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Revision of the montane New Guinean skink genus *Lobulia* (Squamata: Scincidae), with the description of four new genera and nine new species

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The skink genus *Lobulia* is endemic to New Guinea, the largest and highest tropical island in the world. *Lobulia* and its related genera represent an important component of the montane herpetofauna of New Guinea, but it remains understudied and poorly known. We here provide the first, large-scale, systematic revision of *Lobulia*, using molecular phylogenetic and morphological comparisons to assess the monophyly of the genus and the diversity of species within it. We find that *Lobulia*, as currently defined, is polyphyletic. The eight species currently assigned to it form three clades. Furthermore, many specimens from New Guinea of unknown specific affinity are genetically and morphologically distinct from each other. Based on these data, we re-diagnose *Lobulia* and two of its closely related genera, *Prasinohaema* and *Papuascincus*. We erect four new genera (***Alpinoscincus* gen. nov., *Nubeoscincus* gen. nov., *Ornithuroscincus* gen. nov.** and ***Palaia* gen. nov.**) to address the problem of polyphyly and describe nine new species ***Lobulia fortis* sp. nov., *Lobulia huonensis* sp. nov., *Loublia marmorata* sp. nov., *Lobulia vogelkopensis* sp. nov., *Ornithuroscincus bengaun* sp. nov., *Ornithuroscincus inornatus* sp. nov., *Ornithuroscincus pterophilus* sp. nov., *Ornithuroscincus shearmani* sp. nov.** and ***Ornithuroscincus viridis* sp. nov.** We supplement this taxonomic revision by investigating the biogeographic history of *Lobulia s.l.* and find evidence for a large radiation in the accreted terranes of New Guinea, with multiple independent colonizations of montane habitats and subsequent recolonization of lowland habitats. Our study reinforces the uniqueness and richness of the montane herpetofauna of New Guinea and the importance of mountains to biodiversity in the Tropics.

ADDITIONAL KEYWORDS: biogeography – genus revision – Pacific Islands – reptilian.

INTRODUCTION

The largest and highest tropical island in the world, New Guinea, is among one of the most biodiverse regions on Earth (Allison, 2009; Allison & Tallowin, 2015; Cámara-Leret *et al.*, 2020). It is home to ~6.5% of the terrestrial vertebrate fauna of the world, with extremely high rates of endemism (Allison, 2009). The described biodiversity of New Guinea is even more impressive when considering how poorly the biota of this island is known, especially compared to other tropical regions (Allison, 1996; Allison & Tallowin, 2015). Rigorous exploration of the interior of New Guinea, including zoological and botanical collections, only began in the late 1800s, steadily increasing throughout the 20th Century as technological advancements enabled expeditions to scale the towering mountain ranges (Souter, 1963; Allison &

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Tallowin, 2015). However, range-restricted taxa such as reptiles remain poorly known, because there are few taxonomists working on the fauna of the island, and rates of discovery suggest numerous taxa remain unrecognized (Allison, 1982; Allison & Tallowin, 2015). More than a third of the island rises above 1000 m a.s.l. (Allison, 2009), and the steep mountain ranges provide abrupt shifts in climate and habitat structure (Bryan & Shearman, 2015). The geological history of New Guinea is extremely complex (Pigram & Davies, 1987; Hall, 2002; Quarles van Ufford & Cloos, 2005; Baldwin *et al.*, 2012), driven by the movements of the Australian and Pacific tectonic plates, accretion of terranes and orogeny. Many of these processes, particularly the orogeny of the Central Ranges, probably occurred only in the last few million years (Hall, 2002; Hill & Hall, 2003), and heavily influenced the diversification of the flora and fauna of New Guinea (Toussaint *et al.*, 2021). Recent molecular phylogenetic studies have uncovered multiple cases of the mountains of New Guinea serving as barriers to gene flow for lowland taxa, leading to species divergence (McGuigan *et al.*, 2000; Kadarusman *et al.*, 2012; Georges *et al.*, 2013; Tallowin *et al.*, 2018, 2019), but also creating novel, highly fragmented montane habitats, providing opportunities for allopatric speciation (Toussaint *et al.*, 2014; Schweizer *et al.*, 2015; Marki *et al.*, 2017; Oliver *et al.*, 2017; Tallowin *et al.*, 2018; Slavenko *et al.*, 2020).

Lobulia Greer, 1974 is a genus of skinks found in the montane regions of New Guinea that was proposed by Greer (1974) in his revision of the genus *Leiolopisma* Duméril & Bibron, 1839. Greer originally included five species in the genus: *Lobulia brongersmai* (Zweifel, 1972), *Lobulia elegans* (Boulenger, 1897), *Lobulia morokana* (Parker, 1936), *Lobulia phaeodes* (Vogt, 1932) and *Lobulia stanleyana* (Boulenger, 1897), all formerly included in *Leiolopisma*. The generic diagnosis was based on the lack of a post-orbital bone and the presence of 1–3 small lobules on the anterior margin of the ear opening (Allison & Greer, 1986). However, these traits are also shared with at least some members of two other genera Greer (1974) erected in the same revision: *Lipinia* and *Prasinohaema*. Furthermore, major differences in biology occur even within this original version of *Lobulia*—two included species are viviparous (*Lo. elegans* and *Lo. brongersmai*), whereas two (*Lo. morokana* and *Lo. stanleyana*) are oviparous. These latter two, along with *Lygosoma buergersi* Vogt, 1932 and *Lygosoma phaeodes* Vogt, 1932, were later re-assigned to a newly erected genus *Papuascincus* Allison & Greer, 1986, based on a unique synapomorphy—pustulate surfaces on the egg shells in the two species for which reproductive data were available (Allison & Greer, 1986). Indeed, the main unifying feature of *Lobulia* seemed to be the lack of other apomorphic traits, such as expanded subdigital lamellae (found in both *Lipinia* and *Prasinohaema*), prehensile tails or green blood pigment (unique to *Prasinohaema*). Allison & Greer (1986) redefined the genus on putative synapomorphies with respect to *Papuascincus*, namely two pairs of chin shields in medial contact (vs. 1), and the chin shields being separated from the infralabials by anterior extension of small scales to varying degrees.

Since the erection and redefinition of the genus, several more species have been described. First, *Lobulia alpina* Greer *et al.*, 2005, *Lobulia glacialis* Greer *et al.*, 2005, *Lobulia stellaris* Greer *et al.*, 2005 and *Lobulia subalpina* Greer *et al.*, 2005 were described from high elevations on mountains spread widely throughout the island (Greer *et al.*, 2005), although doubt was expressed that all of these were convincingly part of *Lobulia*. Kraus (2020) recently described a new species, *Lobulia sabini* Kraus, 2020, from the south-eastern tip of New Guinea, and redefined *Lo. elegans* to only include populations in the south-eastern Owen Stanley range. He also resurrected *Lobulia lobulus* (Loveridge, 1945) from synonymy and assigned it to the remaining Central Ranges populations of what was previously recognized as *Lo. elegans s.l.* *Lobulia sabini* is unusual in lacking lobules on the anterior edge of the ear opening—one of the defining traits of the genus. Furthermore, numerous specimens that were collected throughout New Guinea have been putatively assigned to the genus in natural history collections as *Lobulia* sp., despite not always fitting the redefinition of the genus by Allison & Greer (1986). Some of these presumably represent undescribed species. Specimens and species currently putatively assigned to *Lobulia* are morphologically highly diverse: some have scaly lower eyelids, whereas others have semi-transparent "windows"; some have fragmented scalation in the temporal region, and others do not; and coloration patterns, body proportions and other scalational features vary widely between species.

Molecular phylogenetic studies have so far been lacking on *Lobulia*. Some have been conducted on other New Guinean reptiles, including relatives of *Lobulia*. Generally, these studies suggest that current diversity of montane reptiles on the island is greatly underestimated (Slavenko *et al.*, 2020) and that *Prasinohaema* and *Lipinia*, as currently described, are paraphyletic (Pyron *et al.*, 2013; Rodriguez *et al.*, 2018). These recent findings, together with the somewhat vague generic diagnosis of *Lobulia*, raise the need to assess both the monophyly of *Lobulia*, and its currently described diversity.

We provide a formal systematic revision of the genus *Lobulia*. We perform large-scale multilocus molecular phylogenetic analyses across the range of *Lobulia* in New Guinea, sampling both described and undescribed taxa and members of the closely related genera, *Papuascincus*, *Lipinia* and *Prasinohaema*. We supplement this with a comprehensive morphological assessment of *Lobulia* and related genera. We provide a redescription of *Lobulia* and *Lo. lobulus*, erect four new genera and describe nine new

species. We also provide a taxonomic key for the genera and species in this large radiation of New Guinean skinks. Finally, we use our phylogenetic reconstructions to infer the biogeographic and evolutionary history of montane skinks in New Guinea.

MATERIAL AND METHODS

Genetic sampling, DNA extraction, amplification and sequence analysis

We sampled 58 *Lobulia* specimens from across its range in New Guinea (Supporting Information, Table S1), both in Papua New Guinea (PNG) and Indonesia. These included representatives of *Lo. alpina*, *Lo. brongersmai*, *Lo. elegans*, *Lo. glacialis*, *Lo. lobulus* and *Lo. sabini* (but not of *Lo. subalpina* and *Lo. stellaris*), as well as multiple samples of specimens not ascribed to any recognized species. We included close generic relatives of *Lobulia* (Greer, 1974; Rodriguez *et al.*, 2018), using three tissue samples of *Prasinohaema virens* (Peters, 1881), two tissue samples of *Lipinia noctua* (Lesson, 1830) and one sample each of *Lipinia longiceps* (Boulenger, 1895), *Lipinia* cf. *longiceps*, *Prasinohaema flavipes* (Parker, 1936), *Prasinohaema prehensicauda* (Loveridge, 1945) and *Prasinohaema semoni* (Oudemans, 1894). We supplemented this data set by retrieving published sequences from GenBank of two specimens of *Lipinia pulchra* (Boulenger, 1903) and one specimen each of nine *Papuascincus* lineages defined by Slavenko *et al.* (2020) and sequences of the outgroups used for time-calibrated phylogenetic analyses in that study (Slavenko *et al.*, 2020). A total of 89 samples were used for all subsequent analyses (Supporting Information, Table S1).

We chose to omit *Fojia bumui* Greer & Simon, 1982, the only member of the monotypic genus *Fojia*, from this analysis despite it being recovered with high support as sister species to the clade containing *Li. pulchra* and *Papuascincus* (Rodriguez *et al.*, 2018). *F. bumui* is a highly derived semi-aquatic species, closely associated with riparian habitats, that is extremely distinct both behaviourally and morphologically not only from its closest relatives, but from the entire skink fauna of New Guinea (Greer & Simon, 1982). It was recovered as sister to some of our examined taxa, but not nested within any (Rodriguez *et al.*, 2018).

We extracted DNA from ethanol-preserved tissue samples using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). We sequenced a total of three mitochondrial markers—the ribosomal 12S rRNA (12S), the NADH dehydrogenase subunit 2 (*ND2*) and the NADH dehydrogenase subunit 4 (*ND4*)—and two nuclear markers—RNA fingerprint protein 35 (*R35*) and the nerve growth factor β polypeptide (*NGFB*). These markers were used in other studies of Australasian sphenomorphine skinks (Linkem *et al.*, 2011; Slavenko *et al.*, 2020) and thus had sequences available for the outgroups. Primers and PCR conditions used for the amplification and sequencing of all markers are as detailed in Linkem *et al.* (2011). Chromatographs were assembled and edited using Geneious v.11.0.5 (Biomatter Ltd). For the nuclear markers, we identified heterozygous positions and coded them according to the standard International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes. We translated protein-coding genes into amino acids, and we detected no stop codons, suggesting that they were not pseudogenes. We aligned sequences for each marker using MAFFT v.7.3 (Katoh & Standley, 2013) with default parameters. We tested the occurrence of recombination for the two-phased nuclear gene alignments using the Pairwise Homoplasy Index (PhiTest; Bruen *et al.*, 2006) implemented in SplitsTree v.4.14.5 (Huson & Bryant, 2006), and we detected no evidence of recombination ($P > 0.6$ for the two genes).

Phylogenetic analyses

We partitioned our data set for the phylogenetic analyses with PartitionFinder v.2 (Lanfear *et al.*, 2016), using the following parameters: linked branch lengths; BEAST models; BIC model selection; "greedy schemes" search algorithm; single partition for 12S, and by codons for the protein-coding genes *ND2*, *ND4*, *R35* and *NGFB*. We performed phylogenetic analyses under maximum likelihood (ML) and Bayesian inference (BI) frameworks. We analysed data sets with the following partitions and relevant substitution models: 12S (HKY+I+G), *ND2*_1+*ND4*_1 (GTR+I+G), *ND2*_2+*ND4*_2 (GTR+I+G), *ND2*_3 (GTR+G), *ND4*_3 (HKY+I+G), *NGFB*_1+*NGFB*_2+*NGFB*_3+*R35*_1+*R35*_2 (TrNef+G), *R35*_3 (HKY+G). We conducted ML analyses in RAxML v.8.1.2, as implemented in raxmlGUI v.1.5 (Silvestro & Michalak, 2012), with the GTRGAMMA model of sequence evolution and 100 random-addition replicates. We assessed nodal support with 1000 bootstrap replicates. We conducted BI analyses with MrBayes v.3.2.6 (Ronquist *et al.*, 2012). Nucleotide-substitution-model parameters were unlinked across partitions, and we allowed the different partitions to evolve at different rates. We performed two simultaneous parallel runs with four chains per run (three heated, one cold) for 10^7 generations, sampling every 1000 generations for the complete concatenated data set. We examined the standard deviation of the split frequencies between the two runs and the Potential Scale Reduction Factor (PSRF) diagnostic, and discarded the first 25% of trees as burn-in. We considered nodes well-supported if they received ML bootstrap values ≥ 70% and posterior probability (pp) support values ≥ 0.95.

We reconstructed a multilocus species tree using *BEAST (v.1.8.4; Heled & Drummond, 2010). We defined lineages based on the results obtained from the complete data set analysis. Outgroups were excluded and only lineages with a full set of genes were included (thus excluding samples 694, 7685, 9254 and CAS236454 from this analysis). The nuclear loci were phased (see below), and the site models, clock models and gene trees were unlinked across loci (tree model linked for the mtDNA partitions). We used Bayesian Information Criterion (BIC), as implemented in jModelTest v.2.1.7 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012), to select the best model of nucleotide substitution for each partition: 12S (TPM1uf+G), *ND2* (GTR+G), *ND4* (TrN+G), *NGFB* (K80+G) and *R35* (TPM1+G). Other prior settings were as follows (otherwise by default): models as listed above, strict clock prior for the nuclear markers, Yule process species tree prior, random starting trees, ploidy type (mitochondrial for the relevant tree), GTR base substitution prior uniform (0, 100) and alpha prior uniform (0, 10). Three individual runs were performed for 10^8 generations with a sampling frequency of 10^4. We assessed convergence by confirming that all parameters had reached stationarity and had sufficient effective sample sizes (> 200) using Tracer v.1.6 (Rambaut *et al.*, 2014). We used LogCombiner and TreeAnnotator (in the BEAST package) to infer the ultrametric tree after discarding 10% as burn-in. All *BEAST analyses were carried out in the CIPRES Science Gateway (Miller *et al.*, 2010).

We explored patterns of intra-specific diversity and nuclear allele sharing within each newly-defined genus (see *Results*) by inferring statistical parsimony networks on the two individual nuclear genes with the program TCS v.1.21 (Clement *et al.*, 2000), implemented in PopART (Leigh & Bryant, 2015) using default settings (connection limit of 95%) and including only full length sequences. To infer haplotypes, we used the online web tool SeqPHASE (Flot, 2010) to convert the input and output files, and we used the software PHASE v.2.1.1 (Stephens *et al.*, 2001; Stephens & Scheet, 2005) to resolve heterozygous single-nucleotide polymorphisms in the phased alignments, with a probability threshold of 0.7 for *NGFB* and 0.5 for *R35*.

We calculated inter- and intraspecific uncorrected *p*-distances between species within all non-monotypic genera (see *Results*) for each sequenced mitochondrial marker in MEGA v.7.0.14 (Kumar *et al.*, 2016).

Estimation of divergence times

We estimated divergence times with BEAST and the concatenated data set, containing one sample per species and one sequence for each of the outgroups (see Supporting Information, Table S1). We set the following five divergence times, as previously estimated in other studies: (a) between the clade containing *Lerista*, *Notoscincus* and *Sphenomorphus solomonis*, and the clade containing *Scincella lateralis* and *Lobulia*, to 29.4–55.8 Mya (normal distribution; mean 37 Mya, SD = 4) (Skinner *et al.*, 2011), (b) between *Scincella lateralis* and the clade containing *Lobulia* to 20.6–43.9 Mya (normal distribution; mean 32 ± 7 Mya) (Skinner *et al.*, 2011), (c) between *Sphenomorphus solomonis* and the clade containing *Lerista* and *Notoscincus* to 24.3–48.5 Mya (normal distribution; mean 33 ± 4 Mya) (Skinner *et al.*, 2011), (d) between *Notoscincus ornatus* and the clade containing *Lerista* to 19.1–53.6 Mya (lognormal distribution; mean 28.2; log(SD) = 0.35, offset 5) (Rabosky *et al.*, 2007) and (e) between *Lerista lineopunctulata* and *Lerista neander* to 12.9–22.1 Mya (normal distribution; mean 17.5 ± 2.8 Mya) (Rabosky, 2014).

We conducted the calibration in BEAST v.1.8.4 (Drummond *et al.*, 2012) with the following partitions and relevant models as determined by PartitionFinder: 12S (HKY+I+G), *ND2*_1+*ND4*_1 (GTR+I+G), *ND2*_2+*ND4*_2 (GTR+I+G), *ND2*_3 (GTR+G), *ND4*_3 (HKY+I+G), *NGFB*_1+*NGFB*_2+*R35*_1+*R35*_2 (TrNef+G), *NGFB*_3 (K80+G), *R35*_3 (HKY+G). Priors were set as follows (otherwise by default): Yule process tree model; random starting tree; alpha prior uniform (0–10), base-substitution parameter (0–100), strict clock prior for the nuclear genes (uniform distribution; mean 1, 0–1) and uncorrelated relaxed-clock model for the mitochondrial genes (uniform distribution; mean 1, 0–1). We conducted three individual runs of 10^8 generations, with sampling at intervals of every 10^4 generations. We evaluated convergence, posterior trace plots, effective sample sizes (ESS > 200) and burn-in, with Tracer. We combined the tree runs in LogCombiner, discarding the first 10% as burn-in and generated an ultrametric tree with TreeAnnotator.

Biogeographic reconstruction

We performed ancestral-range reconstruction analyses in order to assess the biogeographical history of the montane skinks of New Guinea. We performed this reconstruction on a time-calibrated phylogeny using BioGeoBEARS (Matzke, 2013, 2014), as implemented in RASP v.4.2 (Yu *et al.*, 2015, 2020).

We assigned each of the species (see *Results*) in our analyses to one of four discrete geological regions in New Guinea based on their current distribution: (1) Australian Craton (AC); (2) Fold Belt (FB); (3) Oceanic Arc Terranes (OAT); and (4) East-Papuan Composite Terrane (EPCT). In addition, CAS234654, which is a sample of *Li. noctua* from Palau, was assigned to its own region, Palau (P). Species that occur on multiple

geological regions were assigned a combination of regions, e.g. *Li. pulchra* occurs throughout the northern coasts of New Guinea, and so was assigned to OAT+EPCT. We disallowed the combination of P with any of the other geological regions.

We used the consensus concatenated dated phylogeny (see above) to examine six different biogeographic models: BAYAREA, which does not allow dispersal at cladogenesis; DIVA, which allows vicariance [i.e. if parent lineage occurs in (x,y), then one daughter lineage can occur in only (x) whereas the other can occur in only (y)] but disallows subset speciation, in which one daughter lineage inherits a subset of the distribution of the parent [i.e. if parent lineage occurs in (x,y), then one daughter lineage can occur in only (x) or only (y) whereas the other can occur in (x,y)]; DEC, which allows both vicariance and subset speciation; and BAYAREA+J, DIVA+J and DEC+J, which are equivalent to the previous three models but also allow jump dispersal through founder effects at cladogenesis. We compared all six models by their AICc scores, choosing the model with lowest AICc score (and the highest AICc weight) as the best model. We then ran the best fitting model on a random sample of 100 trees from the posterior to generate our final estimates of biogeographic regions at ancestral nodes.

We ran this procedure twice: on an unconstrained and on a time-stratified data set. In the unconstrained data set, all allowed combinations (e.g. FB+EPCT) of regions were available throughout the entire phylogeny. In the time-stratified data set, we adjusted the area-adjacency matrix of the software so that certain combinations were unavailable in specific times, based on the geological history of New Guinea. Specifically, while AC+FB were available throughout the phylogeny, combinations of the above two with EPCT were unavailable prior to 16 Mya, and combinations of the above three with OAT were unavailable prior to 12.5 Mya. These dates were chosen to reflect the earliest estimates of docking of the EPCT and the OAT, respectively, to New Guinea (Pigram & Davies, 1987). No combinations of Palau with any other region were allowed, since Palau is a volcanic archipelago > 1000 km from New Guinea, and was always separated from New Guinea by large swaths of open ocean.

We also performed ancestral-character-state reconstruction of elevational distribution in R v.4.0.3 (R Core Team, 2020). We assigned species to one of three discrete elevational distribution categories based on the minimum elevation of specimens for each species: (1) Lowland (< 1000 m a.s.l.); (2) Montane (1000–2500 m a.s.l.); and (3) Alpine (> 2500 m a.s.l.). These categories were chosen to reflect habitat categorizations in Bryan & Shearman (2015). We fit a meristic model of discrete trait evolution where transitions occur in a stepwise manner, i.e. Lowland → Montane → Alpine, allowing all transition rates to differ, and setting the prior probabilities as 1, 0 and 0 for Lowland, Montane and Alpine categories, respectively, under the assumption that the ancestral skink was a lowland species, reflecting that the sister species to our examined taxa is a lowland Philippine skink [*Lipinia pulchella* (Gray, 1845)]. We reconstructed ancestral states using Stochastic Character Mapping (SCM; Bollback, 2006) with the "make.simmap" function in the *phytools* package (Revell, 2012). We ran 100 iterations on the concatenated dated phylogeny to obtain posterior probabilities for each character state at each internal node.

Finally, to visualize the evolution of minimum elevation as a continuous trait, we generated a phenogram with the *ggtree* package (Yu *et al.*, 2017), where minimum elevation is reconstructed along the phylogeny under a Brownian Motion (BM) model.

Morphological analyses

We examined vouchers for specimens that were sampled for the phylogenetic analyses and additional specimens collected in the same localities by the same research expeditions as the vouchered specimens. We also examined specimens that were not included in the phylogenetic analyses due to lack of tissue samples, as well specimens from unsamples localities, but which nonetheless fit within the examined taxa morphologically. Overall, we included 1002 specimens in the morphological analyses (Supporting Information, Table S2). All specimens were used for meristic comparisons. Only the 771 adult specimens, as determined based on dissection and visual examination of the gonads, were used in the morphometric comparisons, to eliminate potential confounding effects of ontogeny on body proportions. For the dissected adult individuals, we also counted the number of eggs or developing embryos in gravid females. The material studied was obtained from the following collections: the Australian Museum, Sydney, Australia (AMS), the Natural History Museum, London, UK (NHMUK), the Bernice P. Bishop Museum, Honolulu, USA (BPBM), the California Academy of Sciences, San Francisco, USA (CAS) and the South Australian Museum, Adelaide, Australia (SAMA).

We examined specimens for several meristic and morphometric measurements to assess variation in scalation patterns (Supporting Information, Fig. S1) and body proportions. These variables were based on previous research on systematics of New Guinean skinks (Greer *et al.*, 2005; Kraus, 2020), as well as on several additional measurements we supplemented. These two studies differ in how they measure paravertebral scales and supraciliaries. We followed Greer *et al.* (2005) in measuring paravertebrals from

the first scale posterior to the primary nuchal pair (see below) to the first scale in front of the hindlimbs (with the limbs left in the position seen in the fixed specimen), and in defining supraciliaries as the scales divided from the eyelid by small intervening oblique imbricate scales(ventrally) and the supraoculars (dorsally). The scales between the posteriormost supraciliary and the parietals are here termed upper pretemporals, as they do not contact the eyelid (Supporting Information, Fig. S1). The lower pretemporal is defined as the scale wedged between the upper pretemporal, the parietal, the upper secondary temporal and the primary temporal. We followed Miralles (2006) in defining nuchal scales as "enlarged scale[s] of the nape, occupying transversally the place of two or more rows of dorsal cycloid scale[s]". However, we do not offer a distinction 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), and instead report on the total number of nuchal pairs. Since nuchal scales can be asymmetric, with one or two unpaired enlarged scales on either the left or right side, we define the number of pairs 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), but also report on the number of nuchal scales on each side.

The following mensural and meristic characters were taken by the first author (A.S.) on the left side of each specimen (if bilateral). Measurements were taken using a digital calliper, with accuracy to the nearest 0.1 mm, of: snout-vent-length (SVL) with specimens held flat and extended, fore-hindlimb distance (FHD; the distance from the line across the posterior margin of the forelimbs to the line across the anterior margin of the 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 the centre of the ear opening (equidistant from anterior and posterior margins) to the tip of the snout, oblique measurement], head width (HW; width of head at widest point, typically at the level of or just anterior to the ear openings), head depth (HD; dorsoventral depth of the head at the level of the ear openings), upper forelimb (UFL; from the posterior side of the body wall at the axilla to the elbow at a right angle), lower forelimb [LFL; from the elbow at a right angle to the base of the front foot (contact between imbricate scales on the antebrachium and non-imbricate scales on the metacarpus)], front foot (FFOOT; from the base of the front foot to the tip of the longest digit, either III or IV, claw included), forelimb length (FLL; sum of previous three), upper hindlimb (UHL; from the anterior side of the body wall at the groin to knee at a right angle), lower hindlimb [LHL; from the knee at a right angle to the base of the hind foot (contact between imbricate scales on the crus and non-imbricate scales on the metatarsus)], hind foot (HFOOT; from the base of the 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), pronounced supraorbital ridge, made up of the supraoculars forming an arc above the line from the tip of the snout to the parietals in lateral view (yes/no), number of supralabials, number of supralabials posterior to the 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), lobules on anterior edge of ear opening (yes/no), number of midbody (axilla-groin interval) scale rows, number of paravertebral scales [along paravertebral line, counted from the scale posterior to the primary nuchal pair (thus including secondary nuchals) to the scale crossing the imaginary horizontal line connecting the hindlimbs at their anterior point], longest digit on forelimb (III/IV/equal length), number of subdigital lamellae under 4th toe, number of single supradigital scales on 4th toe.

RESULTS

Molecular inferences

Our full molecular data set comprised 89 specimens with a concatenated length of 3305 bp divided into three mitochondrial gene fragments (12S, 395 bp; *ND2*, 1020 bp; *ND4*, 708 bp) and two nuclear gene fragments (*NGFB*, 546 bp; *R35*, 636 bp).

We found that, together, all members of *Lobulia*, *Prasinohaema*, *Papuascincus* and *Lipinia* form a well-supported group, with most internal nodes in the phylogeny receiving strong support with both ML and

BI methods of phylogenetic reconstruction (Fig. 1A). However, *Lobulia*, *Prasinohaema* and *Lipinia* were recovered as polyphyletic, similar to previous results for *Prasinohaema* and *Lipinia* (Rodriguez *et al.*, 2018). Members of these three genera were spread widely throughout the phylogeny.

In particular, the various species of *Lobulia* form several well-supported groups, but the relationships between some of them are poorly resolved and separated by short branches (Fig. 1A). *Lobulia elegans* forms a clade with *Lo. brongersmai*, *Lo. lobulus* and several specimens assigned as *Lobulia* sp. from the New Guinea Highlands and the Huon Peninsula (Clade I). *Lobulia glacialis* (Clade III) is closely related not to other species of *Lobulia*, but to *Pr. prehensicauda* and *Pr. flavipes* (Clade II). *Lipinia pulchra* (Clade V) is sister to *Papuascincus*, which is recovered as monophyletic (Clade IV). *Lo. alpina* is sister to a single specimen assigned as *Lobulia* sp. from Mt Victoria (Clade VI). Finally, the recently described *Lo. sabini* forms a clade with *Li. noctua* and with many specimens assigned as *Lobulia* sp. [but not fitting morphologically with the redefinition of *Lobulia* by Allison & Greer (1986)] from various localities in the Papuan Peninsula (Clade VII). *Prasinohaema semoni* clusters together with these seven clades, but its exact relationship to them is unresolved, whereas *Pr. virens*, *Lipinia pulchella* and *Lipinia longiceps* are recovered as external to these seven clades.

The species tree recovered a similar topology to the phylogeny based on the concatenated data set (Fig. 1B). All seven clades were recovered with high support, and the relationships between the lineages within the clades were identical to those in the concatenated phylogeny. The main difference between the two phylogenies, apart from some differences in support values for a few nodes, was in the position of *Pr. semoni*. Whereas in the concatenated data set *Pr. semoni* was recovered as sister to all seven clades, in the species tree *Pr. semoni* was recovered as sister to Clades I–III (Fig. 1). However, in both phylogenies these nodes were not statistically supported, leaving the phylogenetic position of *Pr. semoni* unresolved.

Our divergence-time estimates indicate that the radiation of the clade containing *Pr. semoni* and the other seven clades began between 18.1–26.3 Mya (Fig. 2; Supporting Information, Table S3). This event was followed by divergences lasting until 10.4 Mya at the latest, the last of them being between Clades IV and V. The seven clades differ somewhat in crown ages, with Clade VII being the oldest (Fig. 2; Supporting Information, Table S3).

Within our major clades, several geographically distinct lineages differ both morphologically (Table 1) and genetically (Fig. 1; Supporting Information, Table S4). Nuclear haplotype networks show little allele sharing between the different lineages (Supporting Information, Fig. S4), with the few exceptions being in Clades I and VII. In Clade I, *Lo. lobulus* shares some *NGFB* and *R35* haplotypes with *Lobulia* sp. from the Huon Peninsula. In Clade VII, two lineages from Mt Victoria and the Kokoda Track share some *NGFB* and *R35* haplotypes and two lineages from the vicinity of Mt Suckling, both known from a single specimen each (BPBM 37741 and 47915), share *NGFB* haplotypes. In all these cases, the lineages are geographically close to one another yet morphologically distinct, and in the pair of lineages from the vicinity of Mt Suckling, ecologically distinct as well. Morphologically, lineages are best distinguished from each other based on relative limb lengths, paravertebral scale counts, midbody scale row counts, subdigital lamellae counts or combinations of the above measurements (Table 1). Many lineages also differ in colour patterns (see *Taxonomic accounts* below).

Genetic distances between the different lineages within clades are higher than within-lineage distances in all three mitochondrial markers (Supporting Information, Table S4). For 12S, between-lineage distances were 8.4–9.9% for Clades II+III, 2.6–7.9% for Clade III, 4.4% for Clade VI and 2.5–10.5% for Clade VII, whereas within-lineage distances were 0%, 0–1.1%, 0.4% and 0.4–0.5% for the same clades, respectively. For *ND2*, between-lineage distances were 19.7–22.7% for Clades I+II, 5.5–16.8% for Clade I, 12.5% for Clade VI and 5.9–23.4% for Clade VII, whereas within-lineage distances were 0.1%, 0.3–2.4%, 0.6% and 1.3–3.3% for the same clades, respectively. For *ND4*, between-lineage distances were 16.8–20.2% for Clades II+III, 7.5–19.6% for Clade I, 12.1% for Clade VI and 1–19.6% for Clade VII, whereas within-lineage distances were 0%, 0.4–3.4%, 0.2% and 0.6–4.5% for the same clades, respectively.

Biogeographic history

The seven clades differ in distribution. Clades I–III are centred around the New Guinea Highlands, Clades VI–VII are found almost exclusively on the Papuan Peninsula and Clades IV–V are more widespread across New Guinea (Fig. 3). Most of the sampled taxa occur in montane regions, in elevations above 1000 m a.s.l., but a few lowland taxa (*Li. pulchra*, *Li. noctua*, *Lo. brongersmai*) are nested within otherwise montane-restricted clades (Fig. 4).

The best supported biogeographic model for both the unconstrained and time-stratified data sets was BAYAREA+J (Supporting Information, Table S5), suggesting no role for vicariance or subset speciation. However, the two data sets resulted in somewhat different biogeographic reconstructions. In the time-stratified data set, the ancestral area for the entire

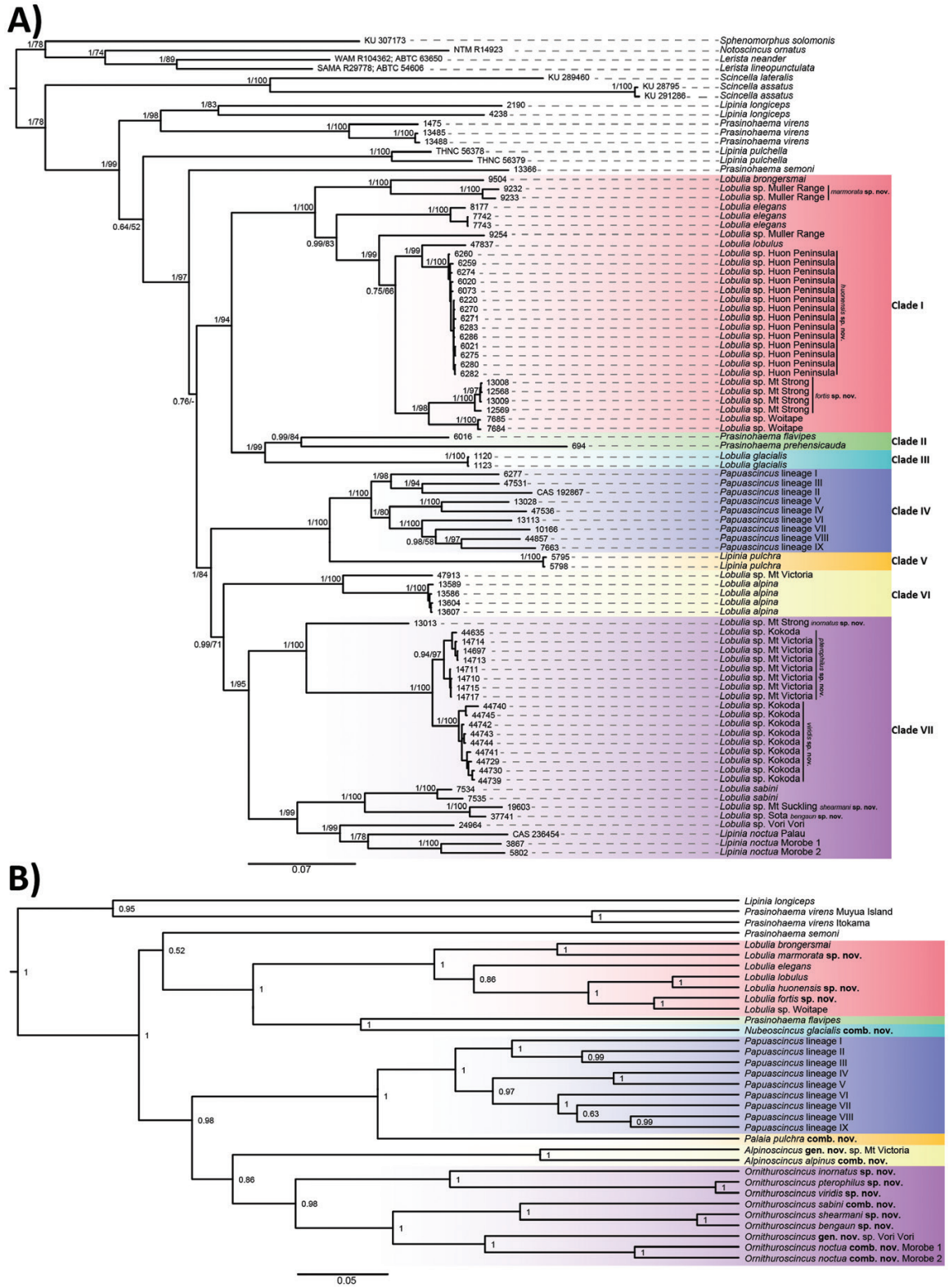

Figure 1. A. Bayesian Inference phylogenetic tree based on the concatenated data set of three mitochondrial and two nuclear markers, with BI posterior probabilities and ML bootstrap support values shown at each node, respectively. B, Bayesian Inference multilocus species tree, with BI posterior probabilities shown at each node. Colours in both panels

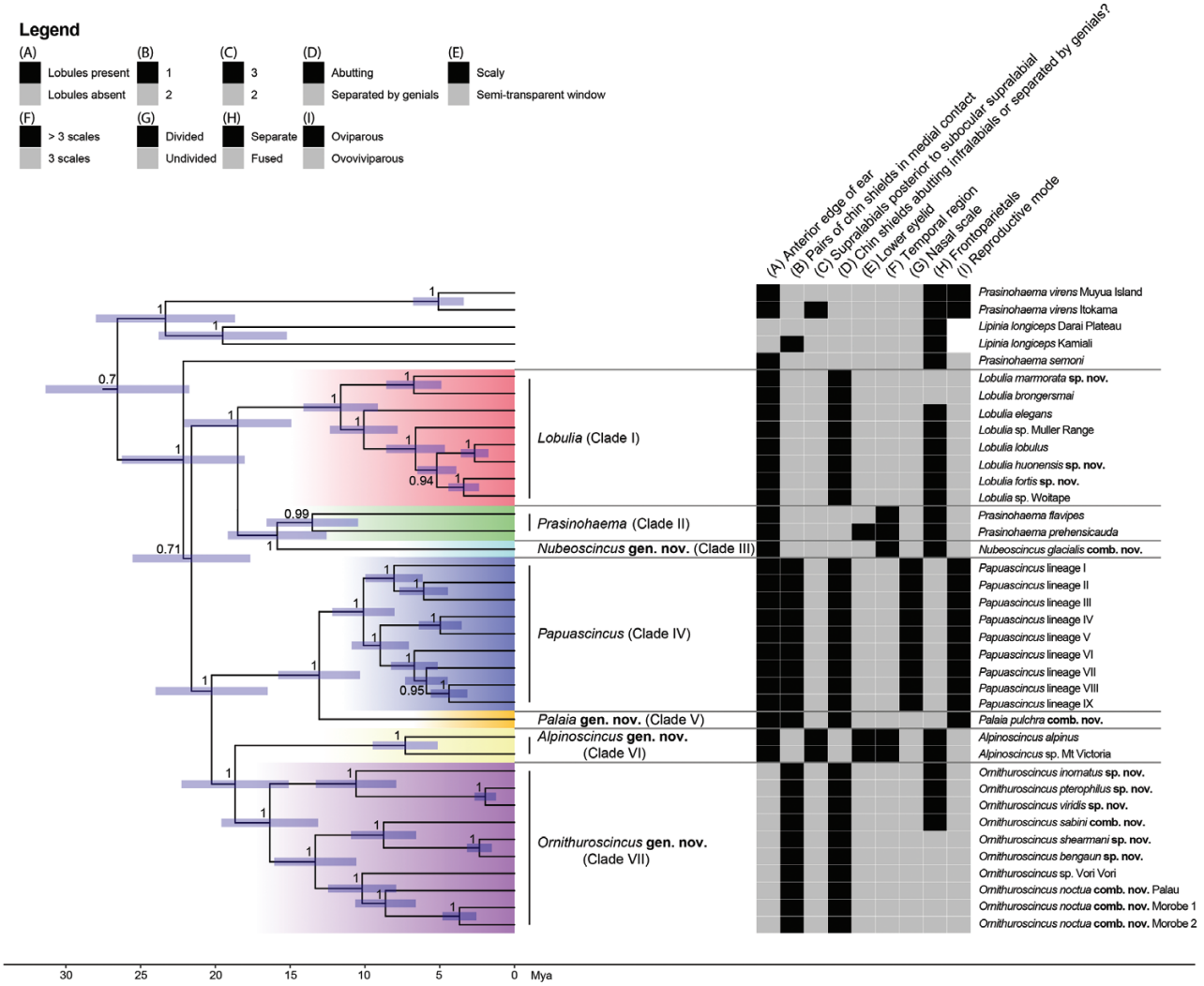

Figure 2. Time-calibrated phylogenetic tree, based on one specimen per species, with posterior probability values indicated above the nodes. Blue bars represent 95% HPD of divergence date estimations. Colours correspond to the same clade assignments as in Figure 1. The matrix on the right represents character states of nine morphological characters for each species. Blank squares represent missing data.

clade was reconstructed as the EPCT, where most major radiations occurred (Fig. 3). Only after the EPCT docked to New Guinea, at ~16 Mya, did we reconstruct dispersal events to the geological regions comprising the western parts of the island, namely AC and FB. This dispersal occurred independently in several lineages in Clades I–V. Conversely, in the unconstrained data set, we recovered the ancestral area for the entire clade as shared between the EPCT and the OAT (Supporting Information, Fig. S5). A dispersal event then occurred to the FB in the ancestor of Clades I–VII, where most radiations occurred. However, there were several independent dispersal events back to the EPCT, most notably in the ancestor of Clades VI–VII.

We assumed the ancestor of our phylogeny to have been a lowland species (Fig. 4). The first split in the phylogeny is between the entirely lowland clade containing *Pr. virens* and *Li. longiceps* and the clade containing the lowland *Pr. semoni* and Clades I–VII. The ancestor for this clade was reconstructed

correspond to each of seven clades representing seven different genera: *Lobulia* (Clade I, red), *Prasinohaema* (Clade II, green), *Nubeoscincus* (Clade III, light blue), *Papuascincus* (Clade IV, blue), *Palaia* (Clade V, orange), *Alpinoscincus* (Clade VI, yellow) and *Ornithuroscincus* (Clade VII, purple).

Table 1. Ranges of morphometrics and meristics for specimens of species treated in this study (mean values in parentheses). Only adult specimens were examined for morphometric measurements, but juveniles were included for meristics

Species	*N* (adult)	*N* (total)	SVL (mm)	Forelimb length (% of SVL)	Hindlimb length (% of SVL)	Midbody scale rows	Paravertebrals	Subdigital lamellae	Single supradigital scales
Nubeoscincus (Clade I)									
N. glacialis	5	5	47.4–58.0 (52.4)	32.2–34.4% (33.1%)	34.6–38.6% (37.1%)	34–36 (34.6)	66–70 (67.6)	13–16 (14.8)	2–3 (2.4)
N. stellaris	1	1	50.9	28.7%	36.2%	36	75	14	2
Prasinohaema (Clade II)									
Pr. flavipes	2	2	59.7–85.3 (72.5)	30.1–30.4% (30.3%)	33.5–34.1% (33.8%)	38–39 (38.5)	66–69 (67.5)	17–20 (18.5)	3–4 (3.5)
Pr. prehensicauda	2	2	57.2–64.5 (60.9)	27.7–31.4% (29.5%)	29.9–33.3% (31.6%)	38–45 (41.5)	70–92 (81)	17–18 (17.5)	3–4 (3.5)
Lobulia (Clade III)									
Lo. brongersmai	1	1	48.7	43.2%	49.7%	30	51	22	4
Lo. elegans	1	1	55.7	34.5%	44.6%	31	55	19	3
Lo. fortis	21	29	45.7–60.5 (53.6)	40.6–47.6% (43.3%)	46.0–54.8% (50.2%)	34–37 (35.3)	55–65 (58.9)	20–25 (22.9)	3–5 (3.5)
Lo. huonensis	17	19	45.2–63.9 (54.0)	37.7–43.6% (42.1%)	46.1–51.9% (49.8%)	33–38 (36.2)	59–68 (62.7)	19–25 (21.3)	3–4 (3.1)
Lo. lobulus	5	10	42.5–55.8 (52.2)	32.9–41.6% (39.6%)	42.0–51.5% (47.7%)	32–40 (35.3)	54–61 (57.7)	19–24 (21)	3–7 (4)
Lo. marmorata	29	33	41.9–56.9 (48.1)	36.8–47.0% (42.4%)	44.1–53.4% (47.5%)	30–34 (31.5)	46–56 (51.2)	20–25 (22.5)	3–4 (3.2)
Lobulia sp. Muller Range	1	1	57.2	41.3%	48.6%	35	63	21	3
Lo. vogelkopensis	3	3	56–58.3 (57.4)	35.7–41.3% (37.7%)	41.6–47.8% (45.0%)	34–36 (35.0)	69–77 (72.7)	19–23 (21)	3–4 (3.3)
Palaia (Clade IV)									
Pal. pulchra	8	8	37.3–41.2 (39.2)	29.9–34.4% (32.0%)	36.7–43.8% (40.5%)	23–25 (23.9)	42–48 (44.3)	19–21 (20.0)	7–8 (7.6)
Papuascincus (Clade V)									
Lineage I	154	198	41.2–56.7 (50.4)	28.1–37.1% (32.9%)	36.8–46.1% (41.3%)	25–43 (29.9)	46–71 (60.1)	19–28 (23.3)	3–13 (9.1)
Lineage II	13	13	36.6–48.1 (45.0)	28.1–35.5% (31.8%)	38.3–45.4% (42.2%)	26–32 (29.8)	52–58 (54.2)	24–29 (25.7)	10–13 (11.5)
Lineage III	95	112	36.3–57.9 (47.0)	25.1–36.8% (31.8%)	33.6–47.4% (41.3%)	24–36 (28.2)	45–67 (52.3)	15–26 (22.2)	7–15 (11.9)
Lineage IV	83	136	44.4–63.7 (55.9)	27.8–38.6% (32.9%)	38.8–48.8% (43.2%)	24–41 (30.4)	57–76 (66.0)	18–27 (22.8)	7–14 (11.0)
Lineage V	66	79	42.6–52.9 (48.8)	27.9–35.9% (32.1%)	34.8–46% (40.1%)	26–42 (29.0)	50–64 (55.1)	19–24 (21.3)	8–14 (11.7)
Lineage VI	25	28	51.6–65.3 (60.5)	29.4–36.3% (33.6%)	37.4–46.5% (41.5%)	29–42 (32.7)	59–72 (65.6)	21–27 (24.1)	8–14 (10.8)
Lineage VII	23	44	45.3–62.6 (56.7)	31.2–37.8% (34.7%)	38.3–46.5% (44.0%)	28–35 (30.2)	55–69 (60.7)	21–28 (23.8)	8–12 (9.9)
Lineage VIII	90	128	45.3–67.8 (58.6)	29.1–38.9% (34.8%)	39.2–49.6% (44.0%)	28–38 (32.9)	58–79 (68.1)	21–29 (25.1)	6–14 (10.5)
Lineage IX	35	40	43.2–65.6 (59.8)	30.3–36.8% (33.9%)	39.5–47.3% (44.1%)	31–51 (35.4)	67–83 (73.6)	21–26 (24.1)	8–11 (9.5)
Pap. morokanus	2	2	42.9–45.6 (44.2)	29.1–30.8% (29.9%)	39.1–41.7% (40.4%)	28–29 (28.5)	44–50 (47.0)	23–24 (23.5)	6–7 (6.5)
Pap. stanleyanus	1	1	57.9	31.4%	42.9%	31	64	23	11
Alpinoscincus (Clade VI)									
A. alpinus	9	10	46.1–64.7 (56.5)	27.0–38.0% (33.2%)	31.7–46.1% (41.0%)	37–51 (44.6)	70–89 78.9)	12–19 (15.7)	4–9 (6.5)
A. subalpinus	37	43	46.5–72.7 (58.2)	30.0–39.8% (35.7%)	40.4–48.7% (44.4%)	35–44 (38.4)	64–84 (74.9)	18–23 (19.2)	3–10 (5.7)
Ornithuroscincus (Clade VII)									
O. bengaun	1	1	48.2	36.3%	47.3%	30	55	20	6
O. inornatus	1	1	47.9	32.7%	41.2%	35	51	21	3
O. noctua Morobe 1	1	1	29.4	31.9%	41.7%	24	49	23	6

Table 1. Continued

Species	*N* (adult)	*N* (total)	SVL (mm)	Forelimb length (% of SVL)	Hindlimb length (% of SVL)	Midbody scale rows	Paravertebrals	Subdigital lamellae	Single supradigital scales
O. noctua Morobe 2	1	2	39.3	32.5%	39.4%	24–27 (25.5)	47–56 (51.5)	22	6–8 (7.0)
O. pterophilus	12	18	50.1–62.3 (55.9)	27.0–33.7% (30.4%)	33.3–42.5% (38.0%)	28–42 (33.4)	50–67 (60.4)	17–23 (19.9)	3–8 (4.3)
O. sabini	2	3	49.2	33.2–34.4% (33.8%)	41.4–42.4% (41.9%)	28–30 (28.7)	56–59 (58.0)	19–20 (19.3)	3–4 (3.7)
O. shearmani	1	1	69.2	28.4%	35.6%	37	83	18	4
O. viridis	16	17	42.1–54.8 (49.7)	25.7–30.8% (28.2%)	29.0–40.6% (35.0%)	32–41 (36.2)	57–70 (62.8)	12–18 (15.8)	3–5 (3.4)

as likely montane, as were the ancestors for Clades I–VII (Supporting Information, Table S3). Overall, we reconstructed at least one transition from lowland to montane distribution, at least four transitions back to lowland distribution (in *Pr. semoni*, *Lo. brongersmai*, *Li. pulchra* and *Li. noctua*) and at least three transitions from montane to alpine distribution (Fig. 4).

Morphological variation

We identified nine morphological characters, the combinations among which differentiate between members of the seven clades and the other species of *Prasinohaema* and *Lipinia* (Fig. 2):

(A) *Presence of lobules on the anterior edge of ear opening*—One to three lobules of varying size are present on the anterior edge of the ear opening for most sampled taxa. Lobules are found in all members of Clades I–VI, as well as in *Pr. semoni* and *Pr. virens*, but are absent from all members of Clade VII and *Li. longiceps*.

(B) *Pairs of chin shields in medial contact*—The anteriormost one or two pairs of chin shields are typically in medial contact, whereas the posterior pairs are separated by small, medial gular scales. The number of separating scales increases posteriorly as chin shields become progressively smaller and the chin widens. In Clades IV, V and VII, as well as *Li. longiceps* from Kamiali, only the anteriormost pair of chin shields is in medial contact. In Clades I–III and VI, as well as in *Pr. semoni*, *Pr. virens* and *Li.* cf. *longiceps* from the Darai Plateau, the two anteriormost pairs of chin shields are in medial contact.

(C) *Position of the subocular supralabial*—Along the row of supralabial scales, one supralabial is in contact with the eyelid, termed the subocular supralabial and bordered on two sides by the presubocular and postsubocular scales. Although the number of supralabials varies widely, even within species, the number of supralabials posterior to the subocular supralabials is more conserved and differentiates clades. In Clades I–V and VII, as well as *Li. longiceps*, *Pr. semoni* and one specimen of *Pr. virens*, there are two supralabials posterior to the subocular supralabial, whereas in Clade VI and the other specimen of *Pr. virens*, there are modally three (with some intraspecific variation in Clade VI).

(D) *Position of chin shields in relation to infralabials*—The anteriormost chin shields always abut the infralabial scales. However, the posteriormost chin shields can either abut the infralabials fully—in which case the posteriormost chin shields are

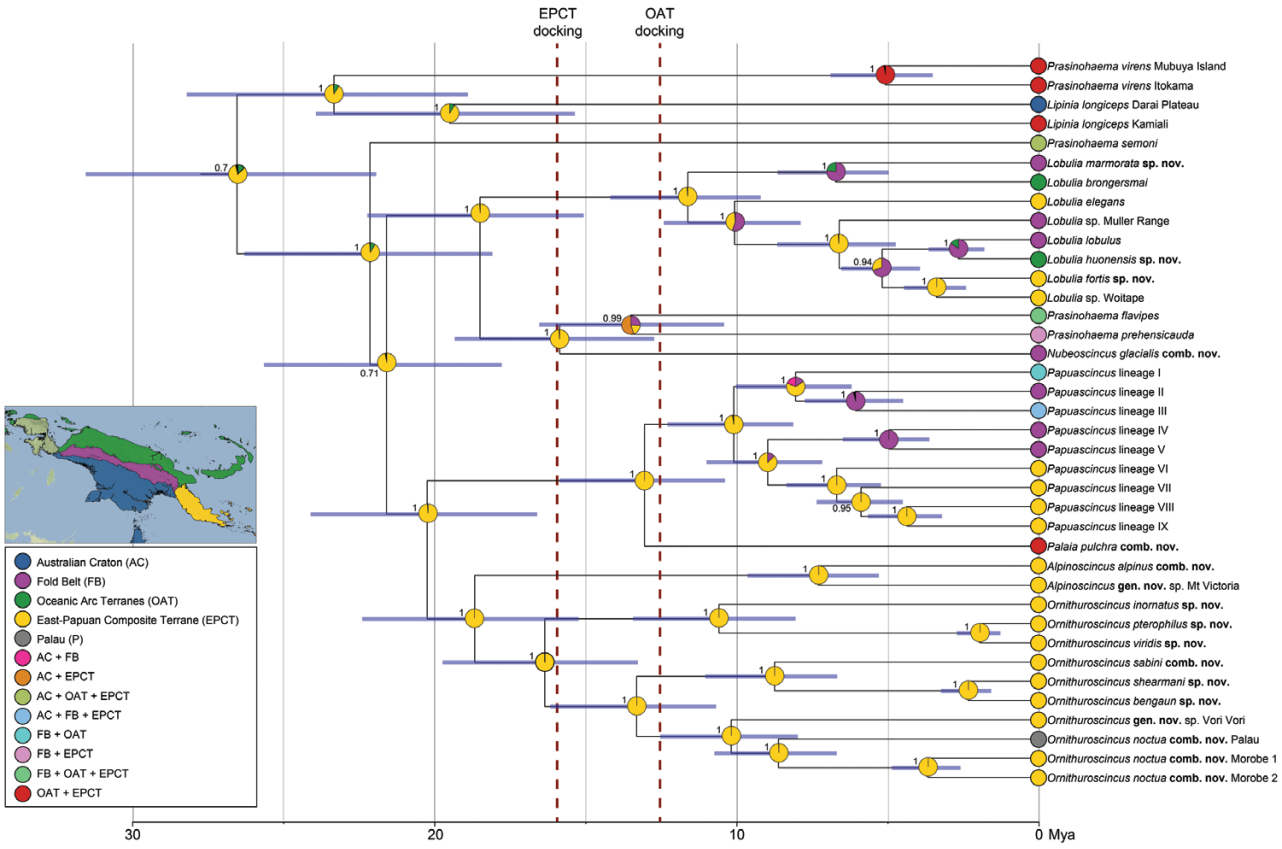

Figure 3. Time-stratified biogeographic reconstruction using a BAYAREA+J model. Tips are coloured according to the extant distribution of each species. Nodes are pie charts, where the sizes of the coloured slices correspond to the relative probability of each state at each node. Earliest dates of docking of the East-Papuan Composite Terrane (16 Mya) and the Oceanic Arc Terranes (12.5 Mya) are designated by the dashed red lines. Posterior probabilities of the nodes are listed next to each node. Four of the geological regions are illustrated in the inset map. Palau, which is further north in the Pacific Ocean, is not pictured.

typically in contact with the penultimate infralabial (although this varies between individuals)—or be separated from the infralabials by an intervening row of genial scales. The former condition occurs in Clades I, IV, V and VII, whereas the latter condition occurs in Clades II–III and VI, as well as in *Pr. semoni*, *Pr. virens* and *Li. longiceps*.

(E) *Condition of the lower eyelid*—The lower eyelid is moveable in all examined taxa, and in almost all specimens has a clear, semi-transparent palpebral disc, either as large as or smaller than the ear opening. However, in all members of Clade VI, and in one species of Clade II (*Pr. prehensicauda*), the lower eyelid is scaly, lacking a palpebral disc.

(F) *Scales of the temporal region*—In Clades I, IV, V and VII, as well as in *Pr. semoni*, *Pr. virens* and *Li. longiceps*, the temporal region is almost always comprised of one primary temporal (in contact with the pretemporals and supralabials) and two secondary temporals, the upper of which is larger and in contact with the parietals, whereas the lower interdigitates between the two posteriormost supralabials. However, in Clades II, III and VI, the scales of the temporal region, particularly the secondary temporals, are further fragmented into > 3 scales. The latter condition is found rarely in individuals of the other clades.

(G) *Condition of the nasal scale*—In almost all examined taxa there is a single, undivided nasal scale, and the nostril is centrally located. In Clade IV (only), the nasal scale is always divided by a horizontal suture extending posteriorly from the upper margin of the nostril to reach the posterior border of the nasal, a condition that is found only rarely in individuals of the other clades.

(H) *Condition of the frontoparietals*—The most common arrangement of parietal scales is of two frontoparietal scales in medial contact, bordered posteriorly by an interparietal (of equal size or smaller than the frontoparietals), which is itself

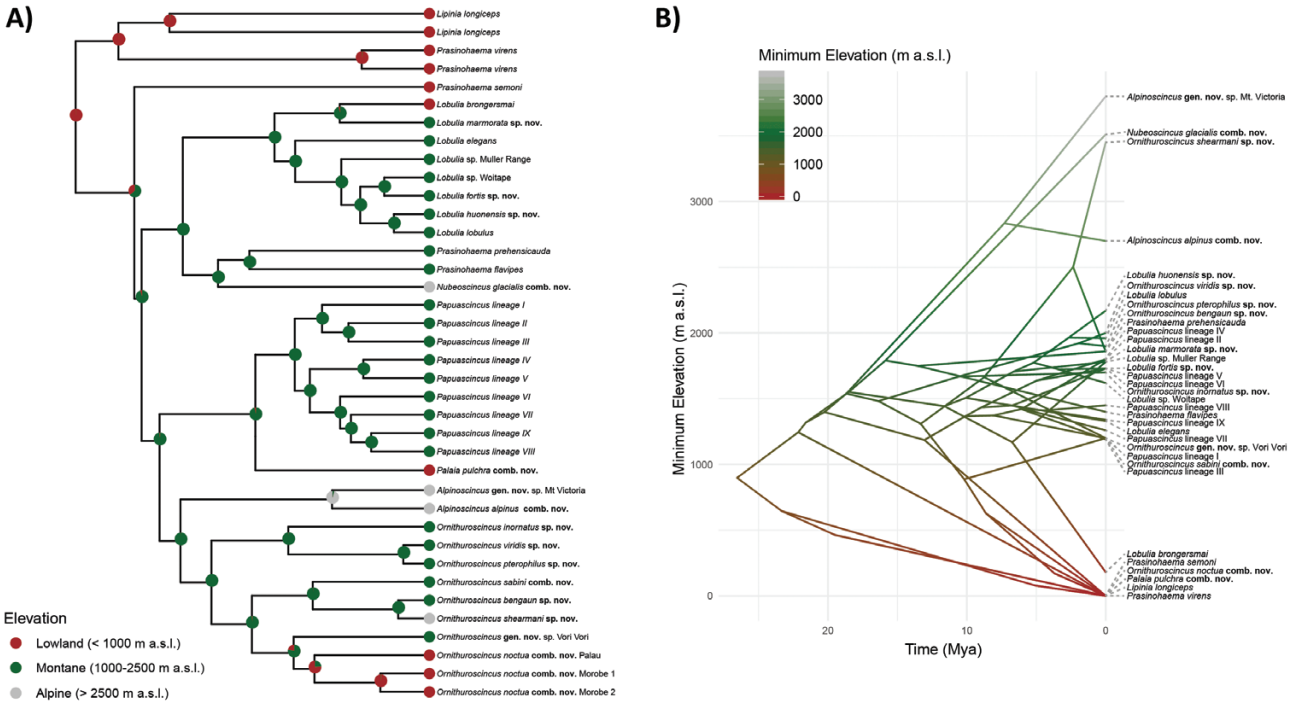

Figure 4. Ancestral-state reconstruction of elevations occupied by this clade of skinks. A, tips are coloured according to the known minimum elevation (m a.s.l.) for each species. Pie charts at each node denote the posterior probabilities of each state, based on 100 simulated character histories. B, phenogram showing evolution of minimum elevation along the time-calibrated phylogeny under a BM model, with branches coloured according to minimum elevation (m a.s.l.).

bordered posteriorly by two large parietals in medial contact. This arrangement is found in all members of Clades II, III and VI, in *Pr. semoni*, *Pr. virens* and *Li. longiceps*, and in some members of Clades I and VII. The alternative condition of the frontoparietals being fused to form a single frontoparietal is found in all members of Clades IV and V, and in some members of Clades I and VII.

(I) *Reproductive mode*—All members of Clades I–III and VI–VII, as well as *Pr. semoni*, are viviparous, with a variable litter size of up to four young (fixed at two in some species), whereas all members of Clades IV and V, as well as *Pr. virens*, are oviparous, with a fixed clutch size of two eggs. Data on the reproductive mode for *Li. longiceps* are missing.

Additionally, the relative length of the limbs as a proportion of SVL, and the ratio between the lengths of the fore- and hindlimbs, vary greatly between species and clades (Supporting Information, Fig. S2). Members of Clades VI and especially I have relatively long limbs compared to other clades. Members of Clade II have unusually short hindlimbs, leading them to having forelimbs and hindlimbs of similar length. Members of Clade IV have the lowest ratio of forelimb-to-hindlimb length, with short forelimbs and moderately long hindlimbs (Supporting Information, Figs S2–S3). Finally, members of Clade II, *Pr. semoni* and *Pr. virens* are unique in having green blood serum and tissues (Greer, 1974; Rodriguez *et al.*, 2018).

Six other taxa that were not genetically sampled fit morphologically with four of the seven clades discovered by us. First, *Lo. stellaris* fits with Clade III based on its original description (Greer *et al.*, 2005) and the holotype, which we examined (AMS R.127522). It has two pairs of chin shields in medial contact, two supralabials posterior to the subocular supralabial, a row of genials separating the chin shields from the infralabials, a fragmented temporal region, an undivided nasal scale, unfused frontoparietals, a viviparous mode of reproduction and relatively short limbs. It differs from the other species in the clade, *Lo. glacialis*, in lacking lobules on the anterior edge of the ear opening and in having scaly lower eyelids but otherwise is similar to it in general morphology and coloration.

Second, an undescribed species of *Lobulia* from the Vogelkop Peninsula in north-western New Guinea fits with Clade I based on three examined specimens (BPBM 6917, 6919, 6920)—it possesses lobules on the anterior edge of the ear opening, has two pairs of chin

shields in medial contact, two supralabials posterior to the subocular supralabial, chin shields abutting the infralabials, a standard three-scale temporal region, an undivided nasal scale, a viviparous mode of reproduction and relatively long limbs. It also has unfused frontoparietals, similar to *Lo. elegans* and *Lo. lobulus* (but not to *Lo. brongersmai*) and is similar to *Lo. lobulus* in general coloration.

Third, *Lo. subalpina* fits with *Lo. alpina* in Clade VI, based on its original description (Greer *et al.*, 2005) and our examination of the type series (BPBM 9647; 9675–76; 9679; 9860; 10726–29; 10736–39; 10742–43; 10746–47; 10750; 10754–62; 10768; 10773–74; 10788; 12662). It has lobules on the anterior edge of the ear opening, two pairs of chin shields in medial contact, three supralabials posterior to the subocular supralabial, a row of genials separating the chin shields from the infralabials, scaly lower eyelids, a fragmented temporal region, an undivided nasal scale, unfused frontoparietals, a viviparous mode of reproduction and relatively short limbs.

Fourth, *Lipinia albodorsalis* (Vogt, 1932), *Lipinia nototaenia* (Boulenger, 1914) and *Lipinia venemai* Brongersma, 1953 all fit in Clade VII based on our examination of BPBM 5799 (*Li. albodorsalis*), photos of RMNH 9649 (holotype of *Li. venemai*), the original descriptions (Boulenger, 1914; Brongermsa, 1953a, 1953b; Vogt, 1932) and subsequent descriptions in Shea & Greer (2002). All are viviparous (Berongersma, 1953a; Shea, 2008), lack lobules on the anterior edge of the ear opening and possess two supralabials posterior to the subocular supralabial, lower eyelid with a semi-transparent window, unfused frontoparietals, chin shields abutting the infralabials, a standard three-scale temporal region and an undivided nasal scale. *Lipinia albodorsalis* and *Li. nototaenia* also have one pair of chin shields in medial contact, whereas *Li. venemai* differs in having two pairs.

Taxonomic accounts

The genetic results of this study present *Lobulia s.l.* as a polyphyletic genus, with species of the genera *Prasinohaema*, *Lipinia* and *Papuascincus* [Figs 1–2; similar to the genomic study of Rodriguez *et al.* (2018)] nested within the clade containing all *Lobulia* species. These genetic results indicate there are up to seven distinct clades that are highly divergent genetically (Figs 1–2; Supporting Information, Table S4). *Lobulia s.l.* also presents strong intrageneric phenotypical divergence, with various combinations of nine morphological characters serving to differentiate between members of the seven major clades and the other species of *Prasinohaema* and *Lipinia* (Fig. 2; Supporting Information, Figs S2; Table 1).

Based on the genetic and morphological evidence presented here, we propose several taxonomic changes to this clade of lizards. We restrict *Lobulia* [type species: *Lobulia elegans* (Boulenger, 1897)] to only include members of Clade I, which includes the type species of the genus, and we formally describe the other clades containing species currently placed in *Lobulia* (III, VI and VII) as new genera. We also recognize *Lipinia pulchra* (Boulenger, 1903) as a new, monotypic genus, as it is most similar to its sister taxon *Papuascincus*, yet lacks its diagnostic pustulate egg shells and nasal scales, and is more arboreal than *Papuascincus*. Further, in light of our findings, we redescribe *Papuascincus* and *Prasinohaema* to include several key morphological characteristics that distinguish between them and the newly described genera.

In addition to this, we describe four new species of *Lobulia* and five new species within Clade VII, based on combined genetic and morphological evidence. Below follows accounts for the new genera and species. Taxonomy of plants mentioned in the habitat descriptions follows Plants of the World Online (POWO, 2021).

Genera accounts

Lobulia Greer, 1974 (Clade I)

(Figs 5–15; Supporting Information, Figs S6–S7; Table 1)

Lobulia Greer, 1974. *Australian Journal of Zoology Supplementary Series* (31): 1–67.

Type species: Lygosoma elegans Boulenger, 1897, by original designation.

Diagnosis: Medium-sized (adult SVL 41.9–63.9 mm) terrestrial or semi-arboreal skinks with long limbs (forelimbs 32.9–47.6% of SVL, hindlimbs 41.6–54.8% of SVL); lobules present on anterior edge of ear opening; two pairs of chin shields in medial contact; two supralabials posterior to subocular supralabial; chin shields abutting infralabials; lower eyelid with semi-transparent window; standard three-scale temporal region; nasal scale undivided; frontoparietals either fused or unfused; viviparous; litter size 1–4.

Lobulia differs from all other genera by its much longer limbs (forelimbs 32.9–47.6% vs. 27.7–39.8% of SVL, hindlimbs 41.6–54.8% vs. 29.9–49.6% of SVL). It further differs from *Prasinohaema* by lacking green blood serum and tissues (Greer, 1974), a prehensile tail with a glandular tip and basally expanded subdigital lamellae. It differs from *Papuascincus* by having two pairs of chin shields in medial contact (vs. one), an undivided (vs. divided) nasal scale and a viviparous (vs. oviparous) reproductive mode.

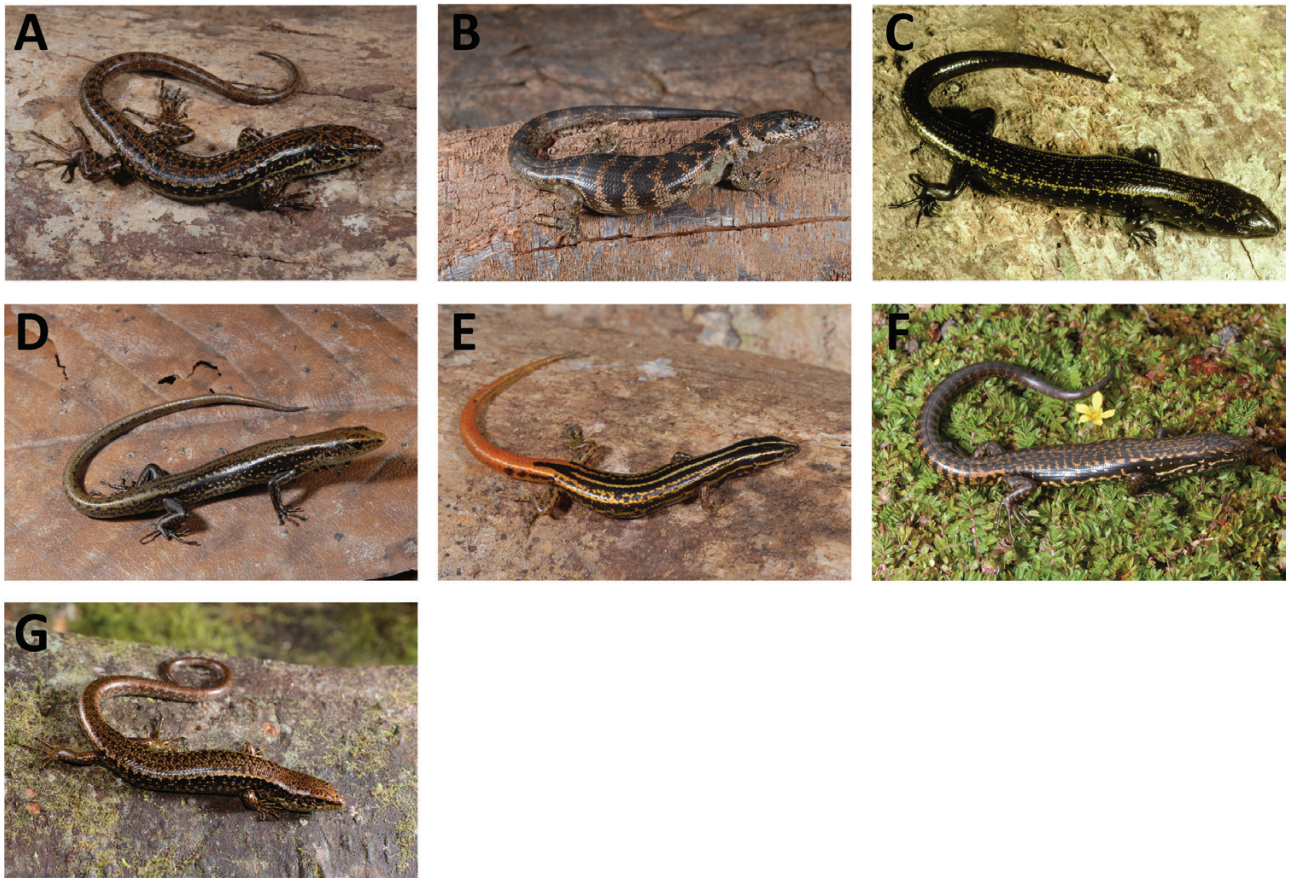

Figure 5. Representatives of each of the seven revised genera, not to scale: (A) *Lobulia huonensis* (BPBM 40322); (B) *Prasinohaema flavipes* (BPBM 40369); (C) *Nubeoscincus glacialis* (BPBM 14712); (D) *Papuascincus* lineage VII (BPBM 44749); (E) *Palaia pulchra* (BPBM 38789); (F) *Alpinoscincus alpinus* (BPBM 44218); (G) *Ornithuroscincus pterophilus* (BPBM 45705). Images by Allen Allison.

Species included: *Lobulia brongersmai* Zweifel, 1972; *Lobulia elegans* (Boulenger, 1897); *Lobulia lobulus* (Loveridge, 1945); and new species described below.

Distribution: Members of *Lobulia* are widespread along most of the montane regions of New Guinea, ranging from the central Owen Stanley Mountains in the Papuan Peninsula in the east (*Lo. elegans*) to the Arfak Mountains in the Vogelkop Peninsula in the west. Most species are montane, found at elevations up to 2700 m a.s.l.; however, *Lo. brongersmai* is found in the lowlands and hill regions of the northern versant of New Guinea (0–1340 m a.s.l.). *Lobulia brongersmai* is the only member of the genus to be found below elevations of 700 m, the lowest recorded locality for *Lo. elegans* (Kraus, 2020).

Remarks: Molecular evidence suggests that at least two other species not already named or described herein occur in the genus: one in Woitape (BPBM 18689–90; WGS 84: 8.545°S, 147.251°E) and one on Mt Yakapi in the Muller Range (BPBM 34161; WGS 84: 5.666°S, 142.643°E). However, since both are only known from a few specimens each, and are not extremely morphologically distinct, we refrain from formally describing them until further material can be collected and examined.

PRASINOHAEMA GREER, 1974
(CLADE II)

(FIG. 5; SUPPORTING INFORMATION, FIG. S6; TABLE 1)

Prasinohaema Greer, 1974. *Australian Journal of Zoology Supplementary Series* (31): 1–67.

Type species: *Lygosoma flavipes* Parker, 1936, by original designation.

Diagnosis: Large (adult SVL up to 103 mm; Meiri, 2018) arboreal skinks with short limbs (forelimbs 27.7–31.4% of SVL, hindlimbs 29.9–34.1% of SVL); lobules present on anterior edge of ear opening;

Figure 6. Pictures in life of (A) *Lobulia brongersmai* (BPBM 34733); (B) *Lobulia elegans* (BPBM 18692); (C) *Lobulia fortis* (paratype; BPBM 41130); (D) *Lobulia huonensis* (holotype; BPBM 40322); (E) *Lobulia lobulus* (BPBM 47837); (F) *Lobulia marmorata* (holotype; BPBM 34150). Images A, B, F by Fred Kraus, images C–E by Allen Allison.

two pairs of chin shields in medial contact; three supralabials posterior to subocular supralabial; chin shields separated from infralabials by a row of genials; lower eyelid with window variable in size, opaqueness and scaliness; temporal region fragmented (> 3 scales); nasal scale undivided; frontoparietals unfused; viviparous; litter size 2–9; green blood serum and tissues; tail prehensile with a glandular tip; subdigital lamellae greatly expanded basally.

Prasinohaema differs from *Lobulia* and *Papuascincus* by having green blood serum and tissues (Greer, 1974), a prehensile tail with a glandular tip and basally expanded subdigital lamellae, by having the chin shields separated from the infralabials

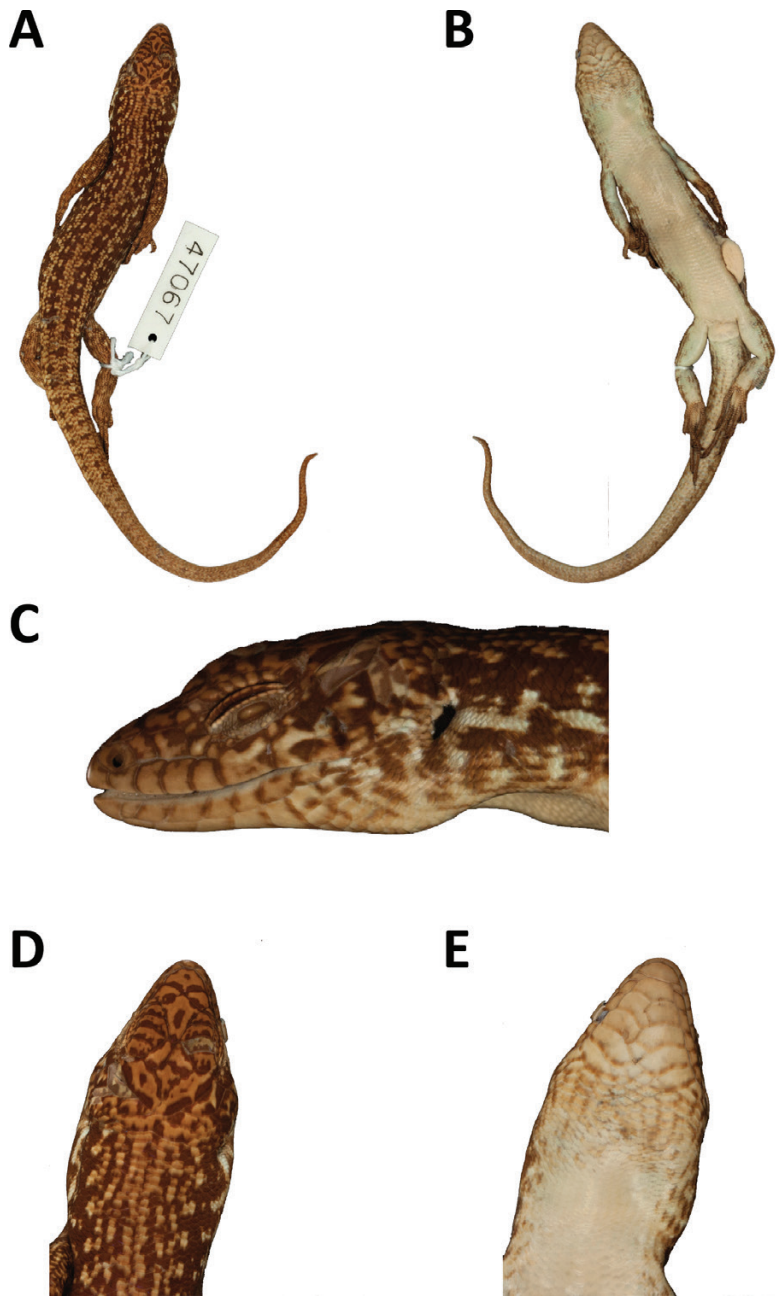

Figure 7. *Lobulia lobulus* holotype (MCZ R-47067), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Museum of Comparative Zoology, Harvard University.

by a row of genials (vs. chin shields abutting the infralabials) and by having a fragmented temporal region (vs. the standard three-scale arrangement). It further differs from *Papuascincus* by having two pairs of chin shields in medial contact (vs. one), unfused (vs. fused) frontoparietals, an undivided (vs. divided) nasal scale and by its viviparous (vs. oviparous) reproductive mode.

Species included: Prasinohaema flavipes (Parker, 1936); *Prasinohaema prehensicauda* (Loveridge, 1897).

Species incertae sedis: Prasinohaema parkeri (Smith, 1937) was originally placed in *Prasinohaema* by Greer (1974), seemingly based on having basally enlarged subdigital lamellae and transverse cross-bands on the dorsum, a coloration pattern it shares with *Pr.*

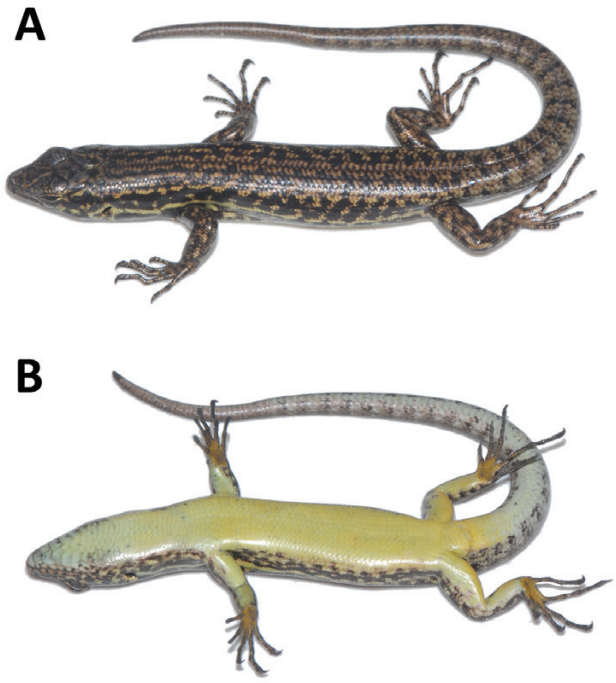

Figure 8. *Lobulia lobulus* (BPBM 47837) in life, (A) dorsal view and (B) ventral view. Images by Allen Allison.

prehensicauda and *Pr. flavipes*, but also with *Pr. semoni* which is phylogenetically distant from the former two species (Fig. 1). However, no information was given in Smith (1937) regarding the condition of its tail or the colour of its blood serum or tissues, data for the latter of which would not have been available for Greer in his revision (Greer, 1974) since the species was never collected after its original description. Furthermore, *Pr. parkeri* lacks lobules on the anterior edge of the ear opening and has a unique arrangement of the frontal (contacting the three vs. two anteriormost supraoculars) and prefrontals (fused with the anterior loreals). *Pr. parkeri* is only known from its type specimen (Meiri *et al.*, 2018) collected in the Utakwa River (Smith, 1937), presumably along the southern slopes of the Sudirman Range (Wollaston, 1914). Although the presence of basally expanded subdigital lamellae and cross-bands may suggest an affinity with *Pr. prehensicauda* and *Pr. flavipes*, these traits are also common in at least some other New Guinean skinks (e.g. basally expanded subdigital lamellae in *Li. longiceps*, cross-bands and basally expanded subdigital lamellae in *Pr. semoni*), and therefore its placement in *Prasinohaema* is uncertain. Similarly, the presence of green blood serum and tissues alone would not be enough to place it in *Prasinohaema*, as both *Pr. semoni* and *Pr. virens* possess this trait but are otherwise morphologically and phylogenetically distant from *Pr. prehensicada* and *Pr. flavipes* (Figs 1–2).

Distribution: The two species in the genus (*Pr. flavipes* and *Pr. prehensicauda*) are widespread in the montane regions of Papua New Guinea. *Prasinohaema prehensicauda* is present in the New Guinea Highlands and on the Papuan Peninsula, whereas *Pr. flavipes* also occurs on the Huon Peninsula.

Remarks: Two other species are currently assigned to the genus *Prasinohaema*: *Pr. semoni* and *Pr. virens*. These species emerge in our analyses as phylogenetically distant from the type species of the genus, *Pr. flavipes* (Fig. 1; Rodriguez *et al.*, 2018), rendering the former concept of the genus polyphyletic. They also differ widely morphologically (Fig. 2), reproductively (*Pr. virens* is oviparous, whereas *Pr. semoni*, *Pr. flavipes* and *Pr. prehensicauda* are viviparous; Fig. 2) and in elevational range (*Pr. semoni* and *Pr. virens* are lowland species, whereas *Pr. flavipes* and *Pr. prehensicauda* are montane species; Fig. 4). Many of these differences, particularly in *Pr. virens*, were mentioned by Greer even in his original description of the genus (Greer, 1974). Therefore, we stress that *Prasinohaema* is in need of taxonomic revision. *Prasinohaema semoni* and *Pr. virens* likely need to be assigned to new genera, although this is beyond the scope of the current work.

NUBEOSCINCUS GEN. NOV.

(CLADE III)

(FIG. 5, SUPPORTING INFORMATION, FIGS S6, S8; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:21B16380-F7EE-48CF-806C-699AAC63F491

Type species: Lobulia glacialis Greer *et al.*, 2005. *Herpetological Monographs* 19: 153–179.

Diagnosis: Medium-sized (adult SVL 47.4–64.0 mm) terrestrial skinks with short limbs (forelimbs 28.7–34.4% of SVL, hindlimbs 34.6–38.6% of SVL); lobules either present or absent from anterior edge of ear opening; two pairs of chin shields in medial contact; two supralabials posterior to subocular supralabial; chin shields separated from infralabials by a row of genials; lower eyelid with window of variable size, opaqueness and scaliness; temporal region fragmented (> 3 scales); nasal scale undivided; frontoparietals unfused; viviparous; litter size up to three.

Nubeoscincus differs from *Prasinohaema* by lacking green blood serum and tissues (Greer, 1974), a prehensile tail with a glandular tip and basally expanded subdigital lamellae. It differs from *Lobulia* and *Papuascincus* by having the chin shields separated from the infralabials by a row of genials (vs. chin shields abutting infralabials) and by having a fragmented temporal region (vs. the standard three-scale arrangement). It further differs from *Papuascincus* by having two pairs of chin shields in medial contact (vs. one), unfused (vs. fused)

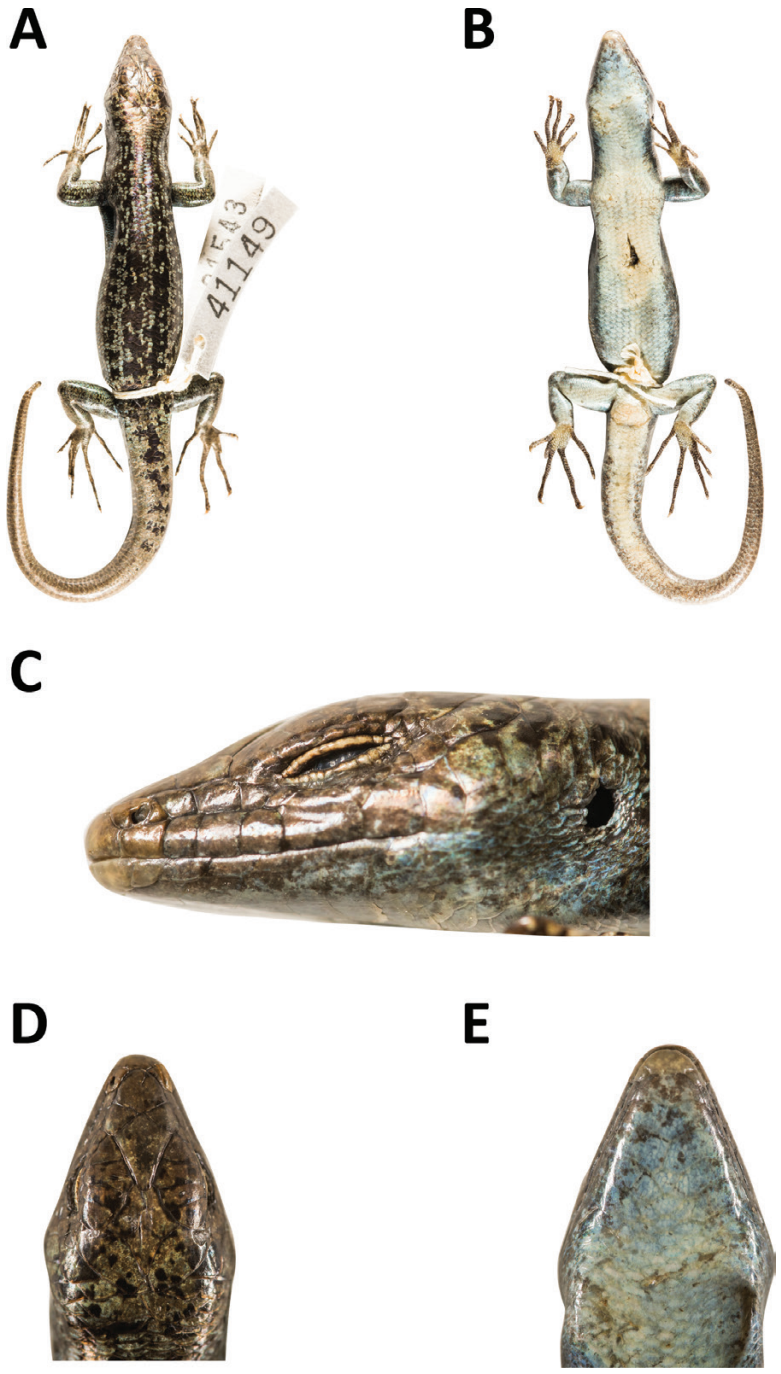

Figure 9. *Lobulia fortis* holotype (BPBM 41149), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

frontoparietals, a viviparous (vs. oviparous) reproductive mode and an undivided (vs. divided) nasal scale.

Etymology: A combinatorial noun derived from the Latin nouns *nubes*, cloud, and *scincus*, a type of lizard, in reference to the extremely high elevations at which species in this genus occur.

Species included: ***Nubeoscincus glacialis*** (Greer *et al.*, 2005) **comb. nov.**; ***Nubeoscincus stellaris*** (Greer *et al.*, 2005) **comb. nov.**

Distribution: Both species of *Nubeoscincus* occur at extremely high elevations from the western New Guinea Highlands to the western (Indonesian) parts

Figure 10. *Lobulia fortis* holotype (BPBM 41149) in life, (A) dorsal view and (B) ventral view. Images by Allen Allison.

of the island and are known from extremely limited distributions: *N. glacialis* near Puncak Jaya in the Sudirman Range, Papua Province (Indonesia), and *N. stellaris* from the Star Mountains in West Sepik Province (Papua New Guinea).

PAPUASCINCUS ALLISON & GREER

(CLADE IV)

(FIG. 5; SUPPORTING INFORMATION, FIG. S6; TABLE 1)

Papuascincus Allison & Greer, 1986. *Journal of Herpetology* 20(1): 116–119.

Type species: Lygosoma stanleyanum Boulenger, 1897, by original designation.

Diagnosis: Medium-sized (adult SVL 36.3–67.8 mm) terrestrial skinks with short forelimbs (forelimbs 25.1–38.9% of SVL) and moderately long hindlimbs (33.6–49.6% of SVL); lobules present on anterior edge of ear opening; single pair of chin shields in medial contact; three supralabials posterior to subocular supralabial; chin shields abutting infralabials; lower eyelid with semi-transparent window; standard three-scale temporal region; nasal scale divided by a horizontal suture extending posteriorly from the nostril; frontoparietals fused; oviparous; clutch size two; pustulate egg shells.

Papuascincus differs from all other genera by having pustulate egg shells and a divided (vs. undivided) nasal scale. It further differs from *Nubeoscincus*, *Prasinohaema* and *Lobulia* by having one pair of chin shields in medial contact (vs. two pairs) and an oviparous (vs. viviparous) reproductive mode. It further differs from *Nubeoscincus* and *Prasinohaema* by having the standard three-scale temporal region (vs. fragmented temporal region) and the chin shields abutting the infralabials (vs. chin shields separated from infralabials by a row of genials). It further differs from *Prasinohaema* by lacking green blood serum and tissues (Greer, 1974), a prehensile tail with a glandular tip and basally expanded subdigital lamellae.

Species included: Papuascincus buergersi (Vogt, 1932); *Papuascincus morokanus* (Parker, 1936); *Papuascincus phaeodes* (Vogt, 1932); *Papuascincus stanleyanus* (Boulenger, 1897).

Distribution: Members of *Papuascincus* are widespread across montane regions of New Guinea, ranging from the Papuan Peninsula to the Central Highlands in Papua Province (Indonesia).

Remarks: The genus *Papuascincus* most likely contains more species than currently recognized (Slavenko *et al.*, 2020). However, members of the genus appear to be more morphologically conservative than the other genera described in this manuscript. A full taxonomic revision of *Papuascincus* is underway.

PALAIA GEN. NOV.

(CLADE IV)

(FIG. 5; SUPPORTING INFORMATION, FIG. S6; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:89741FC3-DB12-469F-8682-C4579D922488

Type species: Lygosoma pulchrum Boulenger, 1903. *Proceedings of the Zoological Society of London* 1903(2): 125–129.

Diagnosis: Small (adult SVL 37.3–41.2 mm) skinks with short limbs (forelimbs 29.9–34.4% of SVL, hindlimbs 36.7–43.8% of SVL); small lobules present on anterior edge of ear opening; single pair of chin shields in medial contact; two supralabials posterior to subocular supralabial; chin shields abutting infralabials; lower eyelid with semi-transparent window; standard three-scale temporal region; nasal scale undivided; frontoparietals fused; oviparous; clutch size two; subdigital lamellae slightly expanded basally.

Palaia differs from *Nubeoscincus*, *Prasinohaema* and *Lobulia* by having one pair of chin shields in medial contact (vs. two pairs) and an oviparous (vs. viviparous) reproductive mode. It further differs from *Nubseoscincus* and *Lobulia* by having slightly basally expanded subdigital lamellae. It further differs from *Nubeoscincus* and *Prasinohaema* by having the standard three-scale temporal region (vs. fragmented temporal region), the chin shields abutting the infralabials (vs. chin shields separated from infralabials by a row of genials) and fused (vs. unfused) frontoparietals. It further differs from *Prasinohaema* by lacking green blood serum (Greer, 1974) and tissues and a prehensile tail with a glandular tip. It differs

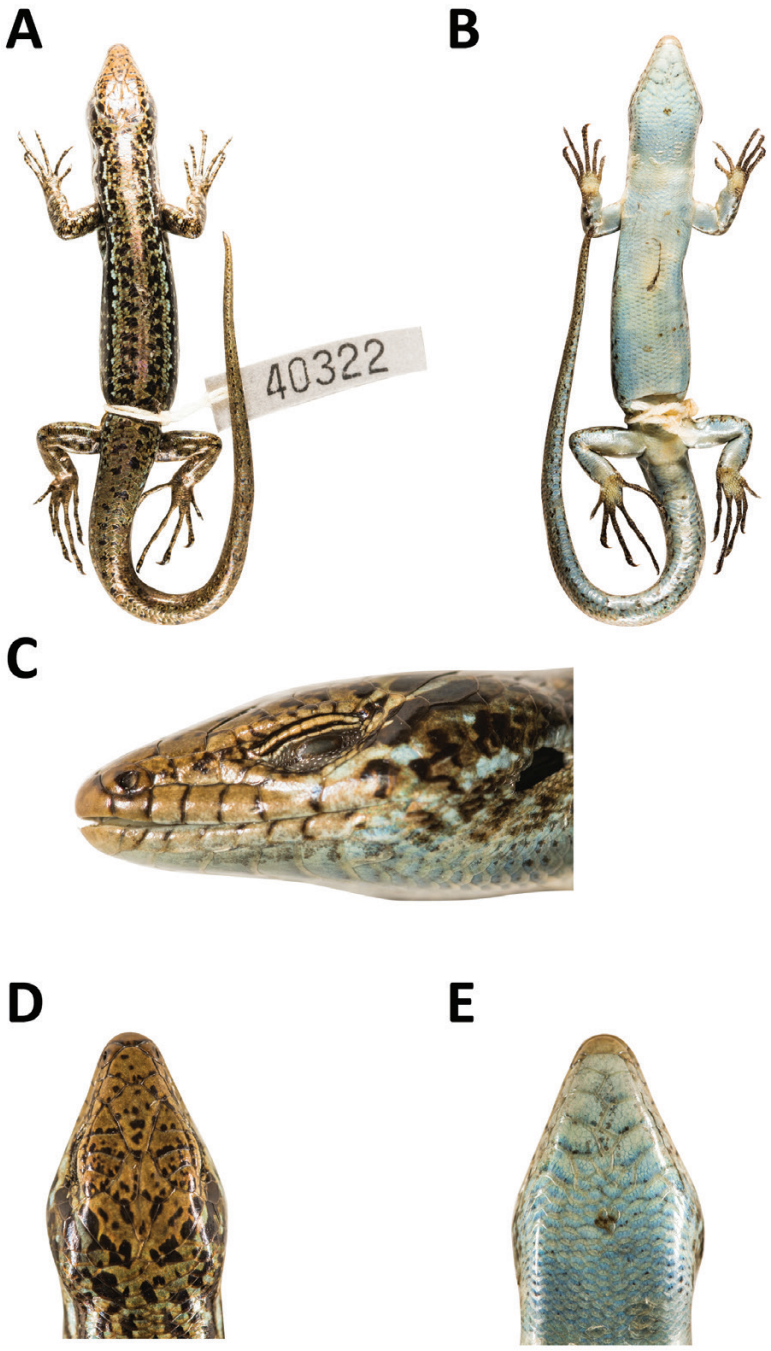

Figure 11. *Lobulia huonensis* holotype (BPBM 40322), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

from *Papuascincus* by having an undivided (vs. divided) nasal scale and slightly basally expanded subdigital lamellae and by lacking pustulate eggshells.

Etymology: Latinized feminine genus from the Tok Pisin *palai*, lizard.

Species included: ***Palaia pulchra*** (Boulenger, 1903) **comb. nov.**

Distribution: The single species in the genus is distributed widely across the lowlands of northern New Guinea.

Figure 12. *Lobulia huonensis* holotype (BPBM 40322), in life, in (A) dorsal view and (B) ventral view. Images by Allen Allison.

ALPINOSCINCUS GEN. NOV.

(CLADE VI)

(FIG. 5; SUPPORTING INFORMATION, FIGS S6, S8; TABLE 1)

Zoobank Registration: urn:lsid:zoobank.org:act:D473AA5B-791E-4C76-A5A9-AE75D78958C0

Type species: Lobulia alpina Greer *et al.*, 2005. *Herpetological Monographs* 19(1): 153–179.

Diagnosis: Medium-sized (adult SVL 46.1–72.7 mm) terrestrial to semi-arboreal skinks with moderate limbs (forelimbs 27.0–39.8% of SVL, hindlimbs 31.7–48.7% of SVL); small lobules present on anterior edge of ear opening; two pairs of chin shields in medial contact; modally three supralabials posterior to subocular supralabial; chin shields separated from infralabials by a row of genials; lower eyelid scaly; temporal region fragmented (> 3 scales); nasal scale undivided; frontoparietals unfused; viviparous; litter size 1–4.

Alpinoscincus differs from all other genera by modally having three (vs. two) supralabials posterior to the subocular supralabial. It further differs from *Prasinohaema* by lacking green blood and tissues, a prehensile tail with a glandular tip, and basally expanded subdigital lamellae. It further differs from *Lobulia*, *Palaia* and *Papuascincus* by having the lower eyelid scaly (vs. lower eyelid with a semi-transparent window), a fragmented (vs. the standard three-scale) temporal region and the chin shields separated from the infralabials by a row of genials (vs. chin shields abutting infralabials). It further differs from *Palaia* and *Papuascincus* by having two pairs of chin shields in medial contact (vs. one pair), unfused (vs. fused) frontoparietals and a viviparous (vs. oviparous) reproductive mode. It further differs from *Palaia* by its longer adult SVL (46.1–72.7 vs. 37.3–41.2 mm) and by lacking basally slightly expanded subidigital lamellae. It further differs from *Papuascincus* by having an undivided (vs. divided) nasal scale.

Etymology: A combinatorial noun derived from the Latin adjective *alpinus*, of high mountains, and Latin noun *scincus*, a type of lizard, in reference to the extremely high elevations in which species in this genus occur.

Species included: ***Alpinoscincus alpinus*** (Greer *et al.*, 2005) **comb. nov.**; ***Alpinoscincus subalpinus*** (Greer *et al.*, 2005) **comb. nov.**

Distribution: The two species of *Alpinoscincus* are restricted to extremely high elevations (> 2700 m a.s.l. in *A. alpinus* and > 2350 m a.s.l. in *A. subalpinus*) in the north-western Owen Stanley Range in the Papuan Peninsula. *Alpinoscincus alpinus* occurs in the Murray Range, the Wharton Range, and on Mt Albert Edward and Mt Yule. *Alpinoscincus subalpinus* occurs farther to the north-west, in the vicinity of Wau and Mt Missim.

Remarks: Molecular evidence suggests that another undescribed species occurs on the summit of Mt Victoria, but the specimen (BPBM 47913) was unavailable for morphological examination at the time of writing.

ORNITHUROSCINCUS GEN. NOV.

(CLADE VII)

(FIGS 5, 16–24; SUPPORTING INFORMATION, FIGS S6, S8; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:D473AA5B-791E-4C76-A5A9-AE75D78958C0

Type species: Lobulia sabini Kraus, 2020. *Zootaxa* 4779(2): 201–214.

Diagnosis: Small to medium-sized (adult SVL 29.4–69.2 mm) terrestrial to semi-arboreal skinks with short limbs (forelimbs 25.7–36.3% of SVL, hindlimbs 29–47.3% of SVL); lobules absent from anterior edge of ear opening; a single pair of chin shields in medial contact; two supralabials posterior to subocular supralabial; chin shields abutting infralabials; lower eyelid with semi-transparent window; standard three-scale temporal region; nasal scale undivided; frontoparietals either fused or unfused; viviparous; litter size 1–3.

Ornithuroscincus differs from all other genera apart from *Nubeoscincus* by the absence of lobules

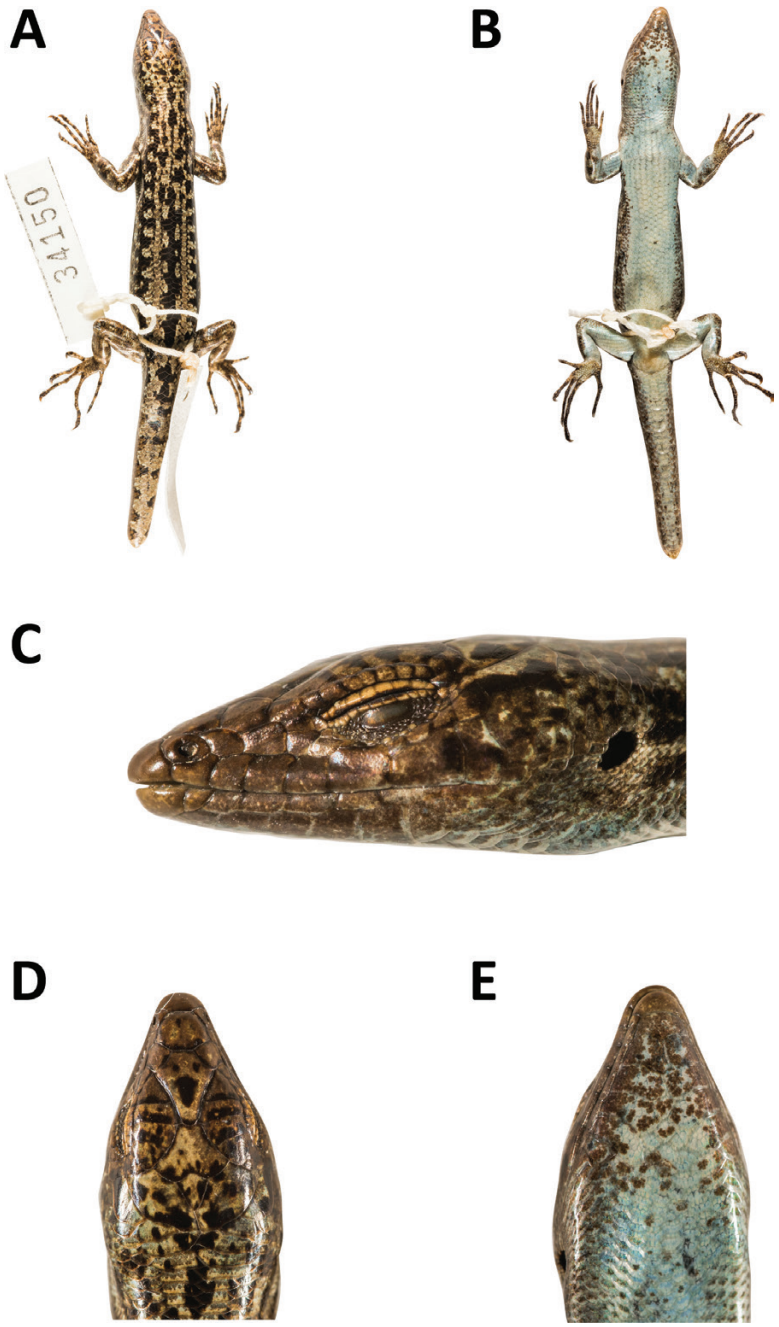

Figure 13. *Lobulia marmorata* holotype (BPBM 34150), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

from the anterior edge of the ear (vs. lobules present)—a character which in *Nuboescincus* only occurs in one species, *N. stellaris*. It further differs from *Alpinoscincus*, *Lobulia*, *Nubeoscincus* and *Prasinohaema* by having one pair of chin shields in medial contact (vs. two pairs). It further differs from *Alpinoscincus*, *Nubeoscincus* and *Prasinohaema* by the chin shields abutting the infralabials (vs. chin shields separated from infralabials by a row of genials) and by having the standard three-scale temporal region (vs. fragmented temporal region). It further differs from *Alpinsocincus* by having two (vs. three) supralabials posterior to the subocular supralabial. It further differs from *Prasinohaema* by lacking green blood serum and tissues, a prehensile tail with a glandular tip and basally expanded subdigital lamellae. It further differs from *Palaia* and *Papuascincus* by its viviparous (vs. oviparous) reproductive mode. It further differs from

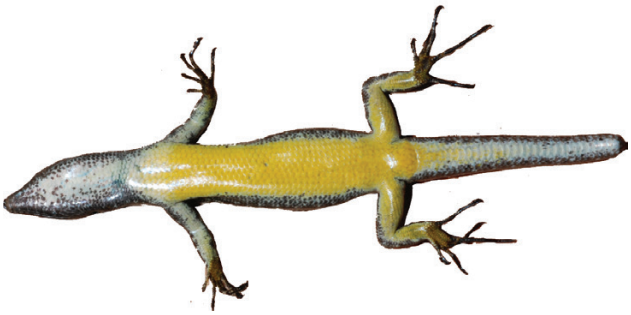

Figure 14. *Lobulia marmorata* holotype (BPBM 34150), ventral view in life. Image by Fred Kraus.

Palaia by lacking basally slightly expanded subidigtal lamellae. It further differs from *Papuascincus* by having an undivided (vs. divided) nasal scale. It further differs from *Alpinoscincus* by having the lower eyelid with a semi-transparent window (vs. scaly).

Etymology: A combined noun formed from the Latinized Greek nouns *ornis*, bird, and *oura*, tail, appended to the Latin noun *scincus*, a type of lizard, referring to the centre of distribution of the genus, as most species occur in the Papuan Peninsula, also known as the Bird's Tail in reference to the general shape of New Guinea resembling a bird-of-paradise.

Species included: ***Ornithuroscincus albodorsalis*** (Vogt, 1932) **comb. nov.**; ***Ornithuroscincus noctua*** (Lesson, 1830) **comb. nov.**; ***Ornithuroscincus nototaenia*** (Boulenger, 1914) **comb. nov.**; ***Ornithuroscincus sabini*** (Kraus, 2020) **comb. nov.**; and new species described below.

Species incertae sedis: *Lipinia venemai* (Brongersma, 1953a) possesses many traits the combination of which is uniquely found among New Guinean skinks in *Ornithuroscincus*, including viviparity, lacking lobules on the anterior edge of the ear opening, two supralabials posterior to the subocular supralabial, lower eyelid with a semi-transparent window, separated frontoparietals, chin shields abutting the infralabials, a standard three-scale temporal region, and an undivided nasal scale. However, the holotype of *Li. venemai* differs from all other members of *Ornithuroscincus* in having two pairs of chin shields in medial contact (vs. one). Since genetic data for this species are unavailable, we tentatively place it as *incertae sedis* in *Ornithuroscincus* but stress that more work is required to fully ascertain its generic affiliation.

Distribution: Most species in the genus have a montane distribution in the Papuan Peninsula, and appear to have narrow distributions restricted to one or a few adjacent mountains. The lowland species appear to be far more widespread, both in New Guinea and elsewhere. *Ornithuroscincus albodorsalis* is known from West Sepik Province (Papua New Guinea), north of the Central Cordillera; *O. nototaenia* is known from the Setakwa River in Papua Province (Indonesia) and from the Palmer River in the Western Province of Papua New Guinea (Shea, 2008), both localities south of the Central Cordillera of New Guinea. *Ornithuroscincus* cf. *venemai* is known from Ajamaroe in the Vogelkop Peninsula, West Papua Province, Indonesia. *Ornithuroscincus noctua* is widespread throughout the northern versant of New Guinea, as well as across many islands in the Pacific Ocean, but it is clearly a species complex in need of taxonomic resolution [see also Zweifel (1979) and Austin (1999) for discussions of morphological and genetic variation in *O. noctua*].

Remarks: Several of the species assigned to this genus have been previously assigned to a different genus by Raymond Hoser, an act which would give Hoser's generic name priority. However, we follow Kaiser *et al.*'s recommendation and completely disregard Hoser's nomenclature due to his broad acts of taxonomic vandalism, which do not stand up to even the slightest level of scientific standard or scrutiny (Kaiser *et al.*, 2013).

Ornithuroscincus albodorsalis had been previously sampled genetically and found to be phylogenetically closest to *O. noctua* (Rodriguez *et al.*, 2018). However, no other members of *Ornithuroscincus* were sampled in that study. Furthermore, *O. nototaenia* is only known from the Setakwa River and the Palmer River, south of the Central Cordillera and far from all other recognized species in the genus (Boulenger, 1914; Wollaston, 1914; Shea, 2008). Similarly, *O.* cf. *venemai* has only been recorded from the Vogelkop Peninsula (Brongersma, 1953a) and has never been collected since. Therefore, the relationships between *O. albodorsalis, O. nototaenia*, *O.* cf. *venemai* and other members of the genus, remain to be resolved.

Molecular evidence suggests that a further undescribed species not treated herein occurs in Vori Vori, a foothills site in proximity to the Kokoda Track in the Papuan Peninsula, but the voucher (BPBM 48589) was unavailable for morphological examination at the time of writing, and so we refrain from formally describing it. Furthermore, *O. noctua* likely represents a species complex, but revising it is beyond the scope of the current work.

Species accounts

Lobulia lobulus (Loveridge, 1945)

Central Range moss skink

(Figs 6–8; Table 1)

Lygosoma (Leiolopisma) elegantoides lobulus Loveridge, 1945: 49.

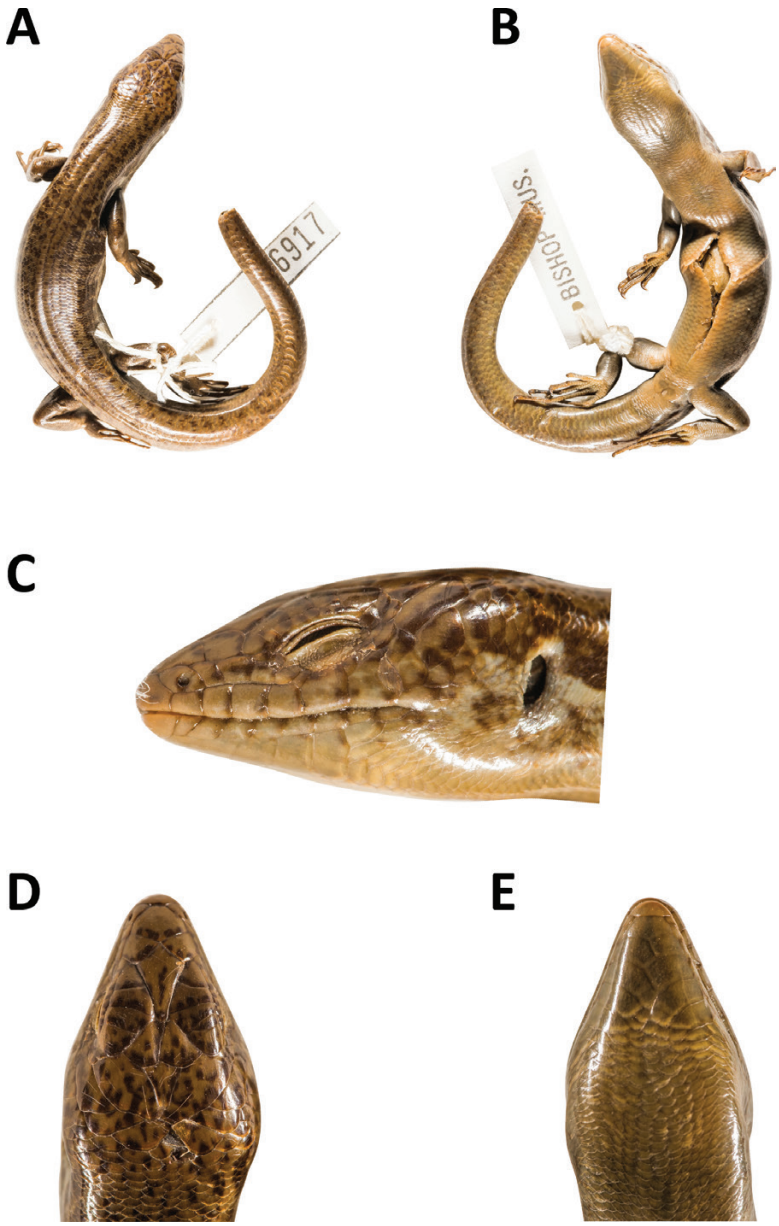

Figure 15. *Lobulia vogelkopensis* holotype (BPBM 6917), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

Type locality: Mt Wilhelm, Papua New Guinea.
Lobulia lobulus, Kraus, 2020: 204.

Material examined for rediagnosis: Papua New Guinea: Madang Province: Bismarck Range: Mt Wilhelm, 2286–2438 m a.s.l. ("7500 to 8000 ft") (MCZ R-47067; male; holotype; photos only); Eastern Highlands Province: Daulo Pass, 6.0409°S, 145.2256°E (WGS 84), 2472 m a.s.l. (BPBM 2577, 2578; two juveniles); Chimbu Province: Bismarck Range: Denglagu, Mt Wilhelm, 5.8424°S, 145.0967°E (WGS 84), 2500 m a.s.l. (BPBM 3901, 3910; one male, one juvenile); Mt Wilhelm, above Keglsugl, 5.8071°S, 145.00631°E (WGS 84) (BPBM 6125–26; one male, one juvenile); vicinity of Keglsugl, 5.8311°S, 145.0981°E (WGS 84), 2652 m a.s.l. (BPBM 10811; juvenile); Western Highlands Province: Trika, 5.812°S, 145.095°E (WGS 84), 2200 m a.s.l. (BPBM 22976; female); Rondon Ridge, 5.8891°S, 144.2521°E (WGS 84), 1960 m a.s.l. (BPBM 47837; male); Hela Province: Ambua Lodge, Tari, 5.9616°S, 143.0677°E (WGS 84), 2100 m a.s.l. (BPBM 23058; female).

Diagnosis: A medium-sized species of *Lobulia* (adult SVL 42.5–55.8 mm), characterized by the unique

Figure 16. Pictures in life of (A) *Ornithuroscincus bengaun* (holotype; BPBM 37741); (B) *Ornithuroscincus pterophilus* (holotype; BPBM 45705); (C) *Ornithuroscincus sabini* (BPBM 16761); (D) *Ornithuroscincus shearmani* (holotype; BPBM 47951); (E) *Ornithuroscincus viridis* (holotype; BPBM 44744). Images A, C by Fred Kraus, images B, D, E by Allen Allison.

combination of frontoparietals unfused; supraorbital ridges usually not pronounced; nuchals 1–3 pairs; paravertebral scales 54–61; mid-body scale rows 32–40; 4th digit on front foot longer than 3rd; subdigital lamellae 19–24 under 4th toe; single supradigital scales 3–4 on 4th toe; mid-dorsum with two rows of large dark brown spots on an olive green background typically joined to form two irregularly-shaped dark brown mid-dorsal stripes; top of tail base with two rows of large dark brown spots; fragmented white dorsolateral stripes present, extending from parietals to base of tail; flanks dark brown with light spots; unbroken white lateral stripes present, extending from occiput to hindlimbs; ventral coloration light blue on chin, occasionally speckled with

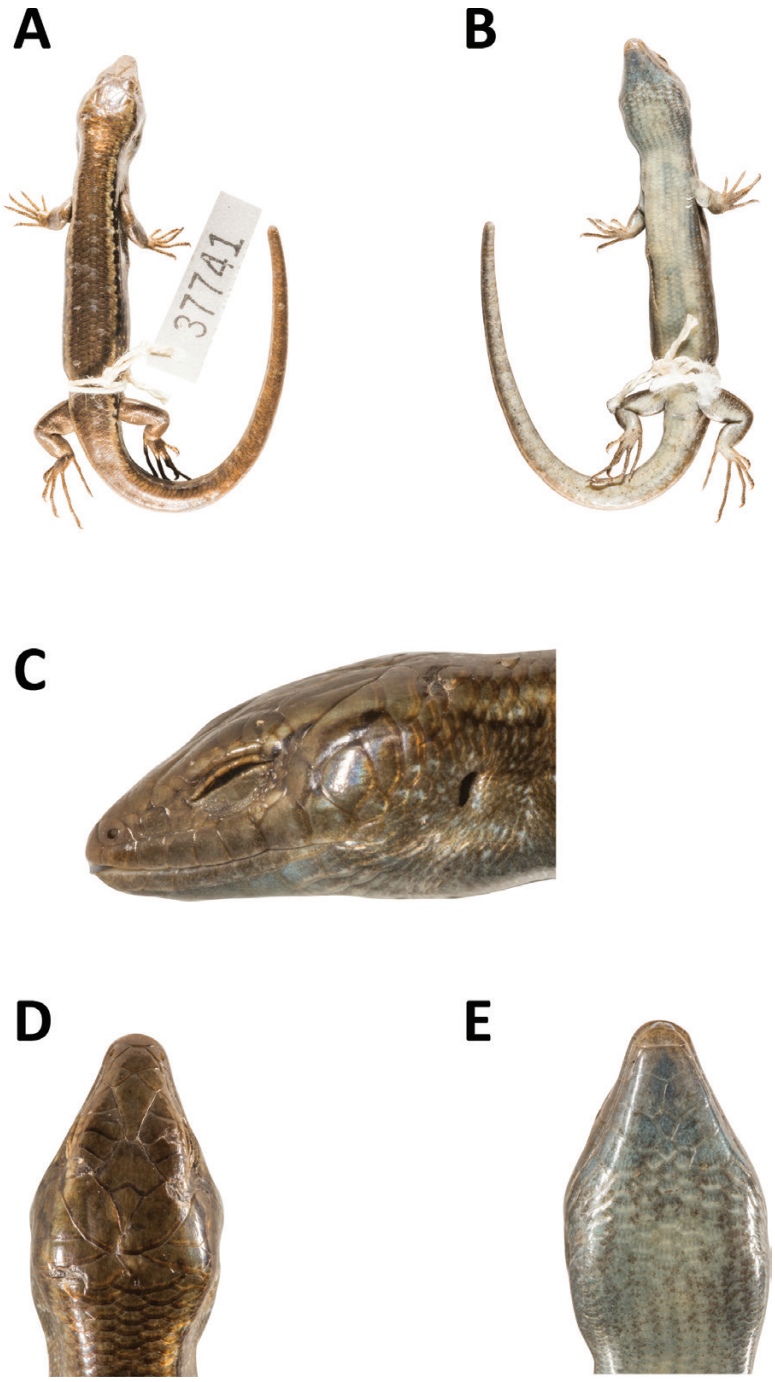

Figure 17. *Ornithuroscincus bengaun* holotype (BPBM 37741), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

dark brown spots, lemon-yellow on abdomen and base of tail in life, uniform light blue in preservative; thighs and precloacal region lack brown spotting; ventral surfaces of tail occasionally speckled with light brown spots; palmar and plantar surfaces lemon-yellow in life, light brown in preservative.

Comparisons: Lobulia lobulus differs from *Lo. brongersmai* in having unfused (vs. fused) frontoparietals. It differs from *Lo. elegans* in having white dorsolateral stripes and lateral stripes (vs. absent), and in having higher counts of midbody scale rows (32–40 vs. 30–32) and paravertebral scales (54–61 vs. 52–54).

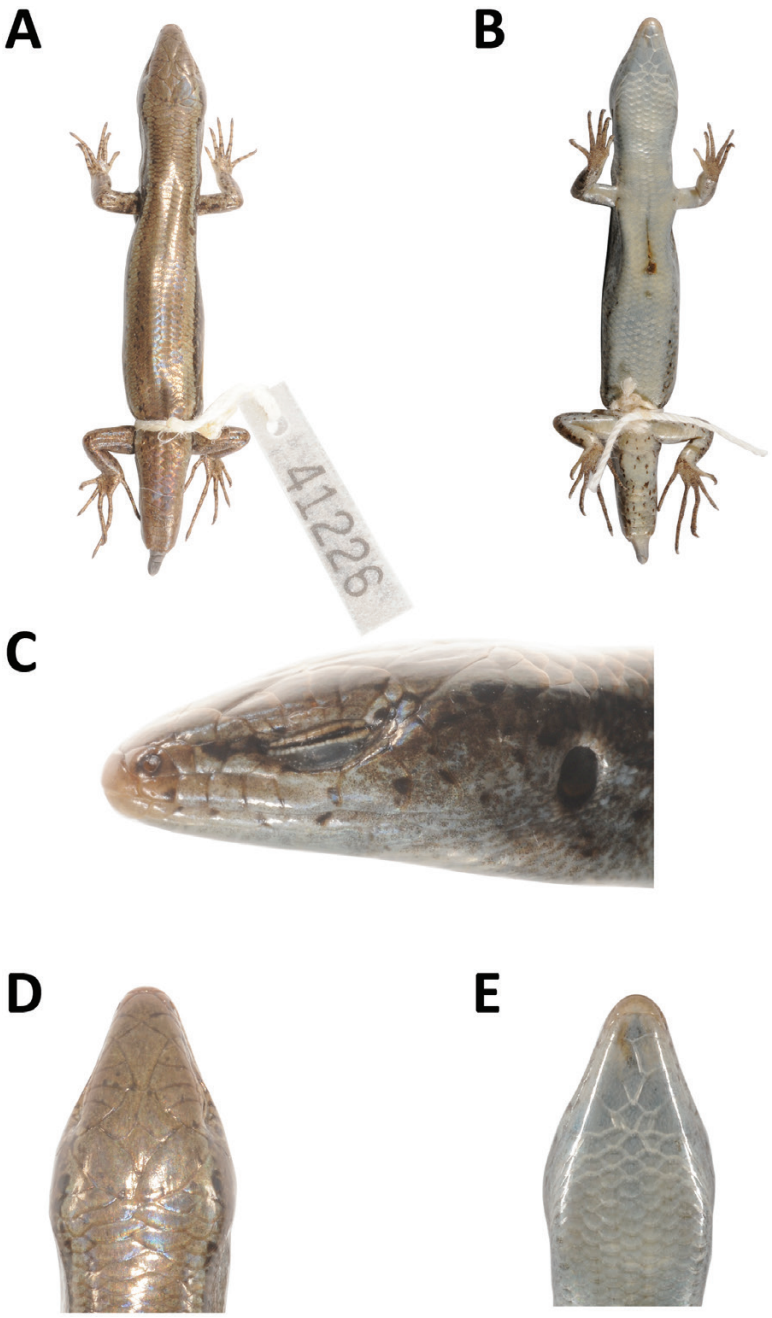

Figure 18. *Ornithuroscincus inornatus* holotype (BPBM 41226), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

Description: This description is based on photographs of the holotype (available online: https://mczbase.mcz.harvard.edu/guid/MCZ:Herp:R-47067) and our examinations of ten specimens in the BPBM collections.

Adult body size 42.5–55.8 mm SVL (mean = 52.2, SD = 5.5, *N* = 5). Females (mean = 49.2, range: 42.5–55.8, SD = 9.4, *N* = 2) have larger maximal size than males (mean = 54.2, range: 53.7–55.0, *SD* = 0.7, *N* = 3), although Loveridge (1945) reports an SVL of 60 mm for the male holotype. Forelimbs 32.9–42.9% of SVL (mean = 39.6%, SD = 3.9, *N* = 5). Hindlimbs 42.0–51.5% of SVL (mean = 47.7%, SD = 3.7, *N* = 5). 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, undivided in all but BPBM 6125; frontonasal

Figure 19. *Ornithuroscincus inornatus* holotype (BPBM 41226) in life, in (A) dorsal view and (B) ventral view. Images by Allen Allison.

large, with eight sides, extending laterally to slightly above the level of nares; prefrontals large, either separated by frontonasal and frontal contact (N = 5) or in narrow contact (N = 4), rarely separated by a single azygous scale (N = 2), bordered lateroventrally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal roughly kite shaped, widest anteriorly; frontoparietals single pair in medial contact, in narrow contact with frontal; interparietal of roughly similar area to single frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and two pretemporals; nuchals 1–3 pairs, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale; nuchals typically symmetrical (N = 7), sometimes one more on left side (N = 3), rarely one more on right side (BPBM 40327). Anterior loreal smaller than posterior loreal, higher than long; posterior loreal usually longer than high; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single; postsuboculars usually three (N = 8), occasionally four (N = 3), lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than the size of the ear opening; supraciliaries typically eight (N = 7), rarely seven (N = 2) or nine (N = 2), anteriormost usually not in contact with frontal (N = 7), sometimes in narrow contact (N = 4), posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporals typically one (N = 9), but rarely two (N = 2) with lower interdigitated between posterior two supralabials; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid, posteriormost fragmented by horizontal suture in BPBM 47837; postsupralabials two; ear opening moderately large, with lobules along anterior margin. Mental single; postmental single, contacting two anteriormost infralabials; infralabials typically seven (N = 7), occasionally eight (N = 4); enlarged chin shields four pairs, the first two pairs in medial contact, third pair narrowly separated by single medial scale, fourth pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial (N = 10), rarely with prepenultimate (N = 1). Body scales smooth, in 32–40 rows at midbody (mean = 35.3, SD = 2.4, N = 10); paravertebral scales 54–61 (mean = 57.7, SD = 2.6, N = 10); medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of fourth toe in two rows proximally, single row distally beginning at third interphalangeal joint, 3–7 single scales (mean = 4, SD = 1.2, N = 10); subdigital lamellae under fourth toe 19–24 (mean = 21, SD = 1.6, N = 10), smooth. In preservative (Fig. 7), base dorsal coloration coppery brown, with two mid-dorsal parallel rows of large dark brown spots two to four scales long, typically joined to form irregular dark brown parallel stripes, extending to base of tail; two parallel rows of dark brown spots become smaller posteriorly on tail; dorsolateral stripes present as light brown or light blue fragmented stripes extending from occiput to base of tail; lateral field dark brown, speckled with light blue spots one to two single scales wide; unfragmented light blue lateral stripe present, extending from postsupralabials, across ear opening, to hind limbs; head similar in coloration to dorsum, with dark brown spotting, mostly in centre of scales and along scale margins; ventral surfaces uniform cream or light blue; light brown dusting occasionally present on chin and ventral surface of tail; scales on palmar and plantar surfaces light brown, contrasting with dark brown digits. In life (Figs 6, 8), dorsal colour coppery brown with black mid-dorsal spots; fragmented dorsolateral stripes, uniform lateral stripes and spots on lateral field pale yellow; chin light blue; ventral surfaces of chest, abdomen, thighs, precloacal region and tail lemon yellow, with tail becoming light blue posteriorly; scales on palmar and plantar surfaces dark yellow.

Distribution: Known from several locations in the Central Ranges of Papua New Guinea at elevations 1960–2650 m a.s.l., mostly around the vicinity of Mt Wilhelm. It likely does not extend to the Huon Peninsula or the Owen Stanley Ranges, where it is

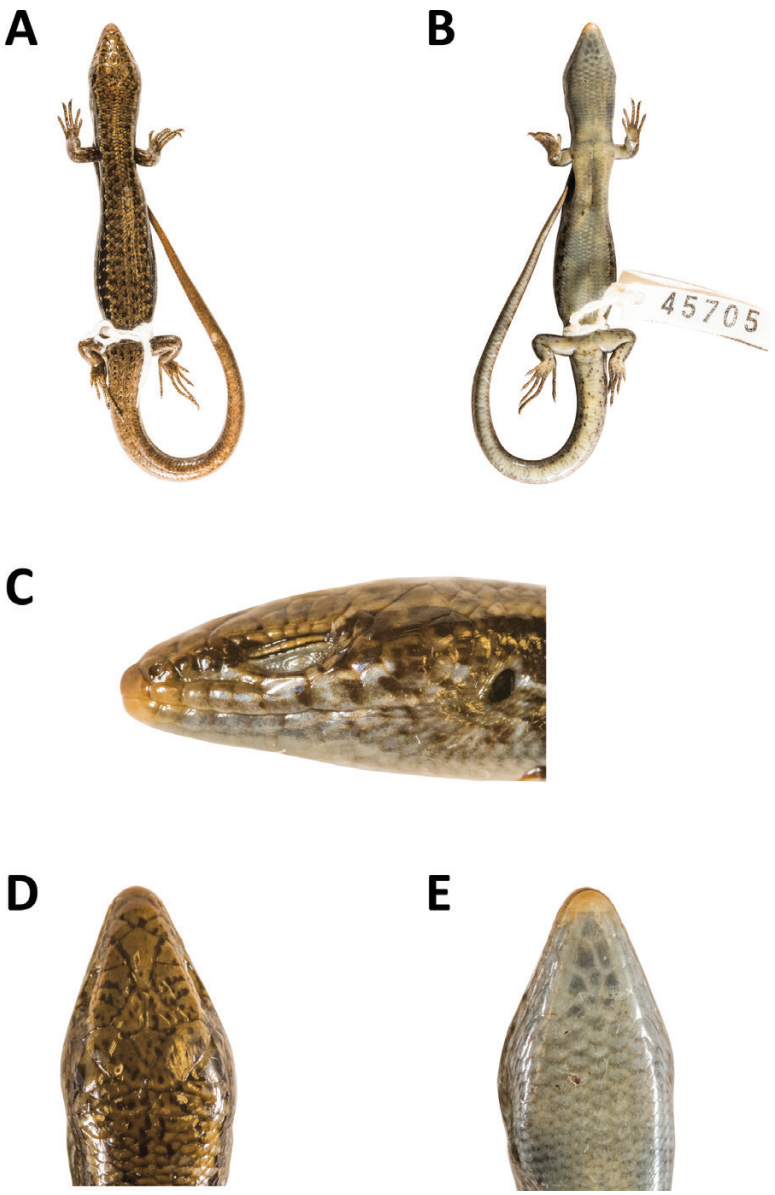

Figure 20. *Ornithuroscincus pterophilus* holotype (BPBM 45705), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

replaced by two newly described species (see below) and *Lo. elegans*.

Reproduction: Viviparous. Only a single gravid female was examined, with three embryos, but litter size is presumably variable in this species, as in other members of the genus.

Conservation status: The species appears locally abundant although the population trend is unknown. Based on the sampled populations *Lo. lobulus* has an extent of occurrence of 4085 km^2 and an area of occupancy of 32 km^2 (based on occupation of 4 km^2 cells; both calculated using http://geocat.kew.org/). However, its distribution almost certainly encompasses more populations throughout the Central Ranges in suitable elevations, including many specimens already deposited in natural history collections, and the true area of occupancy and extent of occurrence are likely much larger than estimated here. The type locality is in the vicinity of a protected area, the Mount Wilhelm National Park, although the National Park only encompasses elevations > 3200 m, and it is unclear if *Lo. lobulus* occurs at such elevations. Since it is locally abundant, with no immediate direct threats to the species or indirect threats to its habitat or location,

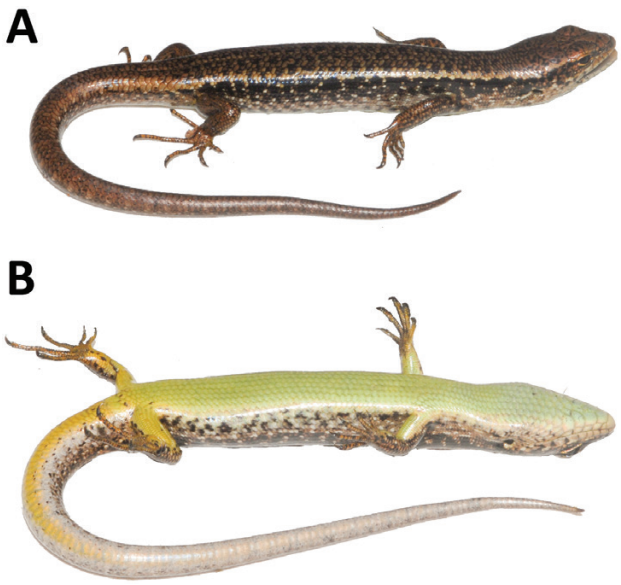

Figure 21. *Ornithuroscincus pterophilus* holotype (BPBM 45705) in life, in (A) dorsal view and (B) ventral view. Images by Allen Allison.

and because it likely occurs over a wide distribution range encompassing at least one protected area, we recommend assigning a status of Least Concern to *Lo. lobulus*, although its true distribution extent needs to be confirmed.

LOBULIA FORTIS SP. NOV.

MOUNT STRONG MOSS SKINK

(FIGS 6, 9–10; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:A3DD9FD2-4D28-4883-A087-249B6C432020

Holotype: BPBM 41149 (field tag AA 21543), adult male, collected by A. Allison at Kesemani, 7.9372°S, 147.0544°E (WGS 84), 1733 m a.s.l., north slope of Mt Strong, Morobe Province, Papua New Guinea, 25 February 2012.

Paratypes (N = 28): Papua New Guinea: Morobe Province: Mt Strong: Arabuka, 7.9838°S, 147.0458°E (WGS 84), 1965 m a.s.l. (BPBM 41127–35, 41141–48; five males, seven females, five juveniles); Lamgatak Camp [Camp 2], 7.9325°S, 147.0399°E (WGS 84), 2161 m a.s.l. (BPBM 41136–40; two males, one female, two juveniles); same locality as holotype (BPBM 41150–55; three males, two females, one juvenile).

Diagnosis: A medium-sized species of *Lobulia* (adult SVL 45.7–60.5 mm), characterized by the unique combination of frontoparietals unfused; supraorbital ridges not pronounced; nuchals 1–2 pairs; paravertebral scales 55–65; mid-body scale rows 34–37; 4th digit on front foot longer than 3rd; subdigital lamellae 20–25 under 4th toe; single supradigital scales 3–5 on 4th toe; mid-dorsum with two rows of large dark brown spots; top of tail base with single row of large dark brown spots; light blue or white dorsolateral stripes absent; flanks dark brown with thin light blue to grey vertical bands; light blue or white lateral stripes absent; uniform coloration on abdomen either lemon yellow (in males) or white (in females) in life, light blue in preservative; thighs and precloacal region without brown spotting; ventral surface of tail lemon yellow in life, becoming white posteriorly, uniform light blue in preservative, either speckled with light brown spots (occasionally forming fragmented parallel longitudinal lines) or with speckling absent; palmar and plantar surfaces lemon yellow in life, light brown in preservative.

Comparisons: Lobulia fortis differs from *Lo. brongersmai* in having unfused (vs. fused) frontoparietals. It differs from *Lo. lobulus* in lacking dorsolateral and lateral stripes. *Lo. fortis* is most similar to *Lo. elegans* in having unfused frontoparietals and lacking light blue or white dorsolateral and lateral stripes but differs from it in having higher counts of midbody scale rows (34–37 vs. 30–32) and paravertebral scales (55–65 vs. 52–54) and a lower number of nuchal pairs (one or two vs. three).

Description of the holotype: 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; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, posteriorly in narrow contact with frontal; prefrontals large, separated by frontonasal and frontal contact, bordered lateroventrally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal roughly kite shaped, widest anteriorly; frontoparietals single pair in medial contact, in narrow contact with frontal; interparietal of roughly similar area to single frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and two pretemporals; nuchals single pair, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale. Anterior loreal slightly smaller than posterior loreal, both longer than high; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single; postsuboculars three, lowest interdigitated between subocular supralabial and

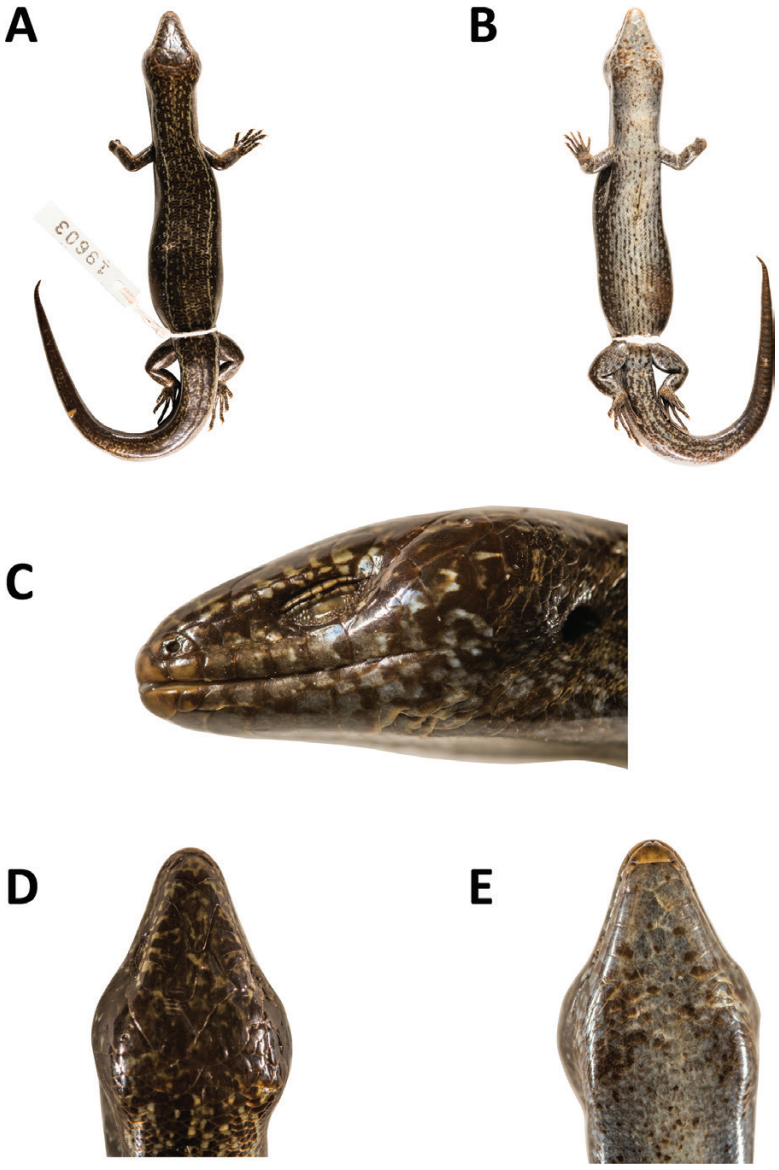

Figure 22. *Ornithuroscincus shearmani* holotype (BPBM 47915), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than 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 ovelapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening moderately large, with lobules along anterior margin. Mental single; postmental single, contacting two anteriormost infralabials; infralabials seven; enlarged chin shields four pairs, the first two pairs in medial contact, third pair narrowly separated by single medial scale, fourth pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial. Body scales smooth, in 36 rows at midbody; paravertebral scales 60; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third interphalangeal joint, four single scales; subdigital lamellae under 4th toe 23, smooth. In preservative (Fig. 9), base dorsal coloration grey, with two mid-dorsal parallel rows of large dark brown spots two to four scales long, extending to base of tail and converging to a single row of blotches along tail; dorsolateral stripes absent;

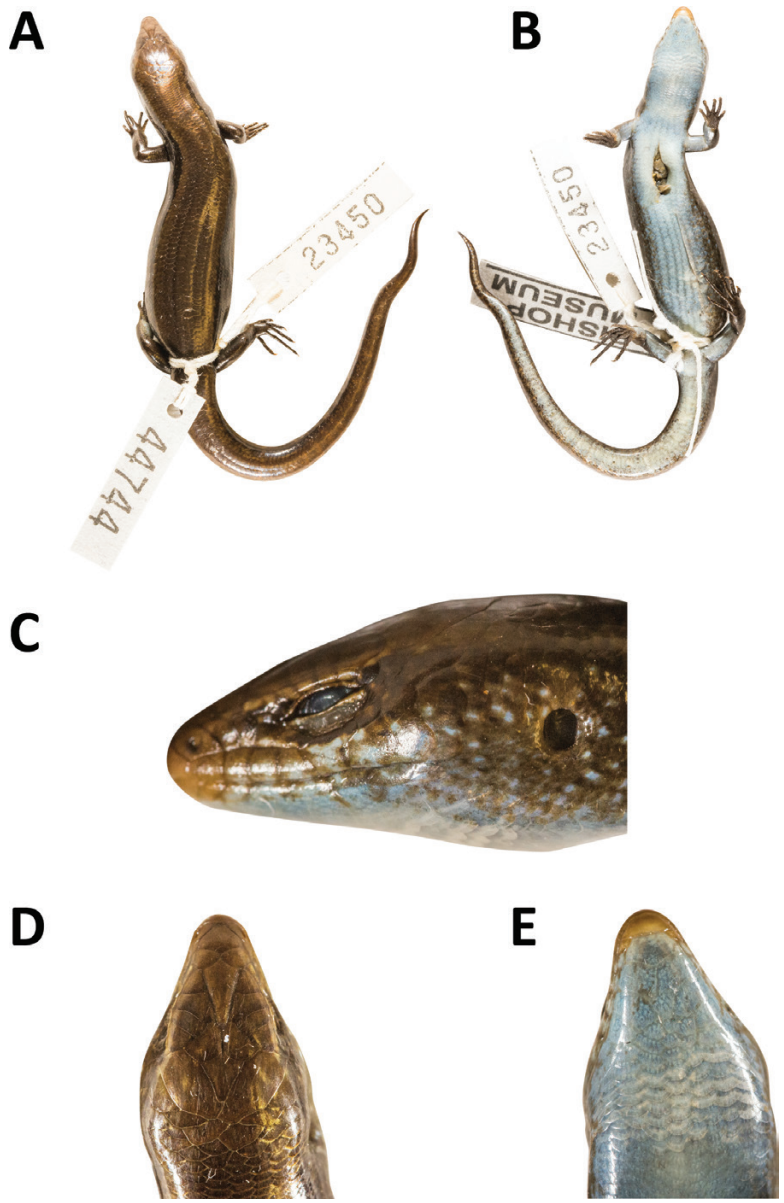

Figure 23. *Ornithuroscincus viridis* holotype (BPBM 44744), in (A) dorsal view, (B) ventral view, (C) lateral view of head, (D) dorsal view of head and (E) ventral view of head. Images by Alex Slavenko.

lateral field composed of smaller dark brown blotches, roughly parallel to dorsal rows, separated by thin vertical grey lines; lateral stripe absent; head similar in coloration to dorsum, with brown snout; dark brown spotting present on head scales, mostly along scale margins; ventral surfaces uniform light blue; light brown dusting present on chin; scales on palmar and plantar surfaces light brown, contrasting with dark brown digits. In life (Fig. 10), dorsal colour reddish coppery brown with black mid-dorsal spots; chin white; ventral surfaces of chest, abdomen, thighs, precloacal region and tail lemon yellow, with tail becoming white posteriorly; scales on palmar and plantar surfaces lemon yellow.

Variation: Adult body size 45.7–60.5 mm SVL (mean = 53.6, SD = 4.9, N = 21). Females (mean = 55.8, range: 47.8–60.5, SD = 4.7, N = 10) larger than males (mean = 51.6, range: 45.7–56.8, SD = 4.4, N = 11; t = 2.1, P = 0.05). Forelimbs 40.6–47.6% of SVL (mean = 43.3%, SD = 1.9, N = 21). Hindlimbs 46.0–54.8% of SVL (mean = 50.2%, SD = 2.4, N = 21). Scale rows at midbody 34–37 (mean = 35.3, SD = 1.0, N = 28); paravertebral scales 55–65 (mean = 58.9, SD = 2.6, N = 28).

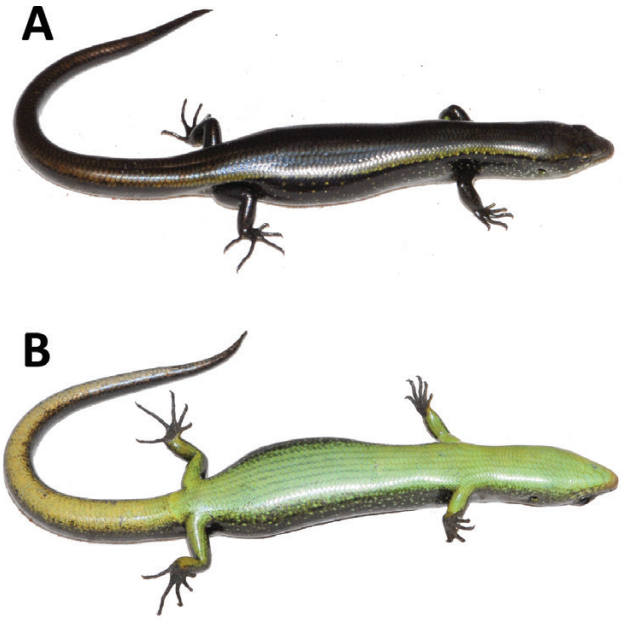

Figure 24. *Ornithuroscincus viridis* holotype (BPBM 44744) in life, in (A) dorsal view and (B) ventral view. Images by Allen Allison.

Lamellae under 4th toe 20–25 (mean = 22.9, SD = 1.2, *N* = 28); single supradigital scales on 4th toe 3–5 (mean = 3.5, SD = 0.6, *N* = 28). Mostly one or two pairs of nuchals, but BPBM 41130, 41135, 41136, 41138, 41145 and 41146 have an asymmetrical number of nuchals, with one more nuchal on left side. Primary nuchals usually separated from secondary temporals by single smaller intercalated scale (*N* = 25), rarely by none on left side and one on right (*N* = 3). Supraorbital ridges not pronounced in all but BPBM 41152. Frontonasal usually wider than long (*N* = 25), rarely as long as wide (*N* = 3). Prefrontals usually separated by frontonasal and frontal contact (*N* = 20), occasionally in narrow medial contact (*N* = 7), rarely separated by a single azygous scale (*N* = 1). Supraciliaries rarely seven (*N* = 1), typically eight (*N* = 23), occasionally nine (*N* = 4). Anteriormost supraciliary usually not in contact with frontal (*N* = 22), sometimes in narrow contact (*N* = 6). Presubocular usually single (*N* = 26), rarely two (*N* = 2). Postsuboculars usually three (*N* = 25), rarely four (*N* = 3). Supralabials typically seven (*N* = 25), rarely eight (*N* = 3). Infralabials rarely six (*N* = 3), typically seven (*N* = 25). Chin shields typically symmetrical (*N* = 23), occasionally anteriormost two on left side fused (*N* = 4), rarely anteriormost two on right side fused (*N* = 1).

Colour pattern of all paratypes generally similar to holotype, with few exceptions. Size of mid-dorsal dark brown spots varies between individuals. BPBM 41136 and 41154 have fragmented lateral stripes, and BPBM 41139 has uniform lateral stripes. BPBM 40334 has dark brown palmar and plantar surfaces.

Colour in life: Dorsal surfaces coppery brown with two parallel mid-dorsal rows of large dark brown spots (Figs 6, 10). Sides dark brown to jet black, usually with thin coppery vertical stripes between dark blotches, which are more or less parallel to dorsal rows of spots. Chin white. Ventral surfaces of chest, abdomen, precloacal region, thighs and base of tail lemon yellow in adult males and white in females and juveniles. Palmar and planar surfaces lemon yellow.

Etymology: From the single-ending Latin adjective, *fortis*, strong, in reference to Mt Strong, where the type series was collected.

Distribution: Specimens examined are from 1733–2161 m a.s.l. on the northern slopes of Mt Strong. Specimens collected from the vicinity of Wau and Mt Kaindi further north in similar elevations and deposited in BPBM as *Lo. elegans* were not examined here, but from photos taken in life and appear to have similar coloration patterns to *Lo. fortis* and therefore possibly also represent *Lo. fortis*. If true, this would make the distribution of this species extend throughout the north-western Owen Stanley Mts.

Natural history: All animals were collected from areas that were covered or formerly covered in lower montane forest (Paijmans, 1975). Trees were generally 20–30 m tall and formed a fairly even, mostly closed canopy. There was a profusion of epiphytic orchids and ferns and a ground flora of scattered herbs and shrubs. Dominant tree taxa included *Castanopsis acuminatissima* (Blume) A.DC., *Lithocarpus celebicus* (Miq.) Rehder, *Elaeocarpus kaniensis* Schltr., *Elaeocarpus pycnanthus* A.C.Sm., *Litsea* sp. and *Saurauia* spp. Southern beech, *Nothofagus* sp., is common on some ridges above 2100 m.

Animals from Langatak were found in forest clearings or in exposed areas along walking tracks. They were exclusively on tree stumps or logs at heights of 2–3 m above the forest floor. The other animals were collected around two villages, Arabuka and Kesemani, within 1–2 km of Langatak, but located within anthropogenous grassland dominated by two native species, *Miscanthus floridulus* (Labill.) Warb. ex K.Schum. & Lauterb. and *Imperata cylindrica* (L.) P.Beauv., with patches of the invasive exotic grass, *Melinis minutiflora* P.Beauv. The lizards were mostly on isolated tree stumps but also occurred on the lower timbers of houses. They were heliothermic and were generally active only during the first few hours of the morning.

Other lizard taxa common in the area included at least two species of *Papuascincus*, *Pr. flavipes*, species of *Emoia* Gray, 1845 and at least four species of *Sphenomorphus* Fitzinger, 1843. A widely distributed montane frog, *Litoria angiana* (Boulenger, 1915), is also common.

Reproduction: Viviparous. Litter size varies between 2–3 (mean 2.5, $N = 6$).

Conservation status: The species appears locally abundant at the type locality although the population trend is unknown. Based on the population described herein from Mt Strong, the extent of occurrence for *Lo. fortis* is 0.3 km^2, with an 8 km^2 area of occupancy (based on occupation of 4 km^2 cells; both calculated using http://geocat.kew.org/). If the species has a wider range in the north-western Owen Stanley Mts as described above, its extent of occurrence would be 1458 km^2 and area of occupancy would be 36 km^2. The putative northern populations occur in a protected area, the Mt Kaindi Wildlife Management Area, approximately 2 km from the McAdams National Park. Since it is locally abundant, with no immediate direct threats to the species or indirect threats to its habitat or location, and because it likely occurs over a wide range encompassing at least one protected area, we recommend assigning a status of Least Concern to *Lo. fortis*, although its true distribution needs to be confirmed through further surveys in the north-western Owen Stanley Mts.

LOBULIA HUONENSIS SP. NOV.

HUON MOSS SKINK

(FIGS 6, 11–12; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:692113B4-B03F-4D41-8620-7DE7852BDA1B

Holotype: BPBM 40322 (field tag AA 20573), adult male, collected by A. Allison at Dopeke, 5.9538°S, 146.5573°E (WGS 84), 2646 m a.s.l., Finisterre Range, Madang Province, Papua New Guinea, 3 October 2010.

Paratypes (N = 18): Papua New Guinea: Morobe Province: Saruwaged Range: Tobo, 6.367°S, 147.37°E (WGS 84), 1600 m a.s.l. (BPBM 2893; male); Madang Province: Finisterre Range: same locality as holotype (BPBM 40320, 40323; one male, one female); Wil, near Teptep, 5.9438°S, 146.5549°E (WGS 84), 2359 m a.s.l. (BPBM 40321, 40330–31; two males, one female); ridge N of Teptep, 5.9369°S, 146.5499°E (WGS 84), 2662 m a.s.l. (BPBM 40324, 40327, 40332; one male, one female, one juvenile); *c.* 1.6 km NW of Teptep, 5.9392°S, 146.5523°E (WGS 84), 2556 m a.s.l. (BPBM 40325; male); *c.* 11 km WNW of Teptep, 5.9365°S, 146.5487°E (WGS 84), 2686 m a.s.l. (BPBM 40326; male); *c.* 2 km NNW of Teptep, 5.9339°S, 146.5567°E (WGS 84), 2564 m a.s.l. (BPBM 40328–29; one male, one female); Siwasiwa, 5.9377°S, 146.5592°E (WGS 84), 2440 m a.s.l. (BPBM 40333; juvenile); Siwasiwa Camp, near Teptep, 5.9464°S, 146.5601°E (WGS 84), 2478 m a.s.l. (BPBM 40334, 40337; two males); vicinity of Teptep Station, 5.9552°S, 146.5595°E (WGS 84), 2173 m a.s.l. (BPBM 40335; female); "ca. 2 km NW of Teptep", 5.9334°S, 146.5336°E (WGS 84), 2687 m a.s.l. (BPBM 40336; male).

Diagnosis: A medium-sized species of *Lobulia* (adult SVL 45.2–63.9 mm), characterized by the unique combination of frontoparietals unfused; supraorbital ridges not pronounced; nuchals 1–3 pairs; paravertebral scales 59–68; mid-body scale rows 33–38; 4th digit on front foot longer than 3rd; subdigital lamellae 19–25 under 4th toe; single supradigital scales 3–4 on 4th toe; mid-dorsum with two rows of large dark brown spots on an olive green background; top of tail base with two rows of large dark brown spots; fragmented white dorsolateral stripes present, extending from parietals to base of tail; flanks dark brown with light spots; unbroken white lateral stripes present, extending from occiput to hindlimbs; ventral coloration light blue on chin, light blue to lemon yellow on abdomen and base of tail in life, uniform light blue in preservative; thighs and precloacal region lack brown spotting; ventral surfaces of tail speckled with light brown spots forming fragmented parallel longitudinal lines; palmar and plantar surfaces pale to lemon yellow in life, light brown in preservative.

Comparisons: Lobulia huonensis differs from *Lo. brongersmai* in having unfused (vs. fused) frontoparietals. It differs from *Lo. elegans* and *Lo. fortis* in having white dorsolateral stripes and lateral stripes (vs. absent). *Lobulia huonensis* is most similar in scalation and general habitus to *Lo. lobulus*. It differs from it in dorsal coloration—whereas *Lo. lobulus* has dorsal rows of dark brown spots joined to form two mid-dorsal stripes, *Lo. huonensis* has large mid-dorsal dark brown spots arrayed in parallel longitudinal rows (not creating stripes), giving it an overall "lighter" appearance—and in having a higher average count of paravertebral scales [62.7 (59–68) vs. 57.7 (54–61)].

Description of the holotype: 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; frontonasal large, with eight sides, extending laterally to slightly above the level

of nares, in broad contact with frontal; prefrontals large, separated by frontonasal and frontal contact, bordered lateroventrally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal roughly kite shaped, widest anteriorly; frontoparietals single pair in medial contact, in narrow contact with frontal; interparietal of roughly similar area to single frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and two pretemporals; nuchals single pair, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale. Anterior loreal smaller than posterior loreal, higher than long; posterior loreal longer than high; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single; postsuboculars four, lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than size of ear opening; supraciliaries eight, anteriormost not in contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporals two, lower 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 lobules along anterior margin. Mental single; postmental single, contacting two anteriormost infralabials; infralabials eight; enlarged chin shields four pairs, the first two pairs in medial contact, third pair narrowly separated by single medial scale, fourth pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial. Body scales smooth, in 36 rows at midbody; paravertebral scales 67; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third interphalangeal joint, three single scales; subdigital lamellae under 4th toe 23, smooth. In preservative (Fig. 11), base dorsal coloration coppery brown, with two mid-dorsal parallel rows of large dark brown spots two to four scales long, extending to base of tail; spots become smaller posteriorly on tail; dorsolateral stripes present as light blue fragmented stripes extending from occiput to base of tail; lateral field dark brown, speckled with light blue spots one to two single scales wide; unfragmented light blue lateral stripe present, extending from postsupralabials, across ear opening, to hind limbs; head similar in coloration to dorsum, with dark brown spotting, mostly in centre of scales and along scale margins; ventral surfaces uniform light blue; light brown dusting present on ventral surface of tail, roughly forming parallel longitudinal rows along tail margins; scales on palmar and plantar surfaces light brown, contrasting with dark brown digits. In life (Figs 6, 12), dorsal colour coppery brown with black mid-dorsal spots; fragmented dorsolateral stripes, uniform lateral stripes and spots on lateral field white; chin light blue; ventral surfaces of chest, abdomen, thighs, precloacal region and tail lemon yellow, with tail becoming light blue posteriorly; scales on palmar and plantar surfaces lemon yellow.

Variation: Adult body size 45.2–63.9 mm SVL (mean = 54.0, SD = 4.7, N = 17). Females (mean = 51.8, range: 45.2–63.9, SD = 7.2, N = 5) have larger maximal size than males (mean = 56.5, range: 51.5–60.2, SD = 3.2, N = 12). Forelimbs 37.7–43.6% of SVL (mean = 42.1%, SD = 1.7, N = 17). Hindlimbs 46.1–51.9% of SVL (mean = 49.8%, SD = 1.6, N = 17). Scale rows at midbody 33–38 (mean = 36.2, SD = 1.3, N = 19); paravertebral scales 59–68 (mean = 62.7, SD = 2.6, N = 18). Lamellae under 4th toe 19–25 (mean = 21.3, SD = 1.3, N = 19); single supradigital scales on 4th toe 3–4 (mean = 3.1, SD = 0.3, N = 19). Mostly 1–3 pairs of nuchals, but BPBM 40323, 40325, 4027, 40328, 40333 and 40325 have an asymmetrical number of nuchals, with either one more nuchal on right side (BPBM 40327) or on left side (all others). Primary nuchals usually separated from secondary temporals by a single smaller intercalated scale (N = 16), rarely by two on left side and one on right (N = 2) or none on left side and one on right (N = 1). Prefrontals usually separated by frontonasal and frontal contact (N = 16), rarely by a single azygous scale (N = 3). Supraciliaries rarely seven (N = 1), typically eight (N = 9), occasionally nine (N = 7) or ten (N = 2). Anteriormost supraciliary usually not in contact with frontal (N = 14), sometimes in narrow contact (N = 5). Postsuboculars usually three (N = 16), rarely four (N = 2) or two (N = 1). Supralabials almost always seven (N = 18), rarely nine (N = 1). Primary temporals either single (N = 13) or two (N = 6). Infralabials rarely six (N = 1), typically seven (N = 13), occasionally eight (N = 3) and rarely nine (N = 1). Infralabials posterior to contact with chin shields usually one (N = 18), rarely two (N = 1).

Colour pattern of all examined specimens generally similar to holotype, with few exceptions. Size of mid-dorsal dark brown spots varies between individuals. BPBM 40320, 40326 and 40328 have unfragmented, as opposed to fragmented, dorsolateral stripes. BPBM 2893, 40325 and 40331 have fragmented, as opposed to unfragmented, lateral stripes. BPBM 40334 has dark brown palmar and plantar surfaces.

Colour in life: Dorsal surfaces coppery brown with two parallel mid-dorsal rows of large dark brown spots (Figs 6, 12). Dorsolateral stripes white to pale yellow. Sides dark brown to jet black with white or pale yellow spotting and white or pale yellow lateral stripe extending from occiput to hind limbs. Coloration of sides becomes gradually lighter ventrally from lateral stripes. Chin pale blue. Chest, abdomen, precloacal region, thighs and base of tail range from pale blue (BPBM 40335) through light lime green to bright lemon yellow. Yellow coloration more prominent in adult males.

Etymology: The Latin adjectival suffix *–ensis* denotes belonging to a place and is used in reference to the Huon Peninsula, Papua New Guinea, where the type series was collected.

Distribution: Known only from 1600–2690 m a.s.l. in the Finisterre Range, Madang Province and the Saruwaged Range, Morobe Province, both on the Huon Peninsula, Papua New Guinea. It is presumed endemic to the Huon Peninsula, where it is the only member of *Lobulia* present. *Lobulia huonensis* appears to be sympatric with one species of *Papuascincus* (lineage I), although *Lo. huonensis* is seemingly more common at higher elevations (most specimens collected > 2200 m a.s.l.), whereas *Papuascincus* sp. is more common at lower elevations (most specimens collected < 2200 m a.s.l.).

Natural history: All animals were collected while basking on old tree stumps and logs within 2 m of the ground along walking tracks through highly degraded lower montane and montane forest or anthropogenic grassland, mostly between Teptep Station (2200 m) and Kawang Bagu Pass at around 3000 m on a track leading to Bumbu. Most of the forest along the track, particularly at lower elevations, had been replaced by tall anthropogenic grassland dominated by *Saccharum* × *edule* Hassk. (pitpit), *Saccharum robustum* E.W.Brandes & Jeswiet ex Grassl and *Miscanthus floridulus* (Labill.) Warb. ex K.Schum. & Lauterb. There were also large expanses of shorter grasses such as *Themeda triandra* Fossk., *Ischaemum polystachyum* J.Presl and *Imperata* sp. Remnant trees included *Pandanus* sp., *Caldcluvia* sp. and *Saurauia* spp. There was fairly intact mossy forest at higher elevations (> 2500 m) dominated by *Nothofagus* sp., with a ground flora fairly typical of montane New Guinea that included as aspect dominants a variety of species of shrubs in the genera *Rhododendron*, *Coprosma* and *Tasmannia*, and an impressively robust ground moss, *Dawsonia* sp.

In much of New Guinea, timberline occurs at around 2800–3000 m. In the Finisterre Mountains, mossy forest extends to around 3200 m or higher. This was in line with our overall impression that the vegetation zones around Teptep were shifted upwards by 200–300 m compared to the rest of New Guinea. This may, at least in part, explain the occurrence of *Lo. huonensis* to nearly 2700 m; *Lo. fortis* and *Lo. elegans*, which are ecologically similar and occur in the central ranges, do not generally occur above 2400 m.

Like the two aforementioned species, *Lo. huonensis* is heliothermic and is exclusively found on tree stumps and logs. However, it is often found close to the ground, unlike *Lo. fortis* and *Lo. elegans*, which generally occur from 2–3 m above the ground. But like these species, *Lo. huonensis* is mainly active in the morning, when the first sun reaches its habitat. It is common.

Lobulia huonensis is sympatric with at least two other species of skinks: a ground-dwelling species of *Papuascincus* and the arboreal *Pr. flavipes*. A terrestrial colubrid snake, *Tropidonophis* sp., occurs to 2500 m. There are only two sympatric species of nocturnal, scansorial frogs above 2200 m: *Choerophryne* sp. and *Cophixalus* sp. Zweifel (1980) has commented on the relatively low diversity of montane frogs on the Huon Peninsula, attributing this to the geological youth of the Saruwaged and Finisterre mountain ranges.

Reproduction: Viviparous. Only a single gravid female was collected, with two embryos, but litter size is presumably variable in this species, as in other members of the genus.

Conservation status: The species appears locally abundant at the type locality although the population trend is unknown. Based on the sampled populations, *Lo. huonensis* has an extent of occurrence of 100 km^2 and an area of occupancy of 16 km^2 (based on occupation of 4 km^2 cells; both calculated using http://geocat.kew.org/). However, its distribution almost certainly encompasses more populations throughout the Huon Peninsula at suitable elevations, and the true area of occupancy and extent of occurrence are likely much larger than estimated here. The type locality is approximately 3 km from a protected area, the YUS Conservation Area. Since it is locally abundant, with no immediate direct threats to the species or indirect threats to its habitat or location, and because it likely occurs over a wide distribution range encompassing at least one protected area, we recommend assigning a status of Least Concern to *Lo. huonensis*, although its true distribution extent needs to be confirmed through further surveys in the Huon Peninsula.

LOBULIA MARMORATA SP. NOV.

MARBLED MOSS SKINK

(FIGS 6, 13–14; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:1E3599CA-0E98-43C5-9BD8-7F977A3E6C65

Holotype: BPBM 34150 (field tag FK 12731), adult male, collected by F. Kraus at 5.639°S, 142.625°E (WGS 84), 1900 m a.s.l., Muller Range, Hela Province, Papua New Guinea, 23 March 2009.

Paratypes (N = 32): Papua New Guinea: Hela Province: Muller Range: same locality as holotype (BPBM 34151–55, 34157; two males, two females, two juveniles); 5.652°S, 142.634°E (WGS 84), 1800 m a.s.l. (BPBM 34156, 34162–23; two males, one female); "Mt Yakapi", 5.666°S, 142.643°E (WGS 84), 1966 m a.s.l. (BPBM 34158–60; two males, one female); "Point 17 = Dickson's Village", 5.64°S, 142.628°E (WGS 84), 1859 m a.s.l. (BPBM 34164–5, 34169–70, PNGNM 25284; two males, one female, two juveniles); "Kunida", 5.6431°S, 142.634°E (WGS 84), 1910 m a.s.l. (BPBM 34166–8; one male, two females); "Dickson's House", 5.6454°S, 142.639°E (WGS 84), 1777 m a.s.l. (BPBM 34171–73, 34177, PNGNM 25281–83; four males, three females); 5.652°S, 142.643°E (WGS 84), 1860 m a.s.l. (BPBM 34174–76; one male, two females); 5.639°S, 142.625°E (WGS 84), 1900 m a.s.l. (BPBM 34178; male); "Top House", 5.6591°S, 142.635°E (WGS 84), 1910 m a.s.l. (PNGNM 25285; male).

Diagnosis: A medium-sized species of *Lobulia* (adult SVL 41.9–56.9 mm), characterized by the unique combination of frontoparietals fused; supraorbital ridges typically pronounced; nuchals 2–4 pairs; paravertebral scales 46–56; mid-body scale rows 30–34; 4th digit on front foot longer than 3rd; subdigital lamellae 20–25 under 4th toe; single supradigital scales 3–4 on 4th toe; mid-dorsum with two rows of large dark brown spots converging to a single row roughly around midbody; top of tail with two rows of dark brown spots joining ventrally with dark lateral stripes along the tail length; light blue or white dorsolateral stripes absent; flanks dark brown spotted with grey; light blue or white lateral stripes absent; uniform coloration on abdomen and base of tail, lemon yellow in life, light blue in preservative; thighs and precloacal region without brown spotting; tail and chin uniform light blue speckled with brown spots; palmar and plantar surfaces dark yellow in life, light brown in preservative.

Comparisons: *Lobulia marmorata* differs from *Lo. elegans*, *Lo. lobulus* and *Lo. huonensis* in having fused vs. unfused frontoparietals. *Lobulia marmorata* is most similar in scalation and coloration to *Lo. brongersmai*, but differs from it in having a higher average count of midbody scale rows [31.5 (30–34) vs. 29 (27–32)], a dark blotch on the nuchal region, posterior to the parietals, and a generally darker coloration due to larger size of the dark brown dorsal spots relative to the base grey coloration.

Description of the holotype: 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; frontonasal large, with eight sides, extending laterally to slightly above the level of nares, in broad contact with frontal; prefrontals large, separated by frontonasal and frontal contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietal; frontal kite shaped, widest anteriorly; frontoparietal single, anteriorly in 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 two pairs, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale, with a third nuchal on the right side. Anterior loreal slightly smaller than posterior loreal, roughly as long as high; posterior loreal longer than high; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single; postsuboculars three, lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc roughly the size of ear opening; supraciliaries nine, anteriormost in narrow contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporal single, ventrally contacting posteriormost supralabial; 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 lobules along anterior margin. Mental single; postmental single, contacting two anteriormost infralabials; infralabials seven; enlarged chin shields four pairs, the first two pairs in medial contact, third pair narrowly separated by a single medial scale, fourth pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial. Body scales smooth, in 31 rows at midbody; paravertebral scales 50; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third

interphalangeal joint, three single scales; subdigital lamellae under 4th toe 20, smooth. In preservative (Fig. 13), base dorsal coloration grey-brown, with two mid-dorsal parallel rows of large dark brown spots two to four scales long, converging posterior to forelimbs to form a single continuous mid-dorsal dark stripe with transverse lateral projections, extending to base of tail; on dorsal surface of tail, two parallel rows of dark brown blotches extending medially from dark brown lateral stripes; light blue or white dorsolateral stripes absent, but parallel dorsolateral rows of dark brown blotches present, extending laterally to lateral fields; lateral field dark brown, speckled with grey spots; light blue or white lateral stripe absent; head similar in coloration to dorsum; dark brown spotting on head scales, mostly along scale margins, with large dark spot in centre of frontal; large dark blotch in nuchal region formed by dark coloration on the posterior margins of parietals and medial margins of nuchals; ventral surfaces uniform light blue; brown dusting present on chin; scales on palmar and plantar surfaces light brown, contrasting with dark brown digits. In life (Figs 6, 14), dorsum greyish with black mid-dorsal spots; lateral field brown with white spotting; chin white; chest, abdomen, thighs, precloacal region and base of tail lemon yellow, with tail becoming white posteriorly; scales on palmar and plantar surfaces dark yellow.

Variation: Adult body size 41.9–56.9 mm SVL (mean = 48.1, SD = 3.8, N = 29). Females (mean = 50.5, range: 42–56.9, SD = 4.0, N = 12) larger than males (mean = 46.4, range: 41.9–50.5, SD = 2.6, N = 17; t = 3.4, P < 0.01). Forelimbs 36.8–47.0% of SVL (mean = 42.4%, SD = 2.5, N = 29). Hindlimbs 44.1–53.4% of SVL (mean = 47.5%, SD = 2.8, N = 29). Scale rows at midbody 30–34 (mean = 31.5, SD = 0.9, N = 33); paravertebral scales 46–56 (mean = 51.2, SD = 2.2, N = 33). Lamellae under 4th toe 20–25 (mean = 22.5, SD = 1.2, N = 32); single supradigital scales on 4th toe 3–4 (mean = 3.2, SD = 0.4, N = 32). Mostly 2–4 pairs of nuchals, but BPBM 34150–51, 34155–56, 34166, 34169–71, 34173, 34178 and PNGNM 25281 have an asymmetrical number of nuchals, with one more nuchal either on left side (N = 6) or on right side (N = 5). Primary nuchals usually separated from secondary temporals by single smaller intercalated scale (N = 27), rarely by none on left side and one on right (N = 1), one on left side and two on right (N = 1), two on left side and one on right (N = 3) or two on both sides (N = 1). Supraorbital ridges usually pronounced (N = 25), but occasionally not (N = 8). Frontonasal usually as wide as long (N = 25), occasionally longer than wide (N = 8). Frontonasal fragmented in PNGNM 25285. Interparietal fused with frontoparietal in BPBM 34151 and 34153. Loreals typically two (N = 29), rarely three (N = 4). Supraciliaries either eight (N = 15) or nine (N = 18). Anteriormost supraciliary usually not in contact with frontal (N = 22), sometimes in narrow contact (N = 11). Postsuboculars rarely two (N = 2), typically three (N = 24), occasionally four (N = 7). Supralabials rarely six (N = 1), typically seven (N = 20), occasionally eight (N = 12). Infralabials typically seven (N = 25), occasionally eight (N = 8). Mental split medially in BPBM 34160. Chin shields typically four on both sides (N = 31), rarely five on right side (N = 2). Infralabials posterior to contact with chin shields occasionally zero (N = 7), usually one (N = 24), rarely two (N = 2).

Colour pattern of all specimens generally similar to holotype, with a few exceptions. Size of mid-dorsal dark brown spots, and location at which two anterior rows converge to form single posterior row vary between individuals. In some individuals, dark blotches form a continuous thick stripe posterior to convergence; in others form a row of dark blotches. BPBM 34174 has continuous, unfrgamented lateral stripes. Degree of brown speckling on chin varies from almost no brown spots (BPBM 34156) to chin shields being almost uniformly brown (BPBM 34152).

Colour in life: Notes for the holotype (BPBM 34150) stated "Dorsum tan with irregular black zigzags vertebrally and dorsolaterally, tan scales margined in black. Face black. Chest, belly, and under rear legs deep orange-yellow; chin and throat white with black spots. Mouth lining and tongue blue-black." Paratypes BPBM 34152 and BPBM 34155 had the venter entirely white.

Etymology: Feminine Latin adjective meaning "marbled", in reference to the marbled grey and dark brown dorsal coloration of the species.

Distribution: Known only from 1777–1966 m a.s.l. on the north-eastern slopes of the Muller Range, Hela Province, where it occurs in sympatry with another, currently undescribed, species of *Lobulia* (BPBM 34161) having unfused frontoparietals.

Natural history: This species was locally common in the village areas and surrounding cleared areas; it was never observed in forested situations.

Reproduction: Viviparous. Litter size varies between 2–3 (mean 2.4, N = 9).

Conservation status: The species is locally abundant in the areas where collected although the population trend is unknown. Based on the available samples, *Lo. marmorata* has an extent of occurrence of 2.5 km^2 and an area of occupancy of 16 km^2 (based on occupation of 4 km^2 cells; both calculated using http://geocat.kew.org/).

However, it is likely distributed in other localities of suitable habitat in the Muller Range. It does not occur near any protected areas. Further research is needed to discern its true distributional boundaries, potential threats and demographic trends for a proper assessment. We recommend assigning a status of Data Deficient to *Lo. marmorata*.

LOBULIA VOGELKOPENSIS SP. NOV.

VOGELKOP MOSS SKINK

(FIG. 15; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:DEBCBB9C-06A3-4E33-B425-C4885ABA72BA

Holotype: BPBM 6917 (field tag MCT 3820), adult male, collected by M.C. Thompson at Kampong Sururae, Lake Anggi Giji, 1.36°S, 133.856°E (WGS 84), ("6200 ft"=)1890 m a.s.l., Arfak Mts, West Papua Province, Indonesia, 8 March 1963.

Paratypes (N = 2): Indonesia: West Papua Province: Arfak Mts: same locality as holotype (BPBM 6919–20; one male, one female).

Diagnosis: A medium-sized species of *Lobulia* (adult SVL 56.0–58.3 mm), characterized by the unique combination of frontoparietals unfused; supraorbital ridges not pronounced; posteriormost supralabial fragmented by horizontal suture; nuchals single pair; paravertebral scales 69–77; mid-body scale rows 34–36; 4th digit on front foot no longer than 3rd; subdigital lamellae 19–23 under 4th toe; single supradigital scales 3–4 on 4th toe; mid-dorsum irregularly spotted with small to medium-sized dark brown spots continuing onto tail; light brown dorsolateral stripes present, either fragmented or continuous, framed medially by dark brown spots; flanks dark brown flecked with small white spots; unfragmented light brown lateral stripes present; in preservative, uniform light brown coloration on abdomen, thighs, precloacal region, tail and chin that lacks brown spotting; palmar and plantar surfaces light brown.

Comparisons: *Lobulia vogelkopensis* differs from *Lo. brongersmai* and *Lo. marmorata* in having unfused (vs. fused) frontoparietals. It differs from all other species of *Lobulia* in having a higher count of paravertebral scales (69–77 vs. 46–68 in all others) and irregularly placed small dark brown spots on the dorsum (vs. one or two mid-dorsal rows of large dark brown spots). *Lobulia vogelkopensis* further differs from *Lo. elegans* and *Lo. fortis* in having light brown lateral stripes (vs. absent).

Description of the holotype: 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; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, separated from frontal by prefrontal contact; prefrontals large, in narrow medial contact, bordered ventrolaterally by two loreals; supraoculars four, anterior three in contact with frontal, posterior two in contact with frontoparietals; frontal kite shaped, widest anteriorly; frontoparietals single pair in medial contact, in narrow contact with frontal; interparietal of roughly similar area to single frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and two pretemporals; nuchals single pair, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale. Anterior loreal smaller than posterior loreal, higher than long; posterior loreal longer than high; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presuboculars two; postsuboculars three, lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc considerably smaller than size of ear opening; supraciliaries nine, anteriormost not in contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporals two, lower interdigitated between sixth and seventh supralabials; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid, posteriormost fragmented by horizontal suture; postsupralabials two; ear opening moderately large and oval shaped, with lobules along anterior margin. Mental single; postmental single, contacting two anteriormost infralabials; infralabials eight; enlarged chin shields four pairs, the first two pairs in medial contact, third pair narrowly separated by single medial scale, fourth pair separated by three medial scales; posteriormost chin shield in contact with antepenultimate infralabial. Body scales smooth, in 34 rows at midbody; paravertebral scales 77; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two paired rows proximally, single row distally beginning at third interphalangeal joint, three single scales; subdigital lamellae under 4th toe 23, smooth. In preservative (Fig. 15), base dorsal coloration coppery brown, with many irregularly placed dark brown spots no more than a single scale long or wide, continuing along dorsum and tail; light brown unfragmented dorsolateral stripes present, framed medially by row of dark brown spots one to two scales long; lateral field

dark brown, speckled with light brown spots a single scale wide; light brown unfragmented lateral stripe present, extending from ear opening to hindlimbs; head similar in coloration to dorsum; dark brown spotting present on head scales; ventral, palmar and plantar surfaces uniform light brown.

Variation: Adult body size 56.0–58.3 mm SVL (mean = 57.4, SD = 1.2, N = 3). Single female (58.3 mm) larger than both males (56.0–57.8 mm). Forelimbs 35.7–41.3% of SVL (mean = 37.7%, SD = 3.2, N = 3). Hindlimbs 41.6–47.8% of SVL (mean = 45.0%, SD = 3.1, N = 3). Scale rows at midbody 34–35 (mean = 35, SD = 1, N = 3); paravertebral scales 69–77 (mean = 72.7, SD = 4, N = 3). Lamellae under 4th toe 19–23 (mean = 21, SD = 2, N = 3); single supradigital scales on 4th toe 3–4 (mean = 3.3, SD = 0.6, N = 3). BPBM 6920 has nuchals as wide as long; primary nuchals separated from secondary temporals by two smaller intercalated scale on left side and one on right. Supraciliaries eight with anteriormost in narrow contact with frontal in BPBM 6920, nine with anteriormost not in contact with frontal in BPBM 6917 and 6919. Presubocular single in BPBM 6920, two in BPBM 6917 and 6919. Primary temporal single in BPBM 6919 and 6920, two in BPBM 6917. Supralabials seven in BPBM 6917 and 6920, eight in BPBM 6919. Infralabials seven in BPBM 6920, eight in BPBM 6917 and 6919. Infralabials posterior to contact with chin shields, one in BPBM 6920, two in BPBM 6917 and 6919. Colour pattern generally similar to holotype, but size of dark brown spots varies between individuals, and BPBM 6920 has fragmented dorsolateral stripes.

Etymology: Suffixed form of Vogelkop with the Latin *–ensis*, denoting place, in reference to the Vogelkop, Dutch for 'Bird's Head Peninsula', West Papua, in reference to where the type series was collected.

Distribution: Known only from the type locality in the Arfak Mountains of West Papua Province, Indonesia.

Remarks: Genetic data for *Lo. vogelkopensis* are not available. Furthermore, it is only known from the Arfak Mts, almost 1000 km west of the other currently described species of *Lobulia*, although this gap in distribution likely represents a lack of sampling in Indonesian New Guinea rather than an actual absence. Therefore, the exact phylogenetic relationship of this species to other species of *Lobulia* is uncertain. However, based on its scalation (unfused frontoparietals) and general coloration, *Lo. vogelkopensis* is likely more closely related to *Lo. elegans* and its related species rather than to *Lo. brongersmai* and *Lo. marmorata*, and the presence of light coloured lateral stripes suggests an affinity to *Lo. huonensis* and *Lo. lobulus*.

Reproduction: Viviparous. Only a single gravid female was collected, with a litter size of two, but litter size is presumably variable in this species, as in other members of the genus.

Conservation status: Population size and trend unknown. The three specimens are only known from a single location, with an area of occupancy of a single 4 km^2 cell. The type locality is roughly 13 km from a protected area, the Pegunungan Arfak Nature Reserve. No records of the species exist later than the 1960s, and Indonesian New Guinea is poorly sampled. Therefore, an assessment of this species will require more information than is currently available, and we recommend assigning a status of Data Deficient to *Lo. vogelkopensis*.

ORNITHUROSCINCUS BENGAUN SP. NOV.

DAGA SMOOTH-EARED SKINK

(FIGS 16–17; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:4DC0258B-AECD-4FFB-899B-C8436002B5A7

Holotype: BPBM 37741 (field tag FK 15374), adult male, collected by F. Kraus at Sota, 9.7580°S, 149.1822°E (WGS 84), 1860 m a.s.l., saddle between Mt Dayman and Mt Suckling, Milne Bay Province, Papua New Guinea, 20 March 2011.

Diagnosis: A moderate-sized species of *Ornithuroscincus* (adult SVL 48.2 mm), characterized by the unique combination of long limbs (forelimbs 36.3% of SVL, hindlimbs 47.3% of SVL); frontoparietals fused; nuchals single pair; paravertebral scales 55; mid-body scale rows 30; 4th digit on front foot no longer than 3rd; subdigital lamellae 20 under 4th toe; single supradigital scales six on 4th toe; dorsal coloration uniform bronze; slightly zigzag unfragmented dorsolateral stripes present, one to one and a half scales wide, extending from orbital region to tail, pale brown in preservative, pale yellow in life; dark brown lateral field present, speckled with light blue spots a single scale wide; ventral surfaces uniform light blue in preservative, darker on the chin; brown spotting absent from chin, abdomen, thighs and precloacal region; light brown spotting present on ventral surfaces of tail; palmar and plantar surfaces light brown.

Comparisons: Ornithuroscincus bengaun differs from all other species of *Ornithuroscincus* by its distinct colour pattern consisting of uniform bronze mid-dorsum with distinct, thick, pale brown dorsolateral stripes. It further differs from *O. albodorsalis*, *O. nototaenia*, *O. sabini* and *O.* cf. *venemai* in having fused (vs. unfused) frontoparietals and by lacking a parietal eye spot (vs. present). It further differs from *O.* cf. *venemai* by having a higher count of

midbody scale rows (30 vs. 24–26; Brongersma, 1953a). It further differs from *O. albodorsalis*, *O. noctua* and *O. nototaenia* by having a higher count of midbody scale rows (30 vs. 22–26, 23–28 and 24–25, respectively; Zweifel, 1979; Shea & Greer, 2002).

Description of the holotype: 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; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, in shallow contact with frontal; prefrontals large, separated by frontonasal and frontal contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal kite shaped, widest anteriorly, suture with frontoparietal shallowly convex; frontoparietals fused, in contact with frontal; 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 pretemporals; nuchals single pair, transversely enlarged, wider than long, separated from secondary temporal by a single intercalated scale of similar size to nuchal. Anterior loreal smaller than posterior loreal, higher than long; posterior loreal roughly as high as long; lower preocular rectangular; upper preocular much smaller, longer than high; presuboculars two; postsuboculars two, lower interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with an opaque palpebral disc of roughly similar size as ear opening; supraciliaries eight, anteriormost in shallow contact with frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporal single, interdigitated between penultimate and posteriormost supralabial; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening moderate sized and oval shaped, without lobules. Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields three pairs, the 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 30 rows at midbody; paravertebral scales 55; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning before third interphalangeal joint, six single scales; subdigital lamellae under 4th toe 20, smooth. In preservative (Fig. 17), dorsum uniform bronze; dorsolateral stripes present as thick (1.0–1.5 scales wide), unfragmented, slightly zigzag pale brown stripes extending from orbital region to tail, framed laterally by thin, dark brown stripes; dark brown lateral field present, extending from dorsolateral stripe ventrally to just above the limbs, and speckled with pale blue spots a single scale wide; head scales similar in coloration to dorsal scales, apart from paler-coloured supraciliaries, which make up anterior edges of dorsolateral stripe; ventral surfaces uniformly pale blue in preservative, darker on the chin, and lacking brown spotting on the chin, abdomen, thighs and precloacal region; light brown spotting present on ventral surfaces of tail; palmar and plantar surfaces light brown.

Colour in life: Dorsal surfaces uniform olive green (Fig. 16). Dorsolateral stripes paler bronze. Lateral field medium brown, darker along dorsal margin, flecked with pale bronze (dorsally) or white (ventrally) spots a single scale wide. Field notes in life stated: "Olive green above with metallic yellow-brown dorsolateral stripe; sides brown with pale yellow-brown spots. Face brown; temporal region brown with metallic green sheen. Chin white with pale green sheen, chest and abdomen metallic green yellow, under tail orange".

Etymology: The name is from the Daga word *bengaun*, a small, dark lizard. Daga is the language spoken in the area from which this species was collected.

Distribution: Known from a single specimen collected at 1860 m a.s.l. on the northern slopes of the Owen Stanley Mts, near the saddle between Mt Dayman and Mt Suckling.

Natural history: The single specimen was collected in primary rainforest, but no information on microhabitat is available.

Conservation status: Only known from a single specimen, and more information is required for a proper assessment. It does not occur near any protected areas, but it occurs in a large, unbroken band of untouched mid-elevation forest that has no serious human habitat disturbance. We recommend assigning a status of Data Deficient to *O. bengaun*.

ORNITHUROSCINCUS INORNATUS SP. NOV.

PLAIN SMOOTH-EARED SKINK

(FIGS 18–19; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:89DE7131-76CC-43C0-95CA-C41541C3563E

Holotype: BPBM 41226 (field tag AA 21402), collected by A. Allison at Kesemani, 7.9372°S, 147.0544°E

(WGS 84), 1733 m a.s.l., N slope of Mt Strong, Morobe Province, Papua New Guinea, 23 February 2012.

Diagnosis: A moderate-sized species of *Ornithuroscincus* (adult SVL 47.9 mm), characterized by the unique combination of short limbs (forelimbs 32.7% of SVL, hindlimbs 41.2% of SVL); frontoparietals separate; nuchals two pairs; paravertebral scales 51; mid-body scale rows 35; 4th digit on front foot no longer than 3rd; subdigital lamellae 21 under 4th toe; single supradigital scales three on 4th toe; dorsal coloration uniform light brown; dorsolateral stripes present as thick, one to two scales wide, unfragmented stripes extending from orbital region to tail, becoming gradually thicker posteriorly, pale brown in preservative, pale green-yellow in life; dark brown lateral field present, lightly speckled with spots, pale blue in preservative, light brown in life; lateral field breaking up to brown spots ventrally; ventral surfaces uniform pale blue in preservative, with dark brown spotting on the thighs, precloacal region and tail; in life, ventral surfaces are green-yellow, becoming lemon yellow on the thighs and base of tail; palmar and plantar surfaces light brown in preservative, dark yellow in life.

Comparisons: Ornithuroscincus inornatus differs from *O. bengaun* in having unfused (vs. fused) frontoparietals. It differs from *O. albodorsalis*, *O. noctua*, *O. nototaenia* and *O.* cf. *venemai* by having a uniform light brown dorsum with thick pale brown dorsolateral stripes (vs. uniform pale yellow dorsum, light brown dorsum with dark brown longitudinal stripes, pale yellow dorsum with single dark vertebral stripe or dark olive grey dorsum powdered with brown with thick white dorsolateral stripes, respectively), by lacking a parietal eye spot (vs. present) and by having a higher count of midbody scale rows (35 vs. 22–26, 23–28, 24–25 and 24–26, respectively; Brongersma, 1953a; Zweifel, 1979; Shea & Greer, 2002). It further differs from *O. noctua* by lacking a light yellow to white patch on the occiput. It differs from *O. sabini* in having uniform dorsal coloration (vs. spotted).

Description of the holotype: 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 anteriorly towards snout; nostril circular, centred within nasal; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, in narrow contact with frontal; prefrontals large, separated medially by frontonasal and frontal contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal kite shaped, widest anteriorly; frontoparietals single pair in medial contact, anteriorly in contact with frontal; interparietal smaller than single frontoparietal, diamond shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and pretemporals; nuchals two pairs, transversely enlarged, followed by a third enlarged nuchal on the left side, wider than long, anteriormost pair separated from secondary temporal by a single smaller intercalated scale. Anterior loreal higher than posterior loreal, higher than long; posterior loreal roughly as high as long; lower preocular rectangular shaped; upper preocular much smaller, longer than high; presubocular single; postsuboculars two, lower interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than 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 penultimate and posteriormost supralabial; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening large and oval shaped, without lobules. Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields three pairs, the first pair in medial contact, second pair narrowly separated by a single medial scale, third pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial. Body scales smooth, in 35 rows at midbody; paravertebral scales 51; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third interphalangeal joint, three single scales; subdigital lamellae under 4th toe 21, smooth. In preservative (Fig. 18), dorsum uniform light coppery brown, extending to tail; dorsolateral stripes present as broad (1–2 scales wide) unfragmented pale brown stripes extending from orbital region to tail, gradually becoming thicker posteriorly, bordered medially by extremely light speckling of small dark brown spots; dorsolateral stripes bordered laterally by dark brown field, extending from preorbital region through eye to base of tail, above level of limbs; dark brown lateral field lightly speckled by pale blue spots, becomes gradually lighter ventrally before breaking up into irregularly placed small dark brown spots on pale blue background; head scales light brown with small, infrequent dark brown spots on margins, paler on snout; ventral surfaces uniformly pale blue with dark brown spotting on thighs, precloacal region and tail; palmar and plantar surfaces light brown.

Colour in life: Dorsal surfaces light brown and lateral field dark brown, as in preservative (Fig. 19). Dorsolateral stripes green-yellow. Ventral surfaces green-yellow, becoming lemon yellow on thighs and base of tail. Palmar and plantar surfaces dark yellow.

Etymology: Combined masculine adjectival form of the Latin *in*, not, and *ornatus,* decorated, referring to its bland and simple colour pattern compared to other members of the genus.

Distribution: Known from a single specimen collected at 1733 m a.s.l. on the northern slopes of Mt Strong, where it occurs in sympatry with at least two lineages of *Papuascincus* (V and VI) and *Lo. fortis*.

Natural history: The single specimen that we collected was from around the village of Kesemani. The village, which is perched on a steep slope high above a river, included around ten bush material houses surrounded by anthropogenic grassland (see account for *Lo. fortis*). The lizard was active in the morning on a steep, *c*. 2 m high moss and lichen encrusted earthen bank along a walking track at the edge of the village.

Conservation status: Only known from a single specimen. However, Mt Strong was well sampled, the village of Kesemani specifically was visited several times and no other *O. inornatus* were observed. Therefore, it appears to be rare compared to sympatric lizard taxa such as *Lo. fortis* or *Papuascincus* spp. This may suggest a small population size and restricted distribution, but more data are required for a proper assessment. It does not occur near any protected areas. We recommend assigning a status of Data Deficient to *O. inornatus*.

ORNITHUROSCINCUS PTEROPHILUS SP. NOV.

MOUNT VICTORIA SMOOTH-EARED SKINK

(FIGS 16, 20–21; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:8D6F7129-1240-4F5A-B31E-0AD103CAA139

Holotype: BPBM 45705 (field tag AA 23742), adult female, collected by A. Allison at grasslands, 8.9592°S, 147.5745°E (WGS 84), 2813 m a.s.l., SE slopes of Mt Victoria, Northern (Oro) Province, Papua New Guinea, 15 August 2015.

Paratypes (N = 17): Papua New Guinea: Central Province: Crest of Owen Stanley Mts along the Kokoda Track: 1900 Crossing Campsite, 9.1288°S, 147.7264°E (WGS 84), 1936 m a.s.l. (BPBM 44634–37, 44843–44, 44855; one male, three females, three juveniles); Myola 2 Guest House, 9.1509°S, 147.7675°E (WGS 84), 2076 m a.s.l. (BPBM 44859; juvnile); Northern (Oro) Province: Chopper Pad Camp, 8.9738°S, 147.5697°E (WGS 84), 2680 m a.s.l. (BPBM 45669, 45710–11; one male, one female, one juvenile); grasslands, 8.9554°S, 147.5764°E (WGS 84), 2805 m a.s.l. (BPBM 45704; female); grasslands, 8.9594°S, 147.5740°E (WGS 84), 2820 m a.s.l. (BPBM 45706; juvenile); 8.9585°S, 147.5751°E (WGS 84), 2817 m a.s.l. (BPBM 45713; male); 8.9591°S, 147.5743°E (WGS 84), 2836 m a.s.l. (BPBM 45714; male); 8.9585°S, 147.5753°E (WGS 84), 2814 m a.s.l. (BPBM 45715; female); 8.95919°S, 147.5742°E (WGS 84), 2830 m a.s.l. (BPBM 45716; female).

Diagnosis: A medium-sized species of *Ornithuroscincus* (adult SVL 50.1–62.3 mm) characterized by the unique combination of short limbs (forelimbs 27.0–33.7% of SVL, hindlimbs 33.3–42.5% of SVL); frontoparietals unfused; nuchals 1–4 pairs; paravertebral scales 50–67; mid-body scale rows 28–42; 4th digit on front foot not longer than 3rd; subdigital lamellae 17–23 under 4th toe; single supradigital scales 3–8 on 4th toe; dorsum light brown with two to four more-or-less transverse longitudinal rows of dark brown to black spots of varying width, at their widest giving the impression of black base coloration with light brown striations, often joining to create two transverse rows of dark spots along tail; dark brown to black lateral stripe or field present; dorsolateral stripes present as thin (up to a single scale wide), unfragmented or zigzag light brown stripes extending from orbital region to tail; flanks marked with parallel fragmented light brown to white vertical bars extending ventrally from dorsolateral stripes; uniform coloration on abdomen, thighs and precloacal region, light to dark blue in preservative, lime green in life; brown spotting occasionally occurs on thighs and precloacal region; ventral surface of tail light to dark blue in preservative, lemon yellow in life, with occasional brown spotting; palmar and plantar surfaces light to dark brown in preservative, light or dark brown to lemon yellow in life.

Comparisons: Ornithuroscincus pterophilus differs from *O. bengaun* in having unfused (vs. fused) frontoparietals. It further differs from *O. albodorsalis*, *O. noctua*, *O. nototaenia* and *O.* cf. *venemai* in lacking a parietal eye spot (vs. present). It differs from *O. inornatus* and *O.* cf. *venemai* in having a light brown dorsum with dark spots and thin (up to a single scale wide) light brown dorsolateral stripes that are clearly distinguished from the base dorsal coloration [vs. uniformly light brown dorsum with thick (one to two scales wide) light brown dorsolateral stripes, extending in thickness towards the base of the tail, diffusely demarcated from the base dorsal coloration in *O. inornatus*; deep olive grey dorsum powdered with brown, with broad dorsolateral white

stripes becoming broader posteriorly in *O.* cf. *venemai* (Brongersma, 1953a)]. *Ornithuroscincus inornatus* also lacks the parallel light brown vertical bars that occur on the flanks of *O. pterophilus*. It further differs from *O. inornatus* in slightly larger size (adult SVL 50.1–62.3 mm vs. 47.9 mm) and from *O.* cf. *venemai* by having a higher count of midbody scale rows (28–42 vs. 24–26; Brongersma, 1953a).

Ornithuroscincus pterophilus is most similar in coloration to *O. sabini*, from which it differs in having less pronounced dorsolateral stripes, a flank pattern composed of parallel fragmented vertical bars (vs. scattered specks in *O. sabini*) and a blue (lime green in life) venter in preservative [vs. white venter in preservative (lemon yellow or white in life) in *O. sabini*].

Description of the holotype: 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; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, in narrow contact with frontal; prefrontals large, separated by frontal and frontonasal contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal wedge shaped, widest anteriorly; frontoparietals single pair in medial contact, in contact with posterior three supraoculars and anteriorly in contact with frontal; interparietal smaller than single frontoparietal, almost triangular shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and pretemporals; nuchals two pairs, transversely enlarged, at least twice as wide as long, anteriormost pair in contact with single secondary temporals. Anterior loreal similar in size to posterior loreal, both higher than long; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single and rectangular in shape; postsuboculars two, lower interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than 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 penultimate and posteriormost supralabial; 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 and oval shaped, without lobules. Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields three pairs, the first pair in medial contact, second pair narrowly separated by a single medial scale, third pair separated by three medial scales; posteriormost chin shield in contact with penultimate infralabial. Body scales smooth, in 42 rows at midbody; paravertebral scales 60; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third interphalangeal joint, three single scales; subdigital lamellae under 4th toe 20, smooth. In preservative (Fig. 20), dorsum light brown, with four transverse longitudinal rows of small dark brown spots no more than a single scale wide, lateralmost rows in contact with dorsolateral stripes and composed of larger spots, one to two scales long; dark brown spots gradually become smaller posteriorly until tail surface becomes uniformly light brown; dorsolateral stripes present in zigzag formation, no more than a single scale wide, extending continuously from orbital region to base of tail; dorsolateral stripes bordered laterally by dark brown fields extending to above limbs, these bordered ventrally by light grey field, itself bordered ventrally by blue venter; lateral fields marked with parallel vertical bars of pale blue spots one to two scales wide and long, extending from dorsolateral stripes ventrally; head similar to dorsum, with dark scale margins and some dark brown spotting, particularly in parietal region; slightly lighter on snout and supraciliaries; labials dark brown at margins and pale blue in centre; venter pale blue, with light brown dusting on proximal third of tail, thighs and precloacal region; palmar surfaces light brown, plantar surfaces white, digits dark brown. In life (Figs 16, 21), dorsal colour light brown, with pale yellow to white dorsolateral stripes; lateral field black dorsally, light brown ventrally, diffusing to ventral surfaces, with parallel heavily fragmented vertical bars extending ventrally from dorsolateral stripes, made up of pale yellow spots; chest and abdomen lime green; ventral surfaces of proximal third of tail, thighs and precloacal region lemon yellow; ventral surface of distal two-thirds of tail white; palmar and plantar surfaces lemon yellow to dark brown.

Variation: Adult body size 50.1–62.3 mm SVL (mean = 55.9, SD = 4.2, N = 12). Females (mean = 57.4, range = 51.6–62.3, SD = 3.8, N = 8) have larger average size than males (mean = 53.0, range = 50.1–57.7, SD = 3.6, N = 4). Forelimbs 27.0–33.7% of SVL (mean = 30.4%, SD = 2.2, N = 12). Hindlimbs 33.3–42.5% of SVL (mean = 38.0%, SD = 2.7, N = 12). Scale rows at midbody 28–42 (mean = 33.4, SD = 4.58, N = 18), with lower counts for specimens from the Kokoda Track (BPBM 44634–37, 44843–44, 44855 and 44859; range = 28–31) vs. Mt Victoria (BPBM 45669,

45704–06, 45710–11 and 45713–16; range = 30–42); paravertebral scales 50–67 (mean = 60.4, SD = 3.91, *N* = 18). Lamellae under 4th toe 17–23 (mean = 19.9, SD = 1.7, *N* = 18); single supradigital scales on 4th toe 4–8 (mean = 4.3, SD = 1.18, *N* = 18). Mostly 1–4 pairs of nuchals, but BPBM 44843 has two nuchals on left side and one on right and BPBM 44844 lacks nuchal on right side, with only single nuchal on left side. Nuchals typically wider than long but roughly as wide as long in BPBM 44635, 44844 and 45713. Primary nuchals usually separated from secondary temporals by single smaller intercalated scale (*N* = 13), rarely by two (*N* = 1) and occasionally by none (*N* = 4). Prefrontals either in narrow medial contact (*N* = 8) or separated by contact of frontal and frontonasal (*N* = 10). Nasal scale single in all but BPBM 44637, where nasal scale is divided by suture extending medioposteriorly from nostril. Presubocular almost always single (*N* = 16), but absent in BPBM 44843, and two in BPBM 44635. Supraciliaries either seven (*N* = 5) or eight (*N* = 13). Anteriormost supraciliary either in contact with frontal (*N* = 11) or not (*N* = 7). Postsuboculars usually two (*N* = 14), occasionally three (*N* = 4). Secondary temporals usually two (*N* = 13), but occasionally one (*N* = 4), and in BPBM 45713 three. Supralabials almost always seven (*N* = 16), rarely six (*N* = 2). Posteriormost supralabial fragmented by horizontal suture on left side in BPBM 44635. Infralabials usually six (*N* = 15), rarely seven (*N* = 2) or eight (*N* = 1).

Dark brown spots on dorsum vary from small and hardly distinguishable (BPBM 44855) to large enough to form the appearance of dark brown base coloration (BPBM 45669 and 45710). In general, populations from higher elevations on Mt Victoria (BPBM 45669–716) have darker dorsal coloration than populations from lower elevations along the Kokoda Track (BPBM 44634–859). Dorsolateral stripes distinct in all but BPBM 44843 and 44845, in which they are indistinguishable in preservative, but were extremely pale in life.

Colour in life: Dorsal surfaces light to dark coppery brown, with small to large dark brown to black spots in two to four more-or-less transverse rows, often extending into two transverse rows along tail (Figs 16, 21). Dorsolateral stripes pale yellow. Sides dark brown to jet black, diffusely giving way ventrally to lighter brown, marked with parallel vertical bars of pale white spots. Venter uniform lime green, often with lemon yellow on tail, precloacal region and thighs. Yellow occasionally absent (BPBM 44843) and lime-green ventral coloration can be pale (BPBM 44843 and 45710). Chin often paler than abdomen. Ventral surfaces of tail and precloacal region occasionally marked with dark brown spots. Juveniles appear to have bright orange tails. Palmar and plantar surfaces light or dark brown to lemon yellow.

Etymology: Masculine Latinized compound adjective derived from the Greek *pteris*, fern, and *philos*, lover of, reflecting that most specimens collected on Mt Victoria were found sheltered between fronds of tree ferns.

Distribution: Known only from 1936–2836 m a.s.l. in the south-eastern Owen Stanley Mountains, Papua New Guinea. Currently two populations are known: one from the south-eastern slopes of Mt Victoria (2680–2840 m a.s.l.) and one from the crest of the Owen Stanley Mountains along the Kokoda Track, at "1900 Crossing" (9.1288°S, 147.7264°E; WGS 84) and a single specimen from the nearby Myola dry lake beds. Presumably, *O. pterophilus* occurs more broadly around Mt Victoria in suitable habitats, but its exact distribution remains to be determined. Nevertheless, it is likely that, similar to most other species of *Ornithuroscincus*, its overall distribution is narrow.

Natural history: On Mt Victoria, most animals were found in the Isuani Basin high-elevation grassland (> 2800 m a.s.l.), dominated by *Gleichenia vulcanica* Blume ferns, together with a variety of grasses and sedges, particularly *Calamagrostis*, *Danthonia*, *Deschampsia*, *Gahnia* and *Poa* together with *Astelia* (Asteliaceae). There are clumps of shrubs, particularly on the grassland margins, dominated by *Gaultheria mundula* F.Muell., *Dimorphanthera* spp., *Rhododendron* spp., *Vaccinium amblyandrum* F.Muell, *Acrothamnus suaveolens* (Hook.f.) Quinn and *Hypericum* spp. Animals were found sheltered between fronds of tree ferns (*Alsophila* spp.) during daytime hours, with air temperatures between 17 and 18°C. Animals were not observed as active, but this may have been due to drought conditions induced by the 2015–16 El Niño.

Three animals were collected from regenerating cloud forest at slightly lower elevations ("Chopper Pad Camp", 2680 m a.s.l.), also under shelter. The area had apparently been cleared 5–10 years previously and was dominated by second growth, particularly *Decaspermum* sp. and other myrtaceous shrubs and small trees. Nearby mature cloud forest was dominated by the conifer, *Dacrycarpus compactus* (Wasscher) de Laub., which forms nearly pure stands in many areas fringing the grassland.

Reproduction: Viviparous. Litter size varies between 2–3 (mean 2.3, *N* = 4).

Conservation status: Population size and trend unknown, but animals were not abundant in sampled localities. Based on the populations sampled herein, *O. pterophilus*

has an extent of occurrence of 156 km^2 and an area of occupancy of 20 km^2 (based on occupation of 4 km^2 cells; both calculated using http://geocat.kew.org/). It does not occur near any protected areas. The species appears to be most common in high-elevation grasslands, and the availability of such habitats would therefore greatly impact its exact distribution boundaries. Shortly after the type series was collected there, the grasslands on Mt Victoria experienced extensive anthropogenically-caused bushfires exacerbated by a drought induced by the 2015–2016 El Niño. This likely damaged the habitat and thus the population there. Future warming and severe ENSO events due to climate change are likely to cause continued degradation of suitable habitat. Therefore, we recommend assigning a status of Endangered B1ab(iii) to *O. pterophilus*.

ORNITHUROSCINCUS SHEARMANI SP. NOV.

SHEARMAN'S SMOOTH-EARED SKINK

(FIGS 16, 22; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:E9C004B6-8694-4984-9FA1-A438E335141D

Holotype: BPBM 47915 (field tag AA 19603), adult female, collected by P. Shearman at 9.7192°S, 148.9846°E (WGS 84), 3456 m a.s.l., Mt Suckling, Milne Bay Province, Papua New Guinea, 5 September 2009.

Diagnosis: A large species of *Ornithuroscincus* (adult SVL 69.2 mm), characterized by the unique combination of short limbs (forelimbs 28.4% of SVL, hindlimbs 35.6% of SVL); frontoparietals fused; nuchals single pair; paravertebral scales 83; mid-body scale rows 37; 4th digit on front foot longer than 3rd; subdigital lamellae 18 under 4th toe; single supradigital scales four on 4th toe; dorsal coloration jet black; medial dorsal golden striations extending posteriorly from occiput to tail, bordered laterally by fragmented golden stripes made up of narrow spots one to two scales long; dorsolateral stripes present as narrow uniform golden stripes, a half scale wide, extending from postorbital region to tail, bordered on both sides by parallel narrow golden striations; flanks jet black, marked with multiple spots one scale wide, pale blue in preservative, pale yellow in life; ventral surfaces pale blue in preservative, with dark brown blotches on chin and dark brown striations on chest, abdomen, thighs, precloacal region and tail, becoming more pronounced posteriorly; palmar and plantar surfaces dark brown.

Comparisons: Ornithuroscincus shearmani is easily distinguished from all other species of *Ornithuroscincus* by its large size (adult SVL 69.2 vs. 29.4–62.3 mm), high paravertebral scale count (83 vs. 47–70) and unique colour pattern consisting of jet black dorsal coloration with golden mid-dorsal striations. It further differs from *O. albodorsalis*, *O. nototaenia*, *O. sabini*, *O. inornatus*, *O. pterophilus* and *O.* cf. *venemai* in having fused (vs. unfused) frontoparietals.

Description of the holotype: 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; frontonasal large, with seven sides, extending laterally to slightly above the level of nares, not contacting frontal; prefrontals large, in shallow medial contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal kite shaped, widest anteriorly, suture with frontoparietal shallowly convex; frontoparietal single, partially cleft by a suture on the posterior edge, in contact with frontal; interparietal smaller than fused frontoparietal, diamond shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietal, posteriormost supraocular and pretemporals; single pair of transversely enlarged nuchals, wider than long, separated from secondary temporal by a single smaller intercalated scale on the left side and two fragmented scales, possibly due to damage, on the right side. Anterior loreal similar in size to posterior loreal, higher than long; posterior loreal roughly as high as long; lower preocular wedge shaped; upper preocular much smaller, longer than high; presubocular single, slightly smaller than lower preocular; postsuboculars two, lower interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with an opaque palpebral disc of roughly similar size as ear opening; supraciliaries eight, anteriormost not contacting frontal, posteriormost projecting medially and interdigitated between posteriormost supraocular and upper pretemporal; primary temporal single, interdigitated between penultimate and posteriormost supralabials; secondary temporals two, upper larger and overlapping lower; supralabials seven, fifth in contact with small scales of lower eyelid; postsupralabials two; ear opening moderate sized and oval, without lobules. Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields four on left side and three on right side, the first right in medial contact with first and second left, second right narrowly separated by single medial scale from second and third left, third right separated by three medial scales from third and fourth left; posteriormost chin shield in contact

with antepenultimate infralabial. Body scales smooth, in 37 rows at midbody; paravertebral scales 83; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of 4th toe in two rows proximally, single row distally beginning at third interphalangeal joint, four single scales; subdigital lamellae under 4th toe 18, smooth. In preservative (Fig. 22), dorsal colour jet black, extending to tail, with medial dorsal golden striations extending posteriorly from occiput to tail, bordered laterally by fragmented golden stripes made up of thin spots one to two scale long; golden striations become less pronounced posteriorly on tail; dorsolateral stripes present as narrow (0.5 scale wide) unfragmented golden stripes extending from postorbital region to tail, bordered on both sides by parallel narrow golden striations, becoming less pronounced posteriorly on tail; flanks jet black, marked irregularly with multiple pale blue spots one scale wide; head scales dark brown to jet black, lighter brown on snout; anterior margins of head scales light brown to golden; labials dark brown at margins and pale blue or light brown in centre; ventral surfaces pale blue with dark brown blotches on chin and dark brown striations on chest, abdomen, thighs, precloacal region and tail, becoming more pronounced posteriorly; golden spots cover dorsal surfaces of limbs; palmar and plantar surfaces dark brown.

Colour in life: Dorsal surfaces dark brown to jet black, with medial golden striations extending posteriorly from occiput to tail, bordered laterally by fragmented pale yellow stripes made up of thin spots one to two scales long (Fig. 16). Dorsolateral stripes pale yellow. Sides dark brown to jet black, marked irregularly with multiple pale yellow to white spots a single scale wide. Pale yellow spots cover dorsal surfaces of limbs.

Etymology: The species is named in honour of Dr Phil Shearman, who collected the sole specimen.

Distribution: Known from a single population near the summit of Mt Suckling in the southern Owen Stanley Mts, at 3456 m a.s.l., of which a single specimen was collected.

Natural history: Our single collection, and all additional sightings of *O. shearmani*, were from a small area on the south-eastern side of a large (*c.* 450 ha) grassy plateau above the tree line enclosed by ridges of Goë Denedeniwa, a peak within the main summit complex of Mt Suckling. The grasslands were dominated by two tussock-forming species, *Chimaerochloa archboldii* (Hitchc.) Pirie & H.P.Linder and *Deschampsia klossii* Ridl., and included pockets of a shrub, *Eurya albiflora* C.T.White & W.D.Francis (Pentaphylacaceae) and scattered populations of the tree fern *Alsophila gleichenioides* (C.Chr.) R.M.Tryon. The area was drained by a small stream, with numerous adjacent bogs.

The lizards appeared to be confined to a small, dry, rocky area dominated by the woody ground creeper *Vaccinium prostratum* Sleumer and several small shrubs including *Acrothamnus suaveolens*, *Hypericum papuanum* Ridl. and *Coprosma papuensis* W.R.B.Oliv.

They were active for only a few hours each day, beginning at around 08:00–09:00 h, when the first sun reached the area. The temperature during the night generally dropped below -5°C and ground frosts were common. The ambient temperature when the lizards were initially active was only around 5–7°C, but the ground quickly warmed under direct sun. The lizards occurred mostly on scattered rocky outcrops and boulders and were occasionally seen on the ground. Although there appeared to be a wide expanse of suitable habitat along the margins of the plateau, the lizards were confined to this one area.

We did not find any other species of amphibians and reptiles on the plateau or on the summit of Goë Denedeniwa. However, the monotreme *Zaglossus bartoni* (Thomas, 1907) was common in bogs along the stream and wallabies were common in the grasslands. We occasionally saw tree kangaroos (*Dendrolagus dorianus* Ramsay, 1883), bandicoots and we found a skull of a quoll, *Dasyurus albopunctatus* Schlegel, 1880.

The lizards were extremely wary and difficult to approach. This was a little surprising because the area is rarely visited by people. Although quolls are voracious predators, they tend to be nocturnal so are unlikely to prey upon the lizards. The bandicoot we observed was diurnal and is a possible but unlikely predator.

Conservation status: We estimate a population of ~50 individuals at the type locality. Another plateaeu with a similar habitat is located ~50–100 m lower in elevation than the topotypic site, but we were unable to survey it to determine if *O. shearmani* occurs there as well. Thus, true population size and trend is unknown. It does not occur near any protected areas. However, the entire area around the collecting locality is wilderness for many kilometres, and human disturbance in this vast area is virtually unknown. The extremely dark pigmentation of *O. shearmani* is only found in four other species with alpine distributions: *A. alpinus*, *A. subalpinus*, *N. glacialis* and *N. stellaris*. This would suggest *O. shearmani* is an alpine specialist, endemic to the summit of Mt Suckling, and is unlikely to occur in lower elevations nearby. Therefore, global warming is likely to cause range contraction. However, this

is also a remote location with few anthropogenic disturbances posing additional immediate threats. Further surveys on Mt Suckling are needed to fully assess its lower distributional boundaries, but since it likely only occurs in a single location, and climate change poses a viable future threat to its persistence, with little suitable habitat to escape to, we recommend assigning a status of Vulnerable D2 to *O. shearmani*.

ORNITHUROSCINCUS VIRIDIS SP. NOV.

GREEN SMOOTH-EARED SKINK

(FIGS 16, 23–24; TABLE 1)

Zoobank registration: urn:lsid:zoobank.org:act:1D260000-8B53-4698-ADC4-A0374C1FD2C1

Holotype: BPBM 44744 (field tag AA 23450), gravid adult female with two embryos, collected by O. Tallowin at Myola 2, 9.1509°S, 147.7678°E (WGS 84), 2075 m a.s.l., crest of Owen Stanley Mts along the Kokoda Track, Central Province, Papua New Guinea, 5 April 2014.

Paratypes (N = 16): Papua New Guinea: Central Province: Crest of Owen Stanley Mts along the Kokoda Track: Myola 2 Guest House, 9.1509°S, 147.7675°E (WGS 84), 2076 m a.s.l. (BPBM 44729–38; four males, five females, one juvenile); Myola 1, 9.1508°S, 147.7675°E (WGS 84), 2057 m a.s.l. (BPBM 44739; female); Myola 1, 9.1506°S, 147.7672°E (WGS 84), 2072 m a.s.l. (BPBM 44740; male); Myola 1, 9.1509°S, 147.7675°E (WGS 84), 2076 m a.s.l. (BPBM 44741–42; two males); same locality as holotype (BPBM 44743; male); Myola 2, 9.1509°S, 147.7679°E (WGS 84), 2076 m a.s.l. (BPBM 44745; male).

Diagnosis: A medium-sized species of *Ornithuroscincus* (adult SVL 42.1–54.8 mm) characterized by the unique combination of short limbs (forelimbs 25.7–30.8% of SVL, hindlimbs 29.0–40.6% of SVL); frontoparietals unfused; nuchals 1–3 pairs; paravertebral scales 57–70; mid-body scale rows 32–41; 4th digit on front foot not longer than 3rd; subdigital lamellae 12–18 under 4th toe; single supradigital scales 3–5 on 4th toe; dorsal coloration light to dark brown in preservative, light to dark greenish brown in life; dark brown to black lateral field present; dorsolateral stripes absent; flanks speckled with spots no more than a single scale wide, blue in preservative, green in life; uniform coloration on abdomen, thighs and precloacal region that lacks brown spotting, light blue in preservative, bright green in life; tail uniformly light blue more or less speckled with light brown spots; palmar and plantar surfaces brown.

Comparisons: Ornithuroscincus. viridis differs from all other species of *Ornithuroscincus* in lacking dorsolateral stripes, having shorter relative limb length (forelimbs 25.7–30.8% of SVL and hindlimbs 29.0–40.6% of SVL vs. forelimbs 27.0–36.3% of SVL and hindlimbs 33.3–47.3% of SVL) and a lower average count of subdigital lamellae under 4th toe (15.8, range = 12–18 vs. 20.2, range = 17–23). It further differs from *O. bengaun* and *O. shearmani* in having unfused (vs. fused) frontoparietals. It further differs from *O. albodorsalis*, *O. noctua*, *O. nototaenia* and *O.* cf. *venemai* by lacking a parietal eye spot (vs. present) and by having a higher count of midbody scale rows [32–41 vs. 22–26, 23–28, 24–25 and 24–26, respectively (Brongersma, 1953a; Zweifel, 1979; Shea & Greer, 2002)].

Ornithuroscincus viridis is most similar in body proportions and scalation to its sister species, *O. pterophilus*. However, it differs by being slightly smaller on average (mean adult SVL 49.7 mm, range = 42.1–54.8 vs. 55.9 mm, range = 50.1–62.3), in having shorter relative limb length (mean forelimbs 28.2% of SVL, range = 25.7–30.8 and hindlimbs 35.0% of SVL, range = 29.0–40.6 vs. mean forelimbs 30.4% of SVL, range = 27.0–33.7 and hindlimbs 38.0% of SVL, range = 33.3–42.5), a lower average count of subdigital lamellae under the 4th toe (15.8, range = 12–18 vs. 19.9, range = 17–23), primary nuchal scales being usually as wide as long (15 of 17) vs. wider than long (15 of 18), and most easily by colour pattern: *O. viridis* lacks dorsolateral stripes (vs. present in *O. pterophilus*), has uniform light to dark brown dorsal coloration (vs. light brown spotted with dark brown to black spots) and in life has a slight greenish tint to its dorsal coloration and bright green ventral surfaces (vs. lime green usually with lemon yellow on precloacal region and thighs).

Description of the holotype: 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 (slightly closer to supralabials than to frontonasal); frontonasal large, with seven sides, extending laterally to slightly above the level of nares, not contacting frontal; prefrontals large, in narrow medial contact, bordered ventrolaterally by two loreals; supraoculars four, anterior two in contact with frontal, posterior three in contact with frontoparietals; frontal kite shaped, widest anteriorly; frontoparietals single pair in medial contact, in narrow contact with frontal; interparietal of roughly similar area to single frontoparietal, kite shaped, widest anteriorly; parietal eye spot absent; parietals in contact behind interparietal, in contact anteriorly with frontoparietals, posteriormost supraocular and two pretemporals; nuchals single pair, transversely enlarged, irregularly shaped, roughly as wide as long, separated from secondary temporal by

a single intercalated scale. Anterior loreal similar in size to posterior loreal, both higher than long; lower preocular roughly square in shape; upper preocular much smaller, longer than high; presubocular single; postsuboculars three, lowest interdigitated between subocular supralabial and penultimate supralabial; lower eyelid scaly, moveable, with a clear palpebral disc smaller than size of ear opening; supraciliaries seven, 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 and oval shaped, without lobules. Mental single; postmental single, contacting two anteriormost infralabials; infralabials six; enlarged chin shields three pairs, the 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 33 rows at midbody; paravertebral scales 70; medial precloacal scales enlarged, overlapping lateral precloacals. Scales on dorsal surface of fourth toe in two rows proximally, single row distally beginning at third interphalangeal joint, five single scales; subdigital lamellae on fourth toe 18, smooth. In preservative (Fig. 23), dorsum uniform light brown; dorsolateral stripes absent; dorsal pattern sharply replaced by dark brown lateral fields, gradually becoming lighter ventrally; lateral field speckled with multiple pale blue spots one scale wide; head similar in coloration to dorsum, slightly lighter on snout and supraciliaries; labials dark brown at margins, pale blue in centre; venter pale blue with slight brown dusting at edges of scales laterally; light brown dusting more pronounced under tail; palmar and plantar surfaces dark brown. In life (Figs 16, 24), dorsum dark brown with green tint, becoming lighter dorsolaterally; lateral field black, speckled with multiple green spots a single scale wide, specks extending to margins of dorsal field; venter bright green, lemon yellow under tail; palmar and plantar surfaces dark brown.

Variation: Adult body size 42.1–54.8 mm SVL (mean = 49.7, SD = 3.7, *N* = 16). Females (mean = 49.9, range = 42.1–54.8, SD = 4.8, *N* = 7) and males (mean = 49.5, range = 44.1–53.4, SD = 2.9, *N* = 9) of similar size. Forelimbs 25.7–30.8% of SVL (mean = 28.2%, SD = 1.5, *N* = 16). Hindlimbs 29.0–40.6% of SVL (mean = 35.0%, SD = 2.6, *N* = 16). Scale rows at midbody 32–41 (mean = 36.2, SD = 2.7, *N* = 17); paravertebral scales 57–70 (mean = 62.8, SD = 3, *N* = 17). Lamellae under fourth toe 12–18 (mean = 15.8, SD = 1.59, *N* = 17); single supradigital scales on 4th toe 3–5 (mean = 3.4, SD = 0.7, *N* = 17). Mostly 1–3 pairs of nuchals, but BPBM 44734 lacks nuchal on left side, with only single nuchal on right side. Nuchals typically roughly as wide as long (*N* = 15), rarely wider than long (*N* = 2). Primary nuchals usually separated from secondary temporals by a single smaller intercalated scale (*N* = 13), rarely by two (*N* = 2) or none (*N* = 2). Prefrontals in medial contact in all but BPBM 44733, where separated by a single, azygous scale. Loreals two in all but BPBM 44740, where loreal single. Supraciliaries either seven (*N* = 7) or eight (*N* = 8), rarely nine (*N* = 2). Anteriormost supraciliary either in contact with frontal (*N* = 9) or not (*N* = 8). Posteriormost supraciliary usually projecting medially (*N* = 15), but rarely in line with all other supraciliaries (*N* = 2). Postsuboculars usually two (*N* = 14), rarely three (*N* = 3). Secondary temporals usually two (*N* = 13), but rarely one (*N* = 2) or three (*N* = 2). Posteriormost supralabial fragmented by horizontal suture on left side in three specimens (BPBM 44729, 44740 and 44743). Infralabials either six (*N* = 12) or seven (*N* = 5). Infralabials posterior to contact with chin shields usually one (*N* = 14), rarely two (*N* = 2) or three (*N* = 1).

Colour pattern of all specimens generally similar to holotype, with few exceptions. BPBM 44732, 44737, 44741 and 44743 have sparse dark brown spotting on dorsum extending to tail, most pronounced in BPBM 44743. BPBM 44743 has a coppery brown dorsum with light margins, bordered medially by dark brown spotting, creating the appearance of light dorsolateral stripes. Palmar and plantar surfaces of BPBM 44735–36 lighter brown.

Colour in life: Dorsum light to dark brown, often with green tint, usually uniform but rarely with sparse dark brown spotting (Figs 16, 24). Green tint not extending to tail, which remains brown. Sides dark brown to jet black, sharply demarcated from dorsum and speckled lightly or heavily with bright green spots a single scale wide. Sides becoming gradually lighter towards venter, dark lateral field of varying width. Venter uniformly bright green, less pronounced on tail and often changing to lemon yellow, with light brown dusting laterally, more pronounced under tail.

Etymology: From the Latin single-ending adjective *viridis*, green, in reference to the diagnostic coloration of the species in life.

Distribution: Known only from high-elevation grasslands at 2052–2076 m a.s.l. on the crest of the Owen Stanley Mountains in the Myola dry lakebeds along the Kokoda

Track. Little is known about its distribution elsewhere, but it appears to be absent from nearby montane habitats (e.g. 1900 Crossing, 9.1288°S, 147.7264°E; WGS 84), as well as from similar high-elevation grasslands on the southern slopes of Mt Victoria, both localities where its sister species, *O. pterophilus*, occurs.

Natural history: All of our specimens of *O. viridis* were collected from underneath logs at the edge of a large (*c.* 800 ha) expanse of partially swampy grassland that is generally interpreted as an ancient lake bed that has filled in with sediment. The grasses include a mixture of native and introduced species, namely *Anthoxanthum horsfieldii* (Kunth ex Benn.) Reeder, *Capillipedium parviflorum* (R.Br.) Stapf, *Dimeria chloridiformis* (Gaudich.) K.Schum. & Lauterb., *Isachne myosotis* Nees, *Miscanthus floridulus* (Labill.) Warb. ex K.Schum. & Lauterb., *Paspalum scrobiculatum* L. and *Sacciolepis indica* (L.) Chase. These grasses, together with a rich array of sedges, formed a continuous, generally low ground cover that was similar in overall aspect to a temperate meadow. This formation, which is unusual in montane New Guinea, has a different appearance from the high-elevation tussock grasslands that dominate most alpine regions.

The area where the lizards were collected was bordered by a rich, upper montane forest about 15–25 m tall, with an uneven canopy. Aspect dominant species of trees included *Saurauia* sp., *Opocunonia nymanii* (K.Schum.) Schltr., *Elaeocarpus angustifolius* Blume, *Elaeocarpus fuscoides* Knuth, *Elaeocarpus murukkai* Coode, *Elaeocarpus sayeri* F.Muell., *Elaeocarpus trichophyllus* A.C.Sm., *Sloanea tieghemii* (F.Muell.) A.C.Sm., *Lithocarpus lauterbachii* (Seemen) Markgr., *Lithocarpus rufovillosus* (Markgr.) Rehder, *Galbulimima* sp., *Litsea albida* (Kosterm.) Kosterm., *Syzygium benjaminum* Diels, *Syzygium callianthum* Merr. & L.M.Perry, *Syzygium homichlophilum* Diels, *Syzygium subalatum* (Ridl.) Merr. & L.M.Perry, *Pandanus* spp., *Melicope conjugata* T.G.Hartley, *Melicope rubra* (K.Schum. & Lauterb.) T.G.Hartley, *Melicope stellulata* T.G.Hartley and *Archboldiodendron* sp. Pulle's southern beech, *Nothofagus pullei* Steenis, occurs on some steep ridges. The understory includes *Decaspermum exiguum* Merr. & L.M.Perry, *Tasmannia piperita* (Hook.f.) Miers and a rich array of Ericaceae.

We visited the area during inclement weather and did not observe the lizards when they were active. We found them only under logs in the grassland, not in the adjacent forest. We therefore infer that they are a grassland species.

Reproduction: Viviparous. Litter size of all three gravid females 2.

Conservation status: The species is locally abundant at the type locality, although the population trend is unknown. It does not occur near any protected areas. We did not find it in other grasslands in the overall area, including another ancient grassland-filled lakebed that was located nearby at a slightly lower elevation. This, along with its apparent absence from nearby localities where sympatric lizard taxa occur (such as *O. pterophilus* or *Papuascincus* sp.), would suggest this species may have a restricted distribution, limited to the *c.* 800 ha grassland. Local landowners, accompanied by dogs, are with increasing frequency establishing hunting camps in the area. Feral pigs were observed foraging nearby. Dogs and pigs are both known to prey on the lizards. Given the relatively small area of occurrence of *O. viridis* and these threats from introduced predators, we recommend assigning a status of Vulnerable D2 to it.

DISCUSSION

The herpetofauna of New Guinea is rich and unique (Allison, 1982, 1996, 2007) and, as our work stresses, it remains poorly known. As recent molecular analyses have shown, many New Guinean reptiles are more genetically diverse than previously assumed (Donnellan & Aplin, 1989; Rawlings & Donnellan, 2003; Metzger *et al.*, 2010; Strickland *et al.*, 2016; Tallowin *et al.*, 2018, 2019; Slavenko *et al.*, 2020). In some cases, as in *Lobulia s.l.*, there is also large morphological variation that has gone unnoticed at least in part due to lack of research (Kraus, 2020).

In its original description, *Lobulia* was not as well defined as were its related genera (Greer, 1974), although that was in part due to the large group of skinks that Greer (1974) was attempting to sort through. Later work reassigned known species to different genera and rediagnosed the genus (Allison & Greer, 1986). However, even after this rediagnosis, newly described species were tentatively placed in *Lobulia* despite ambiguous assignation to the genus (Greer *et al.*, 2005; Kraus, 2020). The taxonomy of sphenomorphine skinks has been notoriously difficult to resolve (Greer & Shea, 2003, 2004), and recent molecular studies have shown that even supposedly well-defined genera such as *Prasinohaema* can be paraphyletic (Rodriguez *et al.*, 2018).

Using a combination of molecular genetic analyses and broad morphological examination (Figs 1–2; Supporting Information, Figs S2–S3) we have restricted *Lobulia* to include only three previously recognized species (*Lo. elegans*, *Lo. lobulus* and *Lo. brongersmai*). We have erected three new genera to reflect the large genetic and morphological differences between *Lobulia s.s.* and other species

previously included in the genus. We assigned two species previously included in *Lobulia* to the new genus *Alpinoscincus* (*A. alpinus* and *A. subalpinus*). Both are restricted to extremely high elevations in the north-western Owen Stanley Range, Papua New Guinea. They are distinguished from *Lobulia* as here redefined based on several key scalation differences relating to the characters of the lower eyelid, temporal scales and supralabials. They also differ from *Lobulia s.s.* in elevational distribution, both occurring at extremely high, alpine altitudes (> 2500 m a.s.l.), whereas species of *Lobulia* are either at montane elevations (~1500–2500 m a.s.l.) or lowland (*Lo. brongersmai*). We assigned two other alpine species to the new genus *Nubeoscincus* (*N. glacialis* and *N. stellaris*). Although they are similar to *Alpinoscincus* in general coloration and habitat requirements [and may share several adaptations to high-elevation habitats (Greer *et al.*, 2005)], they differ in several key characteristics of head scalation, mostly in the number and character of the supralabials. In fact, in terms of scalation, they are most similar to *Pr. flavipes* and *Pr. prehensicauda* but lack their characteristic green tissues and blood serum (Greer, 1974; Greer *et al.*, 2005) and prehensile tail. They also occur geographically distant from *Alpinoscincus* in the central and western portions of the New Guinea Highlands, whereas the latter genus occurs in the south-eastern Papuan Peninsula. Finally, the latest species described in *Lobulia s.l.* (*O. sabini*) we assigned to the new genus *Ornithuroscincus*, which it shares along with four species formerly in *Lipinia* (*O. albodorsalis*, *O. noctua*, *O. nototaenia* and *O.* cf. *venemai*) and several others described herein. These species all lack the lobules on the anterior edge of the ear opening that gave *Lobulia* its name. This genus has the most disparate distribution patterns of the new genera, as it includes both montane species with seemingly extremely small known distributions (such as *O. sabini* and several species newly described herein) and an extremely wide-ranging lowland species (*O. noctua*, although it clearly represents a species complex in need of taxonomic revision).

We also reinforced previous findings that *Prasinohaema* and *Lipinia* are paraphyletic as currently understood (Rodriguez *et al.*, 2018). Thus, both are in need of taxonomic revision, a process that Greer had begun for *Prasinohaema* but never completed. Since we have not sampled these genera as extensively as we did *Lobulia s.l.*, we refrain from making major taxonomic suggestions here. However, we have redefined *Prasinohaema* to better differentiate it from our redefined *Lobulia*, *Papuascincus* and the newly described genera. Under this scheme *Pr. semoni* and *Pr. virens* do not fit the new morphological description of *Prasinohaema* (Fig. 2), nor do they cluster with *Pr. prehensicauda* and *Pr. flavipes* phylogenetically (Fig. 1); we leave them *incertae sedis* in *Prasinohaema* pending future resolution of their taxonomy. Similarly, we leave several New Guinean species, which we did not sample, but which do not appear to fit the generic descriptions provided herein, as *incertae sedis* in *Lipinia*: *Lipinia cheesmanae* (Parker, 1940), *Lipinia longiceps* (Boulenger, 1895), *Lipinia occidentalis* (Günther, 2000), *Lipinia rouxi* (Hediger, 1934) and *Lipinia septentrionalis* (Günther, 2000). We also erected the new genus *Palaia* to include one species (*Pal. pulchra*) formerly placed in *Lipinia*, to differentiate it from its sister genus *Papuascincus*. The two genera differ in egg morphology (Allison & Greer, 1986), in a few scalation features, and in ecology—*Palaia* is decidedly more arboreal than the more terrestrial *Papuascincus*. Indeed, this fact may contribute to *Palaia* having slightly basally expanded subdigital lamellae, which *Papuascincus* do not have.

Biogeographically, our sampled taxa represent several independent cases of colonization of highland habitats and several reversals to lowland distributions (Fig. 4). Lowland taxa are nested within otherwise highland clades, and our time-calibrated phylogeny recovered relatively young ages for montane genera (Figs 2–4; Supporting Information, Table S3), in congruence with the young ages of montane uplift in New Guinea (Hill & Hall, 2003; Quarles van Ufford & Cloos, 2005). However, the geological history of New Guinea is extremely complex, comprising multiple events of tectonic uplift, terrane accretion and subduction of the Australian Plate margin (Pigram & Davies, 1987; Hall, 2002; Hill & Hall, 2003; Quarles van Ufford & Cloos, 2005; Baldwin *et al.*, 2012). Our biogeographic reconstructions support an important role for the accreted terranes of New Guinea in shaping extant diversity, especially the EPCT, which was recovered as being the source of this large radiation of lizards (Fig. 3). A possible scenario is that the major radiation of these skinks occurred in the EPCT, which amalgamated during the Eocene and was separated from the Australian Craton by an oceanic basin (Pigram & Davies, 1987), possibly following dispersal from the Philippines. After the EPCT docked with the Australian Craton, no earlier than the mid-Miocene (Pigram & Davies, 1987) and following subsequent montane uplift (Hill & Hall, 2003; Quarles van Ufford & Cloos, 2005) these skinks were able to disperse further west in New Guinea (Fig. 3). Our results thus support a role for the EPCT as a source for diversification in western New Guinea (Toussaint *et al.*, 2021).

We must note some discrepancies between our biogeographic reconstructions with the time-stratified (Fig. 3) and unconstrained (Supporting Information, Fig. S5) data sets. The unconstrained data set favours early

dispersal to the Fold Belt and subsequent radiation there. However, we find the unconstrained data set to be less likely, since it explicitly allows lineages to occur over several distinct geological regions prior to their actual docking events. We do not think that montane specialist species having continuous ranges over landmasses separated by ocean is a biologically realistic scenario. However, we cannot rule out an early jump-dispersal event to the Australian Craton and the uplifting Fold Belt, and fully unravelling the biogeographic history of these skinks will require more in-depth work. In particular, there is a massive discrepancy between the sampling effort on the mountains in the eastern and western halves of New Guinea (Supporting Information, Figs. S6 & S8). We expect that species richness of reptiles in general and of montane skinks in particular, is greatly underestimated in western New Guinea. A complete understanding of the diversity, biogeography and evolutionary history of the montane skink fauna of the island will never be reached without extensive sampling in the Indonesian provinces of Papua and West Papua.

CONCLUSION

We uncovered evidence of extensive diversity in the New Guinean montane skink fauna, both on the species and generic levels. This diversity was shaped by the complex geological history of New Guinea, and despite our work here, it still remains poorly known, especially in undersampled Indonesian New Guinea. Hence, although our study presents an important and necessary revision, there is yet more work to be done on the montane skinks of New Guinea. More specimens currently categorized as *Lobulia* are found in natural history collections worldwide, which we were not able to examine for the current study. Many of these may represent undescribed species and some will belong to the new genera described herein. Furthermore, many of the species we describe herein are poorly known, and we know little of their natural history, ecology, true distributional boundaries (Meiri *et al.*, 2018), and crucially—their conservation status. Bridging these gaps in our knowledge of the montane fauna of New Guinea will require future study, especially the necessary fieldwork to fully understand these animals.

KEY TO THE GENERA

1. (a) One pair of chin scales in medial contact 2
   (b) Two or more pairs of chin scales in medial contact 4
2. (a) Lobules present on anterior edge of ear opening 3
   (b) Lobules absent from anterior edge of ear opening ..... *Ornithuroscincus*
3. (a) Nasal scale with horizontal suture extending posteriorly from nostril ..... *Papuascincus*
   (b) Nasal scale lacking horizontal suture ..... *Palaia*
4. (a) Chin shields separated from infralabials by a row of genials; temporal region with 4 or more temporals 5
   (b) Chin shields abut infralabials; temporal region with standard pattern of only 1 anterior and 2 posterior temporals ..... *Lobulia*
5. (a) Two supralabials posterior to subocular supralabial 6
   (b) Three supralabials posterior to subocular supralabial ..... *Alpinoscincus*
6. (a) Green blood serum and tissues; prehensile tail with glandular tip; greatly expanded basal subdigital lamellae (over twice width of distal lamellae) ..... *Prasinohaema*
   (b) Pale brown blood serum and pink tissues; tail not prehensile, lacking a glandular tip; basal subdigital lamellae less than twice width of distal lamellae ..... *Nubeoscincus*

KEY TO SPECIES IN *ALPINOSCINCUS*

(ADAPTED FROM GREER *ET AL.*, 2005)

1. (a) Subdigital lamellae 15–23; chin and throat similar in colour to rest of venter; presuboculars modally one; supralabials modally nine ..... *A. subalpinus*—subalpine skink
   (b) Subdigital lamellae 12–19; chin and throat abruptly darker than rest of venter; presuboculars modally two; supralabials modally eight ..... *A. alpinus*—alpine skink

KEY TO SPECIES IN *LOBULIA*

1. (a) Frontoparietals fused 2
   (b) Frontoparietals unfused 3
2. (a) Midbody scale rows 30–34; nuchal region with dark brown patch; large dark brown dorsal patches ..... *Lo. marmorata*—marbled moss skink
   (b) Midbody scale rows 27–32; nuchal region lacking dark brown patch; moderate-sized dark brown dorsal patches ..... *Lo. brongersmai*—Brongersma's moss skink
3. (a) Pale dorsolateral stripes present 4
   (b) Pale dorsolateral stripes absent 6
4. (a) Paravertebrals < 69; two mid-dorsal rows of large dark brown spots running the length of the dorsum, some joining to form two mid-dorsal stripes 5
   (b) Paravertebrals > 68; small dark brown spots on dorsum irregularly placed, not formed into rows ..... *Lo. vogelkopensis*—Vogelkop moss skink
5. (a) Paravertebrals 54–61; large dark brown spots arrayed in two parallel rows, joining posteriorly to form two parallel stripes ..... *Lo. lobulus*—Central Range moss skink
   (b) Paravertebrals 59–68; moderate to large dark brown spots arrayed in two parallel rows, not joining to form stripes ..... *Lo. huonensis*—Huon moss skink
6. (a) Midbody scale rows 30–32; nuchals 3 pairs ..... *Lo. elegans*—elegant moss skink
   (b) Midbody scale rows 34–37; nuchals 1–2 pairs ..... *Lo. fortis*—Mount Strong moss skink

KEY TO SPECIES IN *NUBEOSCINCUS*
(ADAPTED FROM GREER *ET AL.*, 2005)

1. (a) Anterior edge of ear opening with lobules; window on lower eyelid large and semi-transparent; presuboculars modally two ..... *N. glacialis*—glacial cloud skink
   (b) Anterior edge of ear opening without lobules; window on lower eyelid variable in size, opacity and scaliness; presuboculars modally one ..... *N. stellaris*—Star Mountains cloud skink

KEY TO SPECIES IN *ORNITHUROSCINCUS*

1. (a) Light yellow-white patch on occiput absent 2
   (b) Light yellow-white patch on occiput present ..... *O. noctua*–moth skink
2. (a) Frontoparietals fused 3
   (b) Frontoparietals unfused 4
3. (a) Adult SVL < 50 mm; paravertebrals < 70; uniform olive dorsum coloration with thick bronze dorsolateral stripes ..... *O. bengaun*—Daga smooth-eared skink
   (b) Adult SVL > 50 mm; paravertebrals > 70; dark brown to black dorsal coloration with golden striations ..... *O. shearmani*—Shearman's smooth-eared skink
4. (a) Dorsolateral stripes absent 5
   (b) Dorsolateral stripes present 7
5. (a) Parietal eye spot present 6
   (b) Parietal eye spot absent ..... *O. viridis*—green smooth-eared skink
6. (a) Dark vertebral stripe absent from dorsum ..... *O. albodorsalis*—white-backed slender skink
   (b) Dark vertebral stripe present on dorsum ..... *O. nototaenia*—Setekwa slender tree skink
7. (a) Thick dorsolateral stripes (> 1 scale wide) 8
   (b) Thin dorsolateral stripes (1 scale wide) 9
8. (a) Mid-dorsal field dark olive grey spotted with brown; midbody scale rows < 30 ..... *O. venemai*—Brongersma's slender tree skink
   (b) Mid-dorsal field uniform light brown; midbody scale rows > 30 ..... *O. inornatus*—plain smooth-eared skink

9. (a) Parallel fragmented white vertical stripes on flank; venter blue (lime green in life) .... *O. pterophilus*—Mount Victoria smooth-eared skink
(b) Scattered white specks on flank; venter pearl white (lemon yellow or white in life)..... ..... *O. sabini*—Mount Simpson smooth-eared skink

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DATA AVAILABILITY

All genetic sequences used in this study are freely available from GenBank, and accession numbers are listed in Supporting Information (Table S1). All morphological data used in this study are available in Supporting Information (Table S2).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Information on the specimens included in this study and related GenBank accession numbers. Tissue codes correspond to the labels assigned to each sample in the phylogenetic analyses. [a] Representatives used for estimation of divergence times (n = 47). [b] Samples with voucher specimens used in morphological analyses.

Table S2. Measurements for specimens used for morphological comparisons. Listed for each specimen are voucher number, collection number, tissue number (if used for molecular phylogenetic analyses), age, sex, clutch/litter size (if applicable), type status, locality data and collection date. The morphological measurements are as listed in the *Material and Methods*, and morphometric measurements also include relative measures, as a percent of SVL (RFHD, RBW, RHL, RFLL, RHLL) or of head length (RHW, RHD).

Table S3. Divergence-date estimates and ancestral character states of selected nodes in the phylogeny. Each node is the most recent common ancestor of the taxa listed under the "Node" column. In bold are nodes representing the crown ages for five of the seven genera discussed in the manuscript (*Prasinohaema s.s.*, *Lobulia*, *Papuascincus*, *Alpinoscincus* and *Ornithuroscincus*). For each node the median and the 95% HPD of the age estimates, in Mya, are listed. In the "Time-stratified" and "Unconstrained" columns are the best-supported biogeographical regions for the node under the BAYAREA+J model, with relative probability in parentheses, for the time-stratified and unconstrained data sets, respectively. In the "Elevation" column is the best-supported elevational distribution category for the node, with posterior probability from 100 simulated character histories in parentheses.

Table S4. Pairwise uncorrected mitochondrial sequence divergence (*p*-distances in %) between and within lineages for the three mitochondrial gene markers (12S, *ND2* and *ND4*), separated by genus. Within-lineages distances are

only listed where sample size was enough to calculate ($N > 1$). The lower diagonal cells are *p*-distances, and the upper diagonal cells are the corresponding SE values.

Table S5. Results of the model selection for different biogeographical models in BioGeoBEARS, sorted by increasing AICc score. For each model the log-likelihood, estimates for *d* ("dispersal" rate; range expansion), *e* ("extinction" rate; range contraction) and *j* (jump-dispersal rate), the AICc score and the AICc weight are listed.

Figure S1. Head scalation in skinks, based on *Lobulia fortis* BPBM 41149, in (A) lateral aspect from left side, (B) dorsal aspect and (C) ventral aspect. The names of the scales are: 1 – rostral; 2 – nasal; 3 – frontonasal; 4 – loreal; 5 – prefrontal; 6 – preocular; 7 – presubocular; 8 – postsubocular; 9 – supraciliary; 10 – pretemporal; 11 – supraocular; 12 – primary temporal; 13 – secondary temporal; 14 – supralabial (*subocular supralabial); 15 – postsupralabial; 16 – frontal; 17 – frontoparietal; 18 – interparietal; 19 – parietal; 20 – nuchal; 21 – mental; 22 – postmental; 23 – infralabial; 24 – chin shield.

Figure S2. Box plots showing distributions of relative limb length as % of SVL (top) and ratio of length of forelimb divided by length of hindlimb (bottom) for each genus.

Figure S3. Scatterplots showing the relationship between the ratio of forelimb to hindlimb length (forelimb length divided by hindlimb length) to (A) relative forelimb length, and (B) relative hindlimb length, both represented as % of SVL. Dots are coloured based on genera.

Figure S4. Haplotype networks for the two nuclear markers, *NGFB* (left column) and *R35* (right column), for each of four clades, in rows top to bottom: *Alpinoscincus* (Clade VI; yellow colours), *Lobulia* (Clade I; red colours), *Ornithuroscincus* (Clade VII; purple colours) and *Prasinohaema+Nubeoscincus* (Clades II and III, respectively; green and light blue colours, respectively).

Figure S5. Results of the unconstrained biogeographic reconstruction using a BAYAREA+J model. Tips are coloured according to the extant distribution of each species. Nodes are pie charts, where the sizes of the coloured slices correspond to the relative probability of each state at each node. Posterior probabilities of the nodes are listed next to each node. Four of the geological regions are illustrated in the inset map. Palau, which is further north in the Pacific Ocean, is not pictured.

Figure S6. Sampling localities for the current study, with circles coloured according to genus: (A) localities for genetic samples, (B) localities for morphological samples. Base map tiles by Stamen Design, under CC BY 3.0. Basemap by OpenStreetMap, under ODbL.

Figure S7. Distributions of *Lobulia* spp: (A) *Lo. brongersmai*; (B) *Lo. elegans*; (C) *Lo. fortis*; (D) *Lo. huonensis*; (E) *Lo. lobulus*; (F) *Lo. marmorata*; and (G) *Lo. vogelkopensis***.** Black dots represent specimens sampled for this study, either genetically or morphologically. Polygons represent the presumed distribution for each species. Base map tiles by Stamen Design, under CC BY 3.0. Basemap by OpenStreetMap, under ODbL.

Figure S8. Distributions of (A) *Ornithuroscincus*; (B) *Alpinoscincus*; (C) *Nubeoscincus*. For distribution of *O. noctua* throughout New Guinea and the Southern Pacific, see Zweifel (1979). Dots represent specimens sampled for this study, either genetically or morphologically. Base map tiles by Stamen Design, under CC BY 3.0. Basemap by OpenStreetMap, under ODbL.

Figure S9. Map of New Guinea, showing names of mountains (in red) and place names (in purple) referenced in this study, as well as the two major rivers on the island, the Sepik and the Fly (in light blue). Base map tiles by Stamen Design, under CC BY 3.0. Basemap by OpenStreetMap, under ODbL.