured at Kuriva Forestry Station. Several field characters useful in distinguishing *Pharotis* from similar-looking New Guinean species of *Nyctophilus* are visible, including the relatively large nose-leaves with the anterior leaf having a convex dorsal margin (vs. median depression or notch) and the posterior leaf with deep concavities (terminology follows Thomas, 1914), and the uniquely shaped tragus. (Photos: S. J. Richards).

habitats; (3) building on the Oio evidence, the Kuriva data confirm that *Pharotis* can be found in heavily modified landscapes, but the specific habitat features that are required to support the species remain unknown. Kuriva station is a suitable place to explore some of these themes, given its accessibility, the presence of a wide variety of habitats and the confirmed presence of *P. imogene*.

The echolocation call of *P. imogene* is described here for the first time. In general, the pulses of *P. imogene* are relatively short and broadband in structure compared to other species that produce frequency modulated pulses. Nevertheless, the call type is typical of species that forage

within and around the clutter of vegetation and glean insects from surfaces (Denzinger & Schnitzler, 2013), and this species is syntopic with other gleaners that produce broadband calls.

With the echolocation call of *P. imogene* now described, the use of passive acoustic recorders (PARs) may help to detect its presence on other surveys. It also provides the opportunity to re-examine existing recorded datasets to determine if the species has been overlooked elsewhere. However, care must be taken when attempting to distinguish the calls of *P. imogene* from those of other species, especially sympatric vespertilionids with similar call structures such as *Myotis*



Figure 3. Harp trap in position at the Kuriva *Pharotis imogene* capture site, Papua New Guinea. (Photo: I. Woxvold).

moluccarum and *Nyctophilus microtis*. When inspecting a spectrogram, the call of *P. imogene* can be recognized from pulses with a minimum frequency of approximately 30 kHz, which is *ca.* 10 kHz lower than pulses of *M. moluccarum* and *ca.* 20 kHz lower than those of *N. microtis*. However, typical PAR datasets often include wide variation in the characteristics and quality of calls from each species. Low-quality recordings, such as when the bat is close to the edge of the microphone's reception zone, might not be reliably attributable to *P. imogene*; for example, it is possible that a provisional identification of *P. imogene* could be derived from a 'low frequency' example of *M. moluccarum*. With so few data currently available, any false positives may disproportionately influence future assessments of the species' conservation status, and the presence of *P. imogene* should be confirmed through capture whenever possible.

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Figure 4. Satellite image of the *Pharotis imogene* capture site (yellow star) at the Kuriva Station base.

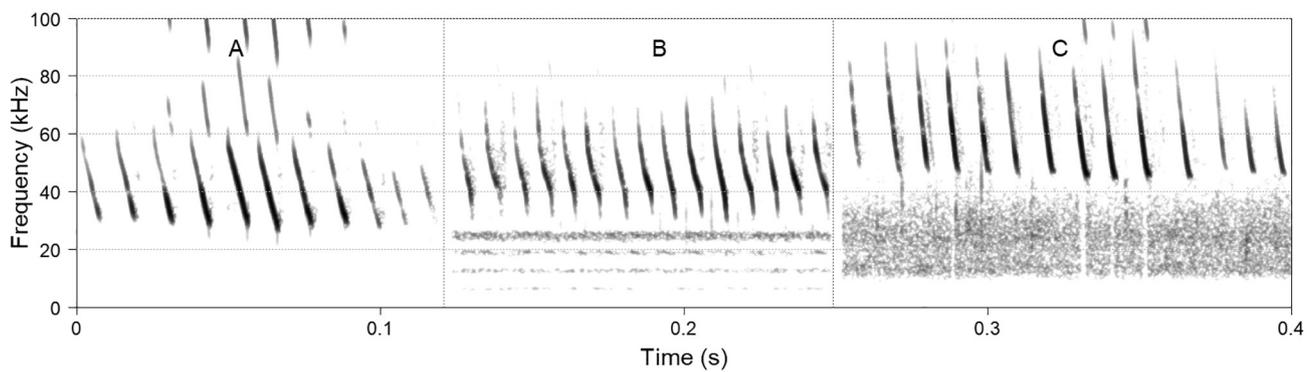


Figure 5. Representative echolocation call sequence portions of *Pharotis imogene* (A), *Myotis moluccarum* (B) and *Nyctophilus microtis* (C). Time between pulses has been compressed.

Table 1. Selected variables extracted from high quality examples of pulses from *P. imogene*, plus representatives from *M. moluccarum* and *N. microtis* (using SCAN'R software; Dur—duration, Fmax—maximum frequency, Fmin—minimum frequency, Fk—frequency at the knee, Tk—time at the knee, Sk—slope at the knee, Fc—characteristic frequency, Tc—characteristic time, Sc—characteristic slope, Supper—slope of upper portion, Slower—slope of lower portion, Se—end slope, Curv—curvature, n—number of pulses measured).

	Dur (ms)	Fmax (kHz)	Fmin (kHz)	Fk (kHz)	Tk (ms)	Sk (kHz/ms)	Fc (kHz)	Tc (ms)	Sc (kHz/ms)	Supper (kHz/ms)	Slower (kHz/ms)	Se (kHz/ms)	Curv ([^] P)
<i>Pharotis imogene</i> n = 6													
mean	6.21	56.13	29.19	40.26	3.17	-4.46	34.44	4.78	-2.94	-5.49	-2.99	-3.24	1.22
sd	0.50	3.48	1.56	7.08	1.69	0.57	7.24	1.61	0.86	1.38	0.78	1.05	0.10
max	6.96	59.97	31.50	52.39	5.57	-3.74	49.17	6.15	-1.43	-4.42	-1.99	-1.43	1.36
min	5.68	51.62	26.86	33.05	0.93	-5.15	30.43	1.74	-3.97	-8.17	-4.29	-4.46	1.07
<i>Myotis moluccarum</i> n = 7													
mean	6.10	71.59	37.78	55.19	1.97	-5.17	46.11	4.48	-2.61	-8.48	-4.20	-4.83	1.35
sd	0.80	1.95	3.12	1.89	0.41	1.05	3.15	0.86	0.86	1.12	0.62	1.57	0.20
max	7.89	75.26	41.40	57.92	3.02	-3.20	50.76	6.38	-0.35	-6.52	-2.99	-0.35	1.62
min	4.87	66.58	32.56	51.37	1.39	-6.86	42.27	3.13	-3.85	-9.90	-5.10	-6.53	1.03
<i>Nyctophilus microtis</i> n = 16													
mean	3.13	83.11	50.73	61.42	1.66	-11.05	56.62	2.42	-8.04	-13.57	-6.66	-8.29	1.35
sd	0.94	4.52	5.43	6.28	0.60	2.13	10.41	1.14	2.88	1.88	1.96	3.11	0.21
max	4.52	89.58	61.75	72.78	2.55	-8.73	76.15	3.94	-2.94	-10.83	-4.39	-2.94	1.59
min	1.97	76.35	46.67	54.96	0.58	-15.06	47.01	0.70	-11.75	-15.91	-10.41	-12.30	1.06

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Towards an Understanding of Marsupial Interchange between Australia and New Guinea

TIM F. FLANNERY , LOUKAS G. KOUNGOULOS ,
AND MARK D. B. ELDRIDGE¹ 

Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

ABSTRACT. A review of the geology, palaeontology, genetic, and morphology studies indicates that during the mid-Miocene to Pliocene, New Guinea consisted of four island Blocks (Vogelkop, Maokop, Central, and Southeastern). The initial dispersal of marsupials from Australia was into the Vogelkop Block. The ancestors of at least six genera (*Dactylonax*, *Microperorytes*, *Myoictis Pseudochirops*, *Spilocuscus*, *Tous*) and three species (*Dendrolagus inustus*, *Dendrolagus ursinus*, *Dorcopsis muelleri*) of endemic New Guinean marsupials are likely to have reached New Guinea via this route. The *Dendrolagus dorianus* complex and two marsupial genera (*Dactylopsila* and *Phalanger*) may have reached New Guinea via the Maokop Block, with *Thylogale* arriving either via the Maokop or Southeastern Block. Four species, or species complexes, of marsupials in the genera *Dendrolagus*, *Dorcopsis*, *Murexia*, and *Peroryctes* may have arrived via the Southeastern Block. The Central Block lacks evidence of Tertiary marsupial transfers from Australia, and may not have been connected with Australia prior to its incorporation into New Guinea. Two possum taxa (*Tous ayamaruensis* and *Dactylonax kambuayai*), which occur in the Vogelkop lowlands, are hypothesized to have been restricted from expansion into the slopes of the Central Cordillera by a combination of tectonics and ecological barriers. A further two species pairs/triplets (*Dactylonax palpator/ernstmayri*, *Pseudochirops albertisii/coronatus/cupreus*) provide evidence of a highly unusual pattern of dispersal within New Guinea, whereby the high-elevation members of each pair have dispersed and speciated, while the mid-elevation members have not. Finally, marsupial distributions indicate that in the early Pleistocene a contiguous mountain range, named here the Northern Cordillera, extended from Vogelkop to the Torricelli Mountains.

Introduction

Australasian marsupials

Marsupials constitute a moderately diverse group of mammals with limited over-water dispersal ability. The Australasian genera *Phalanger* and *Spilocuscus* of the family Phalangeridae and bandicoots of the family Peroryctidae have dispersed over water to non-landbridge islands where they are represented by distinctive insular taxa (Flannery, 1995a; Helgen & Flannery, 2004). Many other insular populations of these and other marsupials are now known

to have originated as prehistoric and historic human introductions (e.g., Flannery & White, 1991; Williams, 1999). The vast majority of Australasian marsupials occur on continental landmasses, or islands of continental origin. Many Melanesian, and a few Australian, taxa are limited to higher elevations, and some clades have unusual distributions that hint to their zoogeographic histories. All of these factors make the marsupials an ideal group with which to investigate faunal interchange between Australia and New Guinea.

It has long been accepted that the marsupial fauna of New Guinea originated from Australia (Schodde & Calaby, 1972;

Keywords: New Guinea, zoogeography, marsupial evolution, Vogelkop, New Guinea-Australia faunal interchange

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ORCID iD: Flannery, 0000-0002-3005-8305; Koungoulos, 0000-0002-5148-0142; Eldridge, 0000-0002-7109-0600

Corresponding author: Tim Flannery tim.fridtjof.flannery@gmail.com

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Flannery, 1995b). However, the number of dispersal events, and which paleo-islands received which faunal elements, remain highly contested. The history of marsupials in Australia offers some constraints on the timing of dispersals to proto-New Guinea. Marsupials arrived in Australia from South America, via Antarctica, *ca.* 54 mya (Godthelp *et al.*, 1992). There is a 29 million year-long gap in their fossil record in Australia between around 54 and 25 mya (Megirian *et al.*, 2010). When the fossil record resumes in the late Oligocene, many of the extant families (as well as those that became extinct in the late Pleistocene) are represented. Several lines of evidence, including the fossil record and phylogenetic studies, suggest that most if not all marsupial migrations from Australia to New Guinea occurred between the late Miocene and the Pleistocene.

Only the later Pleistocene migrations of marsupials are well understood. These interchanges occurred during periods of low sea level when a broad land-bridge opened between Australia and New Guinea. It is likely that savannah woodland dominated the land-bridge, but some gallery forest must also have been present (Schodde & Calaby, 1972). *Notamacropus agilis*, *Thylogale stigmatica*, *Lagorchestes conspicillatus*, *Sminthopsis virginiae* and possibly other marsupial taxa migrated from Australia to New Guinea at this time, while *Echymipera rufescens*, *Spilocuscus maculatus*, *Phalanger mimicus*, and possibly other marsupials, dispersed from New Guinea into northern Australia (penetrating no further south than northern Cape York (Baker & Gynther, 2023).

The precise location, nature and duration of earlier land-bridges between Australia and the paleo-islands that would make up New Guinea remain unknown. But the fact that numerous extant Australian marsupial families, including Myrmecobiidae, Notoryctidae, Chaeropodidae, Thylacomyidae, Phascolarctidae, Vombatidae, Tarsipedidae, Hypsiprymnodontidae, and Potoroidae, are absent from New Guinea, indicates either that severe filtering mechanisms existed, or that extensive extinctions have occurred in New Guinea over the Neogene.

Two pioneering works have inspired our approach to unravelling the zoogeographic history of Melanesian marsupials. The first is Ziegler's (1977) synthesis of the zoogeography of lowland Melanesian marsupials, in which he introduced the concept that the distributions of some taxa might reflect their original dispersion pathways into New Guinea millions of years earlier. Ziegler's argument implies that, despite a lack of ecological competitors, and the historic presence of contiguous rainforest, some marsupial range expansions have been extremely slow. We think it possible that geologically recent tectonic changes, along with the existence of hard to discern zones of unsuitable habitat, may help explain this slow rate of dispersal. The second influence is Aplin's (1998) overview of the vertebrate zoogeography of Vogelkop. Aplin was the first researcher to identify the primacy of Vogelkop as 'a possible major focus of vertebrate speciation during the late Tertiary' (Aplin, 1998: 805). Both recent tectonic shifts and ecological barriers are likely to have been particularly impactful on Vogelkop. The region is geologically complex, leading to edaphic influence on vegetation over short distances, and there is evidence in the mammal distributions we discuss, of marked tectonic changes that have, in the geologically recent past, connected Vogelkop to various regions of New Guinea, as well as severing other connections (Aplin, 1998).

Data bearing on entry points of the New Guinean marsupial radiations

Four sources of information are potentially useful in determining the initial entry points of New Guinean marsupial lineages including: (1) geological evidence, (2) the fossil record, (3) molecular studies, and (4) cladistic assessment of morphological evolution. All four data sets are frustratingly incomplete. For example, while the tectonic evolution of New Guinea is well understood in broad terms, precise details, including the timing of emergence of land bridges and island landmasses, and the coalescence of island landmasses into the single island that is New Guinea, remain unclear (Baldwin *et al.*, 2012). The incomplete fossil record is likewise vexing: the two areas with the highest endemism of marsupials, Vogelkop and southeastern New Guinea, entirely lack a fossil record, while the fossil record elsewhere in New Guinea is severely biased towards larger, now extinct megafauna. Molecular phylogenies are highly useful in determining dispersal events, but in this case a lack of molecular data for key marsupial taxa severely limits its use. Morphological comparisons offer some island-wide comparisons, but even here, detailed analysis is severely limited.

Tectonic evolution of the New Guinean region

New Guinea and surrounding regions are arguably one of the most tectonically complex areas on Earth (Baldwin *et al.*, 2012). On the basis of what is known of its geology, tectonic history and marsupial faunas, we divided New Guinea into four principal 'blocks', which appear to have been islands prior to their incorporation into New Guinea. These four blocks are: (1) the Vogelkop area and its associated 'Northern Cordillera' (newly defined here), (2) the Maokop Block (from the Wissel Lakes to the Hak-Om Divide), (3) the Central Block (from the Hak-Om Divide to the Wau area), and (4) the Southeastern Peninsula.

The Vogelkop Block consists of several continental terranes that collectively comprise the northernmost region of the Australian continental plate. Most of the terranes are composed of deformed Silurian-Devonian marine sediments that are intruded by Permian-Triassic granitoids (Pieters *et al.*, 1983). These continental terranes are fault-bounded by allochthonous blocks of Early Tertiary, oceanic island arc affinity. These oceanic island arc rocks also underlie some zoogeographically important regions—including Yapen, the Wondiwoi Mountains and the Weyland Range. Rocks of oceanic island arc origin also comprise the Foja, Cyclops, and Bewani-Torricelli Mountain Ranges (which, with Yapen, comprise the Northern Cordillera).

The Vogelkop Block is actively deforming via anticlockwise rotation and subparallel sinistral strike-slip faulting at a rate of *ca.* 8 cm/year relative to the rest of the Australian plate (Pigram & Symonds, 1991; Stevens *et al.*, 2002; Bailly *et al.*, 2009). Since *ca.* 6 mya, this process has shifted the Vogelkop Block through 30–40° of anticlockwise rotation and formed the Cenderawasih Rift (Charlton, 2000).

The collision between the Australian Plate and the Melanesian arc is oblique, resulting in diachronous collisional mountain building. The collision, and thus mountain building, began in the west and has moved eastward (Cloos *et al.*, 2005). As a result, the eastern fold-and-thrust belt (part of our Southeastern Block) is now at

the same stage of development as the Maokop Block was at ~4 mya (Baldwin *et al.*, 2012). After the Vogelkop Block, the oldest portion of the New Guinean Central Cordillera is the Maokop Block (Fig. 1.) It is also the highest part of the Central Cordillera, Puncak Jaya reaching 4,884 m above sea level (asl). Mountains have existed in the region of the Maokop Block since *ca.* 12 mya (Cloos *et al.*, 2005). Thick basement sediments indicate that by 8 mya, elevations of up to 2 km asl had been reached, and by 6 mya, elevations of *ca.* 4 km asl existed (Cloos *et al.*, 2005).

The elevation of the Central Block (that part of the Central Cordillera lying between the Hak-Om Divide and the Wau area), is more recent than that of the Maokop, but older than that of the Southeastern Block. The Porgera Intrusive Complex was emplaced in the late Miocene, suggesting that orogenic activity was underway by that time (Baldwin *et al.*, 2012). Uplift of the Southeastern Block is even more recent. The Mt Dayman-Suckling Range (the highest point of the Southeastern Block) appears to have been uplifted during the early-mid Pliocene, between *ca.* 4.6–3.4 mya (Österle, 2019).

The New Guinean fossil record

New Guinea's marsupial fossil record consists of a single possible late Miocene find (Menzies *et al.*, 2008), a single modestly diverse late Pliocene fauna (Hoch & Holm, 1986; Plane, 1967), and a scatter of Pleistocene sites (Flannery, 1994; Menzies & Ballard, 1994; Jackson *et al.*, 2024).

The Miocene fossil record of New Guinea consists of a single, doubtfully dated dentary fragment of a diprotodontid from Yonki, Eastern Highlands Province (Central Block). K/Ar dating of minerals in the breccia adhering to the dentary indicate an age of 13.2 mya. The dentary may well be younger, but volcanic activity in the region ceased around 7.4 mya, providing a tentative youngest date. The dentary is similar in morphology and size to the Plio-Pleistocene New

Guinean taxon *Nototherium watutensis* Anderson, 1937, the phylogenetic affinity of which is disputed. Menzies *et al.* (2008) place it in *Kolopsis* (Zygomaturinae), while Mackness (2012) and Jackson *et al.* (2024) retains it in *Nototherium* (Diprotodontinae).

The only Pliocene marsupial fossil localities in New Guinea occur in the Otibanda Formation, located on the eastern margin of the Central Block. K/Ar dating of pyroclastic rock close to the Watut 3 locality returned an age of 2.9 ± 0.4 mya (late Pliocene) (Hoch & Holm, 1986). Three diprotodontid taxa are recorded from the Otibanda Formation. *Nototherium watutense* is the largest marsupial known from New Guinea. It has also been tentatively recorded from the late Miocene, as well as undated sediments near Nimboran, Jayapura area, Indonesia (Hardjasmita, 1985). *Kolopsis rotundus* and *Kolopsoides cultridens* are both zygomaturine diprotodontids (Long *et al.*, 2002). Species of *Kolopsis* occur in late Miocene deposits in central and southern Australia, while *Kolopsoides* is a New Guinean endemic. Only three extant marsupial lineages, Dorcopsini and Dendrolagini (both Macropodidae), and Dasyuridae, are represented in the Otibanda fauna. The macropodid lineages have complex and disputed taxonomic histories. Kerr and Prideaux (2024) allocate '*Protemnodon*' *buloloensis* to *Dorcopsoides*, as well as placing *Watutia novaeguineae* in Dorcopsini. Regardless of their higher-level classification, neither of these taxa appear to be ancestral to any of the extant New Guinean dorcopsins. *Bohra planei* from the Otibanda Formation is the oldest dendrolagin from New Guinea. It is likewise unlikely to be ancestral to any extant Melanesian dendrolagins (Prideaux & Warburton, 2023). The dasyurid is represented by a dentary fragment with an m2 which was assigned to the New Guinean endemic genus *Myoictis* by Archer (1982).

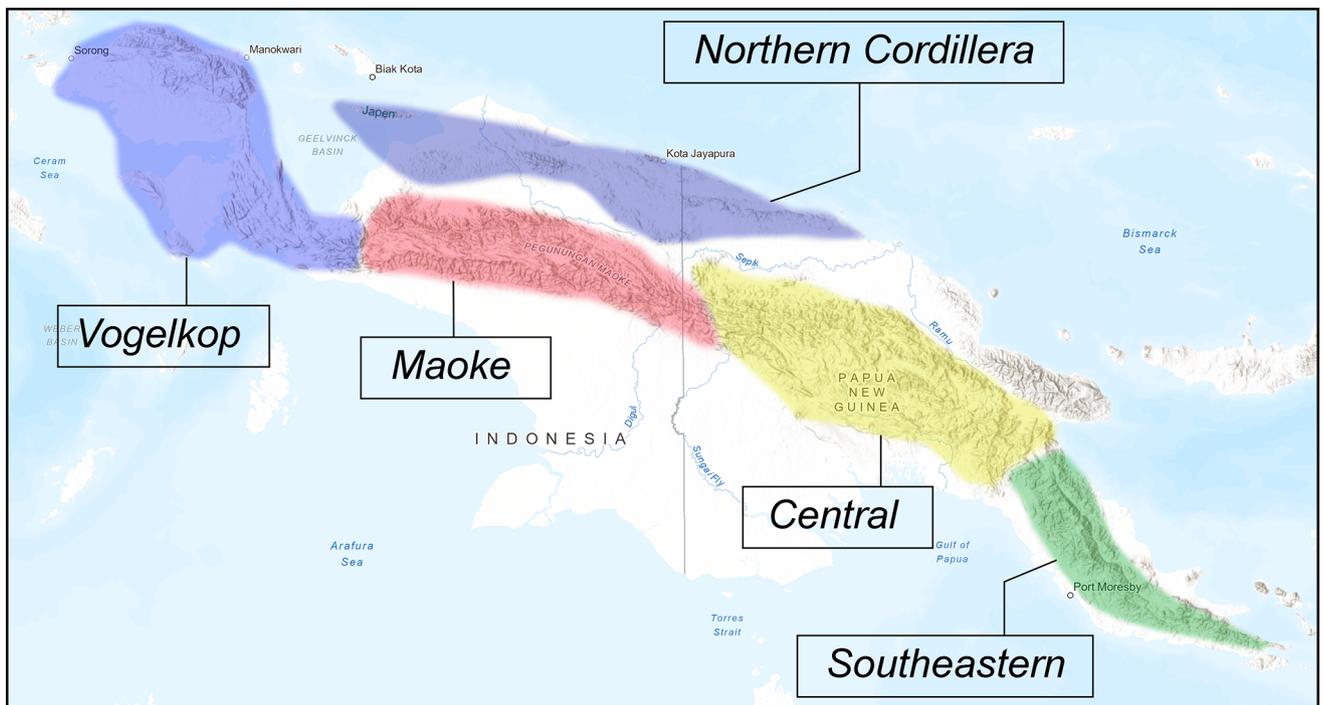


Figure 1. Map of the island of New Guinea, showing the Vogelkop Block and Northern Cordillera (purple), the Maokop Block (pink), Central Block (yellow) and Southeastern Block (green).

Species of *Kolopsis* and *Dorcopsoides* are known only from the late Miocene of Australia and the mid-Pliocene of New Guinea. This strongly suggests a late Miocene migration from Australia into New Guinea, and that by the mid-Pliocene, at the latest, members of these two genera had reached the Central Block, by which time they were extinct in Australia.

Thylacinus (Thylacinidae) is known from late Pleistocene-Holocene archaeological deposits from ‘the Eastern Highlands’, Central Block (Van Deusen, 1963). *Thylacinus* is not known from extensive Pleistocene/Holocene deposits representing subalpine and alpine habitats in the Maokop Block (Hope, 1981; Flannery, 1992, 1999). High elevation, subalpine areas of the Maokop Block offer the most extensive areas of suitable habitat for *Thylacinus* in all of New Guinea, so the absence of the genus there likely indicates that a barrier for *Thylacinus* existed between the Maokop and Central Blocks. Four genera of diprotodontids (*Hulitherium*, *Maokopia*, *Nototherium*, and an unnamed genus) are known from the Pleistocene of New Guinea. *Hulitherium tomasettii* is known from five occurrences, two in the Telefomin area (Maokop Block) and one each in the Hela, Chimbu, and Enga areas (Central Block) (Menzies & Ballard, 1994; Prideaux *et al.*, 2022). *Maokopia* is known from three occurrences (two in the Maokop Block and one from the Central Block (Flannery, 1994; Menzies & Ballard, 1994). An undescribed genus of diprotodontid is known from a single specimen from Mt Kare, Central Block (Menzies & Ballard, 1994). Two genera of extinct macropodines are known from the Pleistocene of New Guinea: *Protemnodon* and *Nombe*. Kerr & Prideaux (2022) reassigned *Protemnodon nombe* to the new genus *Nombe*. The genus *Nombe* is known from a single occurrence in the Central Block (Flannery *et al.*, 1983). *Protemnodon* is represented by two (*P. tumbuna* and *P. sp.*) or possibly three species. Kerr *et al.* (2024) synonymized *Protemnodon hopei* with *P. tumbuna*. If this synonymy is accepted, *P. tumbuna* is known from three occurrences, one in the Maokop Block and two in the Central Block (Flannery, 1994; Menzies & Ballard, 1994). An unnamed species of *Protemnodon* is known from the North Coast Ranges (Koungoulos *et al.*, 2024).

It seems likely that, other things being equal, larger-bodied marsupials should be able to disperse more readily than smaller-bodied forms, leading to less geographic diversification. Conversely, taxonomic lumping may occur in classifying partial fossil remains. The fact that *Hulitherium*, *Maokopia*, and *Protemnodon* are known from multiple occurrences suggests that, at the generic level at least, the Pleistocene megafauna of New Guinea may be relatively completely known (Flannery, 1994; Menzies & Ballard, 1994).

Overall, the fossil record of marsupials in New Guinea is so patchy as to be only marginally useful in investigating the origins of the extant New Guinean marsupial fauna. It is, however, informative in that it supports the hypothesis, as evidenced by the extant fauna, that either a severe filter existed between Australia and New Guinea, or that large-scale extinction has occurred in New Guinea. This is because only two or three extinct Pleistocene megafaunal subfamilies are represented: Macropodinae and Zygomaturinae/Nototheriinae. The following families and subfamilies are notable for their absence from the New Guinean fossil record: Ektopodontidae, Thylacoleonidae, Diprotodontinae, Vombatidae, Phascolarctidae, Propleopinae, and Sthenurinae. Most are abundant and widespread in the late Cenozoic fossil record of Australia.

Molecular studies

Aplin *et al.* (1993) is the earliest molecular study that attempts to elucidate faunal exchange between Australia and New Guinea using divergence times as a guide. It posits major episodes of dispersal of ancestral peroryctids, phalangerids and acrobatids to New Guinea in the early Miocene (*ca.* 20 mya); of some pseudocheirids, petaurids, macropodids and dasyurids in the late Miocene (*ca.* 10–12 mya); and of pseudocheirids, ancestral *Dendrolagus* and *Myoictis* between 4.7–2.7 mya. Diversification within some or all of these clades may, however, have occurred within Australia prior to dispersal to New Guinea.

In the last few decades improvements to molecular genetic techniques and advances in methods of phylogenetic analysis have resulted in a much more comprehensive, robust and detailed understanding of marsupial evolution (Meredith *et al.*, 2009a, 2009b; Mitchell *et al.*, 2014; Duchene *et al.*, 2018). The ancestor of extant Australidelphian marsupials appears to have originated in the Paleocene (66–56 mya), with the diversification of most extant families occurring in the late Eocene and early Oligocene (Duchene *et al.*, 2018). The divergence of many endemic (or near endemic) extant New Guinean genera (*Echymipera*, *Peroryctes*, *Microperoryctes*, *Murexia*, *Phascolosorex*, *Neophascogale*, *Myoictis*, *Spilocuscus*, *Phalanger*, *Dactylopsila*) dates from the mid-late Miocene, except for *Distoechurus* whose divergence from *Acrobates* occurred in the Oligocene (Westerman *et al.*, 2012; Mitchell *et al.*, 2014; Westerman *et al.*, 2016; Kealy *et al.*, 2020). How the extinction of these or related lineages in an increasingly arid Australia impacts these estimates remains unclear.

The divergences of genera with endemic species in both New Guinea and Australia show a more complex pattern, but divergences within genera typically commence in the late Miocene, with the basal lineages often present in Australia (e.g., *Pseudocheirops*, *Pseudochirulus*, *Dendrolagus*, *Dasyurus*, *Thylogale*), or known to have occurred in Australia from fossil evidence (e.g., *Dorcopsis*, *Distoechurus*) (Macqueen *et al.*, 2010; Meredith *et al.*, 2010; Westerman *et al.*, 2016; Eldridge *et al.*, 2018, 2026a). The endemic New Guinean species mostly appear as the result of secondary radiations and date from the late Miocene (e.g., *Pseudocheirops*) through to the Plio-Pleistocene (e.g., *Dendrolagus*, *Petaurus*, *Thylogale*) (Macqueen *et al.*, 2010; Meredith *et al.*, 2010; Eldridge *et al.*, 2018). Regrettably, key Vogelkop endemics remain unsampled in these genetic studies, including *Phascolosorex doriae*, *Microperoryctes murinus/aplini*, *Dactylonax kambuayai/palpator*, *Pseudochirulus schlegeli* and *Pseudocheirops coronatus*, limiting our ability to test our Vogelkop Block origin hypothesis using genetic data.

Morphological evolution

Detailed morphological studies of a few lineages have proved to be useful in discerning phylogenetic divergences. The genus *Dactylonax* is known from three extant taxa, two of which are restricted to Vogelkop. The morphologically most plesiomorphic is *D. kambuayai*, a diminutive species that is restricted to Vogelkop lowlands but may also be present in mid-Pleistocene fossils from central Queensland (Hocknull *et al.*, 2007; Flannery *et al.*, 2026a). It lacks many of the auditory and digital specializations present

in other members of the genus, which facilitate feeding on wood-boring insect larva. *Dactylonax palpator* is a large species restricted to forests above 1,300 m asl in the Arfak Mountains of Vogelkop, while *D. ernstmayri* is widely distributed at elevations above 800 m asl from the Weyland Range to southeast Papua. It is clearly closely related to *D. palpator*, but is even more specialized in its digital and auditory adaptations (Flannery *et al.*, 2026a). *Pseudochirops* is represented in New Guinea by four species, three of which (*P. albertisii*, *P. coronatus*, and *P. cupreus*) are morphologically and ecologically similar and presumably form a clade. *Pseudochirops albertisii* is distributed at mid to high elevations, though with occasional records as low as 300 m (Helgen, 2007) on Vogelkop, Yapen, the North Coast Ranges, and the Weyland Range. It is the most plesiomorphic member of the group, having a relatively elongated skull and unspecialized tail. *Pseudochirops coronatus* is restricted to primary forest above 1,300 m in the Arfak Mountains (Vogelkop), while its putative sister taxon, *P. cupreus*, is widespread above 1,700 m asl on the Central Cordillera from the Weyland Range to the southeast (Flannery, 1995b). Four of the five members of the genus *Spilocuscus* occur on Vogelkop or nearby islands, providing some evidence of a Vogelkop Block point of origination, while the highly morphologically divergent *Microperoryctes aplini*, a Vogelkop endemic, indicates a long history, if not a point of origination, for New Guinean members of the genus.

Taxa with a putative Vogelkop Block entry point

Dactylonax. A recent revision of the genus *Dactylonax* (Flannery *et al.*, 2026a) based on morphological analysis and molecular data, gives us a high degree of confidence that *Dactylonax* originated in Australia, and spread throughout New Guinea from the Vogelkop lowlands. The most plesiomorphic member of the genus, *D. kambuayai*, is restricted to Vogelkop at elevations below 867 m asl. *Dactylonax palpator*, which is restricted to elevations above around 1,300 m asl, is derived from a *D. kambuayai*-like ancestor, while *D. ernstmayri*, which is widespread above 800 m asl on the Central Cordillera and Huon Peninsula, is derived from a *D. palpator*-like ancestor.

Tous. *Tous ayamaruensis* is primarily known from subfossils, but has recently been reported as a living animal (Flannery *et al.*, 2026b). It is distributed in Vogelkop, and the Wutung area (part of the PNG North Coast Ranges, fossil only) and possibly the Torricelli Mts (Flannery *et al.*, 2026b). It is known only from elevations below 400 m asl and is entirely absent from the New Guinean Central Cordillera.

Dendrolagus. *Dendrolagus inustus* is the only member of the long-footed group of tree-kangaroos occurring in New Guinea and is the sister taxon to all other New Guinean tree-kangaroos (Eldridge *et al.*, 2018). It is restricted to lowlands below 1,400 m asl (Flannery, 1995b), and is present in all of the fragments of the putative Northern Cordillera, yet is entirely absent from the Central Cordillera.

Dendrolagus ursinus is endemic to Vogelkop where it occurs at all elevations, and is sympatric with *D. pulcherrimus* and *D. inustus*. It is a member of the short-footed group, but is probably deeply divergent from the other clades.

Pseudochirops. *Pseudochirops albertisii* is present on all the major fragments of the putative Northern Cordillera

(including Vogelkop), where it commonly occurs at elevations above 1,000 m asl, with occasional records from as low as 300 m asl. It can persist in disturbed forest.

Microperoryctes. The genus includes the tiny *M. aplini* (Vogelkop) and *M. murinus* (Weyland Range). No genetic data has been published pertaining to these morphologically divergent taxa, which are similar in body size to mid-late Miocene bandicoots. Vogelkop is also the type locality for *M. longicaudata*, Vogelkop populations of which are unsampled genetically.

Spilocuscus. Four of the five known species of *Spilocuscus* occur on Vogelkop or on nearby islands, suggesting that the Vogelkop Block was the centre of radiation for the genus (Flannery, 1995a, b).

Dorcopsis. Eldridge *et al.* (2026b) reveal deeply divergent lineages within *Dorcopsis*, which is paraphyletic with regard to *Dorcopsulus*. The western species *Dorcopsis muelleri* and *D. hageni* split from the eastern *D. luctuosa* in the late Miocene (6.57 mya), while *Dorcopsulus* split from within *Dorcopsis* in the latest Miocene (5.71 mya). It is likely that the western *Dorcopsis* species arrived via a Vogelkop Block Route, while the eastern *Dorcopsis* species arrived via a Southeastern Block route. As fossils of *Dorcopsulus* sized dorcopsins are known from a 4.46 mya site in Australia, they are likely to have independently dispersed, making it likely that there were multiple independent dispersal events of dorcopsins from Australia. Vogelkop is the only region on New Guinea where two taxa of diminutive montane species (previously *Dorcopsulus*) co-occur (Aplin *et al.*, 1999). All occurrences in Vogelkop are subfossil. More sampling of the modern fauna is required.

Myoictis. The Vogelkop taxon *M. melas* is basal (Phillips *et al.*, 2022). The closest relatives to *Myoictis* are all Australian and have predominantly western or northwestern Australian distributions (*Dasyuroides*, *Parantechinus*, *Dasykaluta*, *Dasyercus*), tentatively suggesting a western (Vogelkop Block) entry for the genus.

Taxa with a putative Maokop Block entry point

Dendrolagus dorianus group. The morphologically most divergent member of the group is *D. mbaiso*, which is endemic to high elevations on the Maokop Block (Eldridge *et al.*, 2026; Flannery *et al.*, 1995).

Dactylopsila megalura is morphologically plesiomorphic, having cranial proportions more similar to basal petaurids than to other members of the genus *Dactylopsila*. It is restricted to a narrow elevational range centred on 1,400 m asl in the Maokop Block (Flannery, 1995b).

Phalanger. The most basal New Guinean member of the group is *Phalanger matanim* (Colgan *et al.*, 1993), which is restricted to mid-elevations (1,400–2,300 m asl) in the Telefomin region of the Maokop Block (Flannery, 1987).

Thylogale. There have been multiple entries from Australia (*T. stigmatica* is likely to be a Pleistocene arrival via the Torres landbridge) The most morphologically distinctive, and possibly the most plesiomorphic of the New Guinean taxa, is *T. christenseni*, which is known only from subfossils from high elevations on the Maokop Block (Hope, 1981). The genus is absent from the Vogelkop Block, but is diverse in eastern New Guinea (where *T. browni*, *T. brunii* and *T. calabyi* occur). A Maokop or Southeastern Block entry, or both, seem possible.

Taxa with a putative Southeastern Block entry point

The *Dendrolagus goodfellowi* complex. This complex includes *D. goodfellowi* (the basal member, inhabits the Southeastern Peninsula, westwards to near Wau), *D. buergeri* (between the Wau area and Mt Bubiari, Sundaun Province), *D. spadix* (low elevations between Lake Murray and the Gulf of Papua), *D. matschiei* (the Huon Peninsula), and *D. pulcherrimus* (Northern Cordillera) (Eldridge *et al.*, 2024). Its most divergent lineages are in the east, with a single lineage reaching Vogelkop. It is possibly absent from the Maokop Block (Eldridge *et al.*, 2024).

Microperoryctes. *Microperoryctes papuensis* is restricted to mid-montane elevations of the Southeastern Block, where it co-occurs with *Microperoryctes ornatus* (Flannery, 1995b). Alternatively, the endemic *M. papuensis* may have evolved more recently from a *M. ornatus*-like ancestor.

Peroryctes. *Peroryctes broadbenti* is restricted to lowlands of southeastern New Guinea and a narrow zone across southeast Papua New Guinea, extending in a latitudinally narrow band along the southern lowlands, west to the Aru Islands. *Peroryctes raffrayanus* is widespread at mid elevations across the Central Cordillera west to Vogelkop. A third species is known from the Maokop Block (Travouillon *et al.*, 2026). The predominantly southeastern distribution of *P. broadbenti* may be evidence of a southwest Papuan origin.

Murexia. *Murexia rothschildi* is endemic to the eastern parts of the of the Southeastern Peninsula, east of the Aroa River (Flannery, 1995b). It is highly divergent within *Murexia sensu lato*, and has no obvious ecological vicars in the rest of New Guinea.

Dorcopsis. The eastern *Dorcopsis* species *D. luctuosa* and possibly *D. phyllis*, are deeply divergent within *Dorcopsis* (Eldridge *et al.*, 2026). Their late Miocene divergence from other *Dorcopsis* and eastern distribution suggest an independent migration to New Guinea via the Southeastern Block.

It is currently not possible to speculate meaningfully about the entry route of *Distoechurus*, *Cercartetus*, and *Pseudochirulus*, all of which have species that are widespread throughout lowland New Guinea. *Cercartetus caudatus*, *Dactylopsila trivirgata*, and *Petaurus breviceps* (*sensu lato*), occur in both Australia and New Guinea. Colgan and Flannery (1992) and Malekian *et al.* (2010) found considerable genetic diversity in *P. breviceps* (*sensu lato*) in New Guinea, suggesting an older migration for this genus. The genus *Echymipera* remains problematic. It has high diversity in southern New Guinea (where *E. kalubu*, *E. rufescens* and *E. echinista* are present), but the most divergent member of the genus (*E. clara*) is restricted to the northern lowlands, where it co-occurs broadly with *E. kalubu* and *E. rufescens*. More genetic analysis is required if zoogeographic patterns within these lineages are to be understood.

The marsupial assemblages of the four tectonic blocks

The Vogelkop Block and 'Northern Cordillera'. This region is unique in New Guinea in having a highly endemic element in its lowland marsupial fauna, *Dactylonax kambuayai* (Vogelkop only) and *Tous ayamaruensis* (Vogelkop and North Coast Ranges) being entirely restricted to lowland rainforests.

Lowland rainforest is (or was prior to logging over recent decades) contiguous from Vogelkop to the southeastern tip of New Guinea. Yet no ecologically similar taxa occur in the lowlands elsewhere on New Guinea, so their absence from the rest of New Guinea cannot be explained, at least at a gross level, by habitat discontinuity or competitive exclusion.

A number of endemics occur in high-elevation forests on Vogelkop (maximum elevation 2,955 m asl), including *Microperoryctes aplini*, *Pseudochirops coronatus*, *Pseudochirulus schlegeli* and *Dactylonax palpator*. Two other endemics, *Dendrolagus ursinus* and the monotreme *Zaglossus bruijnii* occur at all elevations through Vogelkop. A number of other species otherwise known only from Vogelkop (*Dendrolagus inustus*, *D. pulcherrimus*, *Pseudochirops albertisii* and *Tous ayamaruensis*), occur on at least one of a series of isolated ranges across the north of New Guinea, including on Yapen (max. elevation 1,496 m asl) and the Foja Mountains (max. elevation 2,193 m asl) in Indonesia, and the Torricelli Range in Papua New Guinea (max. elevation 1,650 m asl). The distribution of these marsupial clades suggests that in the past a continuous mountain range once extended eastwards from Vogelkop. We refer to this paleo mountain range as the Northern Cordillera, as it paralleled the New Guinean Central Cordillera over its western half.

The nature of the connection between Vogelkop and the Northern Cordillera remains obscure. We have not marked it in Figure 1 because two distinct possibilities exist. One is that the connection lay between the Weyland Range (which is of oceanic arc origin) and the Van Rees/Foja Mountains. The second is that it ran between the Arfak Mountains and Yapen. The Weyland Range is crucial to this problem. It shares *Pseudochirops albertisii* and *Microperoryctes murinus* (possible sister taxon to *M. aplini*) with Vogelkop, suggesting a past connection. Some Weyland taxa are also shared with the Maokop Block (e.g., *Pseudochirops cupreus*, see Flannery, 1995b). No mammal collecting has been done in the Weylands for nearly a century, making it a priority for future research.

The high elevation Vogelkop endemics *Dactylonax palpator* and *Pseudochirops coronatus* are absent from high elevation forests on Yapen, the Fojas and the Torricelli Mountains, suggesting that the Northern Cordillera was bisected by low points which, judging by the distribution of *P. albertisii*, were no lower than 300 m asl. Treeline depression due to glacial cycles, or the Massenerhebung effect, however, may have lowered past vegetational zonation, so these hypothetical breaks in the Northern Cordillera may have been at somewhat lower elevations. Other barriers to the dispersal of marsupials also clearly existed between Vogelkop and the Northern Cordillera, because several Vogelkop taxa that might be expected to occur on the remnants of the Northern Cordillera are absent in both the modern fauna and archaeological record, notably *Dactylonax kambuayai* and *Dendrolagus ursinus*, both of which are widespread and reported from the Vogelkop lowlands.

The majority of the marsupials that occur on both Vogelkop and the Northern Cordillera have a putative Vogelkop Block entry point. The exception is *D. pulcherrimus*, which occurs on Vogelkop, Foja and Torricelli Mts above 700 m asl. It is a member of the *D. goodfellowi* complex, which appears to have entered New Guinea from Australia via the Southeastern Block, migrating thence into the Northern Cordillera and Vogelkop Block. Two marsu-

pials are endemic to the Northern Cordillera: *Dendrolagus scottae*, which is a relatively recently derived member of the *D. dorianus* group (Eldridge *et al.*, 2018), and which occurs only on the Torricelli Mountains and the Menawa Range, and *Petaurus abidi*, the only marsupial endemic to the Torricelli Mountains. It is deeply divergent from other New Guinean *Petaurus* (Malekian *et al.*, 2010) and may have arrived via overwater dispersal while the Torricelli Mountains were islands.

Maokop Block. The Maokop Block appears to have received a basal dactylopsiline (*Dactylopsila megalura*) and possibly species of *Thylogale* from Australia. *Dactylopsila megalura* remains restricted to mid-elevation forests of the Maokop Block. Species of *Thylogale* are absent from Vogelkop, but spread to the Central and Southeastern Blocks, suggesting to us that the Maokop Block joined the Central and possibly Southeastern Blocks prior to connection with the Vogelkop Block. Additionally, the Maokop Block may have been the point of origin of *Phalanger*, which may have spread from there into the Central and Southeastern Blocks. The only montane phalanger to have reached Vogelkop is *Phalanger vestitus*. It occurs at lower elevations than the other montane phalangers, and may have reached Vogelkop at the same time that the murid genera *Mallomys* and *Hyomys* did.

Central Block. The Central Ranges comprise an extensive region including high peaks such as Mt Wilhelm (4,509 m asl). Remarkably, in our analysis, no extant marsupial lineage has a putative origin in the Central Block, suggesting that it may have lacked connections with Australia prior to its docking with the Maokop and Southeastern Blocks. One Holocene extinct taxon, however, may have originated in this region. A species of *Thylacinus* is known from Pleistocene fossils in the Central Ranges. Its systematic status remains uncertain (TF *pers. obs.*). It may be a distinct species which is descended from Pliocene immigrants, or a population of *T. cynocephalus* resulting from Pleistocene immigration from Australia.

Southeastern Block. The Southeastern Block has a scatter of endemic marsupials that indicate a past connection with Australia. It is difficult to date these dispersal events, but the presence of the near-endemic murid genus *Chiruromys* on the Southeastern Block suggests that its marsupial fauna may post-date the arrival of murids in Australia. It is possible that the genus *Peroryctes* arrived in New Guinea at this time, along with *Murexia rothschildi* and the ancestor of the *Dendrolagus goodfellowi* complex. If so, *Peroryctes raffrayanus* spread throughout New Guinea, while its sister taxon *P. broadbenti* remained restricted to the southeast and south. *Murexia rothschildi* remains restricted to the southeast, while the *D. goodfellowi* group has its basal member (*D. g. goodfellowi*) almost entirely restricted to the southeastern block.

Discussion

Baldwin *et al.* (2012) listed a number of regionally significant unanswered questions about the tectonic evolution of the New Guinea region which zoogeographic analysis may help answer. The questions included: (1) how many island arcs existed north of the Australian plate during the Cenozoic, (2) how did they form, (3) what was their polarity, (4) what

was their accretion history, and (5) how are tectonic events in the New Guinea region linked in space and time? Our analysis of marsupial distributions helps shed some light on questions 1 and 4.

In regard to Q1, distributional patterns among New Guinean marsupials are consistent with geological analysis and results in the division of the New Guinean Cordillera into four major 'Blocks' (Vogelkop, Maokop, Central, and Southeastern). These Blocks appear to have originated as islands, each of which has a unique history of connection with the Australian landmass.

In regard to Q4, judging from its high level of endemism and the phylogenetic histories of its lineages, the Vogelkop Block received the earliest migration of marsupial from Australia. Judging from the lack of an endemic murid radiation on Vogelkop, this occurred prior to the arrival of murids in New Guinea, which occurred at some time between the late Miocene and the mid-Pliocene (Roycroft *et al.*, 2022). Prior to the arrival of murids on Vogelkop, a migration of marsupials to the Maokop Block occurred, but it was a highly unusual one that favoured the dispersal of high elevation taxa, over those living at lower altitudes. Among the genera that dispersed were *Dactylonax* and *Pseudochirops*, which gave rise to Vogelkop and Central Cordilleran species pairs (*D. palpator/ernstmayeri*, *P. coronatus/cupreus*). A subsequent dispersal event involved the spread of *Pseudochirops albertisii* and *Dendrolagus inustus* from the Vogelkop Block to the North Coast Ranges of Papua New Guinea. This event involved the orogeny of the Northern Cordillera, which must have connected the Vogelkop, Yapen, the Foja Mountains and the North Coast Ranges into a continuous mountain range. This event was so recent that although some variation in average body size exists between some isolated populations, speciation has not yet been demonstrated among the now isolated populations of these marsupial species.

The genus *Myoictis* offers an intriguing hint to the timing of New Guinea's accretionary history. Its putative point of origin is in Vogelkop and it is known as a 2.9 mya fossil from the Otibanda Formation, on the eastern margin of the Central Block. This suggests that the Vogelkop, Maokop, and Central blocks had established subaerial contact by the late Pliocene.

Temporal constraints. The sequence of dispersal events between Australia and New Guinea, and within New Guinea, as we reconstruct them, are constrained by a number of factors. Molecular studies indicate that the invasion of most if not all marsupial lineages must postdate the mid-Miocene. Two Australasian-wide dispersal events provide the opportunity to constrain the dating of these dispersals. The first is the arrival of hydromyine murids into Australia-New Guinea. Molecular studies date the divergence of Australia/New Guinea hydromyine lineages to the late Miocene (Roycroft *et al.*, 2020, 2022). However, molecular divergence times do not offer unequivocal evidence of entry times of hydromyines into Australo/New Guinea because the lineages may have begun to differentiate prior to their arrival in Sahul, for example in Maluku, Sulawesi, or even further west. The earliest fossils of hydromyine rodents in Australia/New Guinea are from Wellington Caves, NSW and date to the lower Pliocene. The fact that only a single species of hydromyine is represented by dozens of fossils suggests that the site dates close to the time of arrival of hydromyines in Australia (Dawson *et al.*, 1999).

The fact that Vogelkop does not have a radiation of highly endemic hydromyine murids suggests that it received its earliest marsupial migrants prior to the arrival of hydromyines. It is possible that a diverse fauna of marsupials on Vogelkop may have limited opportunities for hydromyine diversification. The Central Cordillera is home to a broad variety of hydromyines, including species of *Anisomys*, *Hyomys*, *Macruromys*, and *Mallomys*. One species each of the genera *Hyomys* and *Mallomys* occurs on Vogelkop, but the Vogelkop populations are only weakly differentiated from their Central Cordilleran relatives, suggesting that the Vogelkop populations result from a Pleistocene dispersal. The North Coast Ranges of PNG, that once comprised the Northern Cordillera, entirely lack these genera. Indeed, thus far the only endemic murids documented from the 'Northern Cordillera' are *Parahydromys rufilatus* and the poorly known *Hydromys zieglerti*. From this we infer that the Northern Cordillera had subsided prior to the arrival of *Hyomys* and *Mallomys* into the Vogelkop.

The second temporal constraint concerns the arrival of *Rattus* in Australia/New Guinea in the early Pleistocene. A few species of *Rattus* (notably *R. praetor*) occur in the lowlands of New Guinea, and a larger number (e.g., *R. niobe*, *R. verecundus*) occur above 1,000 m asl. While *R. niobe* occurs on the Vogelkop, the montane *Rattus* group is entirely absent from the Northern Cordillera. Intriguingly, *Rattus steini* is also absent on the Vogelkop, where it is replaced by *Rattus praetor*. This suggests that the arrival of *Rattus* on the Vogelkop postdates the severance of the contact between the Vogelkop and the Northern Cordillera. Our provisional chronology for mammalian arrivals into New Guinea is as follows:

Vogelkop/ Northern Cordillera. Arrival of *Rattus niobe*, *Phalanger vestitus*, *Hyomys*, *Mallomys* in Vogelkop (**Pleistocene**). Dispersal of *Dendrolagus inustus/Pseudochirops albertisii* to the Northern Cordillera (**Mid Pliocene**). Dispersal of *Dactylonax/Pseudochirops* to the Maokop Block (**Early-Mid Pliocene**). Initial dispersal of marsupials from Australia to Vogelkop (**Mid-Miocene-mid Pliocene**).

Maokop Block. Diversification of New Guinea *Phalanger* species (**Miocene-Pleistocene**). Arrival of *Dactylopsila/Thylogale* (**Pliocene**).

Southeastern Block. Arrival of ancestral *Dendrolagus goodfellowi*, *Murexia rothschildi*, *Peroryctes*, from Australia (**Pliocene**).

Envoi. We consider this work a preliminary assessment. Several important tests of our hypothesis could be made with further fieldwork, the most important of which involve genetic assessment of the numerous Vogelkop endemics whose genetics remain unknown. Species of *Dactylonax*, *Pseudochirops*, *Phascolosorex*, and *Microperoryctes* should be priorities here. Equally urgent is the search for a Tertiary fossil record from the Vogelkop and Southeastern Blocks, especially for small to medium sized marsupials, for it is only the fossil record that can offer unequivocal evidence of the timing of past migrations.

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An Annotated Translation of Georg Stein's, 1933, A Research Trip to the Dutch East Indies

TIM F. FLANNERY¹ , RUDOLF HASLAUER²,
STEPHEN M. JACKSON¹ , AND IAN A. W. MCALLAN³ 

¹ Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

² Independent researcher, Poernbach, Germany

³ Academic Library Services, Macquarie University NSW 2109, Australia

Introduction

Georg Hermann Wilhelm Stein was born in Zittendorf, Germany on 7 April 1897. He became a secondary school teacher who was self-educated in natural history. In 1930, employed by the Botanical Museum in Berlin, he travelled to the Dutch East Indies from 1931–1932. During the expedition he was accompanied by his wife Clara for whom he later named the bandicoot *Echymipera clara*. The highlight of his expedition was an ascent of the Weyland Range in western New Guinea, where he collected at least two mammal species, *Microperoryctes murinus* and *Macruromys elegans*, that have not been sighted before or since. The diaries of his expedition were lost during the Second World War (National Herbarium, Netherlands, no date), making the published account, translated into English here for the first time, a valuable chronicle (Stein, 1933).

In later life Stein became associated with the Humboldt University Museum, Berlin, where his mammal and New Guinea bird specimens are held. During the 1950s and 60s he published on European mammals, including moles and the field mouse (e.g., Stein, 1958). On his 70th birthday the great ornithologist Erwin Stresemann (who had unique privileges to cross the Berlin Wall) gave an encomium which read in part: ‘Now you too have marched with brisk steps over the threshold of old age—a joyful occasion for the circle of your fellow participants and admirers of the long journey you have travelled as a successful, tireless researcher. I have been appointed spokesperson at your beloved place of work because no-one has accompanied your progress as long as I have. It was not mammals that first brought you into the

net of zoological research, but rather birds.’ (Stresemann, 1967). The late Colin Groves told TF of a meeting he had with Stein at the Museum which suggests that relationships with his colleagues were not always rosy. As Stein conducted Groves towards his own office, passing the office doors of other curators, he pointed and said ‘she is a communist; he was a Nazi during the war’, and so on. When they reached Stein’s office, he pulled out a postage stamp which bore the image of Erich Honecker, East Germany’s Head of State, and spat vehemently on it before sticking it to an envelope, saying ‘It is good that they put Honecker on the stamp. I spit on him.’ Stein passed away on 19 April 1976.

Below is a full translation of Stein (1933) in which our edits to his text are in square brackets throughout to include the current taxonomy and other notes. Taxonomy used follows Mittermeier & Wilson (2015) for mammals and Avibase (2025) for birds, with details of the bird collections by Stein available in Roselaar (2003). This translation includes historic language about race and cultural practices. While we would not use this language ourselves, we have retained it here in order to remain faithful to Stein’s original text.

Part I: New Guinea

My journey was intended as a continuation of Dr Ernst Mayr’s expedition to Dutch New Guinea in 1928. It was to consist of ornithological research on several islands in Geelvink Bay, Waigeu Island, and finally the ascent of the Weyland Mountains, the western foothills of the Snow Mountains. Most of the funds were provided by friends of the American Museum of Natural History, New York, at the

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ORCID iD: Flannery, 0000-0002-3005-8305; Jackson 0000-0002-7252-0799; McAllan, 0000-0002-3084-1789

Corresponding author: Tim Flannery tim.fridtjof.flannery@gmail.com

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intercession of Dr L. C. Sanford. My deepest gratitude goes to Prof. Dr Stresemann, whose trust enabled me to undertake this journey. Prof. Dr Diels, Director of the Botanical Museum in Berlin, granted a subsidy for the travel expenses, so that I was able to take my wife with me. Although I still believe that the high mountains of New Guinea, with their demands on physical fitness and willpower, are ill-suited to a European woman, I have not regretted my decision to take my wife with me, and I know that the success of the expedition is largely due to her boundless enthusiasm and constant helpfulness.

After lengthy preparations in the museums of Berlin and Tring, the journey began in early December 1930. The Zoological Museum in Buitenzorg provided us with two taxidermists, including DARNÄ, who had experience in expeditions. Dr Dammerman, to whom we owe our heartfelt thanks for his constant help and care, also provided us with the necessary government recommendations and thus the moral support without which a major expedition in New Guinea cannot function. We made a brief stop in Makassar on Celebes, and eight weeks after our departure from Berlin, we arrived in Manokwari, the capital of Dutch New Guinea.

The day before, we had called at Waigeu [Waigeo]. Gloomy, shrouded in rain clouds and fog, completely covered in jungle, the picturesque limestone peaks of the large island lay before us. Small outrigger canoes, in which dark brown figures with huge hairpieces sat—the first Papuans—swarmed around the ship. To be honest, I did not feel too comfortable when I thought about the fact that we were supposed to go into this eerie, rain-grey, rocky jungle wilderness. We even had a real cannibal from the hinterland of Sorong, who was awaiting trial, in chains on board! Yet the fellow looked quite well-mannered, wore khaki trousers, chewed fruit and looked at everything with eyes that seemed to understand nothing. The Dutch government does not hang such a poor fellow, who acted out of a dark, probably religiously rooted urge, from a tall tree as a deterrent, but instead he is given the necessary number of years of forced labour, ‘service’, as the natives so nicely call it, learns to speak Malay, gets to know European civilization and, if he survives it all, later becomes a great man in his village.

Manokwari

Manokwari is one of the most beautiful places we have seen, especially if you do not know that malaria and dysentery are rife here. Located in a quiet bay, where hundreds of lights from fishing boats flicker on moonless nights, the town is built on terraces, shaded by coconut palms and large Ficus trees. On the coast, under palm trees, are the Chinese shops, the pasar (market) with its colourful bustle of Chinese, Malays, Arabs, and Papuans, with its abundance of bananas, pineapples, vegetables, fish, eggs, and chickens; behind it, separated by a football pitch for the soldiers, barracks, government buildings, hospital, the little church, higher up the houses of the Malays and a few Europeans, well-kept paths, very bright and friendly. Above it all, however, on the other side of the bay, rise steeply from the sea the almost 3,000 m high massifs of the Arfak Mountains, shining blue in the light of the clear sky in the morning, deep green at midday with immeasurable forests and gorges, fading into thunderstorms and clouds in the evening.

We moved into a nice room at the *Pasanggrahan*, the public

rest house, and as soon as my shotguns were unpacked, I set off into the forest early in the morning, eager for action and thirsty for blood. There was remarkably little bird life in the bushes and individual trees in the area. Green honeyeaters with yellow ear coverts (*Meliphaga analoga*), one of the most common birds in New Guinea, were everywhere; but otherwise I only encountered a pair of black flycatchers (*Rhipidura tricolor* [= *R. leucophrys melaleuca*]) with white superciliary stripes, their long tails fanned coquettishly and moving back and forth like a bird of prey; high in the treetops, several oriole-sized yellow and black starlings (*Mino dumontii*) cawed; a crow, *Corvus coronoides orru* [= *C. orru*], with cobalt blue eyes, flew overhead. In the jungle, the same disappointment! Where were the magnificent birds of paradise that I had seen in the museum cabinets? I could not have known that almost everything had been exterminated in the Manokwari area by the zealous activity of Europeans and colonists. Finally, a small flock of birds the size of jackdaws, with mostly white plumage and black wings, descends upon me in a fruit tree. Their calls, melodious and trumpet-like, pierce the forest. I shoot one down: it is a *Cracticus cassicus*, also extremely common in New Guinea and hated by all museums. I shoot another *Manucodia ater*, a bird of paradise, but one that looks desperately like a blue-black crow, and two pitiful white giant cockatoos (*Cacatua triton* [= *C. galerita triton*]).

Gradually, however, you learn how to move around in the jungle. I discovered the little flycatchers *Todopsis cyanocephalus* [= *Malurus cyanocephalus*], which slip through the dense undergrowth almost like blue tits, their tails raised, and I see the first *Tanysiptera hydrocharis*, the light blue kingfisher with the red beak and long central tail feathers, swinging on a thin liana. I watch the little *Aegotheles wallacei* [= *A. wallacii*], which at first glance resemble night swallows, as they flit over the alang-alang of the secondary bush at dusk like large spinners, encountering insects in flight, and even catch some of the rare *Pycnopygius stictocephalus*, large, dark-coloured honey eaters with white stripes on their heads. In the evening, the metallic tjük tjük of the nightjar *Caprimulgus macrurus* can be heard from the roofs of the houses; I have never heard it make the purring sound that is characteristic of our species. I try to catch owls and in doing so shoot a poor chicken in the darkness that was sleeping in a tree, as is customary for chickens there. Later, when I was out at night with my shotgun, it happened to me several times that a dark figure approached me, pointed to a tree and whispered: *Toean awas, ada ajam!* Sir, be careful, there are chickens sitting up there!

One morning, an incredibly dirty Papuan stands in front of the *Pasanggrahan*, grinning from ear to ear. His name is Josepho. Josepho—apparently, he is from Arfak, but of course already a Christian—offers to hunt birds for me. He proves to be very skilled, stalking and shooting with great accuracy, so I decide to take him with me to Yapen. After three days, he asks me for an advance, describing the great hardship his family is in, and receives a guildler. The next morning, he does not show up; as we pass his hut, Josepho is sitting outside, dressed in brand-new swimming trunks, squinting in the sun and looking at me with great cheerfulness. One of his children is sick in the hut, and he cannot leave. The next day, in response to my energetic representations, he explains briefly and concisely that he no longer feels like it and asks for the rest of his earned money. I never gave him an ‘advance’ again.

The island of Yapen

On 17 February 1931, we steam through Geelvink Bay in glorious weather on the small government steamer *Anna* to our first working area, the island of Yapen (Japen) or Jobi, as it is always incorrectly named after the small town on the north coast. In the evening, we drop anchor in a quiet bay on the small, wooded rocky island of Miosnom. The steamer has only one *djuraggan*, a Malay captain who is forbidden to sail at night. The next morning, the long island of Yapen comes into view. To my displeasure, it lies there just as gloomy and rain-shrouded as Waigeu. We sail past Anssus, further west, the former centre of bird of paradise hunting. Here there is only hilly country with gentle slopes. We want to go to Seroei, in the eastern part of the island, the seat of the only Dutch government official in Geelvink Bay. A small bay, protected by rocky islets, a hot and humid coastal plain with lots of sago swamps, crisscrossed by muddy watercourses, open only to the coast, otherwise completely enclosed by mountain ranges that run down to the sea—that is Seroei. The natives here were once considered particularly dangerous and treacherous. On the coast today, they naturally wear cotton cloths bought like everywhere else, and are lazy and indolent. We met better people in the mountains who still knew how to use bows and arrows. There they were still quite reserved, dismissive, even gloomy. The Dutch official had even given us a few policemen as a precaution, but this was not necessary. Some smaller tribes are said to still roam the vast interior of Yapen as nomadic hunters. Everyone knew Dutch money, and most spoke Malay.

Yapen's characteristic bird is *Paradisaea minor jobiensis*, the bird of paradise with its magnificent chrome-yellow tail, the main object of the former ornamental feather trade. If the birds ever suffered in their numbers due to hunting, the gaps must have closed surprisingly quickly. I even saw one in Kampong, the native village, flying slowly over the wide paths, so that the yellow plumage swayed up and down, almost like the white fins of a strange ornamental fish. But hunting is generally not that easy. The old magnificent males are usually found in the company of uncoloured animals. A flock calls through the jungle with *quao quam* and *qua qua*. Slowly, feeding here and there, hopping, fluttering, gliding down into the undergrowth, shooting upwards, the company moves through the forest, and suddenly, to one's surprise, something flashes in the green of the treetops for a moment: an old male! It is gone, covered by thick branches. Now it flies on. Like a white and yellow veil, the bird glides along, disappearing into the shadows. It flashes again; he has spread his decorative plumage! The shotgun trembles, your knees fly with excitement as you rush down a slope where you get caught in vines, where you must bend bushes aside and watch out for boulders so they do not start sliding. Once the younger, uncoloured birds, in the midst of which the old male tends to keep, have spotted the hunter, you can follow the birds for a good hour before you get a shot, unless you prefer to give up, because there is a danger of getting into terrain where it is difficult to find your way home in the heat of the hunt. This happened to me once in Waigeu while pursuing *Paradisaea rubra* and caused me some very unpleasant hours.

In the mountains, my highest camp is located at 1,000 meters above sea level, next to a stream that babbles coolly and clearly along its rocky bed, shaded by bamboo, tall ferns,

and climbing plants. *Paradisaea* no longer lives up here, but another bird of paradise does: *Diphyllodes magnifica*, along with a host of small, colourful fruit doves (*Ptilinopus*); the small red nectar-feeders *Myzomela cruentata* are common here, as are small *Gerygone* species (*G. palpebrosa*, *magnirostris*, *chloronota*), which roam the treetops like leaf warblers. The small silky blue flycatcher *Todopsis wallacei* [= *Sipodotus wallacii*] lives low in the bushes. From the dry peaks of the jungle trees, *Hemiprocne mystacea* glides down like a giant glider and floats through the air in an ethereal flight.

One afternoon, a few old men from some remote mountain village carried a large red cuscus (*Phalanger maculatus* [= *Spilocuscus maculatus*]) on a pole, to which they had simply attached its long naked prehensile tail to the wood with raffia. They did not speak a word of Malay, and the only coin they knew and naturally demanded for the animal was a 'ringget', the largest Dutch silver coin worth 4.25 marks. Of course, I refused this outrageous demand, especially since we already had enough work (the table was full of birds and bats) and a red cuscus, tied to a log, was already waiting for its fate. The group of gaunt patriarchs sat sullenly apart, whispering among themselves with toothless mouths and glaring at me. You could tell they were already annoyed at having come here in the first place and now having to put up with being led around by the nose despite their dignified age. Now it was clear that these white men were all a bunch of swindlers! When they were young, strangers were not allowed to come here, so business would have been concluded quickly; but those good old days were gone, here as everywhere else! My people showed them other types of money, and again there was endless discussion. The guilder coin, also quite large, found favour in their eyes. I did not really want to pay more than the usual price, namely half a guilder, but in the end, not least for psychological reasons, I agreed to pay 95 cents, a nice pile of small change. In vain, they did not even glance at me, said a few words to the people in Japanese and loaded the poor couscous back onto the cart. Barely 50 meters from our camp, in the stream bed, so that we could see it, they beat it to death and roasted it on the spot, out of malice or protest.

Numfor

After a seven-week stay, we leave Yapen with a haul of over 600 birds and 300 mammals. On the return journey, we make a short stop at the small island of Numfor, almost always mistakenly referred to as Mafor, where I hastily shoot a few of the large fruit doves (*Ducula geelvinkiana*) for supper. My wife spots one of the charming, finch-sized green dwarf parrots *Micropsitta geelvinkiana* sitting on a tree trunk, we continue to observe the deep blue long-tailed kingfisher *Tanysiptera carolinae*, so that when the Dutch government official visits the island on an inspection tour sometime later, we join him without further ado, especially as this detour costs almost nothing. Numfor lies in Geelvink Bay on a flat base made entirely of coral limestone. There are no elevations, and the limestone, only sparsely covered with humus, is visible everywhere; nevertheless, the vegetation is truly tropical in its lushness. Unfortunately, the bird fauna did not live up to what it had promised during our first brief visit and can be described as extremely poor. More impressive was the number of individuals. Everywhere, large grey-blue

fruit doves (*Ducula geelvinkiana*) sat in small flocks on the jungle trees, interspersed with literally flocks of various *Ptilinopus* species, small green and colourful fruit doves. The endemic starling *Macruropsar magnus* [= *Aplonis magna*] could have been caught in any number, as could the beautiful bright red parrot *Eos cyanogenys* [= *E. cyanogenia*] with blue cheeks and yellow wing mirrors. The blue of the equally endemic *Tanysiptera carolinae* shone everywhere in the primeval forest.

However, I have very bad memories of the Numfor people; they seem to have reached the peak of indolence. It was impossible to find anyone who was willing to hunt for me, let alone anyone who could do so. When I asked children to help me find a bird that had fallen into dense undergrowth, they explained that there were poisonous snakes there and they had no intention of going in. A man came back from the sea with a few fish he had caught. I wanted to buy one from him, but he calmly explained that he would eat them all himself. On this occasion, I had a minor tantrum, summoned the kapala (village chief) and demanded that he get me some fish for tomorrow. This good man, instead of going himself, naturally first ran around the village, perhaps hoping to find someone else who could be burdened with this task. In the end, however, he had to make the effort himself. We had taken an older boy from Manokwari with us as a ‘jack of all trades’, or perhaps more accurately, a ‘jack of none’, simply because he came from Numfor and claimed to know his way around there. This was indeed the case. When he accompanied me on the hunt and was supposed to search for a shot bird, he often claimed that I had missed, or that the bird must have flown away, or that it was impossible to find. Until I realized that this cunning rascal was sitting peacefully in the bush or only going where his dirty but precious brown skin would not be damaged. I then felt compelled to do some ‘retrieval exercises’ using a sturdy stick that I quickly cut down. In any case, saying goodbye to Numfor was not exactly difficult for us.

Waigeu

To get to Waigeu, we took the Dutch K. P. M. steamer from Manokwari, but only travelled as far as Sorong, a small island on the north-western coast of the Berau Peninsula. From there, we wanted to save on the rather high steamer fare and entrusted ourselves to a small, very small government motorboat for the journey through the Dampier Strait. From early morning until dusk, we rocked back and forth between Salawatti, Batanta, and Waigeu. The *djuraggan* naturally had no idea where we were, but to our relief, he finally brought us—the heavy seas had calmed down in the afternoon—if not exactly to our destination, then at least to Saonek, a small island opposite Waigeu, where I first thoroughly savoured the pleasant feeling of having solid ground under my feet again. The engine had already stopped working on the way there, so I instructed the people to fix it before our departure the next morning. When we were about to board, of course, they had not even started. They certainly could not understand why I expressed my displeasure so vividly. Strange people, these Europeans! Does it really matter whether you sail now or work on the engine? Everything will work out in the end!

We chug along the coast of Waigeu. The green hilltops and wide gorges lie there in the sunshine. Today, the sea is one big reflection of light. Two, three, five sea eagles glide slowly far

out to sea, where fish leap out of the water. On the seabed, we see, as if through clear glass, a fairy-tale carpet of colourful corals, blue starfish, green seaweed, and schools of coral fish in incredible colours, swimming calmly through these meadows. Soon we are travelling along steep cliffs, where the trees lean over and reach into the sea with their branches, soon the black flat edge of mudflats stretches out before our eyes, covered with the stilt roots of the *Rhizophoras*. It becomes more mountainous; a rock gate opens; we enter Majalibit Bay. Fjord-like steep walls rise menacingly to the right and left of the narrow road, hung with dense jungle full of towering palm trees. Often, we pass under overhanging rocks covered with ferns and orchids, whose large flowers, purple with dark spots, nod downwards. Full of trepidation, we remain silent until the blue sky shines again.

We are now deep inside Waigeu. We cross the small ‘sea’ to Kampong Warmek, where we will stay. Even from a distance, we can see a large gap in the giant jungle on the coast, which we are heading towards. A rickety jetty shows us the way, and now we know: we have arrived. A prau disappears, seemingly shooting into the jungle. From the shore, muffled honking sounds reach our ears, but nothing approaches. With the help of the Administrative assistant, the Malay administrative official whom the Lieutenant Governor of Sorong has kindly provided us with, we climb ashore. A brown-skinned man in a cotton jacket and trousers comes running up, breathless and appropriately dirty, of course, for who could have expected such distinguished visitors—the Kapala Kampong, the village chief. With his hand on the area where his heart should be, his back bent and his knees crooked, he greets us with complete subservience—although inwardly, of course, he wishes us to all the devils. The village lies as if dead: the entire population has fled into the forest! People here seem to have a very guilty conscience! The Kapala leads us into his hut and brings us roughly assembled bamboo chairs; and there we sit, with the utmost dignity, sweating, because there is a terrible, humid heat in this village surrounded by swamp forest.

We now make it clear to Kapala that I ‘only’ want to shoot birds here and need porters for the trek into the mountains. He is visibly relieved and promises everything. A hut is cleared for us. We are given double portions of quinine, as the place is swarming with mosquitoes, and then we get to work. The village is surrounded by secondary forest with a rich bird life. From afar, you can already hear the humming *hum hum hum hum* of the large fruit doves *Ducula pinon*; the *budhu budhu* of the small green *Ptilinopus pectoralis* [= *P. viridis pectoralis*] with its grey head and red throat patch, and the loud chirping of the *Sauromarptis gaudichaud* [= *Dacelo gaudichaud*], the loudest screamer among the kingfishers, his *kirr kirr kirr kek kek kek*. Add to that the trill of the small ochre-brown kingfisher *Syma torotoro*, the mocking call of the black fork-tailed drongo *Dicrurus bracteatus*, parrot calls, and we have the whole jungle concert. *Oriolus szalayi* may join in, and *Philemon novaeguineae* [= *P. buceroides jobiensis*], the large honey eater; the other rarer species are quite silent. Only at dusk does the plaintive call of *Melidora macrorrhina* [= *M. macrorrhina*], the large kingfisher with a hooked upper beak, ring out. Rarely and sporadically, the calls of small birds can be heard. At the edge of the village, the blue-black crow *Corvus coronoides orru* [= *C. orru*] calls out its *ra ra ra ra roaaa*; from the mangrove forest, a

similar but different sound echoes: *ö ö ö ö, ga gock, ga gock*. There is already a second crow, but it is larger; agile, bird of prey-like, it swings through the treetops and lands on the highest peak. I sneak after it through the mangrove forest. With every step, bubbles gurgle from the black mud, small crabs scurry over the roots of the mangroves, the air is foul and humid, but I get my crow: it is *Macrocorax fuscicapillus* [= *Corvus fuscicapillus*] with a dark coffee-brown head, noticeably larger than *Corvus*.

The Malay official from Waigeu, who is based on the north coast, visits us and asks about my wishes. He has brought his shotgun with him, a venerable muzzle-loader with an enormous barrel, made in Germany. The next morning, we set off together into the mountains to hunt for the *burung merah, Paradisaea rubra*, the red bird of paradise, endemic to Waigeu. A native who knows a courtship tree leads us. The path first leads through swampy coastal jungle, then into hilly country. Here, for the first time, I hear the mating call of the *Goura cristata*, the great blue crowned pigeon: it is a deep humming sound like *mm mm mm*, also two syllables like *mmpe*. The bird, which is the size of a black grouse, flies off, its wings clapping loudly together, but only on the first few beats, then it continues its flight silently. Green flycatchers, *Microeca papuana* [= *Devioeca papuana*], attract with a soft arpeggio-like *drü drü drü*; a series of soft whistles of equal pitch bubbles out of the undergrowth, and *Monarcha guttula* [= *Symposiarchus guttula*], a flycatcher with the appearance and behaviour of our reed buntings, including their tail twitching, flies in—a harsh screech, characteristic of all *Monarcha*, then the bird notices us and flees back into the darkness of the ground vegetation.

Our guide points to a huge, dry tree: this is where *Paradisaea* is supposed to be courting. From a ravine above, from the treetops, the calls of the females and young bird resound: *ka ka ka ka, ko ko ko, kwao, kwao, kwe, kwe kwe*, it sounds like many voices. Powder, a wad, shot, another wad is laboriously stuffed into the muzzle-loader, the whole thing is tamped down with the ramrod, and we are ready to go. Sure enough, a male is already flying into the courtship tree. It sits high up, hopping and spreading its wings. The bird moves tremulously, now it looks as if it is swaying, then suddenly it hops onto the next branch. The assistant sneaks around the tree, and already a second male is there, but he still does not shoot. The calls of the females and young birds echo from all around. I am now trembling with excitement. I can hardly hold the shotgun. Why isn't the guy shooting yet? Finally, finally, he takes aim—and lowers his gun again, because the birds are hidden by thick branches. The bang of black powder rolls through the forest; my guide has hit his target, and I hold the first *Paradisaea rubra* in my hand, this magnificent creature with a velvety green throat shield, green feather buttons on the front of its head and long decorative feathers like spun red glass.

All the birds have fallen silent. Pangil, pangil, call, call! whispers the assistant to the native. He closes his nose with his fingers, and *nä nä* echoes nasally through the forest, repeatedly, until the chorus of birds of paradise becomes loud again and the second male jumps and dances in the tree. I am far too excited to shoot and must watch again as the official brings it down.

We have yet to find any trace in the plains of the most beautiful bird of paradise, which otherwise only inhabits

the island of Batanta, the small *Schlegelia respublica* [= *Diphylloides respublica*]. The bird with the bare, bright blue crown is called 'Mankombon' by the natives. It lives only in the mountainous interior, and we collect many specimens there, but I have been unable to learn anything about its life. It is always seen, suspicious and very shy, as a black shadow—with a bright yellow collar—darting through the undergrowth and disappearing.

We visit the Lam Lam Mountains in northern Waigeu, go to Kampong Liunssok, located in a vast sago swamp, then to the mountainous Lupin Valley, always on the lookout for the *Aepyodius bruijni* [= *A. bruijnii*], a large bird that no collector has yet found on Waigeu. Only the native hunters of the bird of paradise dealer BRUIJN from Ternate have shot this strange animal and given Waigeu as its location. It is likely that there has been a mix-up regarding the location where it was found, and that the animal's home is somewhere on the Berau Peninsula.

With a haul of around 600 birds, we leave Waigeu after a seven-week stay and return to Manokwari to prepare for our journey to the central mountains of New Guinea.

Departure for the Weyland Mountains

Travelling in New Guinea is a cumbersome and time-consuming affair. Perhaps Kant had formulated his conception of time differently here, attributing to it not only transcendental but also empirical ideality. So, to get from Manokwari to the southern tip of Geelvink Bay, about 250 km, took us over two weeks. First, we are treated once again to the thoroughly enjoyable journey via Numfor and Yapen. From 6 July onwards, we wait patiently in Seroei, the main town on the island of Yapen, to continue our journey. The resident of Amboina was supposed to come and may have wanted to use the government steamer, so the steamer had to be there.

At midnight on 17 June 1931, it finally began. The small coastal steamer with the affectionate name Yvette was packed with people, including a whole collection of young girls from the Waroppe coast, all wearing huge hair ornaments, which constituted the bulk of their clothing, not to mention a few glass beads and the decorative scars on their backs. They had been supposed to dance for the resident, who ultimately did not show up, receiving a very warm ovation, and now, since unmarried young ladies do not yet go out alone there, they were being transported home with their numerous male entourages, who had attached themselves to the back of the steamer with a few praus. It was a lovely jumble; we sat as if in a packed herring barrel, only with different smells. Where my people were, where the luggage was, only Allah knew. In any case, the anchor finally rattled, and we fell asleep reasonably calm, only to wake up quite abruptly.

Little Yvette writhed as if in severe stomach cramps, breakers crashed overhead, bright flashes of lightning were followed by rumbling thunder, accompanied by the occasional screams of fear from the forty Papuan girls. The prau with its men had already been cut loose; heaven knows how they got home! In the end, we had nothing to complain about except the loss of the non-metal part of our tableware.

In the morning, however, the sea was once again infinitely calm, its surface trembling slightly, sunlit and blue. We sailed down the eastern shore of Geelvink Bay and marvelled

at the immense coastal plain stretching endlessly like a green forest sea, until clouds and mist blocked our view. The central mountain range must have been there, and I will always remember how, in the late afternoon, the walls of clouds suddenly parted, the sun flooded through and we saw mountain ranges of gigantic power and imposing dimensions: the snow-capped mountains of New Guinea! Was it seconds, minutes, or was it a mirage? For already the cloud cover had closed in again. But anyone who has seen these mountains once will never forget them; they will be captivated by them. Wainami (Nabire), at the southern tip of Geelvink Bay, is the seat of the Malay administrative officer who had been entrusted with the 'staging' of our train journey. The kampong is a typical coastal Papuan village, carved out of the jungle and towered over by coconut palms. Swallow-tailed kites (*Artamus*) rest on their giant fronds, two or three at a time; here and there, one of the birds swings itself off, glides into the air without flapping its wings and returns to its old place in a gentle arc. *Cinnyris*, the shimmering nectar feeders, buzz tirelessly in the flowering bushes of the natives' gardens; on the giant wall of the jungle in the background, large cockatoos shine like white feathers. Here and there, one glides into the soft twilight green of the forest. Above it all, however, a colony of black starlings (*Aplonis metallica*) make a racket, nesting in a giant tree that stands in the middle of the village. The branches bend under the weight of the pouch nests in the treetops. The kampong consists of palm-leaf-covered huts on stilts, under which pigs, dogs and chickens seek shade. Many of the men can be seen with shaven heads, all of them wearing purchased cotton rags around their hips; none of them carry bows and arrows anymore; the women, however, are 'decently' covered up to their armpits.

And here, where a dull layer of European civilization already covers everything, come three girls, young, swaying as they walk, Polynesian women, without a doubt. Only a dark blue cloth wraps around their hips, tucked in at the back and floating down to the floor like a long train. Red strings of pearls around their slender necks, their long, shiny hair tied up. As I ask them with a smile where they are from and where they are going—they do not understand, but they know what I mean—one of them steps up to me, completely uninhibited, and points to a distant island in the sea. I see her slender bronze arm and feel that Aphrodite, the goddess born of foam, also rose from the waves here.

Meanwhile, my porters' convoy has assembled, brought in from all the accessible villages, about 75 men who speak no fewer than six languages, almost all of them coastal people, skilled sailors. But there is also a group of Tarungares among them, giant figures with the bodies of athletes. They are only coming along because they are forced to and unwillingly. Their tribesmen still live in the hinterland of Geelvink Bay as nomads without permanent homes, true big game hunters of cassowaries and wild boars. The luggage is loaded onto 12 praus, and for two days we travel along the coast with oars and bast sails to the mouth of the Wanggar, the starting point of our trek into the Weyland Mountains. On the way, we see nothing but jungle, jungle on the coast. Once we glide past a Tarungaresen camp. As the praus pass by, everyone flees into the forest, last of all a Papuan woman, a piglet under her arm, a second one and a little dog at her side. The broad laughter of our boatmen accompanies them.

River trip

In Kampong Wanggar, the praus are once again carefully overhauled, the luggage is tied down securely, considerable quantities of coconuts disappear into the deep holds of the vessels, and each porter has taken two weeks' worth of sago with him. Already, the praus are shooting out of a quiet bay into the stream, the first large jungle river in New Guinea that we encounter.

A wide bed, sandbanks in it, on which dead giant trees have washed up, everywhere pairs of black starlings *Aplonis cantoroides* on them, which now have their nests in the hollows. The whole area we are travelling through is covered with forest. Soon it becomes a lighter, lower river forest with casuarinas and acacias, breadfruit trees with large, glossy leaves, isolated clumps of tall reeds, and areas of alang-alang grass; soon dense rainforest approaches the steep bank, and we marvel at the smooth trunks of the giant trees rising, their tops interwoven with lianas, vines, and epiphytes in lush abundance.

At midday, everyone rests on the pebbles of a dry bank in the riverbed, letting the sun shine on their naked brown bodies, dipping dried sago into coconut water and feeling happy. From the forest on the riverbank, the *quao quao* and *quā quā* of the bird of paradise can be heard, and for the first time, the two-syllable *tjui tjuo* call of the bird of paradise *Ptiloris magnifica* [= *P. magnificus*] rings out, to my ears the most beautiful bird song in New Guinea, filling the entire forest with its rich tone. A flock of small grey weaver birds (*Munia castaneothorax* [= *Lonchura castaneothorax*]) sits on the *alang-alang*, the first representatives of the [bird family] Ploceidae that I have seen, for like so many other species, they have not made it to the islands of Geelvink Bay. Wren-like with their tails raised, completely black with white wing mirrors, a pair of *Malurus alboscapulatus* slip through the *alang-alang*, a flight of large starlings, golden yellow and black, falls into the bush forest (*Melanopyrrhus anais* [= *Mino anais*]), and my taxidermists, who consider their day's work with the contemplative prau trip to be finished, look less than pleased when I reach for my shotgun.

Today we reach the mouth of the Djalau River, which flows calmly and deep green into the Wanggar, covered by the crowns of giant trees. Soon tarpaulins and tents are pitched; from the jungle come the sounds of our boatmen's machetes as they gather poles and bushes for their simple shelters. Towards evening, we head back into the jungle. Rain-damp black foliage dampens our steps, twilight reigns and a solemn silence prevails, saplings entwined with tough vines and lianas, snaking upwards, hinder our progress. And here the delicate rattan palm (*Calamus*) climbs and entwines with its beautiful pinnate leaves ending in terrible barbed whips, whose loveless embrace everyone fears.

The stage of absolute speechlessness on such occasions has long since been overcome, as has swearing. But at that moment, one might think of the Bible and the Book of Job, about the righteous man who also had to suffer so much. We struggled on like this for six days. What remains with me is the memory of the heroic deed of a Papuan. Our prau began to spin in a whirlpool and hurtled sideways towards the steep bank with the unwelcome prospect of being smashed to pieces, and above all—the shotguns were in our vehicle! Everyone hung onto the outriggers and tried to brace themselves against the boulders at the bottom

of the river. Then, in dire straits, on the brink of disaster, one man threw himself onto the bank, braced himself with all his might against the speeding prau and absorbed the force of the impact with his own body. Not a word about it, not a movement in his brown face, we continue. We too remain silent. My altimeter reads 200 m. The Wanggar now shoots between dark rock walls from which water trickles, lush ferns and orchids hang down and large white balsam flowers shine. *Monachella mülleriana* [= *M. muelleriana*], the black, white, and brown water flycatcher, sits on the bubbling boulders in the stream. Here, the praus are pushed under quickly constructed roofs. The river journey is over. From afar, the muffled nasal *nā nā* of the large-footed bird *Talegallus fuscirostris* [= *Talegalla fuscirostris*] can be heard. A flock of thrush-like brown birds hops, climbs and flies through the vines of the treetops: *Pomatorhinus isidori* [= *Garritornis isidorei*]. There on the ground, running like a chicken, a large bird disappears into the bushes and twilight, its long tail folded like a roof. It is the beautiful, iridescent ground dove *Otidiphaps nobilis*. A small bird appears, its long tail spread coquettishly, now flying towards a vine, now fluttering along a broken trunk. But it always stays close to the ground: the flycatcher *Rhipidura maculipectus*. It moves low among the huge *Araceae* leaves that cover a trunk up to the treetops; brown, rat-like, it runs across the ground, wanting to cross the trunk that has fallen across a jungle stream. I just manage to shoot it, and my companion brings me a brown marsupial shrew, black and yellow-red with longitudinal stripes on its back (*Phascogale melas* [= *Myoictis melas*]). As early in the morning as the *krükrü* of the colorful pitta (*Pitta mackloti* [= *Erythropitta macklotii*]) sounds from the forest and flocks of parrots screech across the river, life returns to the camp. Tents and tarpaulins are taken down and packed into the boats, and on we go. What remains are porters' huts, pole frames, and a few smouldering fire pits. We have not yet left the plain, but the force of the current is increasing, and it is no longer possible to move forward with oars alone. The praus are pulled through the current by long rattan ropes that the people cut in the jungle yesterday as a precaution. Some of the crew wade in the water, hanging between the outriggers of the prau, pushing, lifting, and shoving. Only the guide stands in the prau and keeps an eye out for whirlpools, blocks, and logs hidden by the water. When the water is deep, everyone climbs into the prau like lightning, and with tremendous effort, they row across. And in doing so, they must manoeuvre from one bank to the other. The people's performance is admirable. Often enough, the crew of a second or even third prau must be called in to help conquer a rapid. There is a huge log lying diagonally across the riverbed. The rushing tide pushes it up and down, and where it ends, there is only a narrow passage to the other bank, through which the dammed water shoots. More rattan ropes are attached to the prau, a few people climb from the bank onto the swaying log and pull from there, others lie down in the rattan ropes from the other bank, and the rest shout enthusiastically and row like mad, so that the outriggers bend and creak. A few more waves crash over the prau, and we were through! The further we go, the more unpleasant it becomes. A prau has crashed into a boulder and developed a crack that needs to be repaired. Every evening, the outriggers are checked and some of them reattached. On the third night, there is suddenly a commotion: *Bandjir, bandjir*, high water! Quickly pull the praus onto the

steep bank! Everyone rushes, pulls, pushes, and clears paths through the bushes on the bank for the praus awkwardly wide outriggers, which bounce and dance in the waves. Shouting, complete darkness. I run around everywhere like a ridiculous, superfluous figure. I can no longer sleep. Again, and again I watch the water rise. If we cannot continue tomorrow morning, everything will lie still, and in the tranquil calm, the porters will consume at least three times more sago than is calculated for the day. And then? Then I will have to break off my march before reaching the mountains! Through numerous such friendly events—and they are as common in New Guinea as showers are here in April—something like a deep Olympic calm gradually descends on my sorely tried mind, and when, for example, in the evening a fellow with infinite caution places the empty petrol container in front of you, in which 10 L of petrol were still gurgling sweetly in the morning, then you just nod your head and say: It's all right, my friend.

March through the low mountain range

For the last time in a while, everyone eats in peace. In large cauldrons, the sago bubbles over huge fires until it boils down to a thick glue. Then everyone squats together in a circle. The tobacco ball moves from the mouth behind the ear, and from their hair, everyone takes out a split wooden arrow with a carved handle, which I had previously thought served as a purely decorative object, 'high in the ideal realm of the useless'. But now, without a thought for the possibilities, they dip it into the cauldron and carefully wrap thick portions of the sticky sago paste around it.

Then it's time to divide up the loads for the walk. Everyone is now remarkably active. The aim is to remember the lightest loads so that you can disappear with them as quickly as possible in the morning. A guy trudges past you, laden with a tin containing cotton wool and other heavy items—all of which are pure extra weight—groaning, and responds to your sympathetic question with nothing more than a nod of his thick Papuan skull. But the next morning, disaster strikes. The porters are already bustling around the luggage, including the brother with the cotton wool tray. He has already had to cut a pole for today! First, you express your regret once again about yesterday's heavy load. He accepts your appreciation with dignity, whereupon you point in a friendly and inviting manner to the heavy tarpaulin, already rolled up and damp from the rain, the sorrowful piece of the entire luggage. Deep consternation now crosses his features. He jumps up and gasps for air, so offended is he, until the diabolical grins of his comrades all around him—even the Papuan greatly appreciates *schadenfreude*—show him that nothing can be salvaged. To reach the Weyland Mountains, we now had to cross several mountain ranges and traverse the Waissai, a tributary of the Wanggar. Then somewhere along the way we would come to the Menoo, a source river of the Wanggar from the Weyland Mountains. Up to that point, the porters were familiar with the land from bird of paradise hunting, and we were able to follow the narrow hunting trails, even though they were almost completely overgrown. On 28 July, we set off with the entire convoy on our march through the jungle, into the low mountain range, which immediately rose steeply to over 1,000 m. After just half an hour, I encountered the people who had been so efficient on the prau trip, resting individually

and in groups, chewing sago leisurely to dry off. I had to persuade them to continue, encountered new groups leaning peacefully on their loads, and so it went on all day. At least we still got far enough, namely to the ridge of the second mountain range. Three months later, I have grown tired of tackling this route, even though my annoying corpulence did not really weigh me down. The bird life here in the low mountain range is extremely poor, the forest is quite light, huge, consisting almost entirely of damar trees (*Agathis*? [= *Agathis labillardierei*]), with sparse undergrowth. All day long, the calls of *Paradisaea* ring out, large-footed chickens call, small flocks of green parrots, *Geoffroyus*, probably *G. simplex*, fly like pigeons through the treetops, the loud flapping of the wings of the large blue crowned pigeons awakens longing thoughts of a full cooking pot—but only forward, forward! Small birds flee from the noise of the passing porter caravan. Every now and then, a *Rhipidura* flits by, its tail fanned coquettishly and its wings hanging down, curious; again and again, I hear the sweet call of my mouse-like, scurrying little brown friend *Crateroscelis murinus* [= *Origma murina*]: *h c h b a*, it whistles softly and melodiously from the tangle of broken trunks, roots and vines on the ground, and sometimes the motif that expresses the name of one of our greatest, sounds modulated and solemn: Bach.

We must call it a day early this afternoon. The sky looks leaden grey through the gaps in the treetops. There is a rumbling in the distance. And as the first heavy drops fall, at least there is a tarpaulin set up to shelter the luggage. My cook WAIKOLE from Ternate—he is supposed to be a hunter and cook—is of course nowhere to be found. Instead of enthusiastically devoting himself to the meritorious task of making coffee, he dignifiedly instructs a few porters on how best to protect his precious camp bed and accessories from the downpour. The fact that some of our belongings are still standing in the rain does not bother him in the slightest. A guy like that has rarely had more than a few copper coins for tobacco in his entire life. But no sooner has he squeezed the first 10 guilders out of someone than he immediately must have a bed frame, a towel, and a pair of cotton trousers, with wide vertical stripes, of course.

The next day, we descended to 400 m and crossed a jungle plateau crisscrossed by countless streams and swampy strips, the system of which will forever remain a mystery to me. The most likely explanation is that it was always the same stream that we waded through an estimated 30 times, from one bank to the other, leaving it once to walk a short distance through the jungle and then returning to it. The forest is filled with thick fog, birdsong rings out from nearby, but you cannot see the animals because everything is ghostly pale. Now it starts to rain, lightly at first, then turning into a downpour; the forest seems to want to dissolve into water and mud. All the leaves flutter in the torrential rain, the whole forest is in a state of trembling excitement, you run, stumble, sink, curse for a while at first, and finally trudge along, a grotesque image of a mule searching for its way in the fog. We then struggled up a 1,400-metre mountain range. In the evening, the blankets were wet, the damp wood would not burn, and we shivered our way into the night, our teeth chattering.

The next morning was cool and clear. There they lay before us, albeit still in the distance, blue chains, promising, exhilarating: our destination, the Weyland Mountains! And I thought I knew how Moses must have felt when he saw the Promised Land. Below us lay a valley through which

the Waissai River flowed. The descent was quick. Menoo could not be far away now. We made our way through the overgrown river forest to the Waissai, which flowed calmly and was soon crossed. Only my protective escort, two Papuan policemen with sabres in wide leather sheaths at their sides, carbines on their backs and gaiters down to their bare feet, had trouble getting through, as no one wanted to help them; and everyone watched with glee as the two heroes poured water out of their carbine barrels. We continued through extensive river forest. Never again have I seen such gigantic jungle trees as there, and we resignedly watched the large hornbills in the treetops, out of reach of our shotguns. Large stretches of alluvial sand crisscrossed the forest floor, traces of violent floods. If the floods from Menoo and Waissai were to pour in here now, it would be impossible to move forward. From then on, there were an extraordinary number of land leeches, which used every crack in our gaiters and even the lace holes in our boots to get to our precious blood. However, one quickly gets used to these tormentors, especially as they are so gentle and painless in their activities.

Several hours passed before we found a crossing over the raging Menoo. The porters did not participate in the search. Apparently, they were not at all happy about us crossing the river. We could understand that, because this was an area they had never been to before. We had been cutting paths all day long. Finally, my brave taxidermist, Darna, found a crossing. Now everything had to be carried across, two or three at a time, with my wife behind, dragged through the current by strong arms.

Stay at Menoo

A wonderful campsite on the other side, high above the floodwaters and close to the jungle. Several meters below us, the Menoo river rushed by. None of the people wanted to help set up camp today; they sat around listlessly and hardly thought about building huts for themselves for the night. Finally, the truth came out: the sago rations had been used up. Some of the people had been starving for two days! That was why they did not want to cross the Menoo! Why bother with all that work when we were going back to the coast tomorrow anyway! At first, I was completely devastated. So close to our goal—the high mountains could hardly be more than three days away—was our expedition going to collapse here? I no longer had the resources for a new venture; all our efforts and struggles had been in vain! I could not deny the difficulty of our situation. What to do with these starving people here in the mountains of New Guinea, where there is no food except for birds and the rare marsupials, where not a single fruit is edible? At noon, I had already seen some porters chewing the woody, bitter seeds of a small palm tree, but I had no idea how bad the situation was. Finally, I told the people that I was prepared to grant their wish and let them return to the coast, which of course made them very happy, because then all the drudgery through the jungle would be over once and for all. Yes, I even suspect that the porters were so careless with their supplies to be able to return home this cheaply. However, I added to my solemn statement that everyone would have to restock their provisions immediately on the coast; I would wait for them at this beautiful place during that time, and then we would continue the march. The two policemen, who also had no food left, were to lead the entire return transport. There was general resentment about my proposal, but since I was

unyielding and also promised them that I would tell the ‘*toean besaar*’ in Manokwari [meaning the ‘big boss’, the assistant resident, the highest official in North New Guinea] about this matter, which would probably result in many soldiers coming, etc., etc., they finally agreed to my proposal, much to my relief. Only the Herculean Tarungares, who had not deemed it necessary to participate in the negotiations, let me know that they had no intention of making the journey twice, that they would stay with me and hunt enough pigs and cassowaries. I saw no way to get rid of these people in a nice way. In any case, the next morning, most of the baggage train set off, accompanied by the two policemen, who were happy to have escaped this eerie situation.

In the afternoon, I saw the Tarungaresen returning to camp in small groups, looking tired; none of them had bagged anything, as is usually the case in such situations. Down at Wanggar a few days earlier, they had shot and eaten several cassowaries without telling me, even though they knew how much I cared about these animals. In the evening, the people squatted and lay under their leaf roofs, some here by the small fire, others there in the dark. The whole situation seemed eerie. I walked through the huts and, to my horror, counted over 30 people. So, around 20 had returned during the day, too lazy to walk to the coast and trusting in my filled rice trays. No one took any notice of me, no one answered, they all sat there brooding, hunger raging in their guts. All it would take was one person to give the signal and we would be lost. It could only be a matter of hours before that happened! My assistants had crawled into their tent—I stood alone facing this hungry horde.

I conferred with my wife for a long time, finally rummaged sorrowfully for my pistol, the only time I did not dislike having it, and summoned the leaders of the people, who trotted bluntly. I explained to them that I would not voluntarily give up a single grain of rice, but if they decided to return to the coast tomorrow morning, I would sacrifice enough of my supplies to feed them on the way. Sensibly (a weight was lifted from my chest!), they accepted my proposal. Everyone immediately received a measure of rice, and soon we were all sitting around the big fire, smoking my tobacco, happy as if nothing had happened at all. My assistants also crawled out of their tent, last of all, the good cook Waikole, but not without first carefully scanning our expressions.

The next day we were ‘finally alone’, and the rest of our stay at Middle Menoo is one of my fondest memories. The river rushed beneath us in wide channels, giant logs washed up and drifted on the stone banks; between the channels, casuarina and alang-alang bushes stretched out. Cool, crystal-clear water bubbled over boulders. There were almost no mosquitoes. How often did I sit on a boulder in the evening, behind us the mountain ranges we had crossed, cloud-covered, fading into twilight. *Harpyopsis* [= *H. novaeguineae*], the giant hawk of New Guinea, flies to its roosting tree in the river forest on the other bank, hornbills fly overhead with a heavy flapping of wings, a nightjar (*Caprimulgus macrurus*) flutters over the alang-alang, and when the last *Trichoglossus* and cockatoo flocks have fallen silent, the large flying foxes arrive with sluggish wings, the polyphonic calls of the tree frogs and the chirping of the cicadas grow louder, fireflies flit rhythmically around individual trees, making them look like large living Christmas trees, and the ever-mysterious New Guinea night envelops everything in starless darkness.

Early in the morning, off on a merry hunt with Teschin and shotgun! My wife stays alone in the camp and works on bellows that could not be finished the day before. The forest lies in twilight, not a bird’s song to be heard, drops fall from the trees, the crowns are shrouded in grey mist, forming a forest above the forest with their epiphytes. Beneath them hang the powerful arches of lianas, and from the ground, young shoots strive upwards towards the light, entwined by vines. Sometimes the tangled undergrowth is almost impenetrable, and whatever flits by there with a flutter of wings flees in haste. Rarely does the eye see a flower on a bush or trunk; only the dusky green of the leaves, in which light reflections play here and there, fills the forest. Only what has fought its way to the light high up in the crowns is allowed to blossom and bear fruit, and then fallen petals cover the ground, large and rich in colour. Here, too, the loud call of *Ptiloris magnifica* [= *P. magnificus*]; *Cicinnurus regius*, the little king bird of paradise with its glass-red plumage, shoots through the treetops, and close to the ground, where the vegetation is sparse, it calls out with a bell-like melody, *ting ting ting*, and responds with a deeper *tōng tōng tōng*. Sometimes the whole forest resounds with these little bells, and yet it takes a long time before I know who is calling. Close to me on the ground, it flutters along, the size of a robin with a bright yellow underside and green back, flying here to a trunk, there to a sapling, disappearing again, and again: *Poecilodryas placens* [= *Gennaedryas placens*]. In the treetops, a rapid *zit zit zit*: already they are chirping away, the tiny parakeets, only the size of a siskin, *Micropsitta pusio*. With *à c f*, easy to whistle, brown and curious, it flies in, *Pinarolestes megarhynchus* [= *Colluricincla megarhycha*], thrush-sized, always morose because it appears daily in the harvest.

Otherwise, most birds in the jungle are extremely shy. No matter how many calls you hear from afar, when you sneak up on them, everything seems dead and deserted. It is as if everything retreats before the hunter’s footsteps and a yawning emptiness gape where he stands. Due to the unfavourable lighting conditions and the dense vegetation of the jungle, the bird has very poor visibility, never feels safe and flees at every sound. Tree snakes, probably the main enemies of birds in New Guinea, jungle sparrow-hawks and hawks (*Accipiter papuanus* [= *Tachyspiza cirrocephalla papuana*], *Astur melanochlamys* [= *Tachyspiza melanochlamys*]), certainly also arrive silently and in a flash; as a bird, you have to be constantly on your guard. Probably the shyest are the old male birds of paradise in their magnificent plumage. With them, one really cannot help feeling that the animals know how exposed they are in their splendour. The obvious hindrance to their flying ability caused by the arrangement and extent of their decorative feathers must also increase their insecurity. It is good for the hunter to crouch patiently in the dark behind a broken tree trunk, shotgun ready to fire. Soon the dead forest comes to life. *Eutrygon terrestris* [= *Trugon terrestris*], the yellow-brown ground dove, scurries along, its plumage ruffled, unaware. A pair of beautiful red parrots, *Alisterus dorsalis* [= *A. amboinensis dorsalis*], glide along, their flight gentle, their tails long. Attentively, they fly towards the trunks, checking the hollows inside for their suitability as nesting sites, peering down from the swaying arch of a liana, gliding on. Noise and screeching from afar: a flock of brown *Pitohuis*, *Paradisaea*, with young birds still without

decorative plumage, shooting down into the undergrowth, hopping in the treetops, climbing—passing by. And there on the ground, with a long supporting tail, a larger mammal hops like a hare in slow jumps. It is about to disappear into the darkness of the ground vegetation: *Dorcopsis* [= sp. cf. *D. muelleri*], the forest kangaroo! There it lies, already shot, and for a while everything around it is once again dead and extinct. In the afternoon, we go down to the riverbed. This is where *Pachycephala aurea*, the golden-winged whistling bird, lives, with its dactylic metallic call like *hüit zick zick* [Stein evidently misidentified this species, from the description of the bird and its call it was *Carterornis chrysomela*]. Green honeyeaters slip into the bushes, *Meliphaga notata* [= *M. analoga*] with yellow ear tufts, and not infrequently the low mountain species *M. montana* with white ear coverts. Bee-eaters sit in small groups on the casuarina bushes, smoke-black swiftlets [= *Aerodramus*] dart back and forth like swallows, and now and then a brown cinnamon pigeon with a long tail (*Macropygia*) flies up from the ground, disturbed in its search for food and disappearing into the dense jungle.

Every day brings heavy rain; you can hear it pattering in the jungle from afar, and it is most beautiful when it falls on the tarpaulin at night, under which you lie in your warm tent. The climate here is like our mild summer days, albeit much more humid. The unpleasant ‘hot and humid greenhouse air’ mentioned in so many writings is something we only know from the coast, and only where sago swamps and mangrove forests predominate. The tropical rainforest of the plains is also a pleasant place to stay, as the dense canopy of leaves shields you from the scorching sun. Absolute calm is another characteristic of the jungle of New Guinea. Here at Menoo, we experience a strong gust of wind. There is a crash throughout the forest; large, rotten knots covered with plant cushions fall—a heavy rumbling: a dead giant tree collapses, and I rush to find a place where I can see the light of the sky above me.

Visit to the primeval forest

One morning, just after returning from a hunt, I hear shouts coming from the riverbed. Far away, four men are standing there with bows and arrows, waving. I hear shouts coming from the forest too. They are highland Papuans, Jabis, inhabitants of the Weyland Mountains. They must have heard the crack of our shotguns during a hunting expedition and have come closer out of curiosity. Full of joy, I go down to them, because I will need these people. They put down their bows and arrows when I wave to them. We greet each other. Everything is a little strange: one of them raises his hand, threatening me with his index finger, so to speak. I do the same, of course, but also raise my other arm, whereupon he conscientiously raises both hands. However, we quickly tire of this. He taps my arm with his finger, but no matter how I try to do the same, he deliberately dodges me. Aha, he’s not good at this! Now he launches into a lengthy speech in which the word ‘marabo’ appears several times. I repeat it after him; after all, it cannot hurt. He is obviously very pleased with my performance. The strange thing is that these primitive people do not realize at all and do not even gradually understand that we do not understand their language. They talk incessantly and are not deterred by our silence or negative gestures. This remained the case during our long stay with these people.

Any request is always presented with increasing urgency; when it comes to business, they assume that we do not want to discuss these matters; at best, they might think—if they think about it at all, which is highly doubtful—that the white man is a little ‘slow on the uptake’. Perhaps, in the great excitement that they regularly get into, they repeatedly forget that they are not being understood. But they are just as unaware that we are gradually speaking their language with them.

Finally, I politely invite the small group to come closer, pointing to our camp. Another long conversation, completely incomprehensible to me; three come with me, the fourth waits, then goes to the steep bank, swings himself up, and is gone. Funny little people, tripping along beside me, bows and arrows over their shoulders. They look almost black, sooty, which they are, since they prefer to lie by the fire and probably never wash. A string around their hips, holding a small bast-woven pouch, is their only clothing. They wear shells around their necks; one, who has an incredibly skinny mutt under his arm, has a ring of human hair around his forehead. I wonder if it is his own hair? They all have short, tightly curled hair and thick, full beards; they are also much smaller than me: real little men from the forest. Each of them has a small raffia bag hanging from their back. I am secretly amused by these funny little men and proud to be bringing the first savages ‘home’. Our cook WAIKOLE, however, looks at them with considerable concern; the good man has never felt quite at ease in the interior of New Guinea: he was in constant fear that, because of his well-fed appearance, he would be the first to be roasted when the time came.

At first, the three Jabis sat quietly by the fire, but they soon seemed convinced that we were extremely peaceful people. Only an outsider could describe the grimaces we all made to communicate and convince each other of our good intentions. Finally, I began to experiment a little. A mirror was presented: what a sensation! Tears ran down our cheeks. So that’s what we look like! Our own tongues and teeth, teeth, teeth—everything was visible! Lost in their newfound discovery, the three of them fiddled with this incredible thing, each wanting to hold it up to their own face. They reached behind it, stuck their fingers in their mouths, pulled the most ridiculous faces, turned the mirror around and were even more amazed when they could not see anything at all. This seemed to be something extremely valuable! One of them was already busy with a hatchet, enthusiastic, completely absorbed, until he finally put it in his bast bag. I took it out, he calmly put it back in, until I gave him a slap on the paw, whereupon he looked at me very offended. The second one was just about to disappear into our tent, while the third was having a great conversation with the cooking pot. With combined efforts, we got the little people back together; they were very excited, their eyes darting around the whole camp. But now it was time to move on to more important things: a stuffed shrew [= *Myoictis melas*] was presented to them, which they immediately examined with interest and objectivity. They determined that it was stuffed and filled with an unknown white substance, whereupon they immediately demonstrated to me how it ran. They called it by an incomprehensible name, and one of them caressed its belly affectionately. Aha, you eat these cute animals? Now I was suddenly very satisfied. Bird skins and kangaroo skins were brought, my people joined in the pantomime,

and despite the truly Babylonian confusion of tongues, all points were clarified: we wanted to go to the mountains, collect rats and birds there and exchange them for knives that my porters would bring. I wisely kept quiet about the fact that we had enough here. They wanted to pick us up and show us the way. They were given a string with 14 knots, which they themselves had requested, and the gesture for sleeping was made, which they also mimicked themselves, pointing to our camp: so, we had to wait here for another 14 days, and soon they wanted to bring us fruit, which we were completely lacking. And then they were gone, disappearing into the forest. My wife did not sleep that night, as has already been mentioned. I saw her peeping through the cracks in the tent until I fell peacefully asleep.

A few days later, our friends returned, this time four men and a little boy; they brought sweet potatoes, yams and wild sugar cane. One of them knelt before my wife, who was embarrassed enough, as if he wanted to propose to her. But the lad only intended to negotiate a small bag of sweet potatoes with my wife and, incidentally, did not even know that he was dealing with a female being. As soon as he saw a thick bundle of small chalk-white glass beads—a fortune, as I soon learned!—he had already grabbed it and refused to give it back. Instead, he flew into a rage, grabbed his bow and arrows and made a move to run into the forest, which I had to prevent at all costs, as I wanted to be on good terms with the locals. Appeasement—but the beads were gone.

The Jabis had only arrived late in the afternoon; now they calmly declared that they wanted to spend the night in our porters' leaf huts, which none of us liked at all. We could not get rid of them amicably; instead, they turned a deaf ear and asked for the leftovers from our spicy dinner, which we gladly gave them, but they did not get any, as we soon heard. And now they sat suspiciously in the dark with stomach aches and dark thoughts. They did not dare to leave either, as it was completely dark, and just stared at us angrily. My wife sat by the tent flap again all night, my people did not sleep either, the Jabis were also terribly afraid, there was an atmosphere of the blackest mistrust, but I slept very well with a clear conscience and as the only reasonable person. The next morning, with the first rays of sunshine, everything was cheerful again, but we always remained people from whom the Jabis would not take a piece of bread. A warm farewell; the string from which the necessary knots, signifying the days that had already passed, have been removed, is shown once more, and we are alone again.

March into the high mountains

Soon the porters and police arrived, cheerful as if nothing had happened. One of the policemen had been replaced because he was showing signs of an unpleasant illness. The journey was to continue the next day. In the evening, the first cases of groin gland inflammation and foot wounds were reported. They were to remain in the Menoo camp and wait for the porters to return. One had even impaled himself on a thorn when he sat down, a highly remarkable injury for a Papuan who is constantly squatting! The next morning, there are even more sick people in front of the tent with completely uncontrollable ailments: head, stomach, knee and who knows what else, but all of them are truly suffering. Now two of them drag a strong lad along, a third

pushes him from behind with a merciful, gentle face. The sufferer collapses in front of me, and all those standing around look as if they have seen a ghost; there is a solemn, serious atmosphere, as if at the funeral of a prince. I also feel somehow when I look at the scoundrels in turn. The cook looks at WAIKOLE, looks at me, grins, becomes serious again, hurries to roll a cigarette, as if he wanted to increase the pleasure he was about to enjoy. Mild as a candidate for the parish priesthood, I ask the sick man about his ailment. The poor man has something everywhere! Unfortunately, I do not have any castor oil, which would also cause unwanted disturbances later during the march. 'I'll give you a good *obat* [remedy],' I promise soothingly and comfortingly, taking the large tin spoon heaped with Karlovy Vary salt. The poor man laboriously opens his mouth, and his head must be supported. I pour in the whole load and command in a thunderous voice: *Makan sarnaskali!* [Eat everything]. The effect is magnificent. In a flash, he is up, gagging, spitting, leaning forward. When I ask: *Ada lagi orang sakit?* [Are there any more sick people?], no one responds. Soon after, it is time to leave. The seriously ill man carries the famous tarpaulin.

Cries echo from the forest: my Jabis are coming, right on time, as promised. They help carry the load and take the lead through the unfamiliar terrain. New mountain ranges, camp by the stream. The next morning it rains. Nevertheless, we set off; we must continue. The first tree ferns; you can hardly see them because it's pouring with rain and you're dirty, wet and exhausted. At midday, we come across some dilapidated Jabi hunting huts with smoke rising from the fires inside. Some of the people have already huddled together there, while the others stand outside, shivering. They have thrown down their loads and stare blankly into the wilderness. But we must keep going, so I fetch the people from the huts one by one. We also make it to the foot of the first major range of the Weyland Mountains, the Kunupi. This night also passes.

The next morning, sunshine, our clothes are drying despite the coolness on our bodies, we are climbing, always climbing, now along the ridge of the elongated Kunupi. Over there, the next range of mountains is even higher, running parallel to the Kunupi. The scenery becomes magnificent. Our feet tread on elastic moss beds, the trees are covered with moss, they are sparser and lower, with nest ferns and orchids growing on them. Bizarre pandanus trees on stilt roots, with strap-like hanging leaf crowns, rattan, and bamboo form a dense tangle. My wife and I do not say a word. We look at each other and point to the wonder forest. Bird calls, strangely shrill, never heard before, strike our ears. The Jabis notice our excitement, smile, say something. I feel drunk! I've never seen anything like this before. All fatigue is gone, all heaviness forgotten—here is the forest of the great Pan!

We are lying on the slope of Kunupi, which we have left behind us at 2,100 meters, in the middle of the Weyland Mountains. 500 m below us, the Menoo River thunders, having carved its way deep into the mountains. In front of us rise further mountain ranges, massifs. There is the Epo, a huge block to our left, and directly opposite the Sumuri, a long ridge with steep slopes, also completely covered in jungle. Behind it, chains and chains. In the distance, a peak can be seen above it, which is probably over 3,000 m high. Clouds and wisps of rain above everything; down in the Menoo Valley, the fog is steaming. The porters stand

silently beside me, staring like me at the wild landscape. More Jabis arrive. Their huts lie scattered around us and below us. The people stay until nightfall. One of them starts a song, the others join in, and their sonorous, deep voices fill the darkness; the last note lingers, drawn out and fading away. We fall asleep happily. Tomorrow we are to descend into the Menoo Valley, towards that distant peak. When we wake up, it is pouring with rain. All the mountain ranges have disappeared in the mist. We cannot continue today, we are tired enough, and so it is decided to wait here for the rain to stop. And it rains for 60 hours! We have never experienced such persistent rain as here. The porters are no longer fetching wood, which is also wet and green and will not burn. The mood is gloomy everywhere. Water drips through the flimsy huts, which are covered only with fern leaves because there are no suitable leaves of sufficient size up here. The people also lack the necessary blankets. I sit under the tarpaulin and stare out. It looks as if the birds are fleeing to the valleys in this downpour: everything is moving downhill. For the first time, I see the bird of paradise *Astrapia splendissima*, not yet in its decorative plumage; its long light brown tail flutters as it moves downhill. Long-tailed flycatchers, black males and brown females (*Rhipidura atra*), flutter in the bushes. Small groups of green weaver birds with red tails (*Erythrura*) appear. Even in the pouring rain, *Peltops montanus* with black, white, and red plumage sit calmly on dry branches. White-eyes (*Zosterops fuscicapillus* [= *Z. fuscicapilla*]), green with blackish cap and white eye rings, flutter and buzz in the trees; small honey eaters, which I do not yet know, fly through—a rich bird life despite the flood of water. But I want to go higher, to where the rarest high-mountain dwellers of New Guinea live. I shoot a few birds, which my wife skins alone. The taxidermists sit gloomily in the tent, probably thinking of their beloved Buiten-zorg with its warmth and streets full of colourful life. Silently, WAIKOLE places rice and coffee in front of us and trots off to the taxidermists' tent.

During the Flood, it is said to have rained for much longer, forty days and nights, and besides, we are too high up for the water to rise so quickly here—so we console ourselves with cheap gallows humour, but it is high time things improved! On the second day, around 25 of the porters are still strong enough to want to continue, on the third day only 10: the leaders of the individual groups, who do not want to abandon me. We also take on a few Jabis as porters and guides. They offer to take us to their friends on the Sumuri. I must give up on reaching the distant heights we have seen. The Jabis point to the arrow scars on their bodies and refuse to take us there. It would be futile anyway to attempt it with so few people, who are also weakened and worn out. Most of my team is allowed to leave for the coast immediately. They disappear quickly!

My wife must stay in Kunupilager with most of the luggage, a policeman, a younger taxidermist, and the cook. The Jabis themselves have made this a condition. All the items for exchange must also remain here. They fear, and rightly so, that I might otherwise attempt to venture further into the mountains to meet people with whom they are at enmity, and then they would lose all the precious things we have brought for them. Ultimately, we have no choice. The thought of any danger to my wife does not even cross our minds.

On the Sumuri

Finally, we can set off: the small remaining group of porters, the Jabis, all heavily laden, the village chief of Wanggar, DARNA the taxidermist, a policeman—and me bringing up the rear. My wife waves us off, and we descend the slope of Kunupi. The forest has been cut down here, the trunks left lying on the ground, weeds growing over them, and there is no end to the stumbling and falling. Bushes, tall clumps of sugar cane, and everywhere the impeccably clean yam and sweet potato plantations of the natives. In the undergrowth, spectacled birds whisper again, green leaf warblers with light longitudinal stripes on their heads (*Phylloscopus giulianettii* [= *P. poliocephalus giulianettii*]) call softly and familiarly, just like in Germany. A dainty chocolate-black cone-billed bird (*Munia tristissima* [= *Mayrimunia tristissima*]) flies to its nest, behind it fluttering a long yellow bast thread like a grotesquely elongated tail. A small flock of green parrots (*Neopsittacus pullicauda*) whizzes past us down into the valley, and high above us we see the flight pattern of the beautiful long-tailed wasp hawk *Henicopernis longicauda*.

We now continue through dense jungle. The Menoo thunders loudly as it foams between the rocks here. After the heavy downpours of the last few days, it is carrying a particularly large amount of water, and we stare hopelessly at the bubbling and swirling. The Jabis now lead us upstream along the Menoo, a gruelling stretch of the journey, until a rock gate opens through which the stream rushes. Here, a tree trunk lies above the floodwaters, crooked, rammed into crevices on both banks, splashed with foam. Over there, a strange Jabi is crouching, covered in soot, with a curly beard—a real forest gnome. He laughs and waves: it is a Sumurimann who has come to greet us. He wears a wonderful large necklace made entirely of animal teeth around his neck, which he has surely put on in our honour. He prances along the first part of the slippery trunk, then settles down, crawls cautiously further, and is with us. He laughs good-naturedly at me. As I am about to step onto the bridge, he holds me back anxiously, speaks excitedly, makes gestures, tells me to wait. Funnily enough, I am reminded of the fairy tale about the bridge of lies, from which anyone who has told a lie that day will fall. I have a clear conscience in this regard, but that is too little consolation for me, so I decide to take the obstacle in a riding position and, if necessary, lovingly embrace the trunk. But already the Jabis are dragging young trunks over, equipped with rattan slings on both sides. These are tied to the side of the tree trunk so that the foot has more grip and cannot slip off so easily. Sand, brought from somewhere, is scattered, although it is quickly washed away again. Another excited conversation among the natives—my new friend takes me by the hand, a second Jabi takes the other—and slowly I am led first, always stepping sideways, across the raging whirlpool. The Jabis themselves must also carry all the loads and the porters. I am terrified for my shotguns. Only Bazi, the Tarungaresen chief, comes to the end upright, almost contemptuous, alone.

It is time to set up camp for the night. I stand aside and ponder how these poorest savages, who have nothing of their own, know nothing of the moral law within us that we 'good Europeans' have recorded in thousands of writings, from the Bible to all philosophical works, have helped me so fraternally, so genuinely humanely.

The Jabi, who brought me across the river with such concern, just like a father, comes up to me. He takes a freshly caught, beautiful pouched shrew [= member of the family *Dasyuridae*] out of his bag, laughs happily and asks me for a knife. I silently hand him a few miserable glass beads, he asks again, then takes them. Perhaps I will be criticized for this behaviour, but I had to economize with my treasures for the sake of the idea for which I am here, as bitter as it has become for me here.

The next day, we climb steep slopes up to Sumuri. The coastal people, panting under their heavy loads, throw themselves down at every rest stop. Only one thing keeps them going here: the fear of being left alone in this strange landscape, among these unknown people. During a rest stop, new natives rush in from all sides—the Sumuri people! They stare at us excitedly. I sit on my tropical suitcase and smoke. I am surprised at how calm I am. After all, there is nothing I can do to change the situation, and everything will be fine. By evening, we have reached an altitude of 1,800 meters. The Jabis do not want to go any further; they sit around, freezing. They are given a few strips of red cotton cloth—and they are satisfied. The next day, our camp is finally set up on the Sumuri at an altitude of 2,300 meters, with the summit still about 300 meters above us. All the porters go back; two Jabis from Kunupi, whom we persuade to stay, have already disappeared the next morning, taking the blankets we gave them with them. Over there lies Kunupi, and on its slope, far below us, I can see a bright spot in the green of the forest when the weather is clear: my wife's camp.

The gorges of Sumuri are filled with gloomy moss forests, all trunks and branches covered with thick layers of damp green moss. There is almost no undergrowth around our camp, and the trunks stand black in the twilight. The whole forest is filled with a solemn, solemn silence, rarely interrupted by a bird call. Then the soft call of the beautiful light green parrot *Psittacella brehmi* [= *P. brehmii*] with dark cross-banding sounds; a slate-blue *Poecilodryas* [an Australasian robin] flits through with a soft chirp; appearing on roots, then disappearing again into moss caves, just like our wren: *Crateroscelis robusta* [= *Origma robusta*]. High up in the foliage sits a black bird the size of a magpie with a slender beak; now it turns, and a white tail root glows. It hops further along the mossy branches, now swoops down into a black ravine, and in amazement I pick up the first magnificent *Astrapia splendidissima* in its brilliant splendour. Wings rustle above me: two black birds with chicken-like short wings flit through the treetops. A soft whistle, one disappears, the other is gone: *Paradigalla curunculata* [probably = *P. brevicauda* at this locality rather than *P. carunculata*], the bird of paradise with black velvet plumage and light green and blue skin flaps on the front of its head. Yesterday, a thick green bird the size of a blackbird hopped along the branches on long legs, the female of the bird of paradise *Loria loriae* [= *Cnemophilus loriae*, now in the family *Cnemophilidae*]; I also saw the male darting through the treetops as a black shadow. Only when you hold it in your hand do you see how the whole bird shines in soft blue-black iridescent velvet.

Time and again, it is hard to comprehend how the most magnificent birds of paradise live here in this wilderness, where the sun does not shine for days on end, where moss and leaves are dripping with moisture and masses of fog envelop the mountain. Even when your clothes are wet and

cold and clinging to your body, you cannot help feeling that no effort was too great, that it is nothing compared to the elation of seeing with your own eyes the pulsating life of creatures that are otherwise preserved only as dead specimens in museum cabinets.

Early afternoon, grey twilight everywhere. The tree trunks appear shadowy. Back home in Germany, all the birds were already asleep, but here there is still whispering everywhere. Close in front of you, red and black plumage flutters in the grey bush: *Myzomela rosenbergi* [= *M. rosenbergii*], it pays no attention to you. Like leaf warblers, the little brown *Sericornis* [scrubwrens] slip by, all still busily searching for food. On the ground, scurrying like a mouse, is a small brown-black marsupial shrew [= from the family *Dasyuridae*]. It quickly disappears again. But I have already learned something, and so I hiss through my teeth: *ss, ss, ss*. Then it reappears, because it is looking for the insect whose buzzing wings it thought it heard in the hissing sounds.

Higher up towards the summit, it becomes brighter and lighter. The trees, weathered and bizarre, stand scattered. Some have died, and then bare, beard lichen-covered spikes protrude, on which *Artamus maximus*, the high mountain swallow thrush, sometimes sits. Many bushes are in bloom here, with small bells tinged with pink, probably a blueberry plant. Trees are also adorned with flowers, dotted with bells. Inside, the army of parrots is making a racket. The rare little *Oreopsittacus arfaki*, with their red foreheads and blue cheeks streaked with white, gather here in flocks; among them the long-tailed, beautiful green and red *Charmosyna josephinae* [= *C. josefinae*], climbing with claws and beaks. Now everything flies up in alarm, screeching, chirping, plunging down into the valley and then returning, again. But the strangest bird is *Paramythia montium* [= *P. olivacea* at this locality], found at altitudes above 2,000 meters. It does not seem to belong to the starlings, near which it has been placed. With loose blue plumage, a yellow belly, and a blue-white cap, it sits there, its posture and behaviour very much like a waxwing, also a berry eater like the waxwing, not shy, always alone. Several species of honey eaters live here: in the crowns of the thrush-sized *Melidectes belfordi* with long beaks and brush-like tongues, in berry-bearing bushes the similarly sized but plumper, dark-coloured *Melipotes fumigatus*, fluttering and feeding. With golden ear tufts and a lively finch-like flutter, a smaller Meliphagidae (*Xanthotis subfrenata* [= *Caligavis subfrenata*]), probably the only bird here with a melodious song. Hunting here is difficult enough given the steepness of the terrain, and finding the shot bird is even more difficult.

A couple of times, Jabis come up. They bring possums, rats and sugar cane to trade, a business that is conducted with vigor, seriousness and a great deal of time wasted. One of their skinny mutts secretly stays here overnight and takes the opportunity to eat at least 30 finished bird and mammal skins. One Jabi loses his composure at the sight of blue glass beads. He jumps at me, waving his arms around, and I have trouble calming him down. As I see afterwards, he has knocked over a bottle of machine oil that we use to clean the rifles. However, it is not until midday that the full extent of the disaster becomes apparent. My taxidermist cheerfully reaches into the rice container to take out the necessary portion for the meal, but withdraws his hand in shock, it is covered in oil and rice in a lovely mixture. We all stand around mourning the good rice and imagine how the soup

will taste now. One filled tray has already fallen into the abyss during the ascent, so we must be very economical. Every morning, the village chief of Wanggar climbs stark naked (he would only unnecessarily soak his precious blanket) into a gorge to fetch the necessary water, which collects there in a hole he has dug. He reappears completely wet, with drops trickling from his shiny brown body. Nevertheless, he laughs every time, which is saying something at a temperature of 7–10°C.

Jabis from Kunupi bring a note from my wife, who writes that she is not feeling well and has a fever. However, as the message does not sound serious, I decide to stay, especially as I have spotted several species of bird that I am keen to shoot: the giant kingfisher *Clytoceyx rex* [= *Decelo rex*] and the small brown *Ifrita* with a blue crest on its head [= *I. kowaldi*]. Once again, Jabis come from across the river, sent by the cook. It is evening when I receive this message, and we cannot set off in complete darkness. So, I have the bellows we have finished packed up, because I want to take them back to Kunupi myself. I decide that the rest of my people must wait here until I can send Jabis up to carry the luggage. After a bleak night, I set off with my guides in the dark to march back to Kunupi. Shaken by the uncertainty of my wife's fate, I hurry inexorably along in the darkness. Slowly it gets lighter, the strap-like leaves of the pandanus trees flutter in the morning wind, water drips from branches and leaves, wisps of mist fly through the forest, we rush on.

We rest for a moment at the huts of the Sumuri people. The men stand around me in silence, and I just keep calculating how long it will take to reach my wife's camp. As we set off, a little boy pushes his way through the crowd. Without me saying a word, he grabs my heavy rucksack and hoists it onto his small, brown back. '*Ubi, ubi!*' (let's go, let's go), he says, smiling at me and coming along [*Ubi* is Bahasa for sweet potato. Perhaps the boy was indicating that he had food in the backpack]. Is he thinking about the knife I will give him later in return? I do not know. We have not agreed on anything, as is always customary when dealing with Papuans.

Now we are already above the roaring Menoo, and the ascent through secondary forest and native plantations begins. The sun is shining brightly today, and I am struggling to move forward. Where a fallen tree provides shade, I throw myself down. I do not remember how I managed the last 500 meters to the camp. The tarpaulin is already shining through the trees. I call out, but get no answer. The campsite lies there as if dead! Finally, the cook stands in front of me, looking at me in disbelief. I manage to choke out a question about my wife, but get no answer. I rush to the tent, tear it open, and there lies my wife on the floor. She cannot lift her head, but she smiles at me. Now the tension eases, I stagger back, it's as if the earth is spinning around me. We cannot say what was wrong with my wife, probably a mild case of typhoid fever because of the protective vaccination. SAAN, the taxidermist, has also been ill. It was high time I came. The Jabis fetch the luggage from the Sumuri, some of it remains there because it cannot be handled. Gradually, my wife is getting better. I attribute this to the incredible soups I composed with great dedication and few ingredients over a smouldering green wood fire, the smoke bringing tears to my eyes.

Camp on Kunupi

Soon, the joy of work returns. First, I devoted myself to the jabis. I had already discovered their excellent hunting qualities on the Sumuri. One of them climbed almost upright, effortlessly, up a barely sloping trunk, at the top of which a flock of parrots was squawking. He stood there freely, waiting until the frightened birds returned to the vicinity, placed the long red arrow on his bow, shot it, and the arrow disappeared somewhere in the foliage. The man calmly climbed down to climb another tree. I really could not say why he chose that tree. At the top, he shook the branches for a while: the arrow fell to the ground, and the bird was brought to me, not shot through, only stuck, and therefore unharmed. There were special arrows for each type of game, and only one or two of each type were available. The bird arrows, about 1.5 meters long, had many hardwood tips at the top, which were tied together at one end and sunk relatively loosely into the hollow of the tube, while the free tips gaped apart. The rat and marsupial arrows had three strong barbed points, and the wild boar arrows had a broad bamboo blade. They also had another type of arrow, carefully crafted with a long, polished, brown hardwood tip. When I asked about their use, they calmly pointed to the heavy scars that each of the people bore on their bodies, as if it were the most commonplace and self-evident thing in the world. Certainly, the people lead a turbulent life. If members of an enemy tribe are encountered in the shared hunting grounds, they fight each other to the death. In a short time, European influences of some kinds were able to bring about peace here. But what did they bring with them? Only unspeakable misery with diseases and vices that are still unknown. The people live happier lives this way, for we never saw even the slightest quarrel among the men within the tribal community.

Obedience without coercion is a matter of course for the younger ones; they helped each other acquire hatchets by hunting together for the mammals I coveted. I sincerely and wholeheartedly wish that anyone who approaches these people without pure motives will break their neck on the coast.

I would have liked to have had some of the Jabis as hunters. There was great excitement when I appeared with my shotgun. So that's the thing that goes 'puh puh'! On the first day of hunting, I had about 20 men following me. They pointed out every bird somewhere in the transparent green of the treetops with outstretched arms and excited gestures. Finally, I saw it too, and when I took aim, everyone respectfully stepped back, but watched the hopping bird with glee, and then it was time to shoot! It had to be made clear to the people that the shotgun was lethal. In and of itself, it does not take any special skill to shoot down the first unsuspecting bird in the jungle, but my excited entourage made the work a little more difficult today. At least the people got their money's worth, and there was great joy when the bird I hit came crashing down. All 18 birds I had hit were brought back; they also searched very carefully for the two that were missing, which of course amused me greatly. Back at camp, I immediately tried to teach the few who had the courage to do so how to shoot with the Teschin. A hopeless and not entirely safe undertaking! But one of them finally got the hang of it, received five cartridges and soon returned with a valuable bird. The next day, he asked for as many cartridges as he had fingers, but only brought

back two, albeit very good birds. On the third day, one of the policemen caught him roasting the birds he had shot! So that's no good, we'll have to do this work ourselves. The huts of our Kunupile people stood scattered on the mountainside between the plantations, solid log cabins made of tree trunks. I never managed to gain access to them—there were always a few men standing in the dark doorway, whose disapproving expressions left me in no doubt that my presence was not welcome. I estimated the entire population of the mountain to be 200, just as many may have lived on Sumuri. On the few clear nights we had up there, we also saw other little lights glowing in the Menoo valley, far away in the interior of the mountains.

Even though we were up here for over three months, I know little, nothing, about the lives of these people. They were completely free in their dealings with me, showing none of the shameful subservience that Europeans know the natives display towards them. It was a great offence to step over bows and arrows. Every time this happened to me, they paused, but immediately realized that it was an oversight on the part of this strange white man and kindly asked me to retrace my steps, once again stepping over the bows and arrows. When sitting with them, it was considered highly inappropriate to pass an object in front of your neighbour. This had to be done from behind, just like we do. We never saw any ritualistic acts or objects that would suggest such practices.

Our little tent camp lost none of its appeal to people during our entire stay. The first visitors arrived at dawn, always armed with bows and arrows, which the Jabi always carry with them. When it rained, everyone wore a giant bag woven from leaves on their heads, with one side extended to cover their entire backs. In addition, everyone had a raffia bag with what appeared to be the same contents: the lower jaws of giant rats (*Mallomys*, *Hyomys*), whose sharp incisors served as knives, a piece of string, a 'lighter', small change, namely a few white shells and a packet of homemade tobacco. The giant penis gourds made from bottle gourds, often in strangely twisted shapes, which people sometimes wore, seemed highly disconcerting.

People immediately sat down by our fire and held their heads over the acrid smoke. It always amazed me how people could stand the sharp smoke from the green wood; there is no dry wood in these rain-soaked heights of New Guinea. They sat there quietly, warming themselves and doing nothing, which caused the greatest bitterness in WAIKOLE, the cook (who, of course, only worked when we saw him). And then the poor people had to make themselves useful. Chop kindling! he mimed to them with a swinging axe, appropriate movements and a reference to the logs lying around. When, instead of reaching for the axe, they worked on the wood with their white teeth and bit it into beautiful splinters until the necessary pile lay there to make coffee for the toean, he kept saying in disbelief: *Ini orang samaskali bodok!* These people are all crazy!

With the wood chopped up, everyone now had a certain right to the embers, so everyone quickly pushed their sweet potatoes into the fire and had breakfast. They had their own tobacco, even though they were careful to try to get some from me first. They poured their rather crumbly tobacco onto the dry, lanceolate leaf of a pandanus, pinched it lengthwise, and a cigarette about a quarter of a meter long was ready. They now took it between their lips, crosswise of course,

so that the ends stuck out far on both sides, which looked incredibly funny. One end was lit with a glowing splinter, and they puffed away merrily. The neighbour took the opportunity to pinch off a piece from the unlit end, which was accepted without objection at any time; indeed, they were happy to share the remaining portion even further. And now everything in the camp was observed with attention and annotated with marginal comments, which we unfortunately did not understand.

A shaving brush attracted particular attention, which is typical of these people's closeness to nature. It was immediately passed from hand to hand, everyone had to examine these strange hairs, and there was lively discussion about which animal they might belong to. Wild boar? General rejection, the hair was too soft for that, nor was it kangaroo or possum; they ran their hands through the hair again to demonstrate its unusual length. Ubukuma, rat? Energetic shaking of heads. Until I drew a horse for them and showed them its size. Finally, one asked: *Nai tekki?* Is the animal good to eat?

Our haul from Sumuri was thoroughly examined. It was immediately explained to me that *Paramythia* did not exist on Kunupi, nor did the small black dwarf bandicoot [= *Microperoryctes murinus*] [Kunupi, in the Mee dialect, means ,swamp + flower. It's a term in daily use among the Mee speakers of the Paniai Lakes (Ms Ance Bom, *pers. comm.*). We suspect here that Stein's informants are referring to the swampy lands around the Paniai Lakes. The western crested berrypecker (*Paramythia olivacea*) occurs both on the high peaks of the Weyland Range and the Maokop. *Microperoryctes murinus*, however, has never been recorded outside of the Weyland Range].

The names of the other species were given to me, and the calls of the birds were whistled. All in all, the people knew much more about the wildlife of their mountain than I did. The names were melodious and easy to pronounce, and the people articulated just like us. The beautiful high-mountain kingfisher was called *Syma megarhyncha* okkurru, the owl kewara, the bird of paradise *Lophorina* [= *L. superba*] kera after its call, the rat *Anisomys* even puradidl, which always made us burst out laughing, while the people looked at us in amazement because they saw no reason for merriment.

Once I asked them how far it was to that distant height that I could not reach. Twenty days, they indicated with their hands and feet, it would take to get there. The trees up there were barely taller than a man, and that was where *Proechidna* [= *Zaglossus bartoni*] lived, the strange monotreme with its spiny coat, whose hedgehog-like silhouette I had sketched for them. His father had once received it from the people who lived back there, one of them explained. And when I expressed my doubts, he picked up the bird of paradise *Epimachus* that was lying on the table, pointed to its enormous beak, and said: 'The animal you have drawn here has a beak just as long as uawa, the bird of paradise!' There really could not have been a more apt comparison. At first, they were very afraid of the camera and kept asking: Bokkai [dead]? Until they found the courage to investigate the lens, while I enlarged and reduced the aperture. Immediately, one of them said in amazement: kewara [owl]! Finding the correct comparison here with the size of the owl's pupil changing with the change in light intensity shows the Jabis' excellent powers of observation and probably also their considerable intelligence.

This acumen could even embarrass me and was the cause of the only impropriety I ever committed towards them.

To collect plants, I used a certain Jabi, my special friend. For every five trees he climbed, from which he had to throw down everything in bloom, he got a pair of scissors. One morning, as I was climbing up the mountain, I saw one of the rare little *Crateroscelis nigrorufa* [= *Aethomyias nigrorufus*] slipping through the tangle of vegetation on the ground. Instead of my shotgun, I was carrying my plant press. If you try to hunt birds and collect plants at the same time, you end up doing neither, so I had left my firearm in the camp for the day and had to ask Jabi, who of course was carrying a bow and arrow, to shoot the little black bird for me. I must have been a little agitated, because when he held out the bird stuck in the arrowheads to me, he scrutinized my expression and asked me to take the bird out. As soon as he knew that the animal was valuable to me, I had to sacrifice the scissors I had in my pocket, which were supposed to serve a completely different, 'higher' purpose today. With feigned indifference, I asked him to remove the bird from the arrow himself. But he was still not reassured. *Ssadakki*, shall I throw it away? he asked probingly and somewhat maliciously. I made a generous gesture with my hand, as one might do when refusing to hand over a two-penny piece. That seemed to satisfy him, and at last I had the precious piece, and the poor man had to climb for another half hour: which, incidentally, did not bother him at all, as those with compassionate hearts here will understand.

Most of our time was spent hunting birds. We set off early in the morning, the cook WAIKOLE, one of the policemen and I. The Kapala from Wanggar was responsible for providing firewood and water, building snares and beat traps with the second policeman, and supervising the small snap traps. DARNA and my wife, who still had to take care of the plants, had to prepare the birds. SAAN, the smaller taxidermist, was master of mice and marsupials. Let's climb the mountains together! You wake up in the small but cozy Klepper tent and stick your nose through the crack in the tent: black night; heavy raindrops fall on the tarpaulin under which the tent stands. After a while, there is a clattering outside: WAIKOLE, the capable one, is making coffee. He squats in front of the ashes, has lit the trusty stable lantern and is gathering the last embers from the hearth, putting green wood on top, blowing long and hard, coughing, placing the kettle on the three stones and staring bitterly at the chaos of petrol cans, pots, hanging skins, shreds of sackcloth covering the floor, wobbly bamboo seats, and tin suitcases. It is getting dark, so out of the warm tent, out of the thick trousers that are only meant for the tent and for sleeping. With slight goose bumps, you drive into the browned and smoky stuff that has just been taken from the fireplace. It is impossible to always have enough dry suits here, not to mention 'matching' socks and the eternally wet mountain boots. For breakfast, there are a few boiled sweet potatoes; every few days, there is even bread, which my wife makes in a petroleum tin. The flour is a bit lumpy, but 'only a little,' as my wife tries to convince me.

We set off, trudging slowly up the 600 m to the summit. Near the camp, there is thick mud, the topsoil has been removed, and the earth is mushy from being trampled by the feet of many Jabi. Every day, it's the same struggle to climb a rock with tired bones. We pass through secondary forest, former indigenous plantations, now overgrown with giant ferns and climbing plants. Here, *Crateroscelis*

murinus [= *Origma murina*] still calls its sweet verse from the plain. In the treetops, a pair of starling-sized *Edolisoma montanum* hop about, the female mouldy blue, the male with a black underside. *Huitihe hui*: *hui*: their calls sound, interspersed with magpie-like chatter. *Peltops montanus* makes its circular flights from dry crags with a shrill *zrii zrii*. In the undergrowth, like leaf warblers, rare, the small *Gerygone*, rarest of all *G. rubra* with its bright red back [= *Eugerygone rubra*, actually an Australasian robin]. This is already the upper limit for *Loboparadisea*, the small silk paradise bird, brown on top and light lemon-yellow underneath [= *L. sericea*, a member of the Cnemophilidae]. As pretty as the bird looks, it is just as boring. The birds can be observed feeding in berry-bearing bushes, then flying into the treetops, always silent. Without striking plumage, the bird is also correspondingly familiar. *Pristorhamphus versteri* [= *Melanocharis versteri*], a Dicaeidae, is common, especially the larger, chaffinch-like females [This species is now in the family Melanochartidae]. The males are rarely seen, and if it were not for the blue-black colouring of their backs and the dove-grey of their undersides, they could almost be mistaken for long-tailed tits. Small birds whisper in a fruit tree and fly on in loose formation, calling like tits. This is *Oreocharis arfaki*, a true high-altitude bird. Everyone thinks the males are beautifully coloured great tits, and A. B. Meyer was probably right to describe the bird as *Parus arfaki*. *Küi küi*, loud and black woodpecker-like, it echoes from a ravine: *Parotia carolae*, the six-rayed bird of paradise. It too rarely goes above 1,800 m. *Kera kera*, it sounds high in the treetops; a black shadow whizzes by, and WAIKOLE, who has been dozing until now, perks up. He loves this bird very much; it is *Lophorina*, the little black bird of paradise with a velvety decorative mantle on its back and an emerald green breastplate, from which lanceolate feathers protrude coquettishly on both sides. WAIKOLE has disappeared, and we wait patiently. Once again, I have thoughtlessly sat down on a tree trunk covered in dripping wet moss, and now I am annoyed because I would have liked to keep the seat of my trousers dry for a little while longer. In the undergrowth, *Chaetorhynchus papuensis*, the black highland drongo, sings. Here, one can truly speak of singing, although it is more of a grasshopper-like mocking. A small long-tailed flycatcher flies in, *Rhipidura albolimbata*, one of the most charming birds in New Guinea. It approaches to within a few meters, tilts its head, looks at us innocently and flutters on. WAIKOLE has fired, the dull roar of black powder echoing from the slopes and gorges. He has his *Lophorina* [= *L. superba*], strokes it tenderly, wraps it in paper and slips it into his shirt. We climb higher, walking along a narrow ridge. Deep in the gorge, a stream rushes by.

Uprooted trees have fallen and torn a gap that is now filled with green thickets, mainly creeping bamboo, ferns with chiselled fronds, and small fan palms above. The moss forest begins. This is home to the most magnificent of paradise birds, *Pteridophora alberti*, which has two long cobalt-blue fern-like feathers on its head that extend slightly beyond its tail. The dark grey young males with pearls on their undersides are not uncommon. From mossy branches high up in the treetops, their strange metallic whirring and hissing sounds can be heard, a back-and-forth pull of tones that bears some resemblance to the song of our corn bunting and is just as difficult to get out of your ear. Except for its moving wings, the bird is concealed by the branch stump

on which it sits. I shot the first male in breeding plumage by chance. I mistook the bird, sitting quietly high up in the dark treetops with its yellowish underside, for an *Edolisoma* [= cicadabird]. Immediately afterwards, I saw the second one shoot through the branches, incredibly shy and restless, until it finally sat completely exposed for a moment—and then it darted into a ravine, its head feathers fluttering after it. The third bird remained stuck in a moss tree, and even the skilled climbers, whom I brought up from our camp to the spot on the same day, were unable to rescue the bird. At an altitude of 1,800 meters, the bamboo jungle begins, which extends to the dome-like summit of Kunupi, and here we spread out, where fog lies all day long, where the ancient weathered trees with clumps of moss in their treetops, in which orchids with yellow and salmon-coloured flowers grow, stand only individually. The undergrowth here is a dense thicket of rattan and bamboo, with smaller deciduous trees in between. In places, layers of hollow bamboo rolls lie rotting, collapsing under the hunter's footsteps, interspersed with fallen branches, crushed by the weight of the moss cushions—decay and mould everywhere. Here, the shy bird of paradise *Amblyornis inornatus* [= *A. macgregoriae* at this locality] beckons, whose mating ground, swept clean like a threshing floor, we found close to the ground with a soft call. High above, the honey sucker *Melidectes belfordi* blares out a lively and rhythmic little song, which is sometimes needed here. Completely in a minor key, it sounds soft and melancholic from up close.

That is *Heteromyias armiti*, hopping on the ground, with a thick beak and white wing mirrors against the brown of its back. You can whistle for it as often as you like, and then there are two or three of them, and you wonder where they all came from, because you rarely see the bird otherwise. It now comes within reach, sitting on a branch close in front of you, so that you think you could kill it with a stick.

Another ground-dwelling bird lives here: *Pachycephala tenebrosa atra* [= *Colluricincla tenebrosa atra*], dark black-brown in colour and highly elegant. I only ever shot it by chance. Twice, when everything nearby became agitated because a marsupial shrew was running through the branches. And now one of the most beautiful high-mountain birds! *Kuit kuit*, it echoes brightly and powerfully between the dark roots of a tree stump, and everyone thinks the caller is a rail until they see it, completely black, round as a ball, long-legged, its head feathers bristling as if brushed: *Melampitta lugubris*, which I would love to see up there again in my lifetime. Now it hops onto a broken trunk, a wren-like trill falling like pearls moves its little throat—already it rolls down, hit, and I gaze in delight at the little singer again, and again. A rail also lives up here, where there is no standing water, where everything is immediately absorbed by moss and humus like a sponge: *Rallicula rubra*, reddish-brown, white-spotted, thrush-sized. The bird runs nimbly over the moss cushions, the lying bamboo rolls, through the stilt roots of the pandanus trees. Hardly any species up here is more common than it. The males are particularly lively, chasing each other with a shrill *chwai chwai chwie*, which is difficult to reproduce. It is rare for a bird to fly more than a few meters.

The rare *Eulacestoma nigropectus* also lives here inconspicuously, and I was introduced to it in a rather amusing way. On my way down to the camp, I meet the cook, who excitedly tells me that a very strange bird was shot today and that it has already been brought to the camp. At my insistence that he

tell me what it looks like, he finally deigns to say succinctly that it is '*satoe roepa ajam*, a kind of chicken'. I imagine all sorts of things, and finally find a very inconspicuous little green bird on the dissection table, smaller than a finch, and ponder what about this animal is supposed to be chicken- or rooster-like, until, to my joyful surprise, I discover two flesh-red flaps of skin on the sides of its head: the bird is the rare *Eulacestoma*! WAIKOLE was teased about his '*satoe roepa ajam*' for a long time.

We return to camp every lunchtime completely soaked. I indignantly and horrified reject a bowl of washing water that my wife has brought me, because I am truly wet enough. Besides, there are more urgent tasks to be done: the ongoing business with the Jabis, more groups of whom have arrived in our absence. They sit with the taxidermists and watch them work. Bows and arrows lean peacefully against the trees. I furtively examine the contents of their bags, but otherwise I do not pay any attention to them—for God's sake, no rushing into business! My wife and my people are shown nothing at all; when they ask the Jabis about the results of the hunt and the setting of snares, they receive only a '*bäu*', a no, in reply. I have already exchanged my soaking wet clothes for the second and last set, which is also 'freshly smoked', and we eat. Every day that God allows us to be here, we have the same huge plate full of wonderfully fluffy white rice with a meter-long broth made from plenty of onions, of which we strangely have a lot, and a cube of bacon that is unfortunately getting smaller every day. Sometimes we even have cucumbers, which the Jabis bring us from time to time. My wife has, of course, put together her own special menu, with sweet potato leaves fried in plenty of water and a little coconut oil to accompany the rice. This infernal dish, which our people also enjoy, is praised to me daily with many words of praise, albeit in vain. For dessert, everyone is allowed to chew as much sugar cane as they like.

The Jabis watched our meal reverently. Every now and then, one of them would furtively reach for his bag to check whether the rat was still there. Then the first one approached, and our painstakingly maintained self-control was gone! With a jerk, he pulls out a huge *Mallomys* with thick, long-haired fur and holds it close to my nose. '*Marabo, tekki*,' he shouts at me, 'friend, something really good!' And with that, he runs over to the other tarpaulin, under which the police are housed in a homemade hut. There are several short strings hanging there. Each Jabi has his own specific string and is allowed to tie a knot in it for a large rat. The second knot earns him one of the highly coveted machetes, of which we have brought a nice supply with us.

Our friend has already disappeared into the hut and is rummaging excitedly among the bush knives. They all have cords with different knots. Each of the people has 'reserved' a knife in advance and marked it with their own mark. Finally, Tabi has found 'his' knife. He shows me his mark, points again to the two knots in his string to document the legitimacy of his actions—he did not forget to quickly tie the second knot before fetching his knife—and now, immensely proud and satisfied, puts it in his raffia bag, of course in such a way that the handle is visible, so that everyone can see how wonderfully far he has come. Those who did not hurry are in a bad way. After all, I have had enough of the giant rats and increasingly frequent cuscus, and I must explain to them 'to my regret' that the terms and conditions have changed somewhat. These animals are no longer accepted

as payment for a machete, but are paid for immediately in cash, and only with a smaller knife. Justified indignation, murmuring (I do not know if there is an expression in the Jabi language for our beautiful ‘*uncoulant*’). But they come to terms with the fact. One of them did it very cleverly. He presents a rat and demands his machete, which I politely refuse. Hesitantly, he takes another little mouse out of his pocket, and then another, until I finally must relent. He gets his knife and now brings out *Pseudochirulus caroli*, a rare marsupial that I am urgently looking for. I will have to credit him for this on the next hatchet. Everyone is grinning, but I make a mental note and from now on I will have them empty their pockets thoroughly before we enter the shop. Another has unpacked a whole bunch of ‘cheap stuff’ in front of me, demands his machete and, when I do not respond, declares that he will give me the animals as a gift. He also refuses to reach an agreement and, energetically and visibly offended, pushes the animals towards me. He also gets his machete, because I do not want to be given anything for free, even though I see right through the guy. But now the fun is over: families must go hunting for the rare *Dactylonax*, the striped possums with one enormously elongated finger, and I realize that only now is the purchase of a machete the real pleasure.

Women are the ones who suffer in this whole situation, as they are mainly responsible for hunting the animals, while men prefer to take care of the more difficult business side of things.

To our amazement, one day a Jabi woman appears, chubby-cheeked, frizzy-haired, a little shy, and brings a *Parahydromys*, a large species of rat of which there were only two in existence in all the museums of the world. As usual, she asks for a hatchet. Not too much to ask for such a precious item, one might think. But the woman probably did not know that there was only one specimen in Berlin and a second in the British Museum. Besides, and this was the decisive factor here, about 10 skins were already drying over our fire. So, I put on a regretful face and politely decline. She smiles again, somewhat embarrassed, as women tend to do in such cases, and quickly considers in her Papuan mind what she could ask for the stupid animal. She does not want a machete at all; her husband just asked her to ask for one. My refusal relieves her of all embarrassment, and so she asks for mani-mani, blue glass beads, which are quite nice and which she would surely have liked to have had a necklace made of long ago. The next best thing after the machete would have been a small knife. Glass beads, small coins in our barter trade, come last.

You can get that for a penny. Her husband, who is sitting nearby—why he did not make the deal is a mystery to me—has hardly heard anything about Mani-mani when he jumps up angrily and yells at his wife that it’s just the way he is. To our deepest regret, we cannot understand what he is saying. In any case, the poor woman goes home saddened and deprived of hope. The rough husband—after all, I cannot interfere in marital disputes—quickly asks me for the knife and, also disappears with a clouded brow. After a while, he reappears, very cheerful, with a relieved expression. My evil taxidermist DARNA, who also has a wife in Java, cannot resist asking him somewhat maliciously where he has been. A merciless, cheerful, and beautiful sweeping gesture of the hand is the answer. I look melancholically at my *Parahydromys*.

Women do not often come to our camp, and only to unload crops; we’ve never seen unmarried women or girls. I often heard them giggling in the bushes during my hunting trips,

but then a call would come from somewhere just in time and everything would fall silent.

One exception was the chief’s wife; the Jabis had several, up to three, although our Kapala from the coast never failed to explain that he only had one, and it would be ‘*soeda, sampe*’ if he had enough with just her! The chief’s wife soon arrived, slim, with a narrow face, from which two dark eyes looked at me calmly and confidently. She wears only a string of raffia around her hips and a blue pearl necklace around her neck, but her body is so perfectly harmonious that one does not realize this woman is almost naked. She kneels next to me and hands me some brown mice she has just caught while working in the fields. Smiling, I give her a mirror and glass beads, which slip into her small, skilled hands. Nothing moves in her face. She gets up, exchanges a few words with her husband and leaves. This woman was the mother of a boy, our little friend, the most beautiful boy we have ever seen, whose grace delighted us time and again. Old women are truly ugly and justify the view of the proverbial ugliness of the Papuans.

Once we even receive post brought up by the coastal people. It took almost two months just to transport it from Manokwari to here, so the newspapers do not exactly contain the latest news, but I still spend the whole afternoon reading in the tent with the greatest pleasure. I give the people a letter to take to Manokwari and ask the assistant resident to expect us in Wanggar 14 days later than agreed, and the porters are also to arrive here two weeks later, as we must make up for what was missed due to my wife’s illness. This, of course, requires us to stretch our already meagre supplies. The police and the man from Wanggar will not be able to get any more rice for a few days and will have to make do with sweet potatoes and rat meat. Whereas the Jabis usually get the bodies of the animals they have caught back, which they value greatly, I now buy the whole animals. Only the bodies of the mice are given back to the people. They are wrapped in a leaf, placed in the fire for a while and then eaten very politely; at the very end, the little tail always hangs melancholically from the lips.

Caterpillars seem to be a particular delicacy for the Jabis. They never miss an opportunity to collect a bagful of them, which is then placed in the hot ashes. Unfortunately, we have not got that far yet. We share with our taxidermists the small and oh-so-skinny bodies of the high-mountain birds that must provide our daily evening soup. Lately, our conversations up there have revolved almost exclusively around food. We remember with nostalgia all the good things we have had the opportunity to eat in our lives, and I solemnly promise my wife that once we get back to Berlin, I will eat my way through the entire two-page menu of a restaurant. In the afternoon, we gather in the secondary forest around the camp. A murky stream winds its way through a small, overgrown gorge; this is the habitat of the rare green ground meliphagids *Euthyrhynchus* [= *Timeliopsis*], which, unlike all other species, slip low through the swamp thicket with their stilted tails, like wrens. Mokoppa, the rare small, dark-colored ground dove *Gallucolumba beccarii* [= *Alopecoenas beccarii*], I shoot here, the green ground shrike *Pachycephalopsis hattamensis* hops along the broken trunks, several species of the small *Microeca* flycatchers catch insects, and the soft, very high-pitched call of the golden cuckoo *Chalcites meyeri* [= *C. meyerii*] rings out. The broad-billed flycatchers *Monarcha frater* and *M.*

axillaris [= *Symposiachrus axillaris*] chirp warningly. In the treetops, several species of honey eaters: the small *Ptiloprora gusei* and *erythropleura*, the larger *Ptiloprora cinerea* [= *Pycnopygius cinereus*]; most commonly, the black *Melipotés fumigatus* (Jabi name bogu) with its chrome-yellow bare skin patches on its head. It is easy to be fooled by this bird, which you only recognize once you hold it in your hand. If you have a Jabi as a companion, it will always warn you in good time in such cases: *Bogu bau!*

One day, I finally bag the second specimen of the bird of paradise *Drepanornis albertisii* [= *D. albertisi*]. The gorge is filled with thick fog, rain pattering through the branches. There, in the distance, a series of whistles like *üe üe üe üe üe üe*, clear and descending, almost like a green woodpecker. I imitate it, something flies towards me, lands a few meters in front of me, but completely hidden by a tangle of leaves and vines. A long beak becomes visible, a small head with dark eyes peeks around searchingly, and then the bird flutters to the ground. I also caught all my *Psittacella modesta*, small parrots, as big as a bullfinch and with the same shape, but light green with dark cross bands in the soft plumage of the back, here while stalking, when their soft *hue hue* sounded. *Syma megarhyncha*, the ochre-coloured high mountain kingfisher with the dark head, blue wings and blue tail, gave me particular trouble. Up to 2,000 meters up, you can hear its *drititititit*, which sounds just like the call of its relative, the *Syma torotoro* from the plains. I never managed to see the bird sitting motionless high up in the canopy. Finally, I hear its soft, *oui*-like call, whistle it back, and the first one shoots over and sits on the front of a tree fern.

Soon, the Jabis also know that I am looking for this bird. A little kid sneaks up, waves at me smartly and whispers: *okkuriu!* The little Jabiman is no more than six years old, but he climbs down a ravine in front of me as skilfully and confidently as the adults. He has inherited an old sleeveless calico shirt from one of the porters, which has become unspeakably dirty and reaches down to his ankles. He must keep lifting it up to free it from the vines, complaining loudly about the time he is losing and the effort it takes, but he would never part with it. The *drrrit it it it it* of the bird now sounds very close. Of course, I cannot find it. It must be sitting quite high up, so I send for the big shotgun. A whole crowd of Jabis comes along, and everyone tries to show me the bird. They put the shotgun to my shoulder, point the barrel somewhere and advise me to pull the trigger, shaking their heads at such a degree of clumsiness; until finally one of them summons all his courage, embraces me, presses his cheek against mine—I think I can already feel a tingling sensation in my hair and as I follow his outstretched arm, I finally see the bird. Only its beak and tail protrude above the thick branch on which it is sitting. Just then, the *drritititit* sounds again, the beak straightens until it is almost pointing upwards, and now the bird sinks back down, only its tail twitching back and forth. At the sound of the shotgun, all the Jabis rush into the ravine, and I can return to camp with peace of mind.

Return march to the coast

We eagerly await the arrival of our porters. We have no more goods to trade; the chief already has my wife's swimsuit, and I have also 'pawned' my pocket knife. We still have a small bag full of beautiful colourful wooden beads, but the Jabis contemptuously bite them with their teeth to show me what

poor quality they are.

Finally, WAIKOLE, the cook, falls ill with kidney inflammation and intestinal catarrh. He is in a very bad way; we hear him moaning through the night. He has my wife to thank for coming down alive. At last, the first group of porters arrives; the others have been held up by a flood wave at Menoo, but should also be here soon. No more work is done that evening. We sit in the tent and do not talk much; finally, I dig out my harmonica, which was among the barter goods, and try to coax silly melodies out of the 30-penny instrument, and in the end we even sing.

We were up here for over three months; 1,300 birds, 300 mammals, bundles of plants, the result of our work, must be packed into metal sheets, tied up, and wrapped in tent fabric. Departure. The place lies desolate, scaffolding stares into the air. The rattan-woven bamboo table and a bark hut still stand, fire pits smouldering. We glance indifferently over everything one last time and then follow the porters, who have long since hurried away with their now light loads. At noon, the two Jabis who accompanied us bid us farewell. We are too tired to feel anything.

It must be the orchids' flowering season; they glow on the ground and from broken stems. Soon I am carrying a whole bunch in my arms to put them in the plant press in the evening. It is afternoon, and we are accompanied only by the cook, who is dragging himself along with difficulty, and Kapala from Wanggar, who is also leaning on a stick, so exhausted is he from the long stay in the mountains with its poor food. There is no sign of the porters—they probably want to return to the coast in a day. We stumble forward listlessly, having eaten nothing all day. Finally—it is already dusk—we hear shouting and see a glimmer of light: the camp is already set up. I put aside the orchids that I have not lost along the way and later find them trampled under the dirty feet of the porters. There is no point in getting upset about it. The next day we walk along a narrow ridge. There is movement among the porters: they point through a gap in the trees. Below us stretches the jungle that we still must cross. Fog brews in the wide green valleys, but at the back on the horizon a narrow silver strip glows, with light blue clouds above it: *Thalatta, Thalatta*, the sea, the sea! For dinner today, we have soup made from leaves that the porters brought from the forest. *Sajoer oetan, bagoes toean*, jungle vegetables, excellent, sir! say my taxidermists, but I am content with just tasting it.

We also happily cross the Menoo, where I am somewhat concerned about my collections, and finally arrive at the Prauen camp. From afar, we can already hear the joyful shouts of the porters who arrived before us. One of the men gives us a delicious banana that he brought up from the coast. We eat dry rice, cooked together with the last mouldy peas, straight from the pot. We speed down the river, past the camps we passed on our way here. In a few hours, we arrive safely at the coast; only one prau has been wrecked on the way! Fortunately, it did not contain any of our collections.

We move into a hut in the kampong, have a feast of chicken prepared, receive delicious bananas and drink the sweet and sour water of green coconuts.

The next morning, we stand at Wanggar and see blue chains in the distance through the clearing in the jungle created by the river. They shine just as mysteriously, untouched and compelling as they did before our journey. We cannot believe that we were up there, we can hardly believe

it, and already we are quietly moved by a longing for those mountains that will never leave us.

The steamer that is supposed to pick us up is already overdue. Finally, we learn from the Malay administrative official in Wainami that it was already here three weeks ago, right on time for the originally scheduled date. Due to a particular mishap, my letter did not reach Manokwari, so we have no idea how long we will have to wait. I consider making the trip to Manokwari by prau. But the journey takes at least 14 days and also involves long stretches along the steep coast, where landing is impossible in stormy weather. I do not want to expose my collections to further coincidences, so we must wait. Resigned, we unpack the shotguns again, gather the last of our ammunition and get back to work. I have been dealt the hardest blow: I have run out of tobacco. I generously gave gifts to the prau people for their safe journey home on the Wanggar and now have to watch others smoke. At least I still have the pleasure of shooting a small series of what is probably the most beautiful kingfisher, *Halcyon nigrocyanea* [= *Todiramphus nigrocyaneus*], which lives in the coastal forest. At high tide, you can bathe in the warm brackish water up to your hips. Small green tree snakes hang in the branches—in general, snakes are very rarely seen in New Guinea—large monitor lizards climb the trunks, a rat swims into the undergrowth, the *boeroeng siang*, the bird that heralds the day (*Philemon novaeguineae*) [= *P. buceroides*] calls its quokke quokke, large fruit doves (*Ducula pinon*) rumble away, and suddenly the eye sees a bright blue splash of colour: this is *Halcyon nigrocyanea* [= *Todiramphus nigrocyaneus*], the blue lister. Except for a white throat and belly patch and its black head, the entire bird is deep blue, and even my wife, who has been very spoiled here, at least as far as the colourfulness of birds is concerned, is delighted.

After waiting for 14 days, we spot a plume of smoke on the horizon. We quickly pack up our few belongings and carry all our luggage to the beach, but the steamer disappears again—it has sailed right across Geelvink Bay without a thought for us, probably so that we can enjoy our Robinson Crusoe experience to the full. Two days later, however, boats take us

to Wainami, where we are greeted by the amiable assistant resident, Sprock, who comes to pick us up himself with the ‘Yvette’. We enjoy a wonderful trip through Geelvink Bay, past the Wandammen Mountains, which rise steeply and cloud-covered from the sea, and past the island of Roon. We make a short stop in Manokwari, where the collections are finally packed. In Ternate, Waikole, the cook, who would have liked to accompany us to Timor, bids us farewell. He remains on board until the steamer departs. He has tears in his eyes and shakes our hands repeatedly.

We have been in New Guinea for almost a year; our total haul amounts to 3,000 birds and 600 mammals. If new destinations, Sumba and Timor, did not beckon, it would be very difficult for us to say goodbye to the land of the birds of paradise.

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