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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

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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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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 (Kuarter 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 Pengunungan 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 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

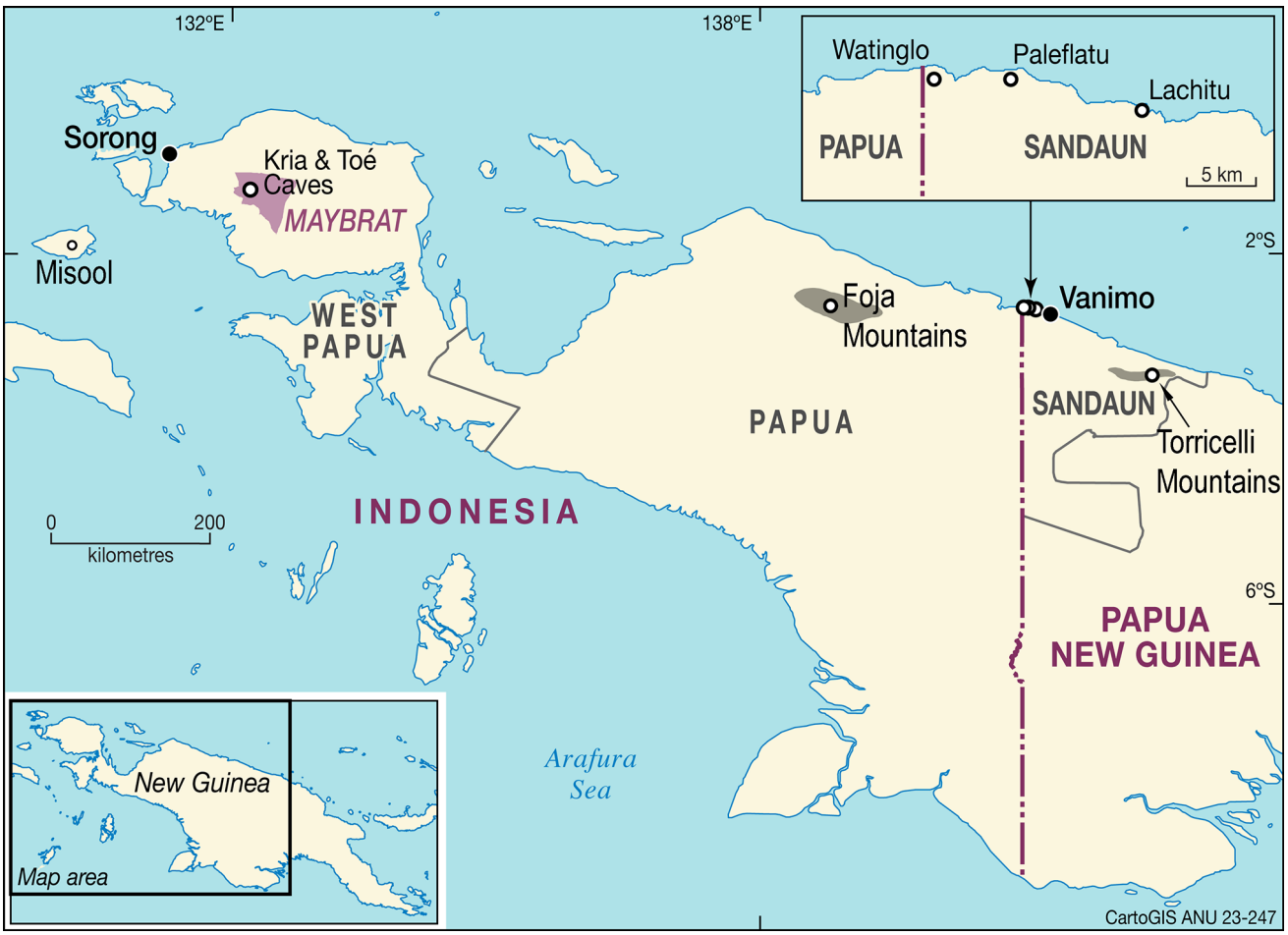

Figure 1. A map of western New Guinea showing localities mentioned, including the Maybrat language region on the Vogelkop Peninsula.

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 toothrows, 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.

	***Tous* gen. nov.**	***Petauroides***	***Hemibelideus***
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 referrable 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).

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

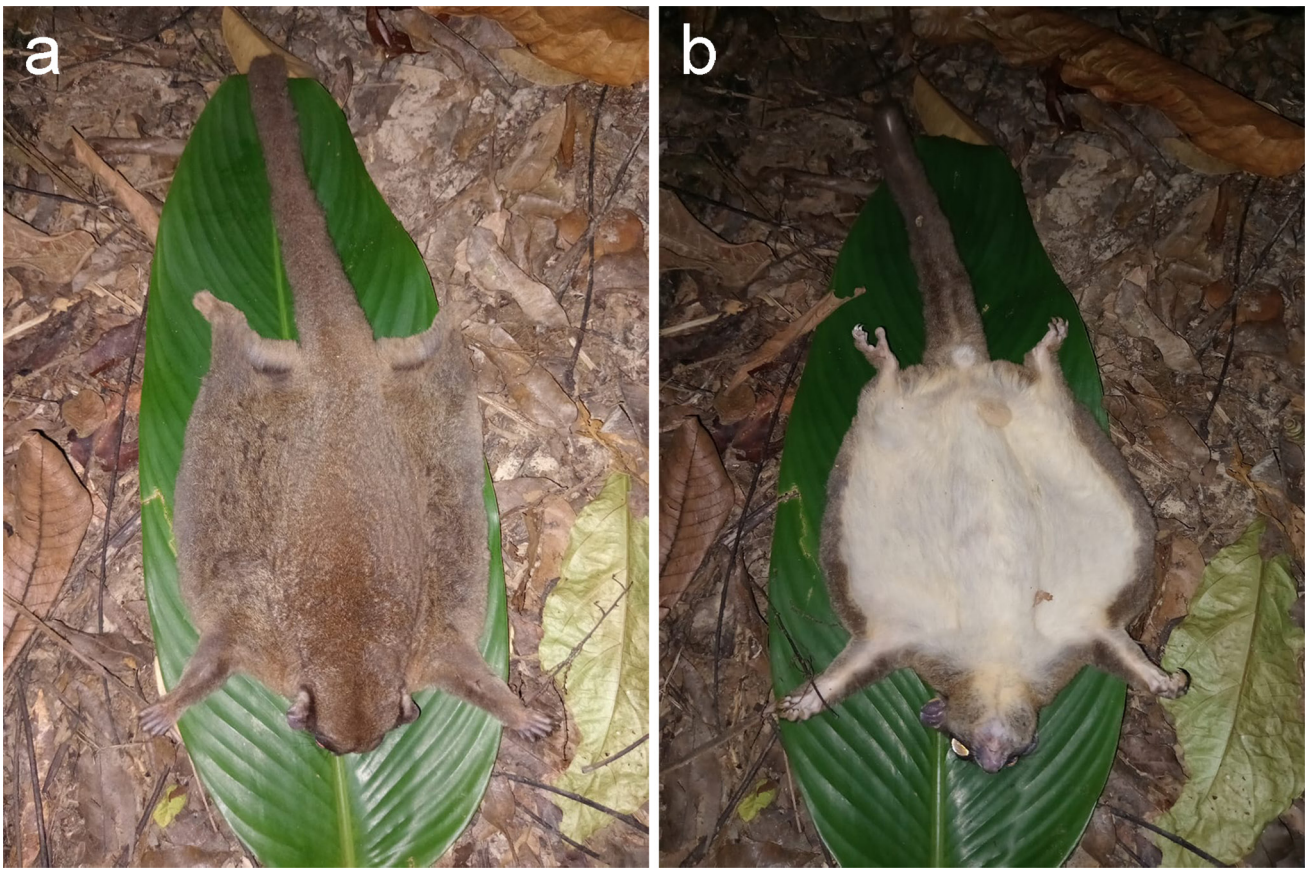

Figure 3. Photos of *Tous ayamaruensis*, adult male, Batkaji forest, Misool Island in (*a*) dorsal and (*b*) ventral views (photo credit Marneks Mjam).

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 Anomarulidae 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

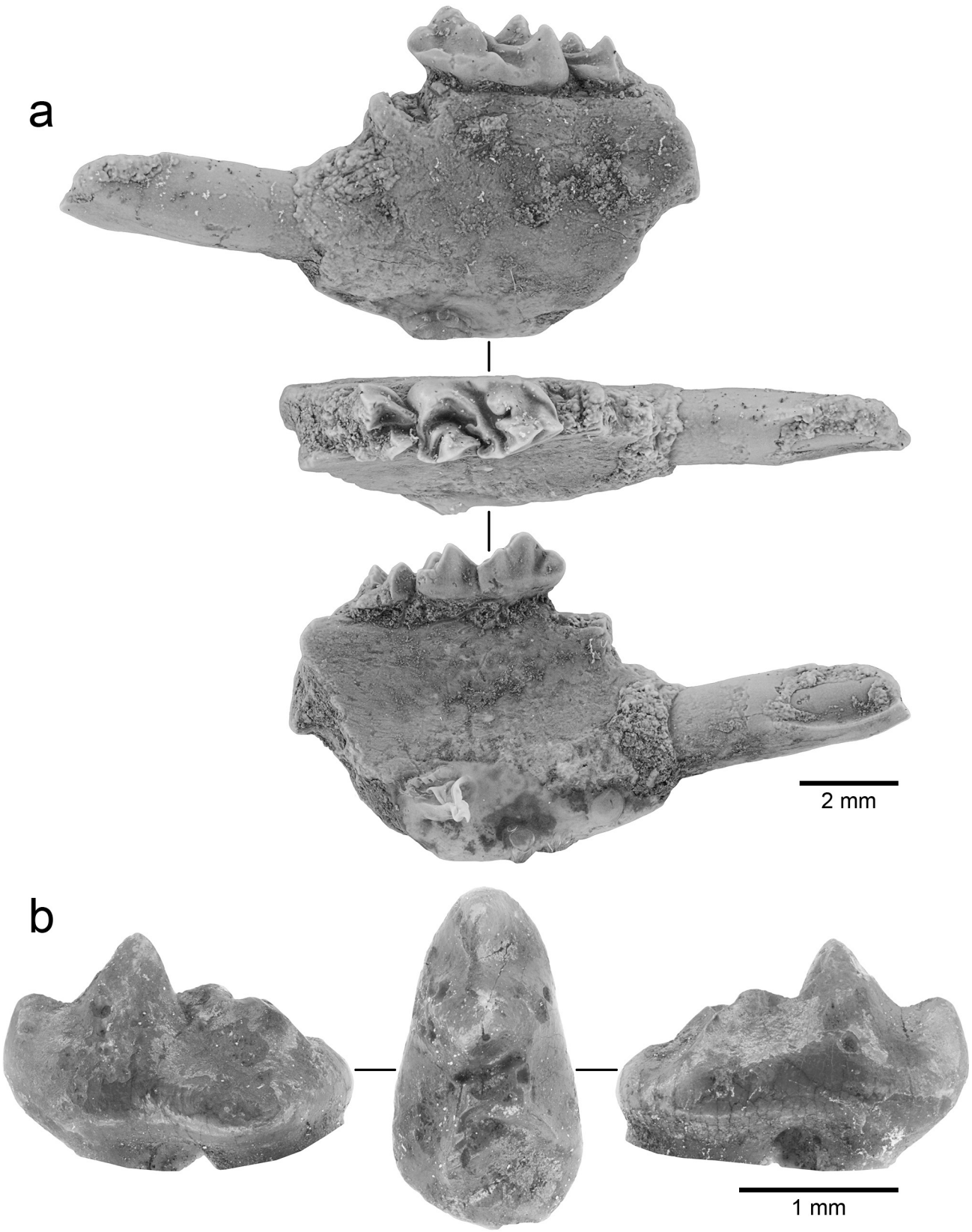

Figure 4. Lower dental material of subfossil *Tous ayamaruensis* from Vanimo sites. (*a*) PM 25697, left dentary preserving i1, m1, and anterior half of m2 in buccal, occlusal, and lingual views; (*b*) isolated view of p3 from PM 26604 in buccal, occlusal, and lingual views.

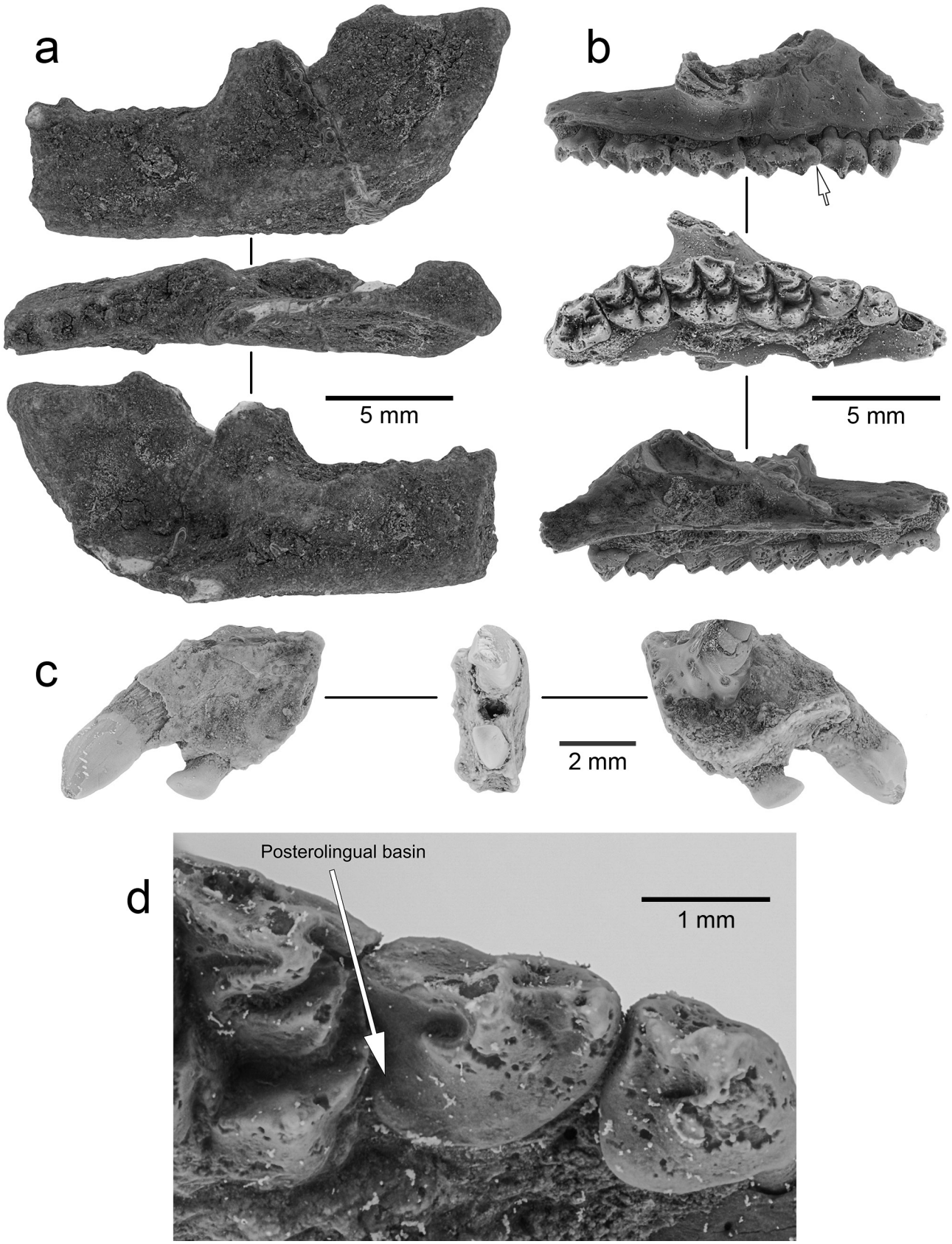

Figure 5. Lower and upper dental material of subfossil *Tous ayamaruensis* from Vanimo sites. (*a*) PM 26646, edentulous left dentary preserving articular facet in buccal, occlusal, and lingual views; (*b*) PM 26619, right maxilla with P2, P3, and M1–4 in buccal, occlusal, and lingual views, parastyle 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.

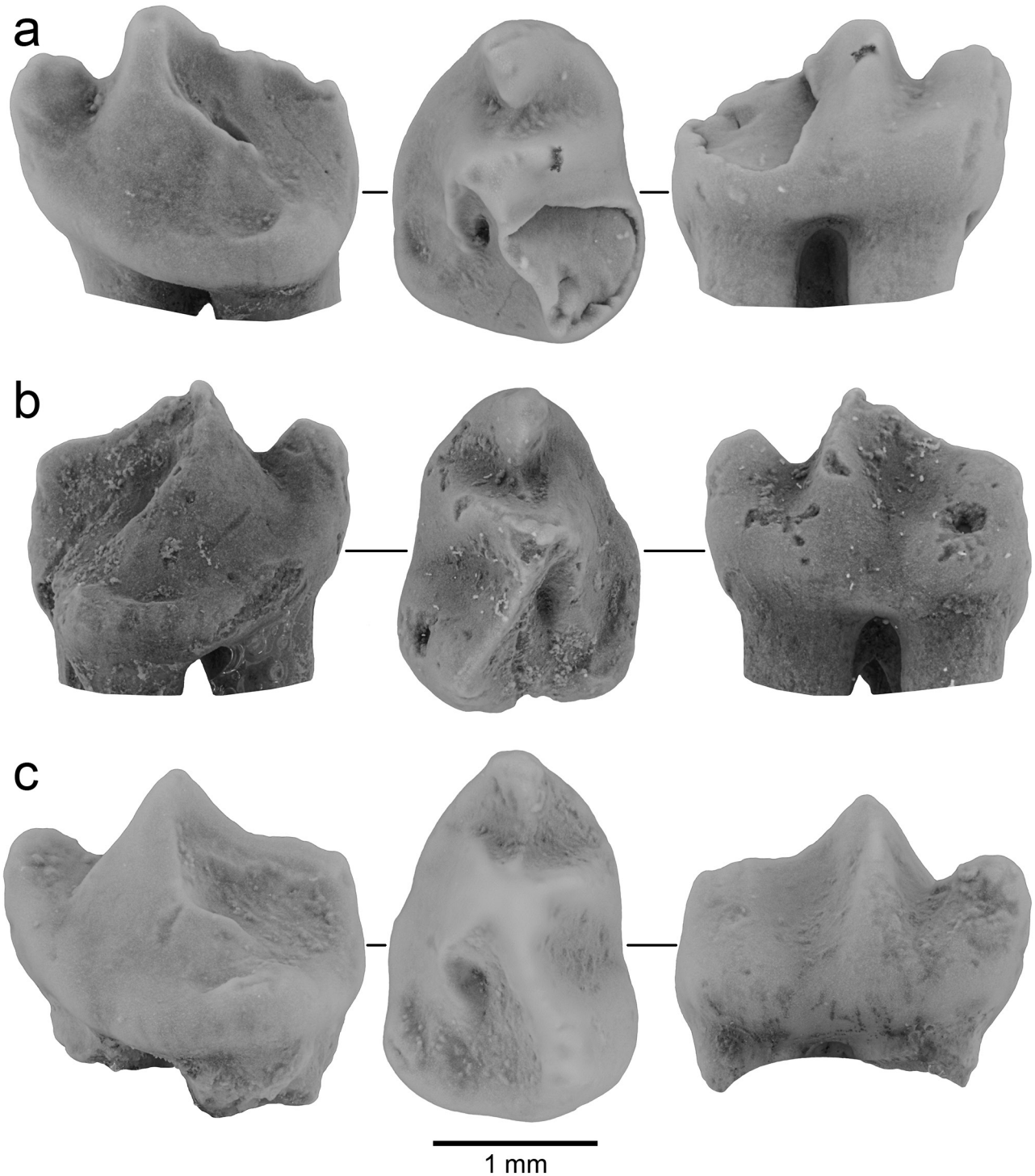

Figure 6. Subfossil *Tous ayamaruensis* isolated P3s from Vanimo sites in lingual, occlusal, and buccal views. (*a*) PM 26640 (left); (*b*) PM 26641 (right); (*c*) PM 26642 (left).

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 Tambrauw speaker, showed a photograph of *T. ayamaruensis* to tribal elders Barnabas Baru and Carlos Yesnat of the Tambrauw and Maybrat language group area, Tambrauw 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 Tambrauw 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 Vanimo-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 paraconule 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 paraconule 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 aenigmanus* (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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