



A new species of *Lepidodactylus* (Reptilia: Squamata: Gekkonidae) from the Kei Islands, Maluku, Indonesia

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Abstract

Lepidodactylus pantai is a new species of gecko from the Kei Islands, Maluku, Indonesia that is closely associated with intertidal habitats. This species does not fit cleanly into any of the three species groups described for the genus because it possesses the unique combination of both divided terminal scansors on all toes and a nearly completely cylindrical tail without fringes or evidence of dorsoventral compression. A phylogenetic analysis including this species demonstrates that it is the sister taxon of a population from Palau, and that this clade is sister to the clade containing Group III species for which we have molecular data.

Key words: Wallacea, Phylogenetics, Gecko, *Luperosaurus*, *Pseudogekko*, Moluccas, intertidal, *pantai*.

Introduction

The genus *Lepidodactylus* Fitzinger, 1843 *sensu stricto* comprises 33 species (Ineich 2008; Uetz & Hošek 2016) of Southeast Asian and Pacific island geckos. They are excellent oceanic dispersers (e.g., Radtkey *et al.* 1995; Ota *et al.* 1995) and have naturally colonized most small Pacific Islands as far eastward as Tahiti (Brown & Parker 1977). Our team has recently conducted a series of expeditions to eastern Indonesia, sampling both the inner and outer Banda Arc islands for reptiles and amphibians. In this paper we describe a new *Lepidodactylus* species from the Kei Islands, thus far found only on limestone rocks in the intertidal zone. The Kei Islands (administrative district Kepulauan Kei) are located in the Maluku Province of eastern Indonesia, and comprise two primary islands, Kei Kecil and Kei Besar, as well as several smaller satellite islands, including Tanimbar Kei, Kei Dulah, Kur, Tam, and Tayando.

The genus *Lepidodactylus* is divided into three species groups based largely on differences in subdigital toe scansor morphology (Brown & Parker 1977). Species in Group I possess undivided scansors, whereas those in Groups II and III have some or all of their scansors divided. Group II species have divided proximal scansors, with the terminal scansors undivided, whereas Group III species have divided terminal scansors. Other characters, such as the presence of a serrated and depressed tail, were used by Brown and Parker (1977) to distinguish Group II and Group III species. Group I comprises *L. listeri* (Boulenger, 1888), *L. magnus* Brown & Parker, 1977, *L. manni* Schmidt, 1923, *L. mutahi* Brown & Parker, 1977, *L. oorti* (Kopstein, 1926), *L. orientalis* Brown & Parker, 1977, *L.*

pumilus (Boulenger, 1885a), *L. browni* Pernetta & Black, 1983, *L. euaensis* Gibbons & Brown, 1988, and *L. flaviocularis* Brown, McCoy & Rodda, 1992. Group II contains *L. gardeneri* Boulenger, 1897, *L. guppyi* Boulenger, 1884, *L. novaeguineae* Brown & Parker, 1977, *L. pulcher* Boulenger, 1885b, *L. shebae* Brown & Tanner, 1949, *L. buleli* Ineich, 2008, *L. intermedius* Darevsky, 1964, *L. lombocensis* Mertens, 1929, *L. paurolepis* Ota, Fisher & Ineich, 1995, *L. vanatuensis* Ota, Fisher, Ineich, Case, Radtkey & Zug, 1998, *L. oligoporus* Buden, 2007, *L. tepukapili* Zug, Watling, Alefaio, Alefaio & Ludescher 2003, and *L. ranauensis* Ota & Hikida Ota & Hikida, 1988. Group III includes *L. moestus* (Peters, 1867), *L. lugubris* (Duméril & Bibron, 1836), *L. woodfordi* Boulenger, 1887, *L. yami* Ota, 1987, *L. aureolineatus* Taylor, 1915, *L. balioburius* Ota & Crombie, 1989, *L. christiani* Taylor, 1917, *L. herrei* Taylor, 1923, and *L. planicaudus* Stejneger, 1905.

Though Groups I, II, and III sensu Brown & Parker 1977 are differentiated on the basis of scissor morphology, it remains unclear whether the groups are monophyletic. This seems particularly relevant given that a recent study has demonstrated the polyphyly of *Lepidodactylus*, with both *Luperosaurus* (Gray, 1845) and *Pseudogekko* (Taylor, 1922) nested within the larger *Lepidodactylus* clade (Heinicke *et al.* 2012). Heinicke *et al.* (2012) did not discuss the implications of their phylogenetic study with respect to the monophyly of the *Lepidodactylus* groups, but their results, and those of Brown *et al.* (2012), definitively show that the *Lepidodactylus*-*Luperosaurus*-*Pseudogekko* clade is in need of taxonomic revision. Furthermore, the phylogenetic estimate provided by Heinicke *et al.* (2012) suggests that the *Lepidodactylus* Groups are likely non-monophyletic (e.g., *L. orientalis* [Group I] far removed from *L. manni* and *L. euaensis*), albeit with weak branch support.

In this paper, we describe a new species of *Lepidodactylus* which, at present, is known only from two of the Kei Islands, Maluku Province, eastern Indonesia. Based on scissor morphology, the new species appears to be a member of Group III, although it differs from all members of this group in having a nearly round tail without fringes or dorsoventral compression. For this description, we take an integrative approach utilizing molecular and morphological data. We include in our molecular analysis representatives of described species for which tissue samples are available, and two additional samples of other currently undescribed *Lepidodactylus* obtained during our field expeditions to Indonesia. Herein, we provide the most comprehensive phylogenetic analysis of the *Lepidodactylus*-*Luperosaurus*-*Pseudogekko* clade yet undertaken by combining the data of Brown *et al.* (2012) and Heinicke *et al.* (2012), and then supplementing these published data with new DNA sequence data generated for undescribed Indonesian *Lepidodactylus* species obtained via our own fieldwork.

Materials and methods

Specimens were field-collected in Indonesia by ALS, BRK and UA in accordance with all pertinent Indonesian laws under a research permit under principal investigator Prof. Jimmy A. McGuire (JAM) through Kementerian Riset, Teknologi, dan Pendidikan Tinggi Republik Indonesia. Animals were sacrificed via intracardiac injection of nembutal in accordance with JAM's IACUC authorization (UC Berkeley), a liver tissue sample was taken, and specimens were fixed in 10% neutrally buffered formalin for approximately one month, rinsed in water, and finally transferred to 70% ethanol for permanent storage approximately one month after collection.

Measurements and scale nomenclature follow Ineich (2008), and include snout–vent length (SVL) measured from the rostral scale to the cloacal opening; head length measured from the anterior margin of the ear opening to the tip of the snout; head width measured at the widest part of the temporal region; head depth measured at the tallest part of the temporal region; jaw length measured from posterior border of jaw to tip of snout; snout–eye length measured from the anterior border of the orbit to the tip of the snout; naris–eye length measured from the anterior border of the orbit to the posterior margin of the naris; eye–ear length measured from the posterior of the orbit to the anterior of the auricular opening; snout width measured as the distance between the nostrils; interorbital width measured from the dorsal-most point between the orbits; snout–forelimb length measured from the anterior margin of the forelimb insertion to the tip of the snout; axilla–groin distance measured from the posterior margin of the forelimb insertion to the anterior margin of the hind limb insertion; tail width and tail depth measured at the widest point after the constriction in the tail. Midbody scale rows were counted as the number of longitudinal scale rows encircling the body at a point midway between the limb insertions. Head scale counts were performed by both ALS and BRK using both a dissecting scope and digital photographs of the specimens taken with appropriate lighting to increase contrast and confirmed on both sides of the body (noted when different). All measurements are presented in mm (to the nearest 0.1 mm), and were obtained with Mitutoyo digital calipers.

We sequenced 1011 bp of the NADH Dehydrogenase Subunit 2 (*ND2*) mitochondrial gene. Genomic DNA was extracted as described in Aljanabi & Martinez (1997) followed by polymerase chain reaction (PCR) using forward primer METF1 (5'-AAGCTTTCGGGCCCATACC-3') of Macey *et al.* (1997) and reverse primer CO1R1 (5'-AGRGTGCCAATGTCTTTGTGRTT-3') of Arevalo *et al.* (1994) under standard conditions. PCR was followed by enzyme clean-up, cycle sequencing using BigDye v3.1 chemistry, and analysis on an ABI3730xl capillary sequencer.

We generated contigs of DNA reads and corrected them for sequencing errors, then aligned the new sequences to all published *Lepidodactylus* ND2 sequences on GenBank (see Table 1). We determined the best partitioning scheme using PartitionFinder v1.1.1 (Lanfear *et al.* 2012) searching for the scheme with the best BIC value. Following the results of PartitionFinder, we treated each codon position as a separate partition for phylogenetic analyses. Phylogenetic analyses were performed in RAXML v8.1.15 (Stamatakis 2006), with 100 rapid bootstrap replicates, and using the GTRCAT model of evolution for each partition.

TABLE 1. List of samples and GenBank accession numbers used for phylogenetic analysis. Abbreviations: ABTC = Australian Biological Tissue Collection, South Australian Museum, ACD = Arvin Diesmos field series, specimen deposited at the National Museum of the Philippines, AMB = Aaron M. Bauer field series, BPBM = Bernice P. Bishop Museum, CAS = California Academy of Sciences Herpetological Collections, HOFH = Hidetoshi Ota genetic samples deposited in the Museum of Nature and Human Activities, University of Hyogo, Japan, ID = Indraneil Das, JAM = Jimmy A. McGuire field series, specimen deposited in the Museum Zoologicum Bogoriense (National Museum of Indonesia, Cibinong, Java), JB = Jon Boone captive collection, JFBM = James Ford Bell Museum of Natural History, KU = University of Kansas Natural History Museum, LSUHC = La Sierra University Herpetological Collections, MNHN = National Museum of Natural History (France), MVZ = Museum of Vertebrate Zoology, MZB = Museum Zoologicum Bogoriense (National Museum of Indonesia, Cibinong, Java), NNUZ = Nanjing Normal University, P = Pui Yong Min field series, deposited at UNIMAS, PNM = Philippine National Museum, RMB = Rafe Brown field number, uncataloged specimen deposited at the National Museum of the Philippines, TNHC = Texas Natural History Collections, University of Texas at Austin, USNM = United States National Museum, ZRC = Zoological Reference Collection, Raffles Museum of Biodiversity Research, Singapore.

Species	Voucher	GenBank Accession
<i>Lepidodactylus pantai</i> sp. nov.	MVZ273692	KY794934
<i>Lepidodactylus pantai</i> sp. nov.	MZB.Lace.14064	KY794935
<i>Lepidodactylus</i> sp.	MZB.Lace.14063	KY794933
<i>Lepidodactylus</i> sp.	MZB.Lace.14062	KY794932
<i>Lepidodactylus euaensis</i>	USNM322126	JX515611
<i>Lepidodactylus guppyi</i>	MNHN2004.0094	JX515612
<i>Lepidodactylus herrei</i>	RMB4330	JQ173539
<i>Lepidodactylus lugubris</i>	ABTC50488	GQ257746
<i>Lepidodactylus lugubris</i>	MVZ247594	JX515614
<i>Lepidodactylus lugubris</i>	CAS198394	JX515613
<i>Lepidodactylus lugubris</i>	ZRC24847	JN393944
<i>Lepidodactylus manni</i>	USNM322638	JX515615
<i>Lepidodactylus moestus</i>	USNM521730	JN019079
<i>Lepidodactylus moestus</i>	USNM.FS	JX515616
<i>Lepidodactylus novaeguineae</i>	BPBM15842	JX515617
<i>Lepidodactylus orientalis</i>	BPBM19794	JN019080
<i>Lepidodactylus</i> sp MPH2012	USNM533293	JX515620
<i>Lepidodactylus</i> sp MPH2012	ACD1226	JX515618
<i>Lepidodactylus</i> sp MPH2012	USNM531971	JX515619
<i>Lepidodactylus vanuatuensis</i>	MNHN2008.0052	JX515622
<i>Lepidodactylus vanuatuensis</i>	USNM323265	JX515621

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TABLE 1. (Continued)

Species	Voucher	GenBank Accession
<i>Luperosaurus anglii</i>	KU322189	JQ437903
<i>Luperosaurus cumingii</i>	RMB3546	JX515623
<i>Luperosaurus cumingii</i>	TNHC61910	JQ437902
<i>Luperosaurus iskandari</i>	MZB2114	JQ437906
<i>Luperosaurus joloensis</i>	KU313978	JQ437900
<i>Luperosaurus macgregori</i>	KU314021	JQ437905
<i>Luperosaurus macgregori</i>	KU304797	JQ437904
<i>Luperosaurus macgregori</i>	KU304850	JX515624
<i>Luperosaurus</i> sp CDS2012	ACD6021	JQ437901
<i>Pseudogekko brevipes</i>	KU302818	KF875323
<i>Pseudogekko brevipes</i>	KU327770	KF875324
<i>Pseudogekko brevipes</i>	RMB3282	KF875325
<i>Pseudogekko compressicorpus</i>	ACD7577	KF875331
<i>Pseudogekko compressicorpus</i>	ACD7637	KF875332
<i>Pseudogekko compressicorpus</i>	KU314963	KF875339
<i>Pseudogekko compressicorpus</i>	KU314964	KF875341
<i>Pseudogekko compressicorpus</i>	KU324426	JQ437898
<i>Pseudogekko compressicorpus</i>	KU326242	KF875340
<i>Pseudogekko compressicorpus</i>	KU326243	KF875335
<i>Pseudogekko compressicorpus</i>	KU326434	KF875336
<i>Pseudogekko compressicorpus</i>	KU326435	KF875334
<i>Pseudogekko compressicorpus</i>	KU326437	KF875333
<i>Pseudogekko compressicorpus</i>	KU330058	KF875327
<i>Pseudogekko compressicorpus</i>	KU330735	KF875337
<i>Pseudogekko compressicorpus</i>	KU331657	KF875338
<i>Pseudogekko compressicorpus</i>	PNM1460	KF875328
<i>Pseudogekko compressicorpus</i>	RMB4365	JX515625
<i>Pseudogekko smaragdinus</i>	JAM973	KF875345
<i>Pseudogekko smaragdinus</i>	KU302819	JQ437897
<i>Pseudogekko smaragdinus</i>	KU302820	KF875343
<i>Pseudogekko smaragdinus</i>	KU302821	KF875344
<i>Pseudogekko smaragdinus</i>	KU303995	JX515626
<i>Pseudogekko smaragdinus</i>	KU307641	KF875346
<i>Pseudogekko smaragdinus</i>	KU313828	KF875342
<i>Pseudogekko smaragdinus</i>	KU326240	KF875347
<i>Pseudogekko smaragdinus</i>	KU326241	KF875348
<i>Gekko athymus</i>	KU309335	JQ173403
<i>Gekko auriverrucosus</i>	NNUZ20050716.004	JN019062
<i>Gekko badenii</i>	JB13	JN019065
<i>Gekko chinensis</i>	LSUHC4210	JQ173409
<i>Gekko crombota</i>	KU304825	JQ173410
<i>Gekko gecko</i>	CAS204952	JN019052

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TABLE 1. (Continued)

Species	Voucher	GenBank Accession
<i>Gekko grossmanni</i>	JFBM9	JN019064
<i>Gekko japonicus</i>	HOFH10061402	JQ173424
<i>Gekko mindorensis</i>	KU302668	JN710490
<i>Gekko monarchus</i>	ACD1278	JQ173501
<i>Gekko petricolus</i>	JB70	JN019066
<i>Gekko porosus</i>	PNM9532	FJ487880
<i>Gekko romblon</i>	KU315348	JN710497
<i>Gekko rossi</i>	KU304876	FJ487871
<i>Gekko smithii</i>	ID8774	JN019054
<i>Gekko subpalmatus</i>	AMB6567	JN019063
<i>Gekko swinhonis</i>	NNUZ20051124.001	JN019061
<i>Gekko vittatus</i>	JAM2171	JQ437899
<i>Ptychozoon kuhli</i>	RMB1134	JQ437918
<i>Ptychozoon lionotum</i>	CAS221168	JQ437914
<i>Ptychozoon rhacophorus</i>	P0500	JQ437913
<i>Nactus sphaerodactylodes</i>	BPBM20759	EU054196

For this study, we define a species using the General Lineage Concept of (de Queiroz 1998, 1999) as an extension of the Evolutionary Species Concept (Wiley 1978), for which phenotypically divergent populations represent distinct and separately evolving lineages. We diagnose a new species based on the possession of non-overlapping morphological characters when compared to closely related species. We corroborate this morphological evidence using genetic data.

Systematics

Lepidodactylus pantai, new species

(Figures 2,3,4)

Holotype. (Museum Zoologicum Bogoriense.Lace.14062, Field number ALS 534) An adult male collected by ALS, BRK, and UA from beachside rocks at Pasir Panjan Beach, Desa Ohoililir, Kei Kecil, Maluku, Indonesia a few hours after sunset at 5.646671° S, 132.638312° E (WGS84) on 16 October, 2011. Liver tissue is preserved in duplicate in RNA-Later at Museum Zoologicum Bogoriense (MZB.Lace.14062) and Museum of Vertebrate Zoology (MVZ 273691).

Paratypes. A series of ten additional specimens were collected at the same locality and time as the holotype (MVZ tissue number and field number in parenthesis): MZB.Lace.14064 (MVZ 273686; ALS 502), MZB.Lace.14065 (MVZ 273687; ALS 505), MZB.Lace.14066 (MVZ 273688; ALS 530), MZB.Lace.14067 (MVZ 273689; ALS 531), MZB.Lace.14068 (MVZ 273690; ALS 533), MVZ 273692 (ALS 501), MVZ 273693 (ALS 503), MVZ 273694 (ALS 504), MVZ 273695 (ALS 532), MVZ 273696 (ALS 535).

Diagnosis. A moderate-sized bisexual species of *Lepidodactylus*, SVL 36.9–40.5 (mean = 38.3) mm for five adult males and 32.0–40.5 (mean = 37.4) for five adult females, distinguished from other species by the following combination of characters: 113 rows of scales around the midbody; subdigital scansors 10–12 on toe IV, and 7–9 on toe I; terminal scansor is divided on digits II through V on both the fingers and toes; 3 scansors on 4th toe divided or deeply notched; interdigital webbing small, less than 1/5th the 4th toe length; 18–24 pores in precloacal and femoral regions of male. Tail nearly cylindrical without lateral serrations.

Description of holotype. MZB.Lace.14062 (measurements in mm, after preservation). Snout–vent length 40.57; head length 11.74; head width 7.56; head height 4.48; jaw length left/right 6.06/6.34; snout–eye length 4.54; naris–eye length 3.13; naris circular, approximately 0.4×0.5; orbit diameter 2.46; eye–ear length 3.38; snout width

1.78; ear opening length×width 0.62×0.41; interorbital width 4.00; snout–forelimb length 14.13; axilla–groin distance 20.05; length of hind limb 15.13 (75.5 % of axilla–groin distance); length of forelimb 10.95; crus length 6.41; tail length 24 (entire); tail width 4.34; tail depth 3.88.

Snout tapered, rounded at tip; three scales touching rostral between left and right nares; supranasals separated by three scales in contact with rostral; rostral entering nares, broader than high, 2.05×0.89 (width about 2.3 times height); no rostral cleft; nares bordered by five scales: three nasals, one rostral, and one supralabial; 34–35 interorbital scales; 11 left and 11 right supralabials, 10th below center of eye; 10 left and 10 right infralabials; mental scale distinct, triangular, its anterior width nearly equal to midline length (0.69×0.72); Mental is bordered posteriorly by two enlarged primary postmentals, each in contact with the first infralabial.

Body slightly depressed; 113 rows of scales (average of 3 counts: 109, 114, 116) around midbody, grading into granular scales on lower lateral surfaces; dorsal and lateral scales granular, without enlarged tubercles; ventral scales almost flat, hexagonal, and 2–3 times larger than dorsal scales; limbs well developed; digits moderately dilated, undersurface (Fig. 3) bearing left/right scansors as follow: fingers—I 9/9, II 9/10, III 12/12, IV 13/13, V 9/9; toes—I 10/(not intact), II 11/11, III 14/14, IV 12/12, V 9/9; distal three scansors, including the terminal one, divided on all digits except the first on fingers and toes; first digit with complete terminal and two divided subterminal scansors; all digits except first with 3 undivided or deeply notched scansors, including the terminal; all digits except first clawed; compressed claw-bearing phalanges arising from distal margin of the dilated part and extending only a short distance beyond; slight webbing 1/6th of the length of the 4th toe; digits elongate and slender, toe pads slightly enlarged.

Twenty five enlarged precloacal and femoral scales; two post-cloacal spurs on each side of vent; tail entire, subcylindrical throughout length, gradually tapering to a blunt tip; lateral margins without spines or skin flanges; tail constricted at base posterior to vent; scales on tail annulate, squarish or rectangular, ventral scales about twice as large as dorsal scales; base of tail distinctly swollen by hemipenes; hemipenes everted, forked with small, flared scales on the midbody of each forked end, transitioning into even smaller distal scales about half the size.

Color in preservative. Color of holotype after about three years in ethanol is similar to coloration in life (Fig. 2). Overall dorsal coloration is pale grey with some lateral streaks of darker pigment. Two pairs of dark spots are clearly visible on the dorsal surface of tail. Venter of body pale cream in color with no distinct pigmentation. Ventral surface of tail slightly darker posteriorly. Slight dark spotting on the dorsal surface of the head. A brown orbital stripe extends from the nostril to the anterior insertion of the forelimb. Three elongated spots on dorsal surface of body between the insertions of the forelimbs.

Variation. The type series varies in SVL (20.6–40.5; n=11), number of precloacal pores in males (17–25; n=5), number of scansors on Toe IV (10–12, n=11), number of lamellae on Toe I (7–9, n=11), number of supralabials (11–14, n =11), number of infralabials (9–11, n=11), head width as a proportion of SVL (18–21%, n=11), and number of scale rows around the midbody (108–127, n=11). Nearly all specimens have two cloacal spurs, however two specimens have an additional cloacal spur on one side of the body. All specimens have three divided terminal scansors. Both males and females of the type series possess enlarged, pale-white, endolymphatic sacs, which are more pronounced in females.

Coloration is similar among the type series (Fig. 4), however patterning is somewhat variable. Some specimens possess distinct dark chevron patterning along the dorsal surface of the body. All members of the type series have three elongate dark spots on the dorsal surface of the body between the insertions of the forelimbs. The lateral surfaces of some specimens have darker brown pigmentation, with a pale cream dorsal band running from the temporal region posterior to the base of the tail. The orbital stripe is variable in conspicuousness, though all specimens possess it to some degree.

Coloration in life (Fig. 2) is very similar to that in preservative (Fig. 4), however some of the darker regions also contain reddish pigment that has been lost in preservation. As with many geckos, these individuals change their level of pigmentation with time of day and light environment. Figure 2 shows a color photograph of this species *in situ* (specimen uncollected) from the type locality taken on a more recent expedition in 2014.

Distribution. The type series are all from Kei Kecil, however we recently collected another series of specimens from Kur Island (~80 km to the northwest) that appears morphologically similar, however further analysis is needed to determine the level of divergence between these two populations. Our phylogeny also indicates that specimens from Palau are remarkably similar genetically but we refrain from assigning members of that population to this species at present time.

Natural history. We have experience with this species only on two islands, Kei Kecil and Kur. Specimens were associated with exposed intertidal limestone rock formations in both cases (see Fig. 1; habitat).



FIGURE 1. Habitat of *L. pantai* sp. nov. at the type locality on Kei Kecil. Specimens were found exclusively in association with limestone rocks in the intertidal zone.

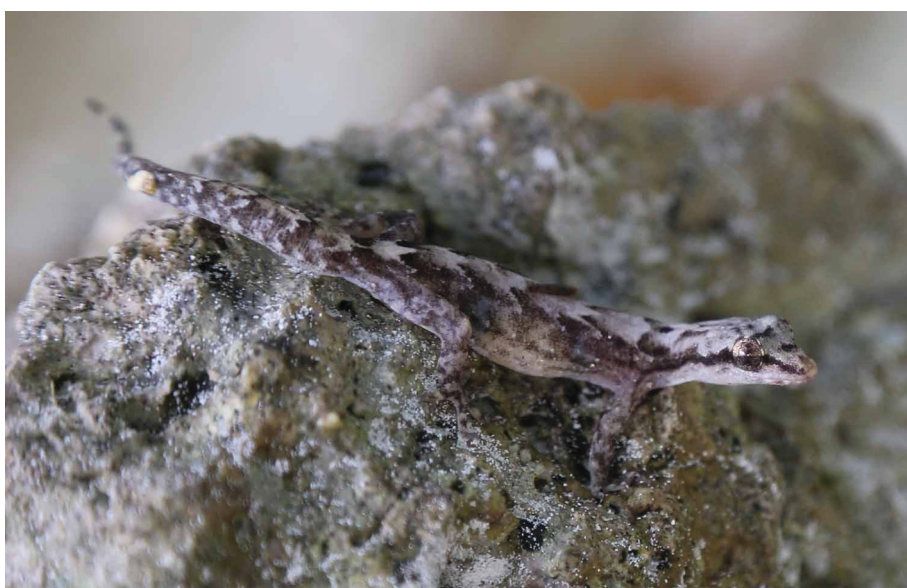


FIGURE 2. Photo in life of *Lepidodactylus pantai* sp. nov. from the type locality. (Photo by LMB, 2014).



FIGURE 3. Plantar view of the right foot of the holotype (MZB.Lace.14069). Note the 3 divided terminal scaps on toes 1-4.

All specimens were found at night on beachside limestone rocks (Fig. 1) or in mangroves within meters of the high tide line. Despite nearly a month of intensive nightly collecting effort (targeting geckos) on Kei Kecil we were unable to find this species in the adjacent disturbed forest. While on Kei Kecil, we resided in a small house approximately 30 meters from the high tide line and collected many other species of geckos on a small wooden shed but *L. pantai* **sp. nov.** were never encountered on this structure. This species was discovered accidentally at the end of our stay on Kei Kecil while surveying for laticaudine sea snakes in the intertidal zone. We think this shows the potential importance of sampling intertidal areas at night, something rarely done by herpetologists. All 11 specimens in the type series were collected over the span of less than one hour, and subsequent visits to Kei Kecil confirmed that this species is locally abundant, occasionally in densities of up to 1 individual per square meter. Terrestrial hermit crabs and marine isopods were also abundant on the same rocks and we believe this resource subsidy of food from the marine environment likely contribute to the locally high densities observed in this species.

On Kur island, only 80 km northwest of Kei Kecil, morphologically similar geckos were also found in association with the intertidal zone and limestone rocks, but they were also numerous in a small patch of mangroves. The roots of these mangroves were submerged during high tide, but specimens were found at an even higher density on mangroves than on exposed limestone rocks (though the small mangroves were themselves growing among limestone rocks). When associated with mangroves, this species appeared to be very abundant close to the water, but trees slightly above the high-tide line were inhabited almost exclusively by another undescribed species of *Lepidodactylus* and members of the gekkonid genus *Cyrtodactylus*.



FIGURE 4. Dorsal color pattern variation in the type series. Specimen tags overlaid with museum accession numbers.

Etymology. The species epithet, *pantai*, is the word for beach in the Indonesian national language (Bahasa Indonesia). It reflects the habitat in which the new species was discovered—a seemingly obligate association with the seashore. All specimens were found within 2 m of the high tide line. We suggest “Beach Scaly-toed Gecko” as the English common name for this species.

Comparisons. The new species is the only member of the genus with divided terminal 4th toe scansors and a cylindrical tail without lateral serrations. Brown & Parker (1977) divided the genus *Lepidodactylus* into three groups but *L. pantai* **sp. nov.** differs from all of the previously recognized groups in having divided terminal scansors on toes 2–5 and a tail that is fully cylindrical without any fringes or compression.

The presence of divided scansors distinguishes *L. pantai* **sp. nov.** from all Group I *Lepidodactylus* (*L. listeri*, *L. magnus*, *L. manni*, *L. mutahi*, *L. oorti*, *L. orientalis*, *L. pumilus*, *L. browni*, *L. euaensis*, and *L. flaviocularis*), which have no divided scansors (Brown & Parker 1977). The presence of divided terminal scansors on toe IV distinguishes *L. pantai* **sp. nov.** from all Group II *Lepidodactylus* which have undivided terminal scansors (*L. gardeneri*, *L. guppyi*, *L. novaeguineae*, *L. pulcher*, *L. shebae*, *L. buleli*, *L. intermedius*, *L. lombocensis*, *L. paurolepis*, *L. vanatuensis*, *L. oligoporus*, *L. tepukapili*, and *L. ranauensis*). The presence of a cylindrical tail without lateral serrations distinguishes *L. pantai* **sp. nov.** from Group III *Lepidodactylus* that have depressed tails with lateral serrations (*L. moestus*, *L. lugubris*, *L. woodfordi*, *L. yami*, *L. aureolineatus*, *L. balioburius*, *L. christiani*, *L. herrei*, and *L. planicaudus*). Lateral serrations are sometimes absent on *L. yami* (Ota 1987), but *L. pantai* **sp. nov.** can be further distinguished from *L. yami* by the number of scansors on Toe IV (10–12 in *L. pantai* **sp. nov.** versus 13–15 in *L. yami*) and the number of midbody scale rows (108–127 in *L. pantai* **sp. nov.** versus 145–148 in *L. yami*).

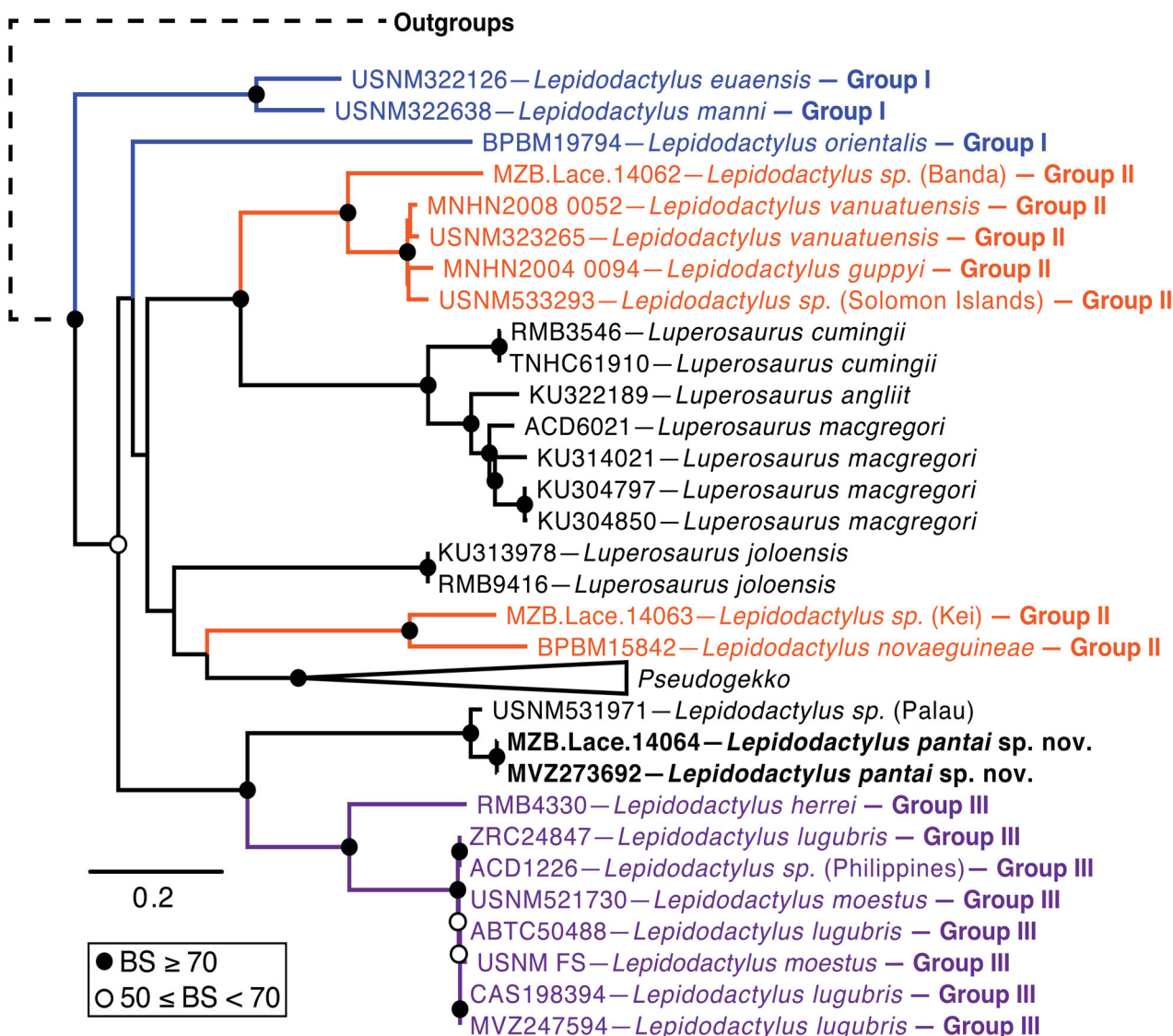


FIGURE 5. Maximum likelihood phylogram of mitochondrial ND2 for the *Lepidodactylus* complex with bootstrap support shown by closed circles (BS ≥ 70), open circles (50 ≤ BS < 70) and no circle (BS < 50). Group I (blue), Group II (orange) and Group III (purple) are colored to emphasize instances of non-monophyly. The new species is indicated in bold.

Results and discussion

Our phylogenetic analysis is concordant with previous results (Heinicke *et al.* 2012) in supporting *Lepidodactylus* as polyphyletic with respect to *Pseudogekko* and *Luperosaurus*. Philippine *Pseudogekko* and *Luperosaurus* are nested within the *Lepidodactylus* complex and the three genera clearly require a comprehensive taxonomic revision. Doing so will call for the creation of new genera or the synonymy of *Pseudogekko* and *Luperosaurus* with *Lepidodactylus*. Interestingly, the Philippine lineages currently placed in *Pseudogekko* and *Luperosaurus* are recognized as morphologically distinctive compared to *Lepidodactylus sensu stricto* (Brown *et al.* 2012), indicating that there may exist disparate rates of morphological evolution across the tree. Because the phylogeny remains unresolved regarding the higher-order relationships within this group and would benefit from greater taxon sampling, we refrain from making any taxonomic recommendations for the group as a whole.

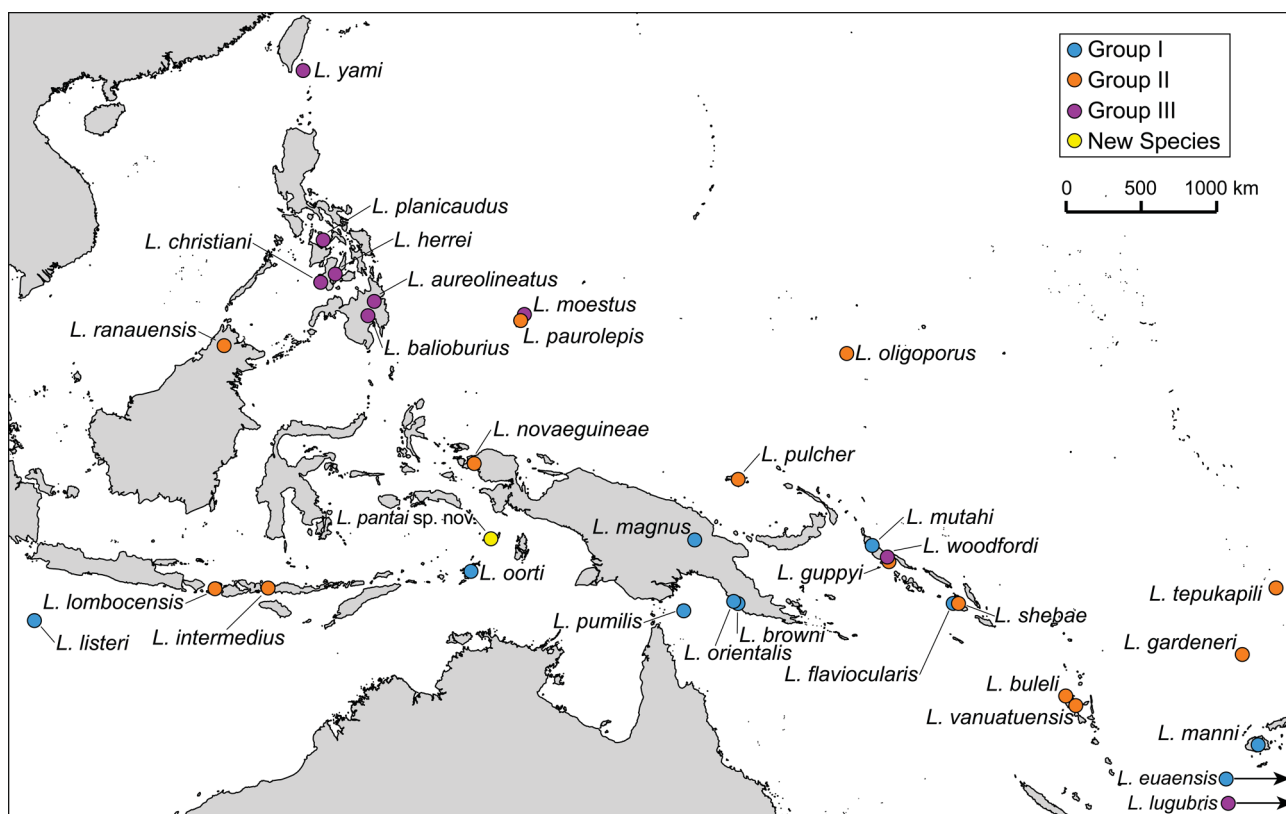


FIGURE 6. Southeast Asia, Australasia, and Pacific islands with type localities of all species of *Lepidodactylus* included. Dots do not represent entire distributions of each species, and many have overlapping ranges. Type localities for *L. euaensis* (Tonga) and *L. lugubris* (Tahiti) are not shown in map limits, but are denoted by arrows pointing to the East. The type locality of *L. pantai sp. nov.* (Kei Kecil) is shown by a yellow dot. The historical *Lepidodactylus* species groups are denoted by colored dots, with Group I (Blue), Group II (Orange), and Group III (Purple). Note that these species groups do not necessarily represent monophyletic groups (see Discussion). The nearest relative of *L. pantai sp. nov.* is in Palau, which is also the type locality for both *L. moestus* and *L. paurolepis*.

Our phylogenetic results (Figure 5) suggest that members of the *Lepidodactylus*-*Luperosaurus*-*Pseudogecko* clade have dispersed multiple times to distant oceanic islands (Fig. 6). With the inclusion of additional sampling in Eastern Indonesia, we find that species groups previously associated with Pacific islands have close relationships to species within Indonesia. For example, another specimen (MZB.Lace.14063), representing an additional undescribed species on Kei, is the extremely divergent sister taxon (18.7% uncorrected patristic-distance) of *L. novaeguineae* from Papua New Guinea. Another individual collected from the nearby Banda Islands (MZB.Lace.14062) shows deep divergence (17.7–18.5% uncorrected p-distance) from its sister clade composed of other geographically distant Group II species (*L. vanuatuensis* from Vanuatu; *L. guppyi* from the Solomon Islands). In contrast, *L. pantai sp. nov.*, is geographically isolated from Palau by approximately 1500 km, and separated by the intervening Bird's Head Peninsula of New Guinea, yet is significantly less divergent (6.2% uncorrected p-distance). Because gene flow between Palau and the Kei Islands is extremely unlikely, we consider these two populations may well represent distinct species, however we have not investigated in this study the possible morphological differences between the new species described here and their close relatives from Palau. This sequence divergence allows for a rough estimate of divergence time following an estimate of 0.47% change per lineage per million years for the ND2 gene (Portik *et al.* 2011), and indicates that the two lineages likely diverged approximately 6 million years ago. Our results highlight how effective multiple lineages of *Lepidodactylus* have been at dispersing out of Southeast Asia to extremely distant islands. Our study also highlights how additional sampling from Eastern Indonesia may be pivotal to fully understand the evolutionary relationships of the Pacific island populations in the genus.

Lepidodactylus sensu stricto has been traditionally separated into three groups based on shared morphology, primarily based on characters associated with their toe scansors (Brown & Parker 1977). Though the majority of

sequences in our phylogeny have been previously published (Heinicke *et al.* 2012, Brown *et al.* 2012) the genetic relationships have never been discussed in the context of the *Lepidodactylus* species groups proposed by Brown & Parker (1977). Combining the mitochondrial data from these two studies and supplementing with new data collected for this analysis, we are able to make a preliminary assessment regarding the evolutionary relationships between the three recognized groups of *Lepidodactylus* with respect to *Luperosaurus* and *Pseudogekko*, though we expect that increased taxon sampling and comprehensive sampling of nuclear genes may resolve the relationships between these species and genera that appear to have rapidly radiated.

The paraphyly of *Lepidodactylus* with respect to *Pseudogekko* and some species currently regarded as *Luperosaurus* has been previously recognized, but our analysis and others (Heinicke *et al.* 2012) provide strong support for the monophyly of *Luperosaurus* (except for the Philippines species *L. gulat* Brown, Diesmos, Duya, Garcia, & Rico, 2010 and the Sulawesi species *L. iskandari* Brown, Supriatna, & Ota, 2000 as noted by Brown *et al.* 2012), *Pseudogekko*, and *Lepidodactylus* relative to other gekkonids.

With respect to Group I, our analysis recovers *Lepidodactylus euaensis* and *L. manni* as sister taxa, but shows low support for the placement of *L. orientalis*. The topology does provide support for Russell's (1972) hypothesis (later elaborated on by Brown & Parker 1977) that undivided scansors represent the ancestral state and that Groups II and III represent more derived forms as the assemblage expanded into Wallacea (Russell, 1972).

Brown & Parker's (1977) Group II clade of *Lepidodactylus vanuatuensis*, *L. guppyi*, and an undescribed species from the Banda Islands of Indonesia are recovered as the well-supported sister group to *Luperosaurus cumingii* Gray (1845), *Luperosaurus angliit* Brown *et al.* (2011), and *Luperosaurus macgregori*, Stejneger (1907), whereas other members of Group II (*L. novaeguineae* and an additional undescribed species from Kei) are placed elsewhere on the tree.

Group III is the only group of *Lepidodactylus* that we found to be monophyletic. However taxon sampling is low in this clade, with only three of the nine currently recognized species having been sampled. *Lepidodactylus pantai* **sp. nov.** is supported as sister to a population of *Lepidodactylus* collected on Palau (Crombie 1999), and these samples together are supported as sister to all of Group III *Lepidodactylus*. The morphological features of *L. pantai* **sp. nov.** do not place it in any of the traditionally defined species groups proposed by Brown & Parker (1997); it shares divided terminal scansors with Group III and cylindrical to semi-cylindrical tail (without lateral serrations) with Group II. One other species previously placed within Group III, *L. yami*, has a tail that sometimes lacks lateral serrations and is only slightly depressed in shape (Ota 1987). Given the genetic placement of *L. pantai* **sp. nov.** as sister to species in Group III along with the shared toe scansor morphology, we tentatively assign the new species to Group III, however, we also emphasize the genetic-morphological inconsistencies associated with the *Lepidodactylus* species group nomenclature.

We hope that the identification of these additional new lineages in eastern Indonesia will stimulate more research in the area, and particularly provide an impetus to conduct herpetofaunal surveys along the intertidal zone at night.

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