



Gold in the mountains: Striking new species of *Papuascincus* (Sphenomorphini: Scincidae) from New Guinea

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Abstract

Skinks are the most diverse component of the reptile fauna in the mountains of New Guinea and many seemingly specialised high-elevation species remain undescribed. Here we describe two spectacular new gold-patterned skinks in the montane-specialist genus *Papuascincus*. Both species can be diagnosed from all congeners by their distinctive colouration, in addition to aspects of scalation and body size. One new species is mainly recorded from lower montane forest in karst habitats spanning more than five hundred kilometres along the southern edge of New Guinea's Central Cordillera and is likely to warrant an IUCN conservation status of Least Concern. The second new species has thus far only been recorded from cloud forest on the summit of Mt. Menawa in the North Coastal Ranges and we suggest it should be considered Data Deficient. However, if further survey work confirms a restricted distribution with little scope for upslope elevational retreat under future warming climates it will likely qualify for Endangered or Critically Endangered status.

Keywords

Central Cordillera, elevational endemism, karst, montane forest, North Coastal Mountains, *Palaia*

Introduction

New Guinea is the world's highest and largest tropical island and is also exceptionally biodiverse, with recent work showing it supports the world's most species-rich insular plant, frog and bird assemblages (Cámara-Leret

et al. 2020; Oliver et al. 2022; Prasetya et al. 2023). The dominant contemporary geographic feature of mainland New Guinea is the vast and high Central Cordillera which extends for over a thousand kilometres in an east-west

axis across most of the island. The uplift of these mountains is widely considered to have played a pivotal role in generating and maintaining the rich biodiversity of New Guinea by providing novel environmental gradients over which species can diverge and accumulate (Toussaint et al. 2014; Tallowin et al. 2018; Slavenko et al. 2020, 2022; Kennedy et al. 2022), and to a lesser extent by isolating lower elevation taxa in northern and southern New Guinea (Tallowin et al. 2020). Across the north and west of New Guinea additional upland areas such as the Huon Peninsula, and Adelbert, Torricelli, Foja, Cyclops and Arfak Mountains, which are much smaller in areal extent, also support numerous endemic montane species (Toussaint et al. 2014; Oliver et al. 2017). Molecular data and patterns of distribution show that montane taxa in these smaller and isolated ranges have divergent origins—some are derived from colonists from other montane areas in New Guinea, while others appear to be related to forms in the surrounding lowlands (Toussaint et al. 2014; Oliver et al. 2017; Kennedy et al. 2022).

The most species-rich component of New Guinea's terrestrial vertebrate fauna is the sphenomorphin skinks (Slavenko et al. 2023). The tribe Sphenomorphini (Shea 2021) is also the richest of the main subdivisions of skinks at a global scale (Chapple et al. 2021). It is distributed throughout Eurasia, Africa, Australia and Oceania, with

prominent hotspots of diversity in Australia and New Guinea, where most skinks are sphenomorphin (Slavenko et al. 2023). However, despite having more species than any other reptile radiation in New Guinea, they remain relatively poorly known, due in part to insufficient sampling, particularly of material suitable for genetic analyses. What is known seems to suggest there are at least two major radiations of sphenomorphin skinks in New Guinea (Slavenko et al. 2023); one poorly-resolved and containing species currently assigned to the paraphyletic genus *Sphenomorphus* Fitzinger, 1843, and another large radiation that includes many species and genera that have localised and elevationally tightly bound distributions in the mountains of New Guinea (Slavenko et al. 2022).

Papuascincus Allison & Greer, 1986 is a genus of moderately small, diurnal and basking skinks that is closely associated with the mountains of New Guinea. At elevations above 2000 m. a.s.l. they are often one of the few reptiles present. This genus is part of the second of the two Melanesian sphenomorphin radiations noted above. The Papuan Peninsula is the likely origin for diversification of this clade, which includes the genera *Papuascincus*, *Lobulia* Greer, 1974, *Prasinohaema* Greer, 1974, *Fojia* Greer & Simon, 1982, *Palaia* Slavenko et al., 2021, *Alpinoscincus* Slavenko et al., 2021, and *Nubeoscincus* Slavenko et al., 2021. Four species of *Papuascincus* are

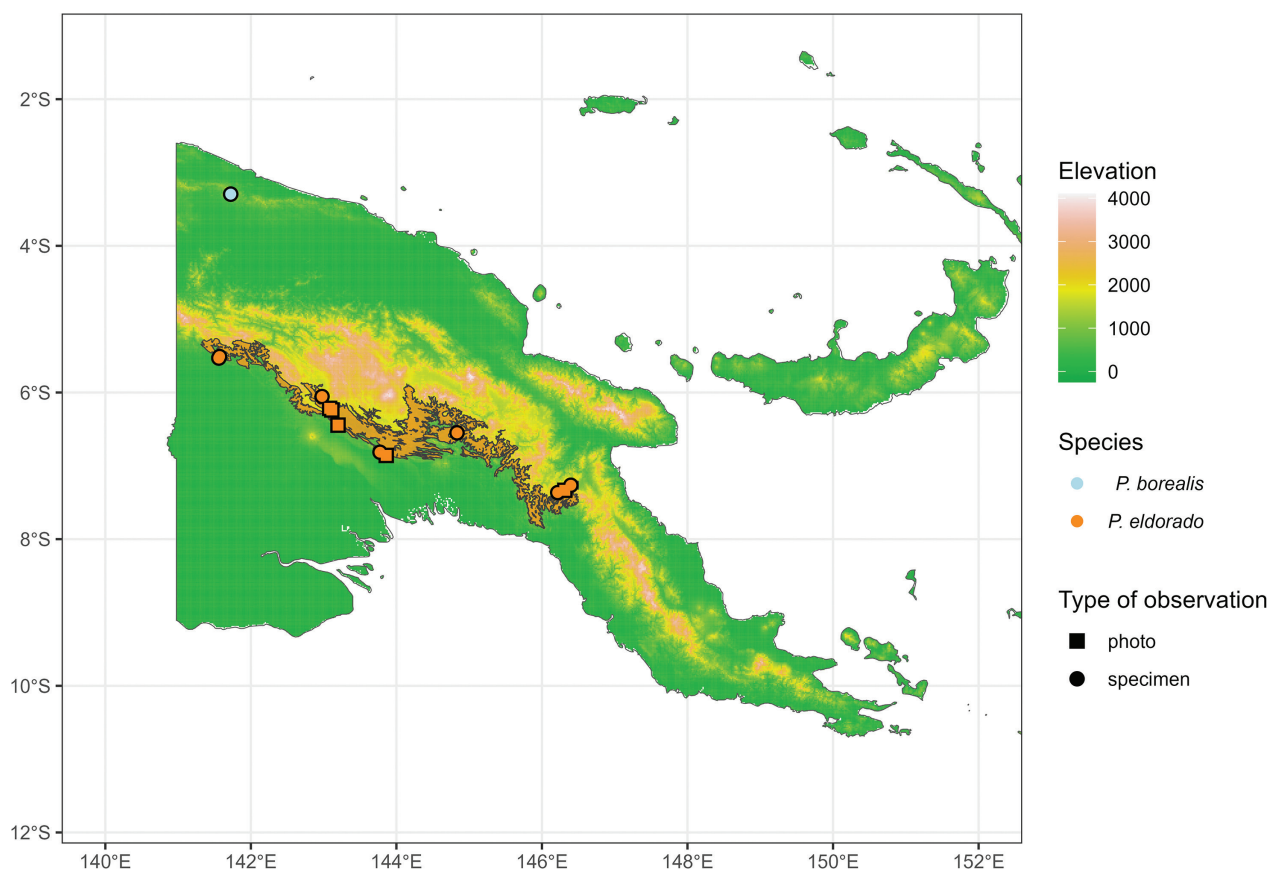


Figure 1. Map of sampled localities in this study, with light blue points representing *Papuascincus borealis* **sp. nov.** and gold points representing *Papuascincus eldorado* **sp. nov.** Circles represent localities where specimens were collected, and squares represent localities where animals were observed and photographed (by Mark O'Shea, Nick Baker and Mattias S Lanas), but not collected. The gold polygon represents an elevational buffer of 700–1600 m a.s.l. along the southern versant of the Central Cordillera, showing the inferred suitable habitat band for *Papuascincus eldorado* **sp. nov.**

currently recognised, but species diversity is considerably underestimated and many undescribed species that vary in body size, colouration, and elevational distribution are known (Slavenko et al. 2020). Here we describe two new, distinctively coloured species of *Papuascincus*. One has a broad distribution across the southern versant of Papua New Guinea's Central Cordillera and occurs at relatively low elevations for the genus (down to less than 800 m a.s.l.; Fig. 1). The other is known only from a single peak in the Bewani Mountains and is to date the only *Papuascincus* species known to be restricted to New Guinea's isolated North Coastal Mountains (Fig. 1).

Material and methods

Material of the new species was collected, euthanised and preserved using standard protocols (as described in Gamble 2014) across three decades of fieldwork in New Guinea. Resultant vouchers are lodged in the collections of the Queensland Museum (QM), Museums Victoria (NMV), South Australian Museum (SAMA), the Australian Museum (AMS), the Bernice P. Bishop Museum (BPBM), and the Papua New Guinea National Museum and Art Gallery (PNGNM). Additional type material for other species of *Papuascincus* was examined in collections at the Museum für Naturkunde Berlin (ZMB) and the Natural History Museum, London (NHMUK). *Papuascincus buergersi* (Vogt, 1932), *P. morokanus* (Parker, 1936), and *P. phaeodes* (Vogt, 1932) are only known from their type series, whereas *P. stanleyanus* (Boulenger, 1897) represents an as-yet unresolved species complex (Slavenko et al. 2020). We therefore restrict our comparison here only to the type material of these species (see Appendix 1).

Specimens were sexed by internal examination of the gonads, and deemed adult if the gonads were large and could be identified as either testes or ovaries. Meristic and mensural protocols followed Slavenko et al. (2022), with the following mensural and meristic characters taken on the left side of each specimen (if bilateral). Measurements were taken using digital callipers with accuracy to the nearest 0.1 millimetre (mm): snout-vent-length (SVL) with specimens held flat and extended, fore-hindlimb distance (FHD; the distance from line across posterior margin of forelimbs to line across anterior margin of hindlimbs) with limbs held at right angles to the body, body width (BW; width of the widest portion of the trunk), head length (HL; distance from centre of ear opening [equidistant from anterior and posterior margins] to tip of snout, oblique measurement), head width (HW; width of head at widest point, typically at the level of or just anterior to ear openings), head depth (HD; dorso-ventral depth of the head at the level of ear openings), upper forelimb (UFL; from posterior side of body wall at axilla to elbow at right angle), lower forelimb (LFL; from elbow at right angle to base of front foot [contact between imbricate scales on the antebrachium and non-imbricate scales on the metacarpus]), front foot (FFOOT; from base of front

foot to tip of longest digit, either III or IV, claw included), forelimb length (FLL; sum of previous three), upper hindlimb (UHL; from anterior side of body wall at groin to knee at right angle), lower hindlimb (LHL; from knee at right angle to base of hind foot [contact between imbricate scales on the crus and non-imbricate scales on the metatarsus]), hind foot (HFOOT; from base of hind foot to tip of longest digit, always IV, claw included), hindlimb length (HLL; sum of previous three), frontonasal wider than long (yes/no), prefrontals in medial contact (no/narrow contact/separated by azygous scale), frontoparietals (fully fused/unfused), number of nuchals on both sides, number of intercalated scales between primary nuchal and upper secondary temporal scale, horizontal suture on nasal scale extending posteriorly from the upper margin of the nostril to reach the posterior border of the nasal (present/absent), number of loreals, anterior loreal wider than long (yes/no), posterior loreal wider than long (yes/no), number of preoculars, number of presuboculars, number of postsuboculars, condition of lower eyelid (window/scaly/opaque), number of supraciliaries, anteriormost supraciliary in contact with frontal (yes/no), number of supralabials, number of supralabials posterior to subocular supralabial, number of infralabials, number of pairs of chin shields in medial contact (with fractions representing an asymmetrical arrangement of chin shield, e.g., a specimen with two chin shields on the left side contacting a single chin shield on the right side would have a count of 1.5), posteriormost chin shield in contact with infralabials (i.e., not separated from infralabials by row of genial scales; yes/no), condition of lobules on anterior edge of ear opening (rounded/pointed), number of midbody (axilla-groin interval) scale rows, number of paravertebral scales (along paravertebral line, counted from the scale posterior to parietals [thus including nuchals] to the scale crossing the imaginary horizontal line connecting the hindlimbs at their anterior point), number of subdigital lamellae under 4th toe, number of single supradigital scales on 4th toe.

As in Slavenko et al. (2020), we defined supraciliaries as the scales separated from the eyelid by small intervening oblique imbricate scales (ventrally) and the supraoculars (dorsally), termed the scales between the posteriormost supraciliary and the parietals as upper pretemporals, defined the lower pretemporal as the scale wedged between the upper pretemporal, the parietal, the upper secondary temporal, and the primary temporal, and did not distinguish between primary nuchal scales (the first pair, present in all skinks), and secondary nuchal scales (all subsequent nuchals posterior to the primary pair, of variable number), instead reporting on the number of nuchal pairs. The number of pairs is defined as the number of paired nuchal scales only (e.g., a specimen with three nuchals on the right side and two on the left would have two pairs). Coordinates presented were taken using the GPS datum WGS 84. All collection and morphological data are available in Appendix 2.

To assess genetic divergence against published data for *Papuascincus* (Slavenko et al. 2020) we generated a dataset for the mitochondrial ND4 gene using tissue for two specimens of each of the new species described here

(QM J97880 and QM J97884; BPBM 23059 and BPBM 23061). DNA was extracted using NucleoSpin DNARapidLyse Kits (Macherey-Nagel). Data for the mitochondrial ND4 locus were generated using the primers (ND4 5'-TGA CTA CCA AAA GCT CAT GTA GAA GC-3' and M246 5'-TTT TAC TTG GAT TTG CAC CA-3') and conditions (annealing at 55°C) as outlined by Skinner (2007). Data were aligned using Muscle multiple-sequence alignment (Edgar 2004) as implemented in MEGA 11 (Tamura et al. 2021), checked for missense mutations and trimmed to only include coding regions (tRNAs were excluded). Genetic distances (p-distances) were calculated in MEGA 11. We partitioned the multiple-sequence alignment by codons and performed model selection using ModelTest-NG (Darriba et al. 2019). We used the selected GTR+G+I model of sequence evolution to run Maximum Likelihood (ML) phylogenetic reconstruction in RaxML v8 (Stamatakis 2014), as implemented in raxmlGUI v2.0.9 (Edler et al. 2021), with 100 runs of 500 bootstrap (BS) replicates. We treated *Palaia pulchra* (Boulenger, 1903) as the outgroup to *Papuascincus* based on the consistently recovered sister relationship between the two genera in molecular phylogenies (Rodriguez et al. 2018; Slavenko et al. 2022). We considered nodes well-supported if they received BS values $\geq 80\%$.

Systematics

Papuascincus eldorado sp. nov.

Golden Mountain Skink

<https://zoobank.org/9F236E82-D4D8-4FFF-9E82-B9740997B8B5>

Figures 2–4

Holotype. QM J97880 (field number PMO 41; GenBank number OR837030), adult male, approximately 9 km east of Kiangibip Village, P'nyang Range, Western Province, Papua New Guinea (5.51°S, 141.57°E, 760 m a.s.l.), collected by P. M. Oliver, M. Sale and K. Aplin on 8 May 2013.

Paratypes (n = 16). All Papua New Guinea. AMS R.115429–30, one adult female, one juvenile, Doido, Chimbu (Simbu) Province (6.550°S, 144.833°E, 1248 m a.s.l.), collected by S. Donnellan and K. Aplin in 1984; SAMA R.71758, adult female, Benaria, Hela Province (6.054°S, 142.978°E, 1330 m a.s.l.) collected by S. Richards on 5 May 2005; BPBM 21668, adult male, Aseki: Piu village, Morobe Province (7.364°S, 146.216°E, 1130 m a.s.l.) collected by A. Allison on 10 August 1988; BPBM 21669–70, adult male, one juvenile, Komagowata: Wau-Aseki road, Morobe Province (7.265°S, 146.397°E 1100 m a.s.l.) collected by A. Allison on 10 August 1988; SAMA R.57406, adult male,

Gobe: SE road above Ridge Camp, Southern Highlands Province (6.814°S, 143.774°E, 830 m a.s.l.) collected by S. Richards on 25 October 2001; field number PMO 8 (to be repatriated to PNGNM), adult male, same locality and collectors as holotype collected on 5 May 2013; NMV D76542–5, QM J97884 (GenBank number OR837031), J97885 and J97891, field number SJR14675 (to be repatriated to PNGNM), six adult males, two adult females, approximately 9 km east of Kaiangibip Village, Western Province: P'nyang Range (5.53°S, 141.56°E, 1075 m a.s.l.) collected by P. M. Oliver, M. Sale and K. Aplin between 20–26 April 2013.

Diagnosis. A species of *Papuascincus* characterised by the unique combination of small size (maximum adult SVL 48.6 mm); 2–3 small rounded lobules on anterior edge of ear opening; supralabials seven; scale rows at midbody 24–28; postsuboculars typically two; paravertebral scales 43–50; lamellae under 4th toe 22–29; single supradigital scales on 4th toe 11–14; and dorsal colour pattern on body consisting of three greenish-gold dorsal stripes on a glossy black background; tail gold with scattered black flecks; limbs black with gold flecking.

Comparisons. *Papuascincus eldorado* sp. nov. differs from all other species of *Papuascincus* in having a dorsal pattern consisting of three light stripes on black background versus two light dorsolateral stripes on light-brown background (*Pap. stanleyanus* and *Pap. buergeri*), two light dorsolateral stripes and two dark-brown medial stripes on light brown background (*Pap. morokanus*), or dark grey-brown blotches on light brown background (*Pap. phaeodes*). It additionally differs from *Pap. stanleyanus* (n = 1) and *Pap. buergeri* (n = 8) in having smaller adult size (maximum SVL 48.6 mm vs. 57.9 and 60.5, respectively) and a lower count of scale rows at midbody (24–27 vs. 31 and 28–31, respectively), from *Pap. stanleyanus* in having a lower count of paravertebral scales (43–50 vs. 64), from *Pap. morokanus* (n = 2) in having a higher count of single supradigital scales on 4th toe (11–14 vs. 6–7), and from *Pap. phaeodes* (n = 1) in having seven supralabials (vs. six), in having 2–3 small rounded lobules on anterior edge of ear opening (vs. 4–5 large, sharply pointed), and in having a much higher count of single supradigital scales on 4th toe (11–14 vs. 2).

In overall colour pattern *Pap. eldorado* sp. nov. is similar to *Palaia pulchra*, a species in a monotypic genus that is the sister lineage to the entire radiation of *Papuascincus* (Slavenko et al. 2022), however it differs in its larger adult size (maximum SVL 48.6 mm vs. 40.8), in having sutured nasal scale (vs. unsutured; see Slavenko et al. 2022), tail gold in life (vs. orange), white lateral stripe absent (vs. present), and limbs overall black with gold mottling (vs. orange with black mottling).

Description of holotype. Adult male, SVL 44.1 mm; tail regenerated, 60.6 mm total length, 30.4 mm regenerated section; FHD 20.5 mm; BW 8.2 mm; HL 10.6 mm; HW 6.7 mm; HD 5.1 mm; FLL 15.2 mm; HLL 21.0 mm.

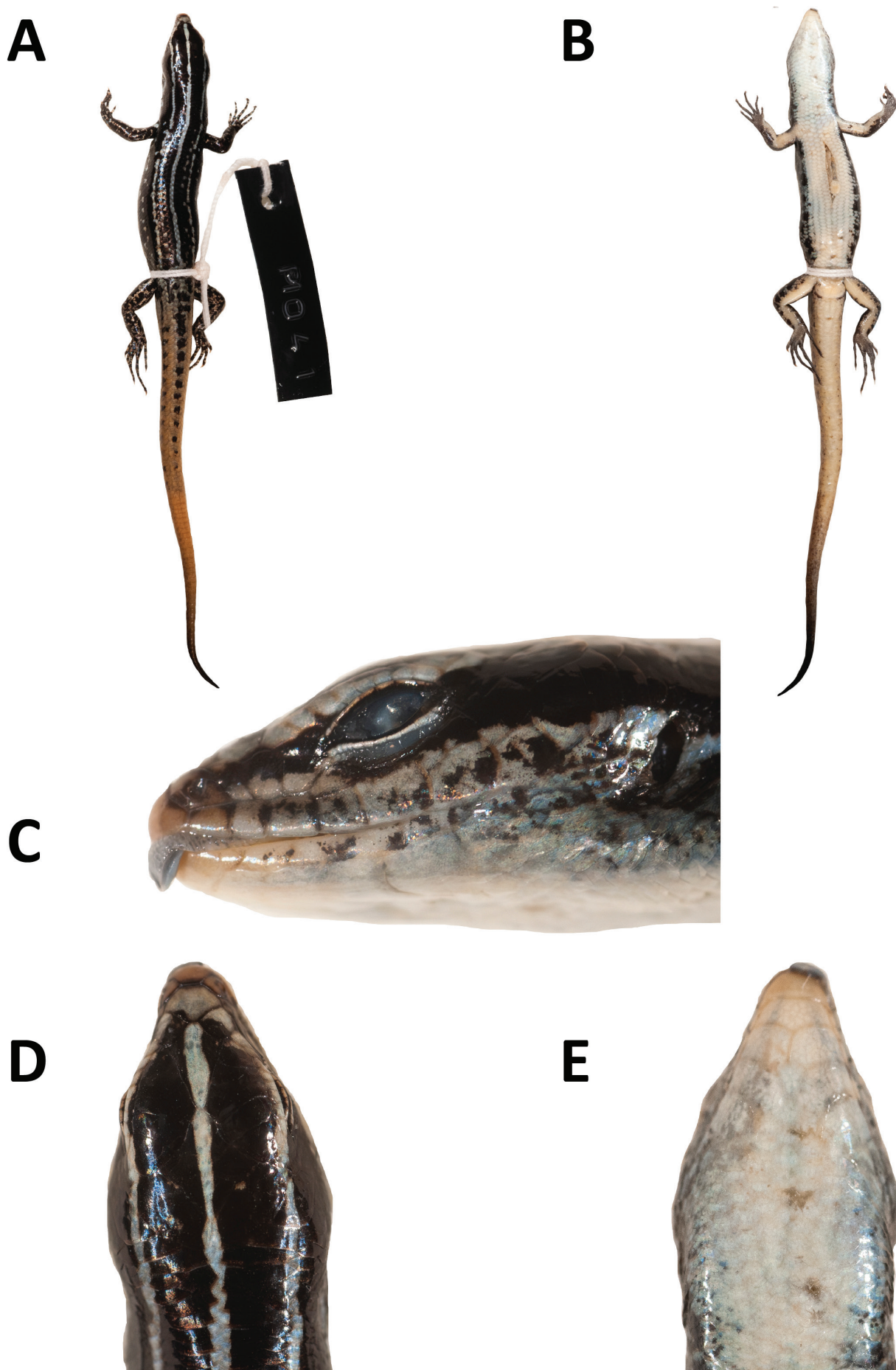


Figure 2. *Papuascincus eldorado* sp. nov. holotype (QM J97880); **A** dorsal view, **B** ventral view, **C** lateral view of head, **D** dorsal view of head, and **E** ventral view of head. Images by Alex Slavenko.

Rostral broad and shallow, wider than deep, projecting slightly onto top of snout; nasals more or less rectangular, separated by rostral and frontonasal contact, projecting anterodorsally onto dorsum of snout; nostril circular, centred within nasal, with suture extending posteriorly from anterodorsal edge of nostril to edge of nasal scale; frontonasal large, with eight sides, extending laterally to slightly above level of nares, posteriorly in narrow contact with frontal; prefrontals large, separated by frontonasal and frontal contact, bordered lateroventrally by two loreals; supraoculars four, of which two contact the frontal and three contact the frontoparietal; frontal roughly kite shaped, widest anteriorly; frontoparietal single, anteriorly in narrow contact with frontal, posteriorly in contact with interparietal and parietals; interparietal smaller than fused frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietal, posteriormost supraocular, and two pretemporals; nuchals in two pairs, transversely enlarged, wider than long, separated from secondary temporal by single intercalated scale.

Anterior loreal slightly smaller than posterior loreal, both higher than long; lower preocular roughly square; upper preocular much smaller than lower preocular, longer than high, separated from prefrontal by anteriormost supraciliary and posterior loreal contact; presubocular single, interdigitated between supralabials; postsuboculars two, lower interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with clear palpebral disc roughly size of ear opening; supraciliaries eight, anteriormost not in contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporal single, interdigitated between posterior two supralabials; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening moderately large, with three small round lobules along anterior margin.

Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields in three pairs, first pair in medial contact, second pair narrowly separated by single medial scale, third pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial.

Body scales smooth, in 26 rows at midbody; paravertebral scales 46; medial precloacal scales enlarged, overlapping lateral precloacals.

Scales on dorsal surface of fourth toe in two rows proximally, single row distally beginning midway along proximal phalanx, 14 single scales; subdigital lamellae under fourth toe 27, smooth.

Colouration in preservative. Base dorsal colouration glossy black, overlain with thin, slightly irregular but unbroken white vertebral stripe extending from snout-tip to base of tail, two thinner dorsolateral stripes with small number of narrow breaks, and small number of additional white flecks, especially in posterior half of body. Lateral surfaces of body largely black overlain with series

of white mid-lateral flecks and further light ventrolateral mottling. Lateral surfaces of head white with prominent black patch in front of eye, and further extensive black flecking on lips. Ventral surfaces of body light buff, unpatterned. Limbs predominately black on dorsal and lateral surfaces with extensive white mottling, pale areas more extensive on hindlimbs than forelimbs. Ventral surfaces of limbs largely buff, but with scattered black flecks. Digits banded white and black on exposed surfaces, black on palmar and plantar surfaces. Original portions of tail faded yellow on exposed surfaces, buff ventrally, with fading series of black dorsal and lateral flecks extending from base to approximately 30 mm along tail. Regrown section of tail dirty yellow, unpatterned.

Variation in the type series. Adult body size 37.8–48.6 mm SVL (mean = 43.0, SD = 3.2, n = 15). Males (mean = 43.7, range = 37.8–48.6, SD = 3.5, n = 11) reach larger size than females (mean = 41.7, range = 40.4–43.6, SD = 1.7, n = 4). FHD 16.4–22.4 mm (mean = 20.0, SD = 1.9, n = 15). BW 6.2–8.5 mm SVL (mean = 7.3, SD = 0.8, n = 15). Forelimbs 31.9–38.4% of SVL (mean = 33.9%, SD = 1.8, n = 15). Hindlimbs 42.1–49.5% of SVL (mean = 45.8%, SD = 2.2, n = 15). Scale rows at midbody 24–27 (mean = 25.5, SD = 0.9, n = 17); paravertebral scales 43–50 (mean = 45.6, SD = 1.8, n = 17). Lamellae under 4th toe 22–29 (mean = 24.2, SD = 1.9, n = 17); single supradigital scales on 4th toe 11–14 (mean = 12.5, SD = 1.2, n = 17). Mostly three pairs of nuchals, but QM J97890, PMO 8, and SJR 14675 have two, NMV D76545 has four, and NMV D765440 has three on left side and two on right side. Primary nuchals usually separated from secondary temporals by single smaller intercalated scale, but BPBM 21670 and SAMA R.57046 have two on left side and one on right side. Prefrontals either separated by frontonasal and frontal contact (n = 9) or in narrow medial contact (n = 8). Presuboculars usually one (n = 15), rarely two (n = 2). Supraciliaries typically eight (n = 14), rarely seven (n = 1) or nine (n = 2). Anteriormost supraciliary typically in narrow contact with frontal (n = 14), occasionally separated (n = 3). Postsuboculars typically two (n = 16), rarely one (BPBM 21668). Chin shields typically symmetrical (n = 16), rarely two on left side contacting one on right side (NMV D76544).

Overall colour pattern is consistent across all specimens, comprising three dorsal stripes on black background on head and body, limbs mottled black and white, and tail yellowish with series of black lateral and dorsal flecks. Some variation in continuity and form of dorsolateral stripes evident, these often broken into series of flecks or blotches or even mottling, especially towards posterior part of body. Considerable variation in how far black flecking extend from the base of the tail, extent ranging between 10–30 mm from the base. Venter typically light buff and unpatterned, occasionally with scattered black flecks under tail and along sides of body. Exposed surfaces of original and regrown tail always dirty yellow.



Figure 3. Photos in life of *Papuascincus eldorado* **sp. nov.**: **A** holotype (QM J97880) from P’nyang, Western Province; **B** paratype (BPBM 21669) from Aseki, Morobe Province; **C** paratype (SAMA R.71758) from Benaria, Hela Province; **D** paratype (SAMA R.57046) from Gobe, Southern Highlands Province; **E–F** uncollected specimen from Moran, Hela Province. Image A by Paul M. Oliver, image B by Allen Allison, images C and D by Stephen J. Richards, images E and F by Mark O’Shea.

Colouration in life. The following description of colour in life is based on photographs of specimens QM J97880, SAMA R.71758, SAMA R.57046, and BPBM 21669, plus additional photographs of uncollected specimens provided by Mark O’Shea and Nick Baker (Fig. 3). Base colouration of dorsum glossy black, light patterning on head and body typically transitions from glossy greenish-yellow on head and anterior body to more yellow or gold on posterior body and tail. Pattern otherwise as per description in preservative.

Genetic comparisons. Based on analyses of a 708 bp region of the ND4 mitochondrial gene *Pap. eldorado* **sp. nov.** is most closely allied (mean p-distance 11.7%) to *Papuascincus* lineage IV, a slightly larger form (SVL typically between 50–60mm) that occurs at higher ele-

vations in the Central Cordillera (1500–2500 m a.s.l.) (Slavenko et al. 2020). The two sequences for *Pap. eldorado* **sp. nov.** were identical.

Etymology. From the Spanish noun phrase meaning “the golden”, in reference to the species’ distinct golden colouration.

Distribution. This species is known from numerous sites spanning 500 km along the southern versant of New Guinea’s Central Cordillera, extending from Western Province, in the west through Southern Highlands, Hela and Chimbu Provinces, and as far east as the Bulolo area, Morobe Province. Given its wide range in PNG, it is possible that it also extends further west into Papua Province of Indonesian New Guinea.



Figure 4. Habitat photos of (A) P'nyang, type locality for *Papuascincus eldorado* **sp. nov.**, and (B–C) summit of Mt. Menawa, type locality for *Papuascincus borealis* **sp. nov.** Image A by Paul M. Oliver, images B and C by Allen Allison.

Natural history. All records of *Pap. eldorado* **sp. nov.** are from foothill and lower montane forest between 760 and 1600 m a.s.l. Records on the P'nyang Range (Fig. 4A) are from between ~760 m a.s.l. and 1075 m a.s.l. (the maximum elevation sampled), and the new species was not observed during extensive searches at 560 m a.s.l. in this same range. In the Moran area of Hela Province the species was encountered up to 1600 m a.s.l. (Mark O'Shea pers. comm.) but it was not observed at sites >2,000 m a.s.l. on Gigira Ridge to the northwest of Moran during extensive surveys there (S. Richards pers. obs.). On the Wau-Bulolo-Aseki road this species was only observed at around 1100 m a.s.l. despite extensive surveys at other elevations along the road during the 1980s. An observation on iNaturalist from along the Aseki road on the south side of the central divide (7.334°S, 146.314°E; <https://www.inaturalist.org/observations/141932949>) was at an elevation of around 1275 m a.s.l. (Mattias S Lanas pers. comm.). These data all suggest that *Pap. eldorado* **sp. nov.** is mostly restricted to a relatively narrow elevational band, but extends broadly along the southern edge of the Central Cordillera in Papua New Guinea. The only exception to the generally southern versant distribution are the specimens from Komagowatta, just north of the main range along the well-travelled road to Aseki.

At most localities in the west of its range this species was collected on karst basement. Due to the very thin soils and complex nature of these landscapes tree cover was in many areas relatively low and quite patchy, with

few very large emergent trees (Fig. 4A). Animals were typically observed basking in patches of sun on the forest floor or atop vegetative debris around campsites. Of the ten specimens in the series from P'nyang eight were males and two were females suggesting that at the time of this survey (April–May) males may be more active or more detectable than females. Other basking skinks collected in sympatry were *Emoia physicina* Brown & Parker, 1985 and *E. physicae* (Duméril & Bibron, 1839) at 760 m a.s.l. and *E. brongersmai* Brown, 1991 at 1075 m a.s.l. Similarly, our specimens from the vicinity of Aseki, in the eastern part of the range, were from relatively open secondary growth areas amidst towering columns of karst. They were typically observed basking on the ground in patches of sun, where they co-occurred with at least two species of widely distributed mid-montane ground skinks, *E. physicae* and *E. pallidiceps* (De Vis, 1890). We also collected *Lygisaurus* cf. *novaeguineae* (Meyer, 1874) from the interior of patches of adjacent forest.

Lineages III and IV of *Papuascincus* (Slavenko et al. 2020) occur in close proximity to *Pap. eldorado* **sp. nov.**, but typically occur at higher elevations and differ greatly in colouration. Lineage IV, which is widely distributed in the Central Cordillera, is phylogenetically close to *Pap. eldorado* **sp. nov.** but is much larger (adult SVL 44.4–63.7 mm) and differs in colouration (it exhibits the “classic” *Papuascincus* dorsal pattern of two light dorsolateral stripes on light brown background) and elevational range

(> 1800 m a.s.l.). Lineage III is similar in size to *Pap. eldorado* **sp. nov.** (36.3–54.4 mm), but also has the “classic” *Papuascincus* dorsal pattern and almost all Central Cordillera populations of this form sampled by Slavenko et al. (2020) occur at elevations above 1700 m a.s.l. At ~1075 m a.s.l. In the P’nyang area we photographed a single specimen of *Papuascincus* that we tentatively assign to lineage III based on colour pattern, providing evidence of sympatry. We are also aware of populations of lineage III on Mt. Missim, Morobe province at elevations of 1190–1300 m a.s.l., slightly above the known distribution of *Pap. eldorado* **sp. nov.** in Morobe Province (1100–1130 m a.s.l.). These data suggest that the elevational distributions of lineage III and *Pap. eldorado* **sp. nov.** abut, but do not extensively overlap where the species occur in close proximity. Three other potentially undescribed species of *Papuascincus* were collected on the Wau-Aseki road at higher elevations than BPBM 21668–70.

Suggested IUCN status. The populations described herein represent an extent of occurrence of 19,986 km² and an area of occupancy of 80 km² (based on occupation of 4 km² cells; both calculated using <http://geocat.kew.org>). The species occurs over a wide area, on multiple substrates, and at an elevational band that suggests a considerable scope for upslope retreat as global temperatures rise in coming decades. We therefore recommend assigning an IUCN red list conservation status of Least Concern for *Pap. eldorado* **sp. nov.**

Papuascincus borealis **sp. nov.**

Northern Ranges Gold-striped skink

<https://zoobank.org/0425A3EE-D2B6-4774-8E0D-23AD-AC9C6427>

Figures 4–6

Holotype. BPBM 23059 (field number AA 11963; GenBank number OR837029), ovigerous adult female with two eggs, at summit of Mt. Menawa, approximately 10.5 km N and 15.7 km E of Utai, Bewani Mountains, Sandaun (West Sepik) Province, Papua New Guinea (3.295°S, 141.723°E, 1950 m a.s.l.), collected by A. Allison on 19 October 1986.

Paratypes (n = 3). BPBM 23016, 23060, 23061 (GenBank number OR837028) (three adult males), same locality and collection data as holotype.

Diagnosis. A species of *Papuascincus* characterised by the unique combination of large size (maximum adult SVL 58.2 mm); 2–3 small rounded lobules on anterior edge of ear opening; postsuboculars typically three; scale rows at midbody 26–28; paravertebral scales 46–47; lamellae under 4th toe 20–25; single supradigital scales on 4th toe 14–15; dorsal colour pattern on body consisting of

three yellow-gold dorsal stripes on a black background; tail gold with diffuse black speckling not extending more than 10 mm along tail; limbs black with gold flecking.

Comparisons. *Papuascincus borealis* **sp. nov.** differs from *Pap. stanleyanus* (n = 1), *Pap. buergeri* (n = 8), *Pap. morokanus* (n = 2), and *Pap. phaeodes* (n = 1) in having a dorsal pattern consisting of three light stripes on black background versus two light dorsolateral stripes on light brown background (*Pap. stanleyanus* and *Pap. buergeri*), two light dorsolateral stripes and two dark brown medial stripes on light brown background (*Pap. morokanus*), or dark grey-brown blotches on light brown background (*Pap. phaeodes*). It additionally differs from *Pap. stanleyanus* and *Pap. buergeri* in having a lower count of scale rows at midbody (26–28 vs. 31 and 28–31, respectively), from *Pap. stanleyanus* in having a lower count of paravertebral scales (46–47 vs. 64), from *Pap. morokanus* and *Pap. phaeodes* in achieving larger adult size (maximum SVL 58.2 mm vs. 45.6 and 44.5, respectively), from *Pap. morokanus* in having a higher count of single supradigital scales on 4th toe (14–15 vs. 6–7), and from *Pap. phaeodes* in having 2–3 small rounded lobules on anterior edge of ear opening (vs. 4–5 large, sharply pointed), and in having a much higher count of single supradigital scales on 4th toe (14–15 vs. 2).

In overall colour pattern *Papuascincus borealis* **sp. nov.** is most similar to *Palaia pulchra* and *Pap. eldorado* **sp. nov.**, from which it differs in having larger adult size (maximum SVL 58.2 mm vs. 40.8 and 48.6, respectively). It further differs from *Pal. pulchra* in having sutured nasal scale (vs. unsutured; see Slavenko et al. 2022), tail gold in life (vs. orange), white lateral stripe absent (vs. present), and limbs overall black with gold mottling (vs. orange with black mottling). It further differs from *Pap. eldorado* **sp. nov.** in having modally three postsuboculars (vs. two), a less distinct yellow canthal stripe, face densely patterned with diffuse and extensive black areas (vs. distinct glossy black blotching and flecking on a light background; Figs 2C, 5C), dorsal stripes grading from gold to yellow (vs. greenish-yellow to yellow; Figs 3, 6), and tail of adults with diffuse black speckling not extending more than 10 mm along tail (vs. tail with clear black flecks extending up to 30 mm along tail; Figs 2A, 5A).

Description of holotype. Ovigerous adult female, SVL 56.2 mm; tail regenerated, 81.5 mm total length, 16.2 mm regenerated section; FHD 28.9 mm; BW 10.4 mm; HL 12.6 mm; HW 7.8 mm; HD 6.0 mm; FLL 19.4 mm; HLL 25.5 mm; two eggs in abdomen.

Rostral broad and shallow, wider than deep, projecting slightly onto top of snout; nasals more or less rectangular, separated by rostral and frontonasal contact, projecting anterodorsally onto dorsum of snout; nostril circular, centred within nasal, with suture extending posteriorly from anterodorsal edge of nostril to edge of nasal scale; frontonasal large, with seven sides, extending laterally to slightly above level of nares, posteriorly in narrow contact with frontal; prefrontals large, in narrow medial

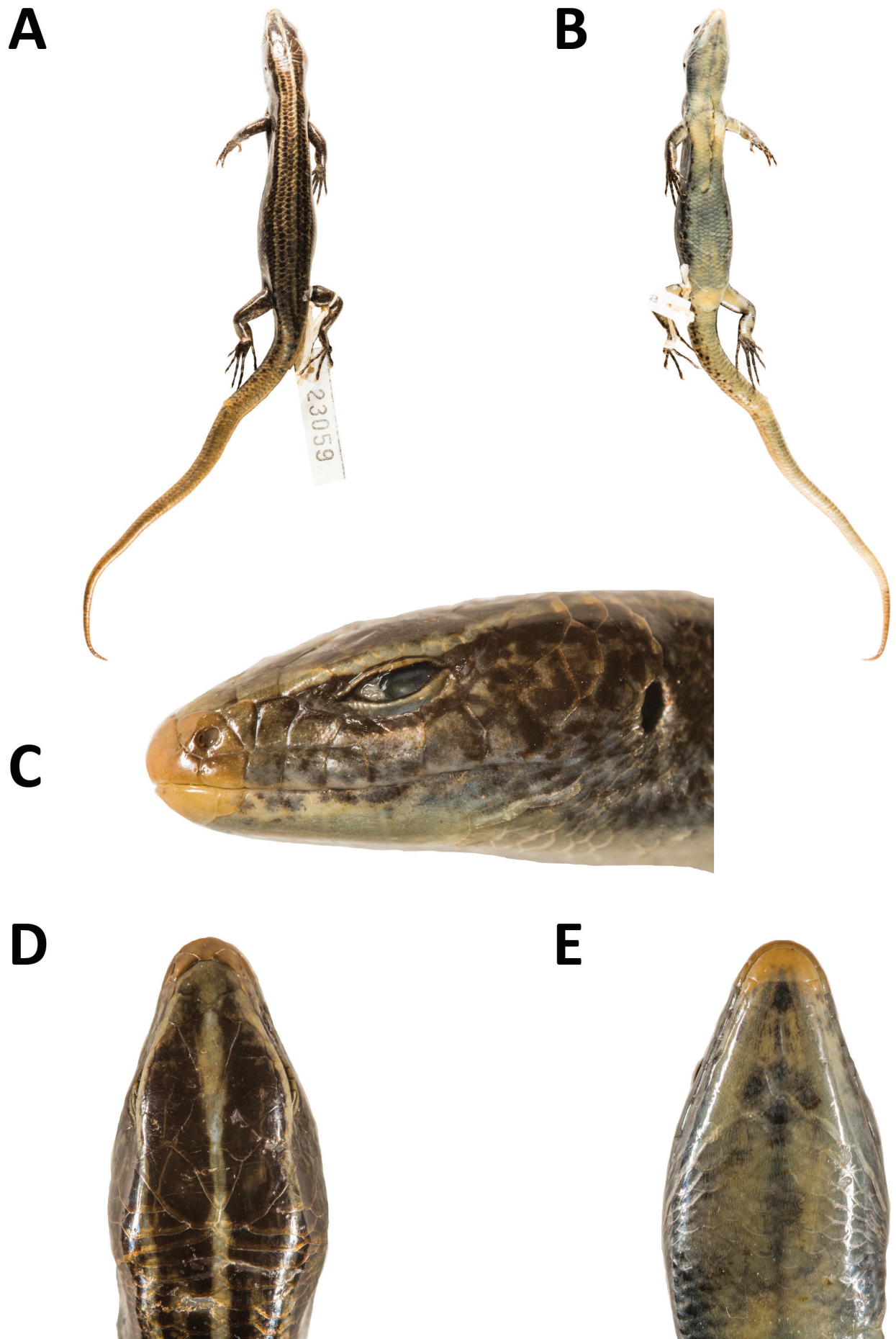


Figure 5. *Papuascincus borealis* sp. nov. holotype (BPBM 23059); **A** dorsal view, **B** ventral view, **C** lateral view of head, **D** dorsal view of head, and **E** ventral view of head. Images by Alex Slavenko.



Figure 6. Photos in life of *Papuascincus borealis* sp. nov.: **A** holotype (BPBM 23059); **B** paratype (BPBM 23061); **C** paratype (BPBM 23016), all from Mt. Menawa, Sandaun (Sepik) Province. Images by Allen Allison.

contact, bordered lateroventrally by two loreals; supraoculars four, of which two contact the frontal, and three contact the frontoparietal; frontal roughly kite shaped, widest anteriorly; frontoparietal single, anteriorly in narrow contact with frontal, posteriorly with interparietal and parietals; interparietal smaller than fused frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietal, posteriormost supraocular, and two pretemporals; nuchals in four pairs, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale.

Anterior loreal slightly smaller than posterior loreal, both higher than long; lower preocular roughly square in shape; upper preocular much smaller, longer than high, separated from prefrontal by anteriormost supraciliary

and posterior loreal contact; presubocular single, abutting supralabials; postsuboculars three, lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with clear palpebral disc roughly size of ear opening; supraciliaries eight, anteriormost in narrow contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporal single, interdigitated between posterior two supralabials; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening moderately large, with three small round lobules along anterior margin.

Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin



Figure 7. Photo of *Palaia pulchra* (BPBM 38789), image by Allen Allison.

shields in three pairs, first pair in medial contact, second pair narrowly separated by single medial scale, third pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial.

Body scales smooth, in 28 rows at midbody; paravertebral scales 46; medial precloacal scales enlarged, overlapping lateral precloacals.

Scales on dorsal surface of fourth toe in two rows proximally, single row distally beginning midway along proximal phalanx, 14 single scales; subdigital lamellae under fourth toe 23, smooth.

Colouration in preservative. Base dorsal colouration black, with a narrow unbroken yellow vertebral stripe extending from snout-tip to base of tail, two narrower unbroken yellow dorsolateral stripes, and small number of additional yellow flecks between vertebral and dorsolateral stripes, forming faded stripes on posterior half of body. Lateral surfaces of body largely black overlain with series of yellow mid-lateral flecks and additional pale ventrolateral mottling. Lateral surfaces of head with diffuse black and yellow mottling, and prominent yellow canthal stripe. Body venter light buff, unpatterned. Limbs black on dorsal and lateral surfaces with extensive yellow mottling. Ventral surfaces of limbs buff. Digits banded white and black on exposed surfaces, black on palmar and plantar surfaces. Original portions of tail faded yellow on exposed surfaces, buff ventrally, with few black dorsal and lateral flecks extending from base to approximately 10 mm along tail. Regrown section of tail dirty yellow, unpatterned.

Variation in the type series. Adult body size 53.8–58.2 mm SVL (mean = 55.7, SD = 2.0, $n = 4$). FHD 25.3–28.9 mm (mean = 26.7, SD = 1.5, $n = 4$). BW 8.9–10.3 mm (mean = 9.6, SD = 0.6, $n = 4$). Forelimbs 32.4–34.5% of SVL (mean = 33.5%, SD = 0.9, $n = 4$). Hindlimbs 40.6–45.4% of SVL (mean = 43.0%, SD =

2.0, $n = 4$). Scale rows at midbody 26–28 (mean = 27, SD = 1.15, $n = 4$); paravertebral scales 46–47 (mean = 46.25, SD = 0.5, $n = 4$). Lamellae under 4th toe 20–25 (mean = 23, SD = 2.2, $n = 4$); single supradigital scales on 4th toe 14–15 (mean = 14.25, SD = 0.5, $n = 4$). BPBM 23016 with three pairs of nuchals, BPBM 23060 with two nuchals on left side and four on right, BPBM 23061 with three nuchals on left side and two on right. Primary nuchals usually separated from secondary temporals by single smaller intercalated scale, but BPBM 23060 has two on left side and one on right. Prefrontals either separated by frontonasal and frontal contact ($n = 2$) or in narrow medial contact ($n = 2$). Supraciliaries either seven ($n = 2$) or eight ($n = 2$). Anteriormost supraciliary in narrow contact with frontal in all but BPBM 23060 where it is separated. Postsuboculars typically three ($n = 3$), occasionally two (BPBM 23016). Pretemporals typically two, occasionally one (BPBM 23060). Supralabials typically seven ($n = 3$), occasionally six (BPBM 23016).

Overall colour pattern highly consistent across all specimens, always including three dorsal stripes on black background on head and body, limbs mottled black and yellow, and tail yellowish with minimal black lateral and dorsal flecks. Some variation in continuity and form of yellow flecks along posterior of dorsum between vertebral stripe and dorso-lateral stripes, often, but not always, forming indistinct stripes extending to base of tail. Venter always light buff, unpatterned. Exposed surfaces of original and regrown tail always dirty yellow.

Colouration in life. The following description of colour in life is based on photographs of specimens BPBM 23016, 23059, and 23061 (Fig. 6). Base colouration of dorsum glossy black, light patterning on head and body typically transitions from glossy golden-yellow on head and upper body to gold on posterior body and tail.

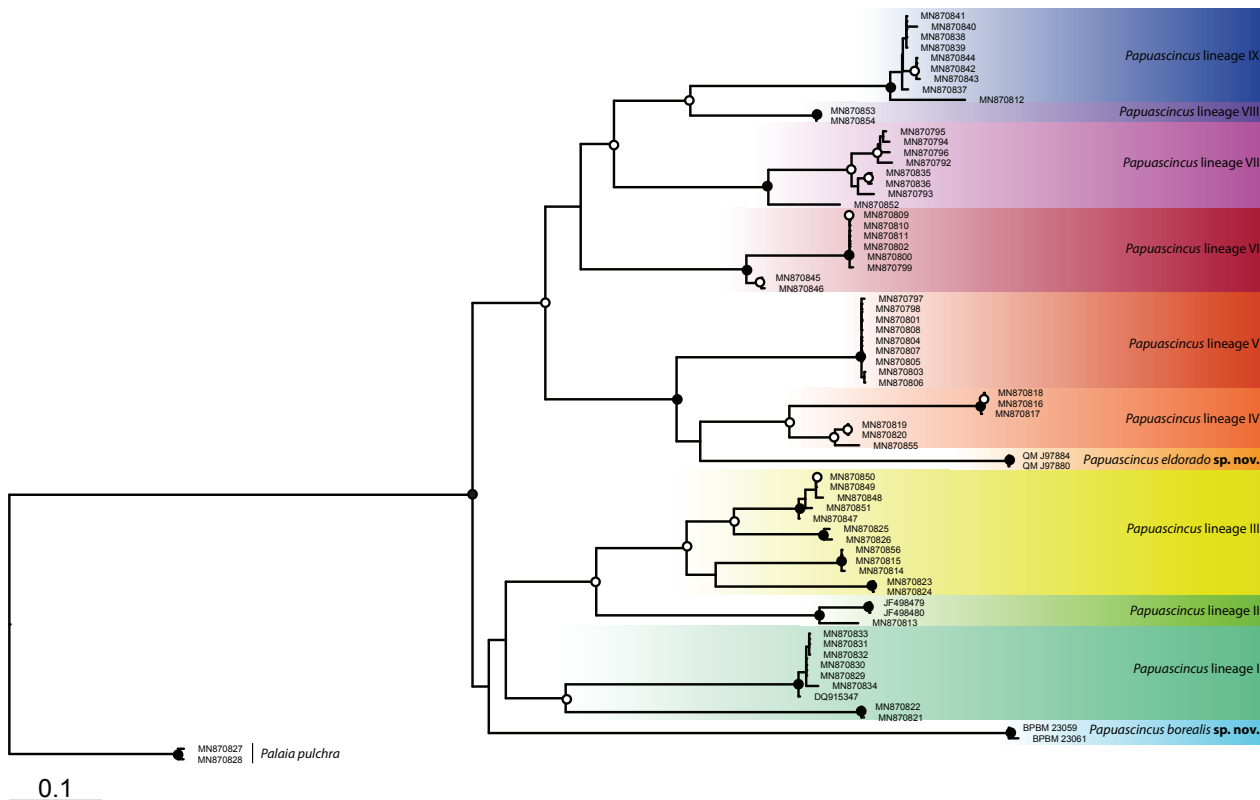


Figure 8. Maximum Likelihood phylogenetic reconstruction of *Papuascincus* based on a 708 bp region of the ND4 mitochondrial gene. Filled circles represent nodes with a bootstrap (BS) value of 100%, empty circles represent nodes with BS values between 80% and 100%, and no circles represent unsupported nodes (BS < 80%). Clade labels for the different lineages of *Papuascincus* follow Slavenko et al. 2020. The raw tree file in Nexus format is available in Appendix 3.

Genetic comparisons. Based on analyses of a 708 bp region of the ND4 mitochondrial gene *Pap. borealis* **sp. nov.** is deeply divergent from all other sampled *Papuascincus* (minimum p-distance 14.4% being to *Papuascincus eldorado* **sp. nov.**, and other taxa being more divergent). The within-species p-distance was 0.4%.

Etymology. Masculine Latin adjective meaning “northern”, in reference to the species’ distribution on the Bewani Mountains, the most northerly location of any known species of *Papuascincus*.

Distribution. Only known from the summit of Mt. Menawa (~1950m a.s.l.), in the Bewani mountains on the northern versant of New Guinea. This is the only species of *Papuascincus* known to occur on the North Coastal Ranges (excluding the Huon Peninsula).

Natural history. Mt. Menawa is an isolated mountain and the highest peak in the otherwise low-lying Bewani Range and was originally covered in cloud forest, with stands of *Nothofagus grandis* and *Lithocarpus* sp. prominent on the adjoining ridges (Fig. 4B–C). The summit was cleared some years prior to collection of the type series to create a helicopter landing area to support the installation of a small solar-powered repeater for Papua New Guinea’s radio-telephone system along the border with Indonesia. The landing area was being encroached on by an assemblage of early succession montane shrubs and trees

including *Homalanthus novoguineensis*, *Melicope elleryana*, *Alphitonia incana*, and *Caldcluvia* sp., together with gingers (*Alpinia* spp.), and a pitcher plant (*Nepenthes* sp.). Two species of successional ferns, *Diplopterygium* and *Dipteris*, were common in open areas as was a prostrate species of *Vaccinium*.

Pap. borealis **sp. nov.** was observed basking ca. 50 cm above the ground on the base of a tree stump and on other similarly raised perches suggesting that it may be partially arboreal. It appeared to be uncommon. The ground skink *Emoia irianensis* Brown, 1991 was also found on the summit. It was previously known only from montane areas at the western end of the Central Cordillera (1200–2000 m a.s.l.). We observed *E. irianensis* basking in open areas within a prostrate species of *Vaccinium* and it appeared to be uncommon. The occurrence of *E. irianensis* on Mt. Menawa suggests that there have been dispersal pathways between the Bewani Mountains and the mountains of north-east Indonesian New Guinea. This area of Indonesian New Guinea remains poorly known and *Papuascincus borealis* **sp. nov.** may also occur there.

Suggested IUCN status. Population size and trend unknown. The four specimens are only known from a single location, with an area of occupancy of a single 4 km² cell. The true extent of the species’ distribution in the Bewani mountains, and potentially in the other peaks in the Torricelli mountains or even the Cyclops and Foja mountains (in Indonesia) needs to be determined. Repeated surveys will

also be needed on Mt. Menawa - since the 1980s, a network of roads has been constructed in the lowlands north of the Bewani Mountains and extensive areas of forest have been cleared for oil palm. If, as is likely, these developments facilitate logging that extends into the Bewani Mountains, this may adversely impact the only known population of *Pap. borealis* **sp. nov.** If further survey work confirms a restricted distribution with little scope for upslope elevational retreat under future warming climates it will likely qualify for Endangered or Critically Endangered. In the absence of good survey data we recommend assigning a status of Data Deficient to *Pap. borealis* **sp. nov.**

Discussion

Papuascincus eldorado **sp. nov.** and *Pap. borealis* **sp. nov.** share a similar colour pattern of three gold dorsal stripes on a black background. This pattern is atypical for *Papuascincus*, which are generally less brightly coloured with fewer dorsal stripes (with the exception of *Pap. morokanus*). These colour patterns are, however, similar to *Palaia pulchra* (Fig. 7), a distantly related and much more arboreal species from lower elevations. This similarity suggests parallel or convergent evolution of bright colouration that is almost certainly disruptive and may potentially draw attention to the striking yellow tail (Murali and Kodandaramaiah 2016).

Pap. eldorado **sp. nov.** occurs at elevations (700–1300 m a.s.l.) lower than is typical for most species of *Papuascincus*, which have elevational distributions centred above 1500 m. a.s.l. (Slavenko et al. 2020). Phylogenetically, *Pap. eldorado* **sp. nov.** is nested within the genus, and forms a clade with *Papuascincus* lineages IV and V (Fig. 8). These phylogenetic data suggest that *Pap. eldorado* **sp. nov.** is derived from ancestors that occurred at higher elevations. The elevational distribution of *Pap. eldorado* **sp. nov.** also provides an example of how elevational segregation may be important in the accumulation of species diversity in this genus. While this species has a huge extent of occurrence, it occurs in a tightly bounded elevational band, potentially in part because there are other *Papuascincus* at higher elevations in the Central Cordillera of similar size to *Pap. eldorado* **sp. nov.** (lineage III). Most populations of *Pap. eldorado* **sp. nov.** are also associated with karst landscapes, suggesting a possible specialisation to that habitat, a situation not unknown from New Guinea (Nielsen and Oliver 2017). Slavenko et al. (2020) have previously posited that different lineages of *Papuascincus* are very similar morphologically and ecologically, and therefore sympatry only occurs between lineages that diverge in body size. Given that the Central Cordillera is home to two other lineages of *Papuascincus* that are divergent in size (lineages III and IV), substrate niche separation in *Pap. eldorado* **sp. nov.** may be another mechanism for avoiding competition in the genus.

Pap. borealis **sp. nov.** is currently the only species of *Papuascincus* known from the North Coastal Rang-

es. Recent systematic and phylogenetic work has revealed several instances of putative or confirmed sister lineages distributed across seemingly isolated montane (> 1000 m) habitats in the North Coastal Ranges and the Central Cordillera (*Cyrtodactylus boreoclivus* Oliver, Krey, Mumpuni & Richards, 2011 and *Cyrtodactylus medioclivus* Oliver, Richards & Sistrom, 2012; Oliver et al. 2012; *Litoria pinnochio* Oliver, Günther, Mumpuni & Richards, 2019 and *Litoria pronimia* Menzies, 1993; Oliver et al. 2019; possibly also *Lobulia brongersmai* (Zweifel, 1972) and *Lobulia marmorata* Slavenko et al., 2021, fide Slavenko et al. 2022). The phylogenetic affinities of *Pap. borealis* **sp. nov.** within the genus remain unresolved (Fig. 8) but suggest it is more deeply divergent than the afore-mentioned north and south taxon pairs of montane taxa. Additional genetic data, including nuclear loci and genomic sequencing is required to better understand when and how low-vagility montane lineages have been able to move across these isolated ranges. *Pap. borealis* **sp. nov.** is currently known only from the top of the highest peak in the Bewani Mountains. There has been moderately extensive survey work in the Bewani Mountains and, to date there are no records from lower elevations. It was also not seen during extensive surveys at around 1500 m. a.s.l. in the Foja Mountains, although survey effort at higher elevations in this range (>1700 m a.s.l.) was limited to four days and it was mostly overcast or raining (P. Oliver and S. Richards pers. obs.). Available data suggest that this species is restricted to high elevations, and confirming its presence or absence on the high peaks of nearby mountain ranges (Torricellis, Cyclops, Foja) should be a high priority. If it is restricted to a small area of high elevation habitat, then this species is likely vulnerable to climatic change. Lack of knowledge about the biology and distribution of this species means it will join a long list of Data Deficient skinks in New Guinea, despite this region being one of the prominent hotspots of global skink diversity (Slavenko et al. 2023). Many more species of skinks await discovery and formal description in New Guinea and we urge more research in this extremely biodiverse but poorly-studied island.

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References

- Allison A, Greer AE (1986) Egg shells with pustulate surface structures: Basis for a new genus of New Guinea skinks (Lacertilia: Scincidae). *Journal of Herpetology* 20: 116–119. <https://doi.org/10.2307/1564142>
- Boulenger GA (1887) Catalogue of the lizards in the British Museum (Natural History) III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae. British Museum (Natural History), London.
- Boulenger GA (1903) Descriptions of new reptiles from British New Guinea. *Proceedings of the Zoological Society of London* 1903: 125–129.
- Brown WC (1991) Lizards of the genus *Emoia* (Scincidae) with observations on their evolution and biogeography. *Memoirs of the California Academy of Sciences* 15: 1–94.
- Brown WC, Parker F (1985) Three new lizards of the genus *Emoia* (Scincidae) from southern New Guinea. *Breviora* 480: 1–12.
- Cámara-Leret R, Frodin DG, Adema F, Anderson C, Appelhans MS, Argent G, Guerrero SA, Ashton P, Baker WJ, Barfod AS, Barrington D, Borosova R, Bramley GLC, Briggs M, Buerki S, Cahen D, Callmander MW, Cheek M, Chen C-W, Conn BJ, Coode MJE, Darbyshire I, Dawson S, Dransfield J, Drinkell C, Duyffjes B, Ebihara A, Ezedin Z, Fu L-F, Gideon O, Girmansyah D, Govaerts R, Fortune-Hopkins H, Hassemmer G, Hay A, Heatubun CD, Hind DJN, Hoch P, Homot P, Hovenkamp P, Hughes M, Jebb M, Jennings L, Jimbo T, Kessler M, Kiew R, Knapp S, Lamei P, Lehnert M, Lewis GP, Linder HP, Lindsay S, Low YW, Lucas E, Mancera JP, Monroe AK, Moore A, Middleton DJ, Nagamasu H, Newman MF, Lughadha EN, Melo PHA, Ohlsen DJ, Pannell CM, Parris B, Pearce L, Pennneys DS, Perrie LR, Petoe P, Poulsen AD, Prance GT, Quakenbush JP, Raes N, Rodda M, Rogers ZS, Schuitman A, Schwartzburd P, Scotland RW, Simmons MP, Simpson DA, Stevens P, Sundue M, Testo W, Trias-Blasi A, Turner I, Utteridge T, Walsingham L, Weber BL, Wei R, Weiblen GD, Weigend M, Weston P, de Wilde W, Wilkie P, Wilmot-Dear CM, Wilson HP, Wood JRI, Zhang L-B, van Welzen PC (2020) New Guinea has the world's richest island flora. *Nature* 584: 579–583. <https://doi.org/10.1038/s41586-020-2549-5>
- Chapple DG, Roll U, Böhm M, Aguilar R, Amey AP, Austin CC, Balasing M, Barley AJ, Bates MF, Bauer AM, Blackburn DG, Bowles P, Brown RM, Chandramouli SR, Chirio L, Cogger H, Colli GR, Conradie W, Couper PJ, Cowan MA, Craig MD, Das I, Datta-Roy A, Dickman CR, Ellis RJ, Fenner AL, Ford S, Ganesh SR, Gardner MG, Geissler P, Gillespie GR, Glaw F, Greenlees MJ, Griffith OW, Grismer LL, Haines ML, Harris DJ, Hedges SB, Hitchmough RA, Hoskin CJ, Hutchinson MN, Ineich I, Janssen J, Johnston GR, Karin BR, Keogh JS, Kraus F, LeBreton M, Lymberakis P, Masroor R, McDonald PJ, Mecke S, Melville J, Melzer S, Michael DR, Miralles A, Mitchell NJ, Nelson NJ, Nguyen TQ, Nogueira C de C, Ota H, Pafilis P, Pauwels OSG, Perera A, Pincheira-Donoso D, Reed RN, Ribeiro-Júnior MA, Riley JL, Rocha S, Rutherford PL, Sadler RA, Shacham B, Shea GM, Shine R, Slavenko A, Stow A, Sumner J, Tallwin OJS, Teale R, Torres-Carvajal O, Trape J-F, Uetz P, Ukwela KDB, Valentine L, Van Dyke JU, van Winkel D, Vasconcelos R, Vences M, Wagner P, Wapstra E, While GM, Whiting MJ, Whittington CM, Wilson S, Ziegler T, Tingley R, Meiri S (2021) Conservation status of the world's skinks (Scincidae): Taxonomic and geographic patterns in extinction risk. *Biological Conservation* 257: 109101. <https://doi.org/10.1016/j.biocon.2021.109101>
- Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T (2019) ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* 37: 291–294. <https://doi.org/10.1093/molbev/msz189>
- De Vis CW (1890) Reptiles from New Guinea. *Proceedings of the Linnean Society of New South Wales* 5:497–500.
- Duméril AMC, Bibron G (1839) *Erpétologie générale ou histoire naturelle complète des reptiles*. Tome Cinquième. Roret, Paris.
- Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Eidler D, Klein J, Antonelli A, Silvestro D (2021) raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAXML. *Methods in Ecology and Evolution* 12: 373–377. <https://doi.org/10.1111/2041-210X.13512>
- Gamble T (2014) Collecting and preserving genetic material for herpetological research. *Society for the Study of Amphibians and Reptiles*.
- Greer AE (1974) The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology Supplementary Series* 31: 1–67. <https://doi.org/10.1071/AJZS031>
- Greer AE, Simon M (1982) *Fojia bumui*, an unusual new genus and species of scincid lizard from New Guinea. *Journal of Herpetology* 16: 131–139. <https://doi.org/10.2307/1563805>
- Kennedy JD, Marki PZ, Reeve AH, Blom MPK, Prawiradilaga DM, Haryoko T, Koane B, Kamminga P, Irestedt M, Jönsson KA (2022) Diversification and community assembly of the world's largest tropical island. *Global Ecology and Biogeography* 31: 1078–1089.
- Menzies JI (1993) Systematics of *Litoria iris* (Anura: Hylidae) and its allies in New Guinea and a note on sexual dimorphism in the group. *Australian Journal of Zoology* 41: 225–255. <https://doi.org/10.1071/ZO9930225>
- Meyer AB (1874) Eine Mittheilung von Hrn. Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1874: 128–140.
- Murali G, Kodandaramaiah U (2016) Deceived by stripes: Conspicuous patterning on vital anterior body parts can redirect predatory strikes to expendable posterior organs. *Royal Society Open Science* 3: 160057. <https://doi.org/10.1098/rsos.160057>
- Nielsen SV, Oliver PM (2017) Morphological and genetic evidence for a new karst specialist lizard from New Guinea (*Cyrtodactylus*: Gekkonidae). *Royal Society Open Science* 4: 170781. <https://doi.org/10.1098/rsos.170781>
- Oliver PM, Krey K, Mumpuni M, Richards SJ (2011) A new species of bent-toed gecko (*Cyrtodactylus*, Gekkonidae) from the North Papuan Mountains. *Zootaxa* 2930: 22–32. <https://doi.org/10.11646/zootaxa.2930.1.2>
- Oliver PM, Richards SJ, Siström M (2012) Phylogeny and systematics of Melanesia's most diverse gecko lineage (*Cyrtodactylus*, Gekkonidae, Squamata). *Zoologica Scripta* 41: 437–454. <https://doi.org/10.1111/j.1463-6409.2012.00545.x>

- Oliver PM, Iannella A, Richards SJ, Lee MSY (2017) Mountain colonisation, miniaturisation and ecological evolution in a radiation of direct-developing New Guinea Frogs (*Choerophryne*, Microhylidae). *PeerJ* 5: e3077. <https://doi.org/10.7717/peerj.3077>
- Oliver PM, Günther R, Mumpuni M, Richards SJ (2019) Systematics of New Guinea treefrogs (*Litoria*: Pelodyadidae) with erectile rostral spikes: An extended description of *Litoria pronimia* and a new species from the Foja Mountains. *Zootaxa* 4604: 335–348. <https://doi.org/10.11646/zootaxa.4604.2.6>
- Oliver PM, Bower DS, McDonald PJ, Kraus F, Luedtke J, Neam K, Hobin L, Chauvenet ALM, Allison A, Arida E, Clulow S, Günther R, Nagombi E, Tjaturadi B, Travers SL, Richards SJ (2022) Melanesia holds the world's most diverse and intact insular amphibian fauna. *Communications Biology* 5: 1182. <https://doi.org/10.1038/s42003-022-04105-1>
- Parker HW (1936) V. – A Collection of reptiles and amphibians from the mountains of British New Guinea. *Annals and Magazine of Natural History* 17: 66–93. <https://doi.org/10.1080/03745481.1936.10801389>
- Prasetya AM, Moritz C, Joseph L, Stelling MW, Oliver PM (2023) Birds and barriers: Present and past seas are dominant correlates of avian turnover in the Indo-Australian Archipelago. *Frontiers of Biogeography* 15: e58189. <https://doi.org/10.21425/F5FBG58189>
- Rodríguez ZB, Perkins SL, Austin CC (2018) Multiple origins of green blood in New Guinea lizards. *Science Advances* 4: eaao5017. <https://doi.org/10.1126/sciadv.aao5017>
- Shea GM (2021) Nomenclature of supra-generic units within the family Scincidae (Squamata). *Zootaxa* 5067: 301–351. <https://doi.org/10.11646/ZOOTAXA.5067.3.1>
- Skinner A (2007) Phylogenetic relationships and rate of early diversification of Australian *Sphenomorphus* group scincids (Scincoidea, Squamata). *Biological Journal of the Linnean Society* 92: 347–366. <https://doi.org/10.1111/j.1095-8312.2007.00843.x>
- Slavenko A, Tamar K, Tallowin OJS, Allison A, Kraus F, Carranza S, Meiri S (2020) Cryptic diversity and non-adaptive radiation of montane New Guinea skinks (*Papuascincus*; Scincidae). *Molecular Phylogenetics and Evolution* 146: 106749. <https://doi.org/10.1016/j.ympev.2020.106749>
- Slavenko A, Tamar K, Tallowin OJS, Kraus F, Allison A, Carranza S, Meiri S (2022) Revision of the montane New Guinean skink genus *Lobulia* (Squamata: Scincidae), with the description of four new genera and nine new species. *Zoological Journal of the Linnean Society* 195: 220–278. <https://doi.org/10.1093/zoolinnean/zlab052>
- Slavenko A, Allison A, Austin CC, Bauer AM, Brown RM, Fisher RN, Ineich I, Iova B, Karin BR, Kraus F, Mecke S, Meiri S, Morrison C, Oliver PM, O'Shea M, Richmond JQ, Shea GM, Tallowin OJS, Chapple DG (2023) Skinks of Oceania, New Guinea, and Eastern Wallacea: An underexplored biodiversity hotspot. *Pacific Conservation Biology*. <https://doi.org/10.1071/PC22034>
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Tallowin OJS, Meiri S, Donnellan SC, Richards SJ, Austin CC, Oliver PM (2020) The other side of the Sahulian coin: Biogeography and evolution of Melanesian forest dragons (Agamidae). *Biological Journal of the Linnean Society* 129: 99–113. <https://doi.org/10.1093/biolinnean/blz125>
- Tallowin OJS, Tamar K, Meiri S, Allison A, Kraus F, Richards SJ, Oliver PM (2018) Early insularity and subsequent mountain uplift were complementary drivers of diversification in a Melanesian lizard radiation (Gekkonidae: *Cyrtodactylus*). *Molecular Phylogenetics and Evolution* 125: 29–39. <https://doi.org/10.1016/j.ympev.2018.03.020>
- Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* 38: 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Toussaint EFA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J, Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications* 5: 4001. <https://doi.org/10.1038/ncomms5001>
- Vogt T (1932) Beitrag zur Reptilienfauna der ehemaligen Kolonie Deutsch-Neuguinea. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1932: 281–294.
- Zweifel RG (1972) A new scincid lizard of the genus *Leiopisma* from New Guinea. *Zoologische Mededelingen* 47: 530–539.

Supplementary Material 1

Appendix 1

Authors: Slavenko A, Richards SJ, Donnellan SC, Allison A, Oliver PM (2024)

Data type: .docx

Explanation notes: Comparative material examined for this study.

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Link: <https://doi.org/vz.74.e112782.suppl1>

Supplementary Material 2

Appendix 2

Authors: Slavenko A, Richards SJ, Donnellan SC, Allison A, Oliver PM (2024)

Data type: .xlsx

Explanation notes: Information on the specimens used in this study, including morphological measurements and related GenBank accession numbers for newly generated sequences.

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Link: <https://doi.org/vz.74.e112782.suppl2>

Supplementary Material 3

Appendix 3

Authors: Slavenko A, Richards SJ, Donnellan SC, Allison A, Oliver PM (2024)

Data type: .tre

Explanation notes: Rooted maximum likelihood phylogeny in Nexus format with bootstrap values.

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