

Systematics and biogeography of Lesser Sunda paddy frogs (Dicroglossidae: *Fejervarya*)

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ABSTRACT – The Lesser Sunda Archipelago is one of the world’s most tectonically complex regions and hosts a unique assemblage of amphibian species. Paddy frogs (genus *Fejervarya*) occur throughout the region, but the systematic position and distribution of each constituent species remains unclear. We present a set of comprehensive mtDNA and morphometric data on the three paddy frog species in the Lesser Sundas: *F. cancrivora*, *F. iskandari* and *F. verruculosa*. We clarify the phylogenetic position of *F. verruculosa*, placing it as the sister species of *F. cancrivora*. We also confirm that *F. iskandari* occur in the Lesser Sundas. Molecular data suggests that *F. cancrivora* is panmictic across Java and the Sunda Arc, while *F. verruculosa* and *F. iskandari* comprise multiple highly divergent populations within the Lesser Sundas. Phylogeographic results appear to support at least two natural colonisations of *Fejervarya* in the Lesser Sunda Archipelago, one by *F. iskandari* and one by *F. verruculosa*, whereas contemporary *F. cancrivora* populations likely arose from human-mediated movement. Our results demonstrate the biogeographic complexity of the Lesser Sunda Archipelago and identify key knowledge gaps in Lesser Sunda *Fejervarya*.

KEYWORDS: Amphibian, Mitochondrial DNA, Phylogeography, Species distribution, Wallacea

INTRODUCTION

The Lesser Sunda (LS) Archipelago is a chain of islands occupying the southern portion of Wallacea and home to biological communities distinct from neighbouring regions (Lohman et al. 2011; Ali and Heaney 2021). One factor leading to the region’s biological distinctiveness is that the LS Archipelago draws upon fauna from two zoogeographic continents: the Oriental region of the Sunda Shelf, dominated by mainland Asian species; and the Australo-Papuan region of the Sahul Shelf, dominated by Australian species (Ali and Heaney 2021; White et al. 2021). The intermediate Wallacean region acts as a two-way filter, containing its own unique transitional species and facilitating two-way

exchanges between zoogeographic continents (sensu Whittaker and Fernández-Palacios 2007). Recent genetic studies revealed that a number of wide-ranging reptile and amphibian species from the region documented solely based on morphology (e.g. Kaiser et al. 2011; O’Shea et al. 2012) actually comprise multiple species with localised distributions (Reilly et al. 2019a, 2022a, 2022b, 2022c, 2023), suggesting that true herpetofaunal diversity of the region is underestimated.

Geologically, the LS Archipelago can be divided into four distinct regions: 1) the eastern end of the volcanic Sunda Arc (Bali, Lombok, Sumbawa, Flores); 2) Sumba Island, an anomalous continental plate fragment (Abdullah et al. 2000); 3) the western end of the Inner Banda Arc (IB), consisting of the volcanic

islands of Pantar, Alor, Atauro, and Wetar; and 4) the western end of the Outer Banda (OB) Arc, consisting of the islands of Rote, Timor, and several islands that lie east of Timor (Figure 1). Portions of the volcanic Sunda Arc islands are thought to have become continuously emergent beginning 10–12 million years ago, while Sumba and the Banda Arcs first arose 3–5 million years ago (Hall 2011). Several of the larger Sunda Arc islands including Sumbawa and Flores likely formed as separate islets before coalescing into the larger islands (Muraoka et al. 2005; Lohman et al. 2011; Reilly et al. 2019a, 2022c). The intricate geologic history of the LS Archipelago presents an intriguing model system of animal dispersal and vicariance. Dispersal pathways between LS islands are thought to be influenced by ocean currents from the Indonesian throughflow and surface wind patterns. However, movement between islands is supplemented by human-mediated dispersal, including components of the herpetofauna (Brown 2010; Linkem et al. 2013; Reilly et al. 2017, 2019b). Human-mediated dispersal was likely facilitated by a sea-faring culture in the LS Archipelago, which has existed in the region for the last 40,000 years (O'Connor et al. 2011).

The genus *Fejervarya* Bolckay, 1915 currently consists of 14 Asian ground frog species (Frost 2024), three of which are found in the Lesser Sundas: *F. cancrivora* (Gravenhorst, 1829), *F. verruculosa* (Roux, 1911) and *F. iskandari* Veith et al., 2001. *Fejervarya cancrivora* are found throughout South-East (SE) Asia (Yodthong et al. 2019a), while *F. verruculosa* appears to be restricted to the Lesser Sunda (LS) archipelago and is morphologically similar to *F. cancrivora* (van Kampen 1923). *Fejervarya iskandari* was described by Veith et al. (2001) from West Java and was referred to as a Java Island endemic but has subsequently been found to occur in the LS Archipelago (Hasan et al. 2022). Taxonomic and phylogeographic relationships of *Fejervarya* west of Wallace's Line (Figure 1) has been thoroughly examined (Dubois and Ohler, 2000; Veith et al. 2001; Kotaki et al. 2008, 2010; Kurniawan et al. 2010, 2014; Köhler et al. 2019; Yodthong et al. 2019a), whereas *Fejervarya* east of Wallace's Line remains poorly understood with imprecisely-known species distributions. This is due to limited sampling in the LS Archipelago and the morphological conservatism of frogs of the genus *Fejervarya*, which makes species assignment challenging.

This study uses molecular and morphological data to delineate phylogeographic structure and systematic relationships of the three LS *Fejervarya* species, while evaluating the intraspecific molecular and morphological diversity. We also use our findings to hypothesise how both dispersal and human-mediated introduction explains the contemporary distributions of LS *Fejervarya* lineages.

MATERIALS AND METHODS

SAMPLE COLLECTION

Institutional acronyms: Western Australian Museum, Perth (WAM); Museum of Vertebrate Zoology, Berkeley (MVZ); Museum Zoologicum Bogoriense, Bogor (MZB); Institut Teknologi Bandung, Bandung (ITB).

Fejervarya tissues and vouchers were obtained from two sets of field surveys: one set conducted by WAM and MZB between 1988 and 1991 and another set conducted by MVZ, MZB, and ITB between 2010 and 2013 (Figure 2). This study uses both tissues and vouchers from the WAM 1988–1991 survey but only tissues (not vouchers) from the MVZ/MZB 2010–2013 surveys. All vouchers are housed at WAM or MVZ (Appendix Table 1). Liver, muscle, or heart tissues were obtained from specimens prior to formalin-fixation and stored in 70% ethanol or RNAlater in transit to WAM/MVZ. No audio recordings (site or individual) were taken. All vouchers were identified to species based on morphology or left unidentified and housed as *Fejervarya* sp. in their respective institutions.

MOLECULAR ANALYSES

Genomic DNA was extracted from liver tissue using either a salt extraction technique or using a Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California, USA). Mitochondrial COI gene sequences were generated from 329 WAM specimens by the University of Guelph (Ontario, Canada). A preliminary COI tree was generated in Barcode of Life Data (BoLD) Systems, version 4 (Ratnasingham and Hebert 2007; <https://www.boldsystems.org/>). Individuals with sequences of <200 bps were removed from the tree, leaving a total of 303 COI sequences. A portion of the 16S ribosomal RNA gene was PCR-amplified for all MVZ samples as well as a subset of 25 WAM specimens representing each major clade identified from preliminary analyses of the COI dataset. The 16S gene was amplified using the primers 16sc-L (5'-GTRGGCCTAAAAGCAGCCAC-3') and 16sd-H (5'-CTCCGGTCTGAACTCAGATGACGTAG-3') (Palumbi et al. 2002). PCR products were purified using ExoSAP-IT (USB, Cleveland, Ohio, USA) before being sequenced in both directions using cycle sequencing reactions with BigDye v3.1 (Applied Biosystems, Foster City, California, USA). The cycle sequencing reactions were then cleaned by ethanol precipitation before being sequenced on an ABI 3730 sequencer (Applied Biosystems). COI and 16S sequences from the same individuals were concatenated in GENEIOUS v11.1.5 (Biomatters Ltd.).

To place our samples into a broader phylogenetic context, additional 16S and COI sequence data from GenBank were downloaded for lineages of *Fejervarya cancrivora*; *F. iskandari*; *F. kawamurai* Djong et al., 2011; *F. limnocharis* (Gravenhorst, 1829); *F. moodiei* (Taylor, 1920); *F. multistriata* (Hallowell, 1861); and an

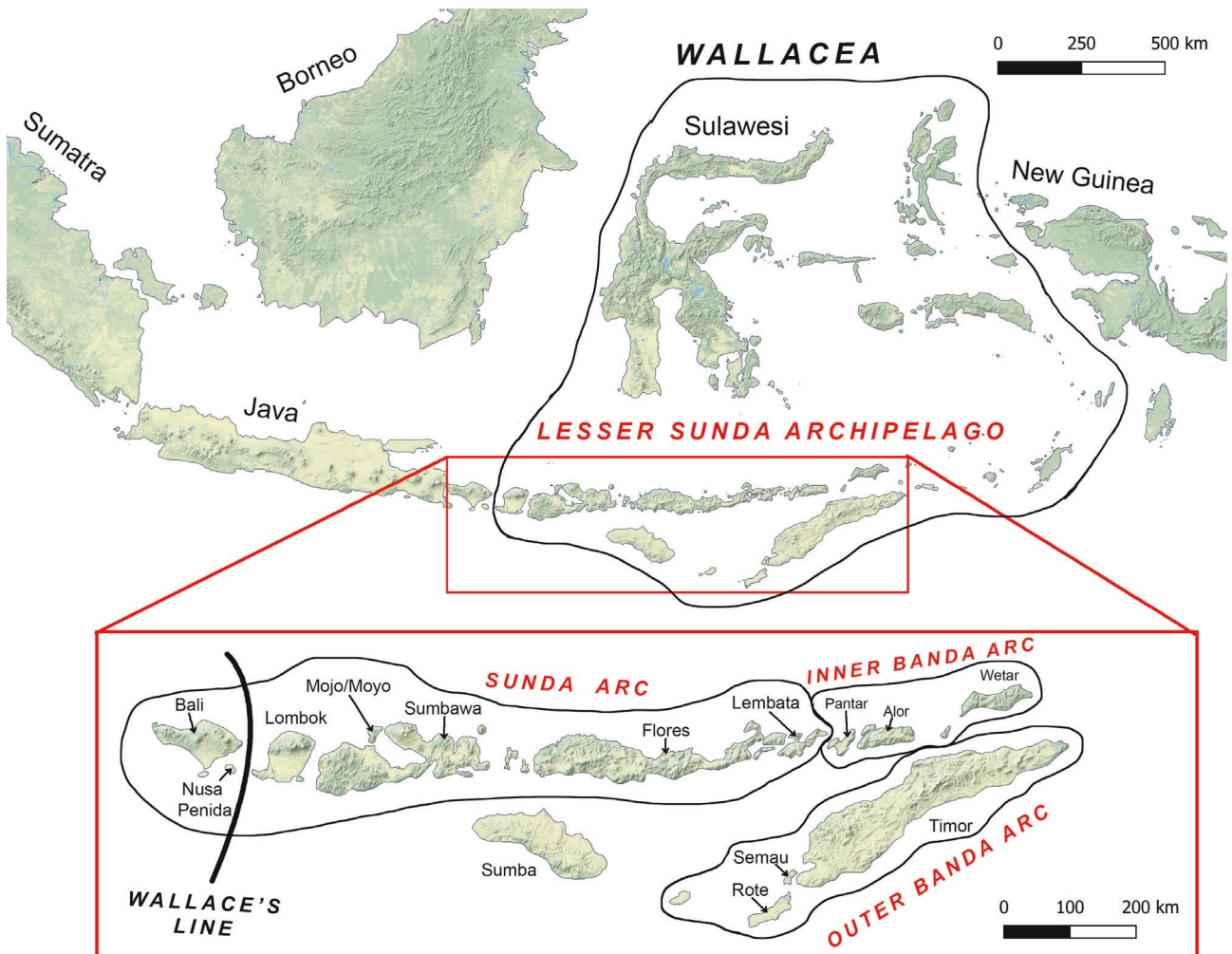


FIGURE 1 Map of Wallacea and the Lesser Sunda Archipelago (inset, within red box). All three island arcs and Wallace's Line extend beyond the Lesser Sundas, but these areas are not depicted in the inset map. Note: Sumba is not a part of an island arc but an anomalous continental fragment (Abdullah et al. 2000).

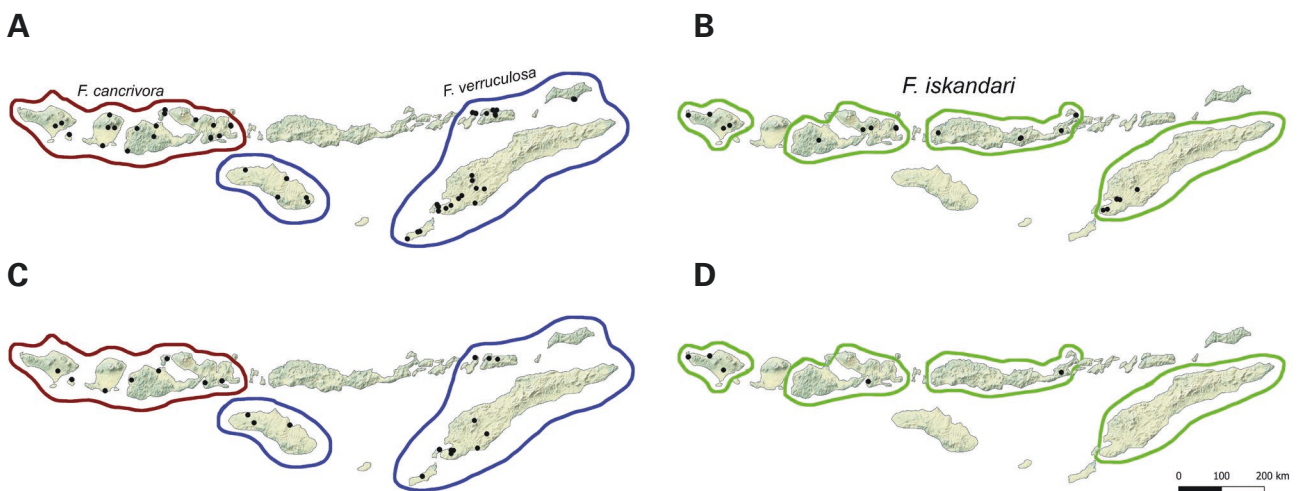


FIGURE 2 Molecular sampling localities: A) *Fejervarya cancrivora* (brown) + *F. verruculosa* (blue); B) *F. iskandari* (green). Morphological sampling localities: C) *F. cancrivora* (brown) + *F. verruculosa* (blue); D) *F. iskandari* (green).

outgroup of *Hoplobatrachus tigerinus* (Daudin, 1802) (Sumida et al. 2002; Chen et al. 2005; Liu et al. 2005; Che et al. 2007, 2009; Kotaki et al. 2008, 2010; Ren et al. 2009; Alam et al. 2010; Kurniawan et al. 2010, 2014; Matsui et al. 2010; Cheng et al. 2018; Jiang et al. 2020; Flury et al. 2021; Zhang et al. 2021) including sequence data from introduced and commercially-harvested *F. cancrivora* (Wostl et al. 2016; Ohler and Nicolas, 2017). These sequences are listed in Appendix Table 2. Taxonomic assignments of outgroup sequences follow the Yodthong et al. (2019a, 2019b) revision and corrigenda of mainland SE Asia *F. cancrivora* populations. GenBank sequences AB444963 and EU979849 were re-attributed to a divergent lineage within the *F. cancrivora* group which is commonly considered to be an undescribed species (Kurniawan et al. 2010; Yodthong et al. 2019a). We have followed these sources and treated them as the Sulawesi- (or Pelabuhan Ratu-) *F. cf. cancrivora*. The outgroup sequences DQ45822, AF206473, AB070738 (directly reassigned in Yodthong et al. 2019b), alongside sequences that group with these individuals were attributed to *F. moodiei*. MW007342 (Borneo) is sister to and well-diverged from *F. moodiei*, suggesting that it represents an undescribed species of Bornean *Fejervarya*. These sequences were aligned with Clustal Omega (Sievers et al. 2011) with a final alignment length of 1601 bp containing 506 *Fejervarya* samples, 462 of which are from the Lesser Sundas. All newly generated 16S

sequences have been deposited in GenBank (accession numbers: OP984408–OP984466, OP984467–OP984614, OP995445–OP995471).

Maximum Likelihood (ML) phylogenetic analysis was performed using the software IQ-TREE v1.6.12 (Nguyen et al. 2015) with model selection (model TIM2+F+I+G4) according to Bayesian information criterion (BIC) scores (Kalyaanamoorthy et al. 2017). Nodal support was determined with 1,000 ultrafast bootstrap replicates (UFBoot; Hoang et al. 2017) and 1,000 replicates of the single branch test (SH-aLRT). DNA alignments and full results files from IQ-TREE are found in the DRYAD digital repository (Reilly 2024). Based on the phylogeographic lineages found within *F. iskandari* and *F. verruculosa*, we obtained rough estimates of lineage divergence times using the Bayesian phylogenetic software BEAST2 v2.7 (Bouckaert et al. 2019). We chose a subset of samples representing the major mitochondrial lineages identified by the ML analysis and chose samples with both genes sequenced when available. The program was run under the GTR+G model of sequence evolution, which was the highest supported model from IQ-TREE implemented in BEAST2. Because we are examining intrageneric divergence, we used a strict molecular clock model assuming a rate of 1.3% lineage divergence per million years (estimated for the 16S gene in a group of ranid frogs; Macey et al. 2001). Two separate analyses were run for 50 million generations, sampled every 5,000 generations. After completion the log files were viewed in TRACER v1.7 (Rambaut et al. 2018) to confirm that parameters had converged by checking that the effective sample size (ESS) values for each parameter were greater than 200. Both runs were confirmed to have converged on the same posterior distribution. After discarding 25% of the samples as burn-in from each of the two runs, the remaining 15,000 trees were combined to generate a maximum clade credibility tree for which the branch lengths represent time, specifically millions of years ago (Ma). DNA alignments, log files and tree files are found in the DRYAD digital repository (Reilly 2024).

Sequence divergence between phylogeographic lineages were estimated by uploading the concatenated alignment on the web server DIVEIN (Deng et al. 2010) and calculated using PhyML v3.0 (Guindon et al. 2010). Mean uncorrected divergence levels were based on pairwise distances calculated with a GTR substitution model and four substitution rate categories.

MORPHOLOGICAL COMPARISONS

Morphological characters were measured for 67 sexually mature WAM *Fejervarya* specimens (Table 1) using MITUTOYO Absolute Coolant-Proof IP67 0-150 mm digital callipers. Sexual maturity was identified by the presence of secondary sexual characteristics. Adult male *F. cancrivora* and *F. verruculosa* were identified by the presence of paired dark triangular gular blotches,

TABLE 1 Morphometric sampling by island. Cells left blank indicates that species does not occur on island.

	<i>F. cancrivora</i>	<i>F. iskandari</i>	<i>F. verruculosa</i>
Bali	3	11	
Nusa Penida	7		
Lombok	1		
Mojo	1		
Sumbawa	6	3	
Flores		2	
Pantar			1
Alor			4
Wetar			0
Sumba			6
Rote			6
Semau			3
Timor		0	13
Total	18	16	33

while adult male *F. iskandari* were identified by the presence of paired grey vocal sacs on both sides of the mandible or a brown-grey streak forming a loose 'M'-shape across the throat. Females of all three species were identified by the presence of eggs. Foot webbing was examined following the notation used in Savage and Heyer (1967) following Veith et al. (2001) and Yodthong et al. (2019a).

Measurements: snout-vent length (SVL) — distance between snout tip and vent; head length (HL) — distance between snout tip and inner edge of tympanum, measured from dorsal midline; head width (HW) — measured level with anterior edge of tympana; snout-tympanum length (STL) — distance between snout tip and posterior edge of tympanum, measured obliquely; interocular distance (IOD) — distance between each eye measured along anterior of each eye opening; eye diameter (EYD) — measured between anterior- and posterior-most point of eye opening; internares distance (IND) — distance between each nares measured along anterior of each nares; tympanum-eye distance (TED) — distance between inner edge of tympanum and posterior of eye opening; tympanum diameter (TYD) — measured at midpoint level; upper arm length (UAL) — distance between base of limb to elbow, measured from the ventral surface; forearm length (FAL) — distance between elbow to midpoint between third and fourth palmar tubercles; forelimb length (FLL) — sum of upper arm and forearm lengths; hand length (HAL) — distance from midpoint between second and third palmar tubercles to tip of Finger III; thigh length (THL) — distance between groin fold and start of patella, measured parallel to femur; tibia length (TIL) — distance between end of patella and ankle; hindlimb length (HLL) — sum of thigh and tibia lengths; tarsus and foot length (TFOL) — distance between ankle and tip of Toe IV. Snout-vent length (SVL) was measured to the nearest millimetre, while all other characters were measured to the nearest 0.1 mm. Mensural values were standardised as a ratio (r) against SVL to adjust for size variation (e.g. rHL = relative head length; HL/SVL). Principal component analysis (PCA) among species was performed separately by sex using FactoMineR (Lê et al. 2008; Husson et al. 2017) and its subsequent add-ons. This PCA methodology was repeated for the major lineages within *F. verruculosa* but not for *F. iskandari* since there were not enough samples of each divergent lineage of *F. iskandari* housed at WAM.

Kruskal-Wallis tests were performed on standardised morphological measurements and morphometric ratios (rHL/rHW, rIOD/rHW, rTYD/rEYD, rTED/rEYD, rFLL/rHLL, rUAL/rFAL, rHAL/FAL, rTHL/rTIL, rTFOL/rTIL) between species with females and males analysed separately. Mann-Whitney U-tests were performed to determine whether size differences between females and males of each species are statistically significant. Kruskal-Wallis and Mann-Whitney tests were not repeated for divergent lineages of *Fejervarya*

verruculosa and *F. iskandari* since there were not enough samples of both species from each island for meaningful statistical analysis. All statistical tests were performed in RStudio 2023.06.0 (RStudio Development Team 2023) with a significance threshold of 0.05.

RESULTS

TAXONOMIC ASSIGNMENTS

The ML phylogenetic estimate grouped all Lesser Sunda *F. cancrivora* together with all additional (including introduced and commercially harvested) *F. cancrivora* sequences, corroborating this species assignment. Lesser Sunda individuals belonging to the most inclusive monophyletic clade sister to *F. cancrivora* and grouping with *F. verruculosa* topotypes (Iliwaki, Wetar Island, Indonesia) were assigned to *F. verruculosa*. Individuals belonging to the most-inclusive clade with individuals from the type locality of *F. iskandari* (Cianjur, West Java, Indonesia; Veith et al. 2001), which is sister to *F. limnocharis* and *F. multistriata*, were assigned to *F. iskandari* following phylogenetic estimates in Djong et al. (2007, 2011) and Sanchez et al. (2018).

PHYLOGEOGRAPHIC STRUCTURES

Both ML and Bayesian phylogenetic trees recover *F. iskandari* as a well-supported monophyletic clade, and recover *F. verruculosa* as a monophyletic sister group to *F. cancrivora*. Intraspecific variation and biogeographic patterns vary between the three species (Figures 3–5). *Fejervarya cancrivora* is recovered as a monophyletic widespread lineage (BS [bootstrap value] = 98) (Figure 3). All Lesser Sunda individuals are recovered as part of this lineage, intermingled with samples from Malaysia, Taiwan, Sumatra, Java, Guam and commercially harvested *Fejervarya*. Private haplotypes from Sumbawa (BS = 81) and Nusa Penida individuals are nested within this lineage.

Unlike *F. cancrivora*, phylogeographic structure is present in both *F. iskandari* and *F. verruculosa*. *Fejervarya iskandari* is recovered as monophyletic (overall BS = 100; PP [posterior probability] = 1) and samples sort into three distinct clades (Figure 5). Samples from Java, Bali and Timor are only moderately supported as a single clade in the ML tree but are fully supported in the Bayesian tree (BS = 56; PP = 1). Sister to the Java + Bali + Timor clade is a Sumbawa + Flores clade (BS = 99; PP = 1), with well-supported Sumbawa (BS = 93; PP = 1) and Flores (BS = 100; PP = 1) sister groups. The split between the Java + Bali + Timor and the Sumbawa + Flores lineages is estimated to have occurred ~5 Ma and they are ~4.6% divergent from one another (Figure 5B; Table 2). The Sumbawa and Flores lineages are estimated to have diverged ~2 Ma and the mean divergence between them is ~2.2% (Figure 4; Table 2).

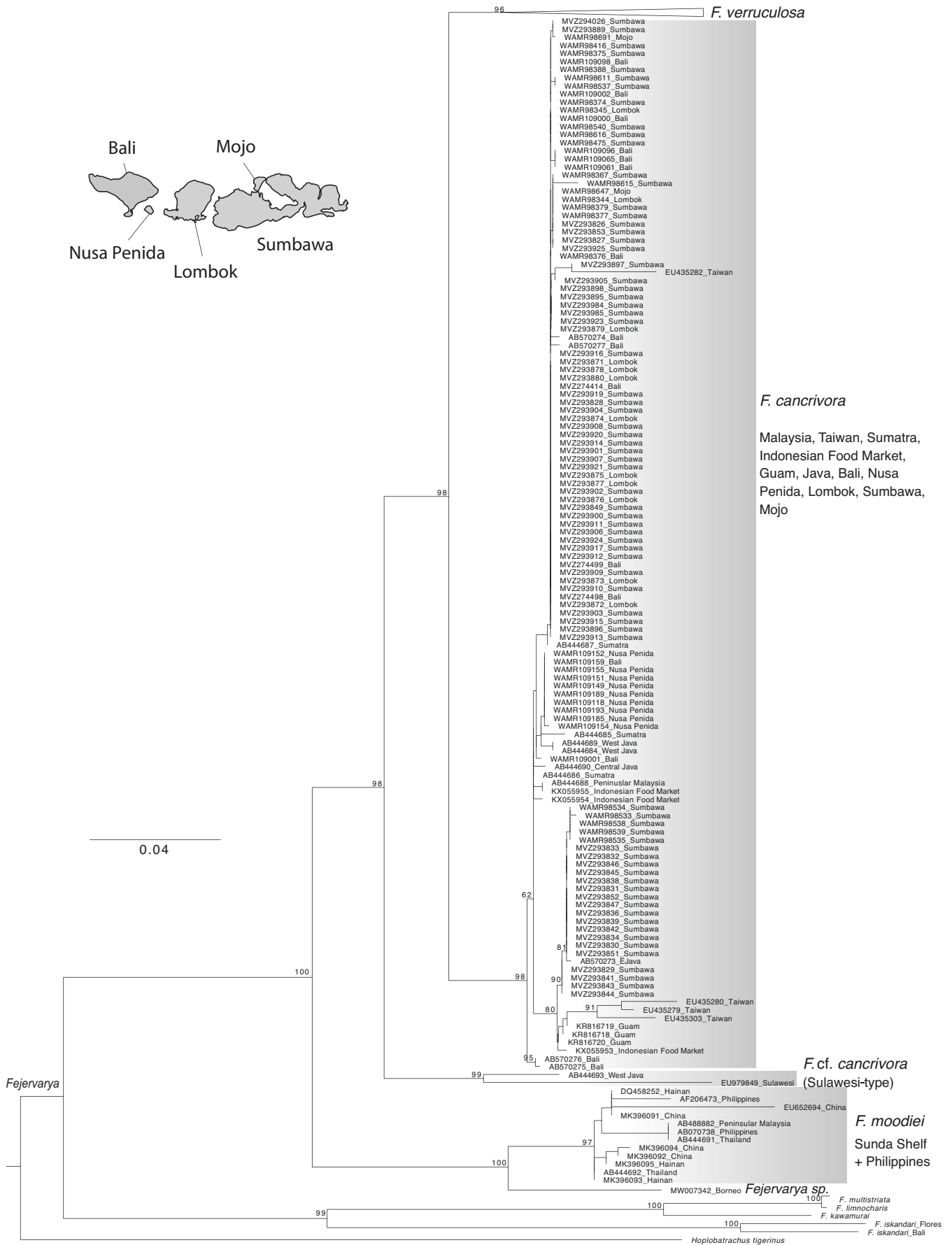


FIGURE 3 Maximum Likelihood majority rule consensus phylogeny of the CO1 and 16S mitochondrial genes for *Fejervarya cancrivora* samples. Numbers at nodes represent bootstrap support.

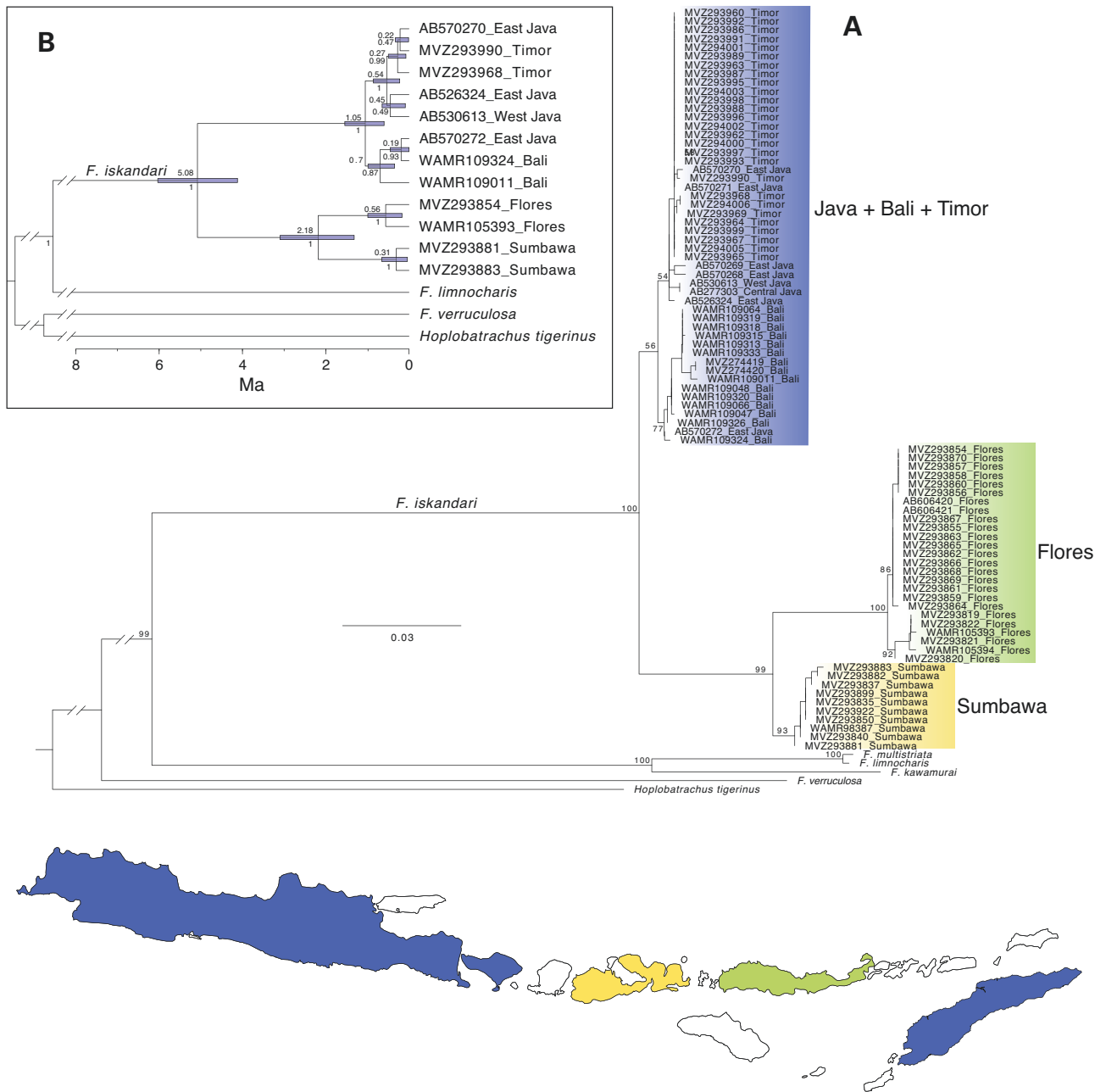


FIGURE 4 Phylogenies of the concatenated CO1 and 16S mitochondrial genes for *Fejervarya iskandari* samples: A) Maximum Likelihood majority rule consensus phylogeny where numbers at nodes represent bootstrap support; B) Bayesian time-calibrated phylogeny for a subset of samples representing the major clades. Note: numbers above nodes represent mean node ages and numbers below nodes represent posterior probability support.

Fejervarya verruculosa is monophyletic and sister to the *F. cancrivora* clade (overall BS = 96; PP = 1), and composed of three well-supported subclades: 1) an early-diverging Rote lineage (BS = 100; PP = 1); 2) a Sumba lineage (BS = 99; PP = 1); and 3) a Banda Arcs (Timor, Semau, Alor, Pantar, and Wetar) lineage (BS = 100; PP = 0.83) (Figure 4). The Sumba lineage is the sister to the Banda Arcs lineage (BS = 100; PP = 1), with the latter clade composed of multiple weakly divergent phylogeographic groups. The only monophyletic island population within the Banda Arcs

clade is Wetar (BS = 99), though they are minimally divergent (note: Wetar Island is the type locality of *verruculosa*; Roux 1911). Populations from Alor, Pantar, Timor and Semau were each recovered as paraphyletic. PhyML divergence of concatenated sequences shows the Rote lineage is approximately 8% divergent on average from all other *F. verruculosa* and is estimated to have diverged ~5.4 Ma, while the Sumba lineage is approximately 6% divergent from the Banda Arcs lineage and is estimated to have diverged from it ~3 Ma (Figure 5; Table 2).

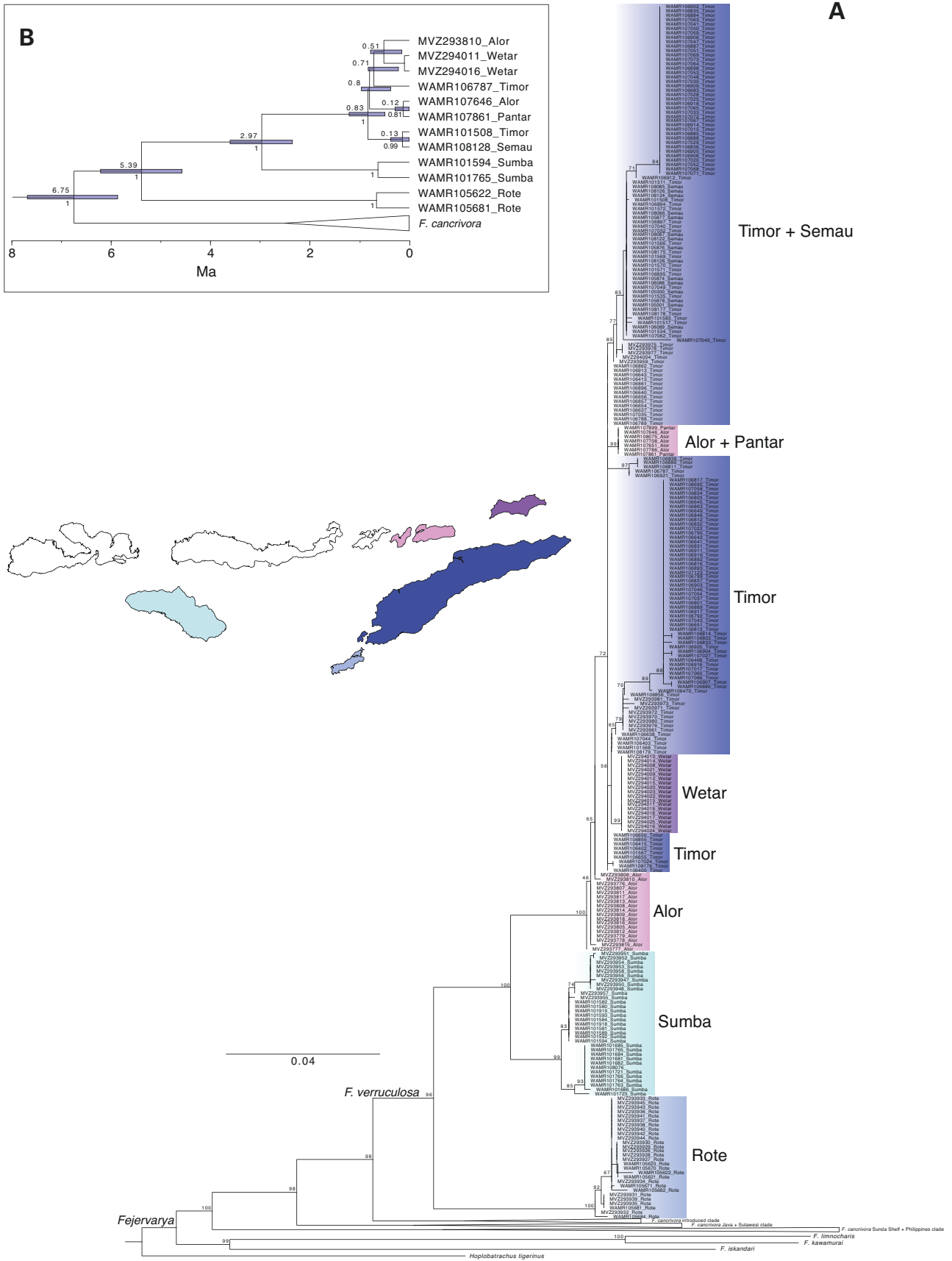


FIGURE 5 Phylogenies of the concatenated CO1 and 16S mitochondrial genes for *Fejervarya verruculosa* samples. A) Maximum Likelihood majority rule consensus phylogeny where numbers at nodes represent bootstrap support; B) Bayesian time-calibrated phylogeny for a subset of samples representing the major clades. Numbers above nodes represent mean node ages and numbers below nodes represent posterior probability support.

TABLE 2 Mean uncorrected divergences between divergent populations of *Fejervarya iskandari* and *F. verruculosa* analysed from concatenated alignment containing both CO1 and 16S genes. Divergence values presented as proportions.

	Java + Bali + Timor (n = 50)	Sumbawa (n = 10)	Flores (n = 25)	Rote (n = 28)	Sumba (n = 33)	Banda Arcs (n = 216)
<i>F. iskandari</i>						
Java + Bali + Timor	0	0.042	0.048	-	-	-
Sumbawa	0.042	0	0.022	-	-	-
Flores	0.048	0.022	0	-	-	-
<i>F. verruculosa</i>						
Rote	-	-	-	0	0.080	0.086
Sumba	-	-	-	0.080	0	0.063
Banda Arcs	-	-	-	0.086	0.063	0

MORPHOLOGY

PCA analysis between LS *F. cancrivora*, *F. iskandari* and *F. verruculosa* separated by sex revealed minimal morphological differences. There is considerable overlap between *F. cancrivora* and *F. verruculosa* across both sexes, while *F. iskandari* did not overlap with the rest of the samples with the exception of a single outlier male voucher (Figures 6A–B). The first three principal components (PCs) accounted for 64.7% and 65.9% of observed variance in females and males, respectively (Table 3). SVL mirrors species clusters in both correlation circles for females and males, suggesting that body size is the primary distinguishing characteristic between the three species (Figures 6C–D). Observed differences in SVL were more pronounced in females (cos-squared [\cos^2] value: 0.040 in PC1, 0.688 in PC2) than in males (\cos^2 value: 0.234 in PC1, 0.338 in PC2). Female *F. cancrivora* are much larger than male *F. cancrivora*, which are approximately the same size as female *F. verruculosa*. Male and female *F. iskandari* are usually smaller than male *F. verruculosa* (Table 5). We only identified four *F. iskandari* males in the WAM collection. These were slightly smaller than their female counterparts, agreeing with previous descriptions (Veith et al. 2001). Mann-Whitney U-tests between female and male SVL were statistically significant in *F. cancrivora* (U-stat = 78, $p = 0.008$) and *F. verruculosa* (U-stat = 286.5; $p < 0.0001$), but not in *F. iskandari* (U-stat = 38; $p = 0.100$).

PCA analysis on divergent *Fejervarya verruculosa* populations (Rote, Sumba and Banda Arcs) separated by sex showed little morphological differentiation between clades except for a single outlying female from

Rote (Figures 6E–H). Description of each measured character can be found in the main text. The first three PCs explained 70.0% and 69.7% of observed variance within female and male *F. verruculosa*, respectively (Table 3). \cos^2 values for in the first PC were generally higher in females than in males, but this can be attributed to the outlying female.

Descriptive statistics for all morphometric characters of adult females and males are presented in Table 4. Kruskal-Wallis tests between species were statistically significant in SVL in both sexes, reinforcing body size as the primary distinguishing characteristic between LS species. Most other morphometric characters were conserved between species. There were differences in dorsum rugosity between *F. cancrivora* and *F. verruculosa*, with long dorsal furrows on the former and raised, short oblong patches on the latter. Additionally, foot webbing between Toes III and IV in *F. iskandari* is more incised than *F. cancrivora* or *F. verruculosa* (see species accounts and Figures 7–11).

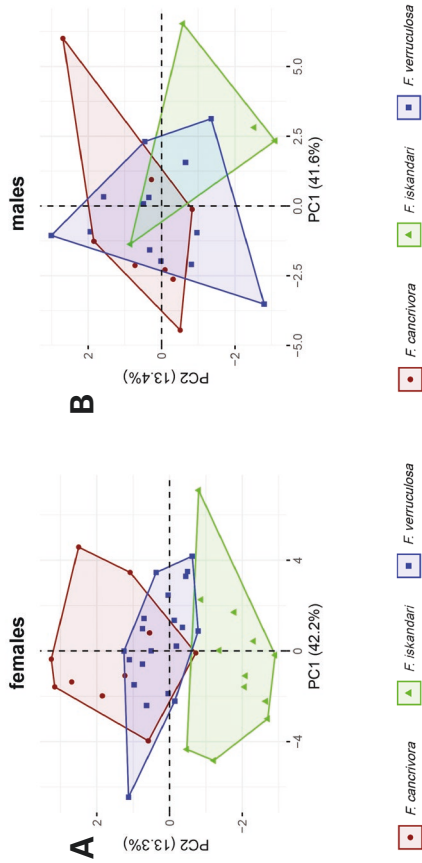
SPECIES ACCOUNTS

The combination of strong phylogenetic support, discontinuous geographic distribution and morphological differences provides multiple independent lines of evidence to recognise at least three current Lesser Sunda *Fejervarya* species. We provide new descriptions in this section, presented in chronological order of their original descriptions. Morphometric measurements are presented as relative to SVL (e.g. rHL = relative head length; see Materials and Methods). A history of synonyms for all three species can be found in Frost (2024).

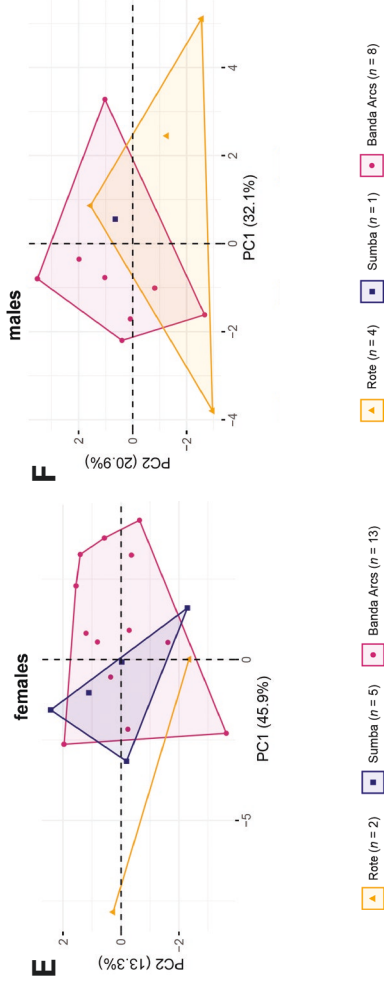
TABLE 3 Cos² values on the first three principal components (PCs) of 17 morphological measurements for female and male *Fejervarya cancrivora*, *F. iskandari* and *F. verruculosa* (left) and *Fejervarya verruculosa* (right) separated by major island clades. Higher cos² value indicates variables with high contribution to observed variance.

Morphological character	<i>F. cancrivora</i> + <i>F. iskandari</i> + <i>F. verruculosa</i>						<i>F. verruculosa</i> only					
	Females			Males			Females			Males		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
SVL	0.040	0.688	0.027	0.234	0.338	0.101	0.4071	0.3952	0.0193	0.2728	0.1833	0.323
rHL	0.295	0.215	0.011	0.402	0.008	0.268	0.1674	0.2805	0.4176	0.5837	0.2054	0.0066
rHW	0.445	0.079	0.047	0.359	0.078	0.270	0.5081	0.0377	0.1347	0.0316	0.2588	0.3413
rSTL	0.492	0.116	0.140	0.773	0.010	0.014	0.5426	0.3607	0.0339	0.7029	0.0731	0.1303
rIOD	0.444	0.003	0.013	0.233	0.249	0.068	0.5071	0.0056	0.0566	0.4205	0.0186	0.0977
rEYD	0.199	0.036	0.433	0.343	0.300	0.002	0.2279	0.1459	0.0224	0.0797	0.5143	0.0058
rIND	0.178	0.552	0.012	0.405	0.058	<0.001	0.3909	0.1437	0.1417	0.3853	0.0199	0.1196
rTED	0.136	0.228	0.002	0.133	0.474	0.036	0.0214	0.0135	0.0144	0.049	0.6219	0.0465
rTYD	0.045	0.024	0.559	0.362	0.160	0.065	0.0149	0.3599	0.2072	0.0272	0.0064	0.6257
rUAL	0.572	0.002	0.006	0.407	0.007	0.356	0.5732	0.2026	0.1924	0.2425	0.165	0.1558
rFAL	0.656	0.007	0.021	0.327	0.267	<0.001	0.5928	0.0958	0.0515	0.1584	0.4608	0.0256
rFLL	0.729	0.004	0.014	0.596	0.077	0.146	0.6724	0.055	0.1389	0.4891	0.0574	0.1814
rHAL	0.470	0.110	<0.001	0.081	0.001	0.354	0.7574	0.003	0.0454	<0.001	0.0516	0.6036
rTHL	0.511	0.088	0.094	0.248	0.090	0.135	0.5746	0.0776	0.1087	0.0011	0.5335	0.064
rTIL	0.695	0.004	0.076	0.846	<0.001	<0.001	0.5946	0.1314	0.0773	0.8998	0.0355	0.0096
rHLL	0.724	0.045	0.105	0.741	0.033	0.049	0.6919	0.1153	0.1135	0.5444	0.3231	0.0061
rIFOL	0.541	0.018	0.011	0.580	0.130	<0.001	0.566	0.0268	0.0498	0.5757	0.0247	0.0951
Eigenvalue	7.168	2.268	1.568	7.073	2.279	1.864	7.8104	2.2683	1.8243	5.4643	3.5531	2.8377
Percentage of variance	42.167	13.340	9.225	41.608	13.408	10.967	45.9436	13.3428	10.7311	32.143	20.9007	16.693
Cumulative proportion	42.167	55.570	64.732	41.608	55.106	65.892	45.9436	59.2863	70.0175	32.143	53.0437	69.736

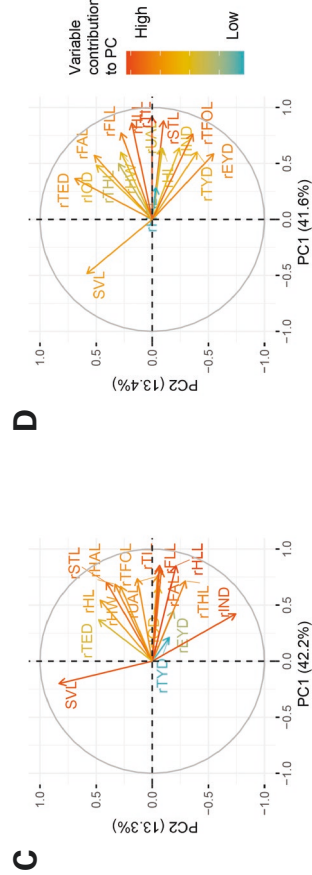
F. cancrivora* + *F. iskandari* + *F. verruculosa



***F. verruculosa* only**



F. cancrivora* + *F. iskandari* + *F. verruculosa



***F. verruculosa* only**

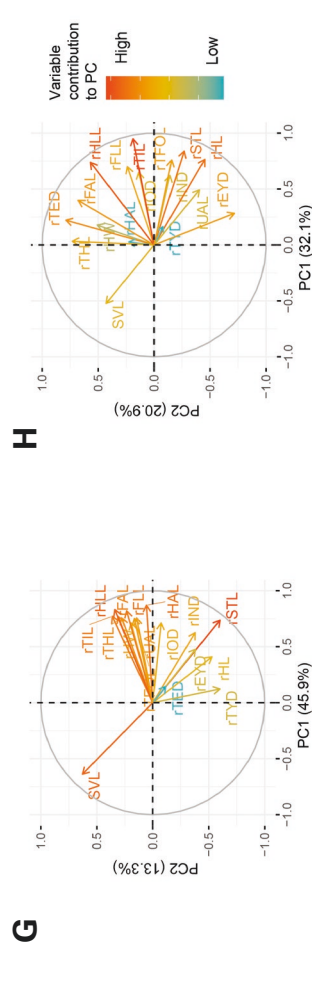


FIGURE 6

Left: Principal components plots (A, B) and correlation circles (C, D) between the first two PCs against morphological measurements from female (A, C) and male (B, D) *Fejervarya cancrivora*, *F. iskandari*, and *F. verruculosa*. Right: Principal components plots (E, F) and correlation circles (G, H) between the first two PCs against morphological measurements from female (E, G) and male (F, H) *Fejervarya verruculosa*, separated by major island clades. See main text for measured values. See main text for measured values.

TABLE 4 Summary of mensural data for examined WAM *Fejervarya cancrivora*, *F. iskandari*, and *F. verruculosa*. Values are means ± SD, followed by range in parentheses. SVL values in mm, all other values standardised as ratio against SVL. *indicates statistical significance from Kruskal-Wallis test.

Morphological character	Females (n = 42)			Males (n = 25)			p-value	x ²	p-value
	<i>F. cancrivora</i> (♀ = 10)	<i>F. iskandari</i> (♀ = 12)	<i>F. verruculosa</i> (♀ = 20)	<i>F. cancrivora</i> (♂ = 8)	<i>F. iskandari</i> (♂ = 4)	<i>F. verruculosa</i> (♂ = 13)			
SVL	73.2 ± 13.6 (59–94)	46.4 ± 2.8 (42–51)	60.6 ± 6.8 (50–75)	60.2 ± 3.8 (56–66)	37.3 ± 7.9 (31–49)	48.9 ± 5.3 (39–56)	17.2	<0.01*	
rHL	0.23 ± 0.04 (0.20–0.33)	0.20 ± 0.03 (0.16–0.25)	0.21 ± 0.02 (0.19–0.25)	0.23 ± 0.02 (0.20–0.27)	0.22 ± 0.02 (0.20–0.24)	0.22 ± 0.03 (0.19–0.28)	1.9	0.40	
rHW	0.34 ± 0.02 (0.32–0.37)	0.32 ± 0.03 (0.28–0.37)	0.34 ± 0.03 (0.29–0.38)	0.34 ± 0.02 (0.32–0.39)	0.37 ± 0.03 (0.34–0.41)	0.34 ± 0.02 (0.30–0.38)	4.3	0.12	
rSTL	0.33 ± 0.06 (0.29–0.48)	0.33 ± 0.03 (0.28–0.40)	0.35 ± 0.02 (0.31–0.38)	0.37 ± 0.02 (0.33–0.42)	0.38 ± 0.23 (0.35–0.42)	0.36 ± 0.02 (0.33–0.40)	3.5	0.18	
rIOD	0.15 ± 0.01 (0.14–0.17)	0.15 ± 0.01 (0.14–0.17)	0.16 ± 0.01 (0.13–0.19)	0.16 ± 0.01 (0.14–0.17)	0.15 ± 0.00 (0.15–0.16)	0.16 ± 0.01 (0.14–0.18)	0.1	0.93	
rEYD	0.11 ± 0.02 (0.08–0.13)	0.11 ± 0.01 (0.09–0.14)	0.12 ± 0.01 (0.07–0.15)	0.12 ± 0.01 (0.10–0.13)	0.13 ± 0.01 (0.12–0.14)	0.12 ± 0.01 (0.11–0.13)	5.0	0.08	
rIND	0.06 ± 0.01 (0.06–0.07)	0.07 ± 0.01 (0.06–0.09)	0.07 ± 0.01 (0.06–0.08)	0.06 ± 0.01 (0.06–0.07)	0.08 ± 0.01 (0.07–0.10)	0.07 ± 0.01 (0.05–0.08)	5.4	0.06	
rTED	0.04 ± 0.01 (0.03–0.05)	0.04 ± 0.01 (0.01–0.06)	0.04 ± 0.01 (0.02–0.06)	0.04 ± 0.01 (0.03–0.06)	0.04 ± 0.00 (0.04–0.05)	0.04 ± 0.01 (0.02–0.06)	0.6	0.74	
rTYD	0.08 ± 0.01 (0.07–0.09)	0.08 ± 0.01 (0.06–0.10)	0.08 ± 0.01 (0.06–0.09)	0.08 ± 0.01 (0.07–0.09)	0.09 ± 0.01 (0.07–0.10)	0.08 ± 0.01 (0.07–0.09)	2.5	0.28	
rUAL	0.23 ± 0.03 (0.19–0.28)	0.23 ± 0.02 (0.19–0.27)	0.23 ± 0.02 (0.20–0.26)	0.24 ± 0.02 (0.20–0.27)	0.25 ± 0.02 (0.23–0.27)	0.24 ± 0.02 (0.21–0.26)	1.1	0.59	
rFAL	0.22 ± 0.02 (0.19–0.25)	0.22 ± 0.02 (0.19–0.25)	0.23 ± 0.02 (0.20–0.26)	0.23 ± 0.02 (0.20–0.28)	0.23 ± 0.02 (0.22–0.26)	0.23 ± 0.02 (0.17–0.25)	0.5	0.79	
rFLL	0.45 ± 0.04 (0.40–0.53)	0.45 ± 0.04 (0.38–0.52)	0.44 ± 0.04 (0.39–0.51)	0.47 ± 0.04 (0.40–0.52)	0.48 ± 0.03 (0.46–0.53)	0.47 ± 0.03 (0.42–0.50)	0.2	0.90	

Morphological character	Females (n = 42)			Males (n = 25)			p-value	χ ²	p-value
	<i>F. cancrivora</i> (♀ = 10)	<i>F. iskandari</i> (♀ = 12)	<i>F. verruculosa</i> (♀ = 20)	<i>F. cancrivora</i> (♂ = 8)	<i>F. iskandari</i> (♂ = 4)	<i>F. verruculosa</i> (♂ = 13)			
rHAL	0.22 ± 0.02 (0.19–0.24)	0.19 ± 0.02 (0.17–0.26)	0.22 ± 0.02 (0.19 ± 0.44)	0.23 ± 0.02 (0.20–0.28)	0.24 ± 0.02 (0.21–0.26)	0.23 ± 0.07 (0.19–0.44)	4.4	0.11	
rTHL	0.43 ± 0.04 (0.35–0.47)	0.45 ± 0.05 (0.34–0.52)	0.45 ± 0.05 (0.31–0.53)	0.42 ± 0.05 (0.36–0.52)	0.45 ± 0.04 (0.40–0.48)	0.45 ± 0.02 (0.40–0.48)	5.5	0.07	
rTIL	0.49 ± 0.04 (0.39–0.53)	0.51 ± 0.05 (0.43–0.61)	0.49 ± 0.03 (0.42–0.55)	0.49 ± 0.04 (0.44–0.57)	0.53 ± 0.05 (0.46–0.57)	0.48 ± 0.03 (0.44–0.53)	2.6	0.27	
rHLL	0.91 ± 0.08 (0.74–1.02)	0.96 ± 0.09 (0.80–1.13)	0.94 ± 0.08 (0.73–1.08)	0.91 ± 0.09 (0.80–1.09)	0.98 ± 0.07 (0.92–1.05)	0.94 ± 0.04 (0.87–0.99)	3.7	0.16	
rTFOL	0.74 ± 0.04 (0.68–0.80)	0.71 ± 0.07 (0.62–0.84)	0.71 ± 0.07 (0.55–0.81)	0.73 ± 0.07 (0.67–0.89)	0.82 ± 0.12 (0.66–0.95)	0.73 ± 0.05 (0.62–0.84)	2.1	0.34	
rHL/rHW	0.67 ± 0.11 (0.60–0.97)	0.63 ± 0.10 (0.51–0.79)	0.62 ± 0.08 (0.49–0.86)	0.65 ± 0.04 (0.57–0.70)	0.60 ± 0.06 (0.55–0.68)	0.65 ± 0.10 (0.51–0.87)	2.0	0.37	
rIOD/rHW	0.45 ± 0.02 (0.41–0.47)	0.48 ± 0.04 (0.39–0.54)	0.46 ± 0.03 (0.41–0.51)	0.46 ± 0.02 (0.43–0.51)	0.42 ± 0.03 (0.38–0.46)	0.47 ± 0.04 (0.42–0.54)	4.5	0.10	
rTYD/rEYD	0.72 ± 0.08 (0.60–0.81)	0.67 ± 0.07 (0.53–0.82)	0.67 ± 0.12 (0.47–0.97)	0.73 ± 0.06 (0.67–0.86)	0.71 ± 0.07 (0.63–0.77)	0.68 ± 0.06 (0.57–0.80)	2.5	0.29	
rTED/rEYD	0.40 ± 0.14 (0.22–0.65)	0.32 ± 0.09 (0.13–0.45)	0.41 ± 0.09 (0.29–0.68)	0.37 ± 0.09 (0.24–0.50)	0.34 ± 0.04 (0.30–0.38)	0.36 ± 0.10 (0.21–0.54)	0.3	0.88	
rFLL/rHLL	0.49 ± 0.05 (0.42–0.57)	0.47 ± 0.02 (0.13–0.45)	0.49 ± 0.04 (0.42–0.55)	0.51 ± 0.04 (0.44–0.60)	0.49 ± 0.03 (0.45–0.52)	0.50 ± 0.02 (0.46–0.53)	1.5	0.48	
rUAL/rFAL	1.06 ± 0.02 (0.86–1.20)	1.05 ± 0.07 (0.92–1.19)	1.02 ± 0.07 (0.93–1.15)	1.03 ± 0.05 (0.96–1.13)	1.06 ± 0.05 (1.03–1.13)	1.04 ± 0.16 (0.87–1.45)	1.0	0.59	
rHAL/rFAL	1.01 ± 0.08 (0.91–1.22)	0.89 ± 0.10 (0.71–1.04)	0.95 ± 0.06 (0.86–1.07)	1.00 ± 0.10 (0.82–1.13)	1.02 ± 0.09 (0.93–1.14)	0.99 ± 0.30 (0.75–1.88)	2.8	0.24	
rTHL/rTIL	0.87 ± 0.07 (0.77–0.97)	0.90 ± 0.09 (0.70–1.04)	0.91 ± 0.08 (0.75–1.03)	0.86 ± 0.07 (0.73–0.92)	0.86 ± 0.11 (0.77–1.02)	0.94 ± 0.07 (0.85–1.04)	5.3	0.07	
rTFOL/rTIL	1.51 ± 0.10 (1.34–1.75)	1.40 ± 0.10 (1.27–1.55)	1.45 ± 0.10 (1.15–1.60)	1.51 ± 0.12 (1.32–1.73)	1.55 ± 0.19 (1.43–1.83)	1.51 ± 0.08 (1.30–1.61)	0.5	0.80	

Fejervarya cancrivora* (Gravenhorst, 1829)*Crab-eating Frog**

Figures 7–8

MATERIAL EXAMINED

Specimens collected from Lombok (WAM R98345), Mojo (R98691), Sumbawa (R98416, R98397, R98611, R98616, R98533, R99843), Bali (R109000, R109002, R109003), and Nusa Penida (R109193) (see Appendix 1 for collection details).

Neotype

Indonesia: West Java: FMNH 256688 (Field Museum of Natural History, Chicago, USA) from Cianjur. Designated by Dubois & Ohler (2000).

DIAGNOSIS

A species of the genus *Fejervarya* (sensu Sanchez et al. 2018) identified by the following characters: maximum male SVL 66 mm; maximum female SVL 94 mm; head large, mean rHL 0.23, mean rHW 0.34; tympanum-eye distance short, mean rTED = 0.04; dorsal furrows continuous, interspersed with raised oblong patches extending to the flanks; forelimbs moderately robust, mean rFLL 0.45 in females and 0.47 in males; mean rHAL 0.22 in females and 0.23 in males; hindlimbs robust; tibia slightly longer than thigh; tarsus and foot longer than hindlimb, mean rHLL 0.91; mean rTFOL 0.74 in females and 0.73 in males; dermal fringe on postaxial side of Toe V variably expressed, from absent to well-developed (Figure 8C); inner metatarsal tubercle prominent and elongate, outer metatarsal tubercle absent; foot webbing formula I (1–1.25) II (1–1) III (1–2) IV (2–1) V.

Fejervarya cancrivora differs from Lesser Sundas congeners as follows: from *F. verruculosa* by its larger size (SVL 39–75 mm in *F. verruculosa*), dorsum rugosity (furrows broken into small oblong patches in *F. verruculosa*), a relatively longer head (rHL/rHW 0.23 in *F. cancrivora*; 0.21 in female *F. verruculosa*, 0.22 in males) and degree of fringing in the post-axial side of Toe V (reduced to a ridge in *F. verruculosa*); from *F. iskandari* by larger size (SVL 31–51 mm in *F. iskandari*), absence of an outer metatarsal tubercle, a relatively longer head (rHL/rHW 0.20 in female *F. iskandari*, 0.22 in males) and longer forelimbs relative to hindlimbs (rFLL/rHLL = 0.49 in female *F. cancrivora*, 0.51 in males versus 0.47 in female *F. iskandari*, 0.49 in males).

DESCRIPTION

Male SVL 47–66 mm; female SVL 59–94 mm. Dorsum slightly rugose with scattered long furrows forming irregular longitudinal rows (Figure 8D). Ventral surface smooth. Head long and wide; side

profile acute. Nares semi-ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length; distinct fold present at anterior edge of eye. Tympanum circular with raised annulus. Supratympanic fold emanates from posterior edge of eye and extends posteriorly to axillary region, terminating before shoulder. Upper arm, forearm and hands approximately same relative lengths. Hands approximately same length as lower arm. Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles elongate. Relative finger lengths I < II < IV < III. Prepollax present on Finger I, indistinct. Palmar tubercles circular on Finger II, ovoid on Fingers III + IV. Thighs well-developed and slightly shorter than tibia. Combined tarsus and foot length shorter than combined thigh and tibia length. Toes long, thin, with moderate webbing deeply excised between digits. Relative toe length I < II < V < III < IV. Subarticular tubercles elongate. Toe I webbed to midpoint of distal phalanx; webbing of pre-axial side of Toe II extends slightly beyond distal phalanx; continuing as narrow fringe to tip of digit. Post-axial side of Toe II fully webbed. Pre-axial side of Toe III webbed to distal point of distal subarticular tubercle. Post-axial side of Toe III fully webbed. Webbing on pre-axial and post-axial sides of Toe IV ends at second distal-most subarticular tubercle, where it narrows to lateral fringe which often wraps distal-most parts of digit. Toe V webbed to distal subarticular tubercle, extending as lateral fringe to end of digit. Dermal flap originates from post-axial side of Toe V, wraps around post-axial side of sole, and terminates at base of foot. Inner metatarsal tubercle prominent, elongated; outer metatarsal tubercle absent. Tarsal tubercles and supernumerary tubercles absent.



FIGURE 7 *Fejervarya cancrivora*, Sumbawa, Indonesia (Photo: Ron Johnstone).

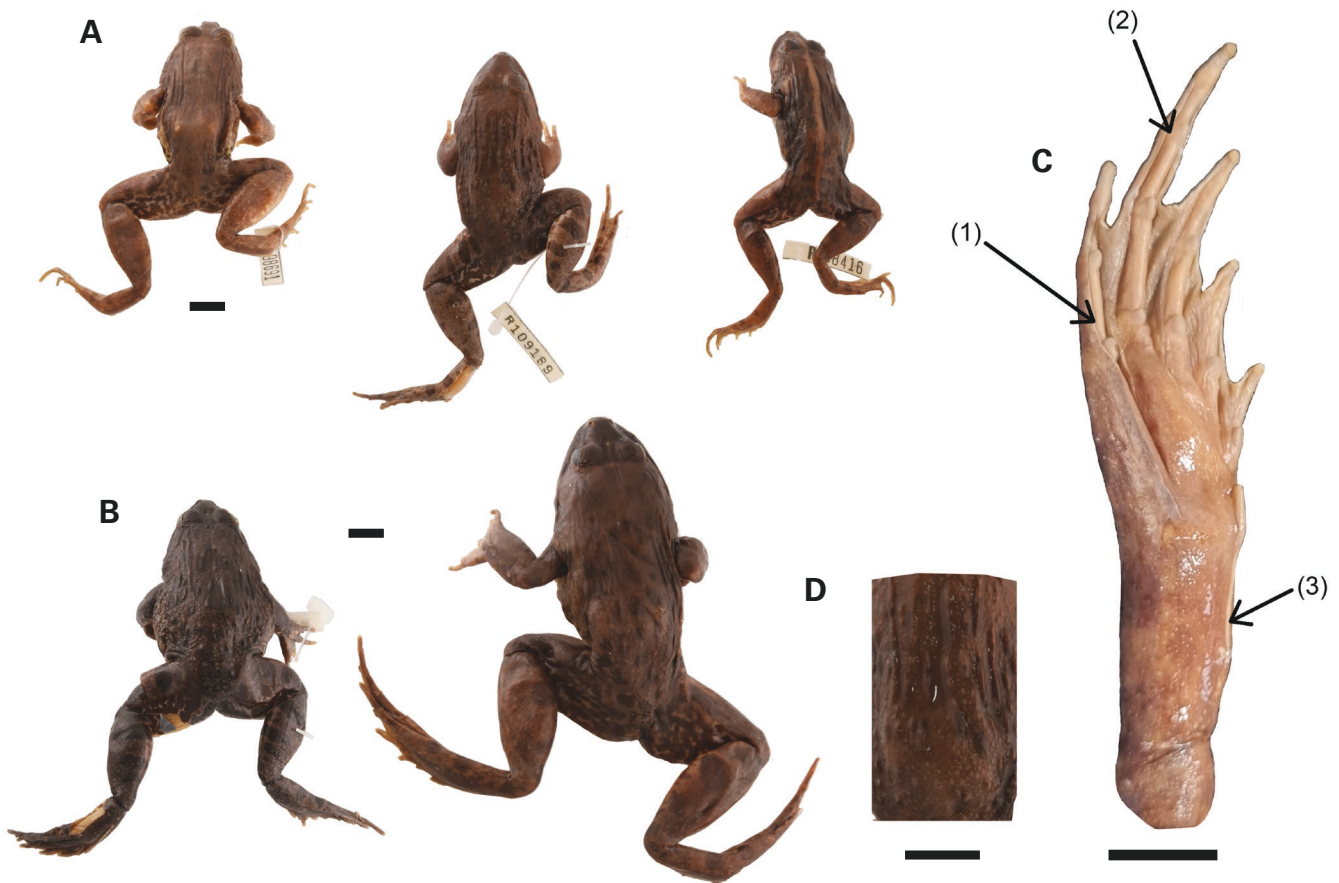


FIGURE 8 Preserved specimens of *Fejervarya cancrivora*. A) males (WAM R98691, R109189, R98416); B) females (WAM R109185, R109000); C) hindlimb (WAM R109189), arrows indicate: (1) post-axial dermal fringe (2), lateral fringing wedded to Toe IV, and (3) inner metatarsal ridge; D) dorsum rugosity (WAM R109000). Scale bars = 10 mm.

Colouration (in preservative)

Dorsum dark brown with darker brown pigmented blotches tending to occur with irregular longitudinal furrows. Ventrums off-white. Sides heavily stippled with dark pigment. Labial region light brown, interspersed with wide dark brown bars extending to lower jaw margin. Forearms covered with dark brown blotches forming loose longitudinal rows. Inside of thigh marbled, pale brown on dark brown. Thighs and tibia covered with transverse rows of round dark brown ovoid spots.

Variation

Females markedly larger than males. Sexually mature males with large, paired triangular blotches on posterior side of each lower jaw, absent in females. Some individuals (2 of 19 examined) with vertebral stripe. Ventral surface of mandible variably stippled with dark brown reticulations. Dermal flap on post-axial side of Toe V variably expressed, with the monophyletic Nusa Penida and Sumbawa populations possessing the flap, whereas it is absent in other populations.

DISTRIBUTION AND ECOLOGY

Fejervarya cancrivora is found in Taiwan, the Malay Peninsula, Sumatra, Java, the Lesser Sunda Archipelago, and is introduced to Guam (Wostl et al. 2016). Its distribution in the Lesser Sundas includes Bali, Nusa Penida, Sumbawa and Mojo Islands (Figure 2A,C), but it does not occur in the Banda Arcs. *Fejervarya cancrivora* is known to inhabit rice paddies and human settlements. It is consumed as a food throughout its range (Kusrini 2005) and one of the primary species exported to European food markets, notably to France (Ohler and Nicolas 2017).

Fejervarya verruculosa (Roux, 1911)

Banda Arc Wart Frog

Figure 9

MATERIAL EXAMINED

Specimens collected from Sumba (WAM R101763, R101805, R101681, R101682, R101589, R101593), Rote (R105671, R105681, R105684, R105604, R105611,

R105606, R105600), Semau (R105000, R105876, R105878), Timor (R101508, R101511, R101535, R107045, R107024, R107027, R107035, R107040, R106470, R106651, R106884, R106836, R106855), and Alor (R107785, R107787, R107987) (see Appendix 1 for collection details).

Lectotype

Indonesia: Maluku: SMF 6538 (Naturmuseum Senckenberg, Frankfurt, Germany) from Ilwaki, Wetar Island. Designated by Mertens (1967).

DIAGNOSIS

A species of genus *Fejervarya* identified by the following characters: maximum male SVL 56 mm; maximum female SVL 75 mm; head large, rHL 0.21 in females and 0.22 in males; rHW 0.34; tympanum-ear distance short, rTED 0.04–0.05; dorsal furrows broken into raised oblong patches covering the dorsal surface and flanks; forelimbs moderately robust, rFLL 0.44 in females, 0.47 in males; rHAL 0.22 in females 0.23 in

males; hindlimbs robust, tibia longer than thigh; tarsus and foot longer than both thigh and tibia, rHLL 0.94; rTFOL 0.71 in females, 0.73 in males; dermal ridge on the postaxial side of Toe V poorly developed, if present; inner metatarsal tubercle prominent and elongate, outer metatarsal tubercle absent; foot webbing formula I (1–1.25) II (1–1) III (1–2) IV (2–1) V.

Fejervarya verruculosa differs from Lesser Sundas congeners as follows: from *F. cancrivora* by smaller size (SVL 47–94 mm in *F. cancrivora*), dorsum furrows arranged in longer ridges in *F. cancrivora*, degree of fringing in the post-axial side of Toe V (reduced to a ridge; Figure 9C), shorter head (rHL 0.23 in *F. cancrivora*), shorter thighs (rTHL 0.45 in *F. verruculosa*, 0.42 in female *F. cancrivora*, 0.43 in males); from *F. iskandari* by larger size (SVL 31–51 mm in *F. iskandari*), absence of an outer metatarsal tubercle, longer upper arm relative to lower arm (rUAL/rFAL 1.02 in female *F. verruculosa*, 1.04 in males; 1.05 in female *F. cancrivora*, 1.04 in males) and hindlimbs (rHLL = 0.94 in *F. verruculosa*, 0.96 in female *F. iskandari*, 0.98 in males).

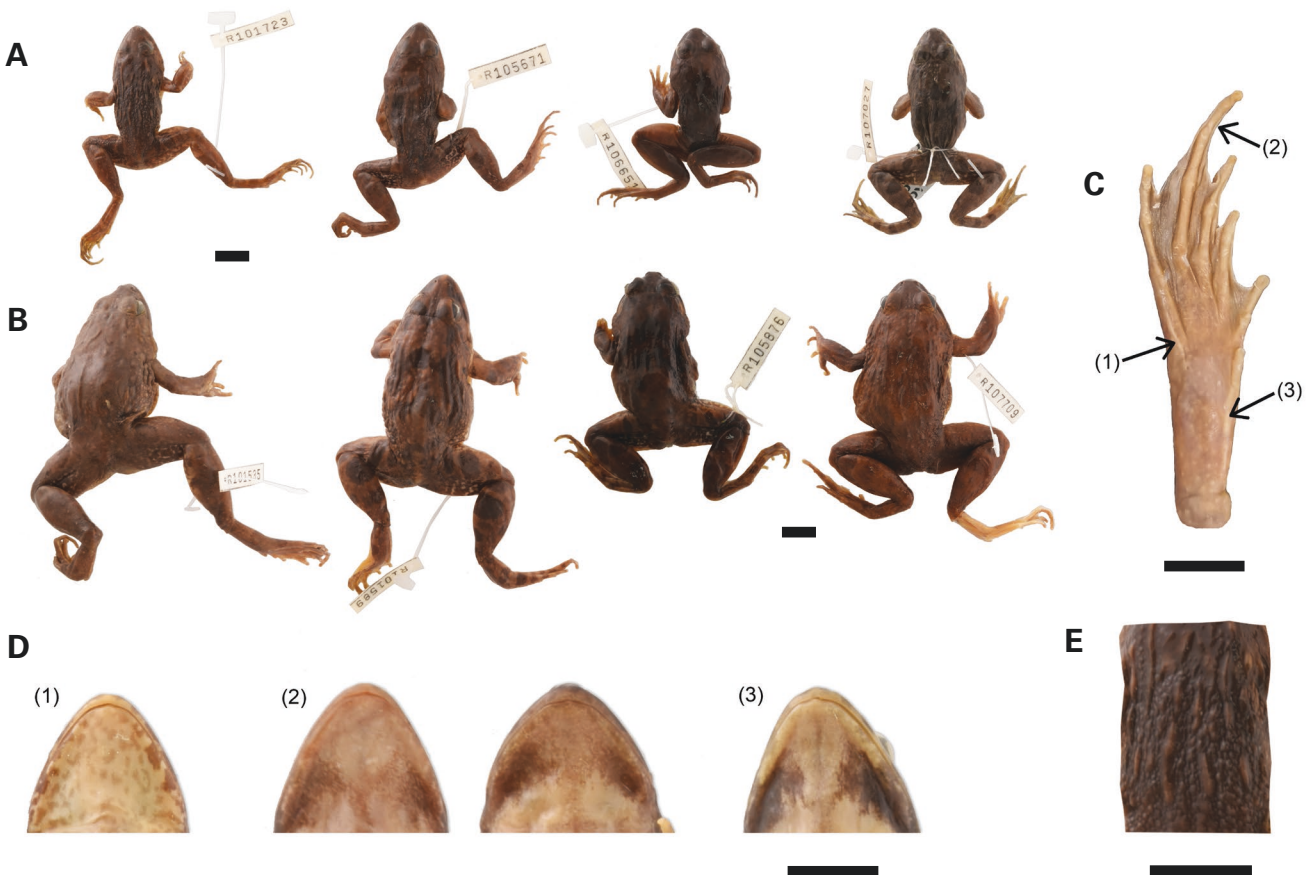


FIGURE 9 Preserved specimens of *Fejervarya verruculosa*. A) males (WAM R101723, R105671, R106651, R107027); B) females (WAM R101535, R101589, R105876, R107709); C) Hindlimb (WAM R101535); arrows indicate: (1) outer toe ridge, (2) distal lateral fringe in Toe IV, and (3) inner metatarsal ridge; D) ontogeny of males: (1) immature (WAM R101723), (2) subadults (WAM R105671, R106651), (3) mature adult (WAM R107027); E) dorsum rugosity (WAM R101723). Scale bars = 10 mm.

DESCRIPTION

Male SVL 39–56 mm; female SVL 50–75 mm. Dorsal furrows broken into raised oblong patches covering dorsal surface and flanks (Figure 9E). Ventral surface smooth. Head long and wide; side profile acute. Nares semi-ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length; distinct fold present at anterior opening of eye. Tympanum circular with raised annulus. Supratympanic fold from posterior edge of eye extending to axillary region, terminating before shoulder. Upper arm longer than the forearm. Hands approximately same length as lower arm. Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles elongated. Relative finger length $I < II < IV < III$. Prepollax present on Finger I. Palmar tubercles circular on Finger II, oval on Fingers III + IV. Hindlimbs robust. Thighs slightly shorter than tibia. Combined tarsus and foot length shorter than combined thigh and tibia length. Toes long, thin, with moderate webbing not deeply excised between digits. Relative toe length $I < II < V < III < IV$. Subarticular tubercles elongate. Toe I webbed to the midpoint of the distal phalanx; webbing of pre-axial side of Toe II extends slightly beyond the distal phalanx; continuing as a narrow fringe to digit tip. Post-axial side of Toe II fully webbed. Pre-axial side of Toe III webbed to distal point of distal subarticular tubercle. Post-axial side of Toe III fully webbed. Webbing on pre-axial and post-axial sides of Toe IV ends at second distal-most subarticular tubercle, narrowing to thin fringe on both sides of digit. Toe V webbed to distal subarticular tubercle extending into lateral fringe reaching tip of digit. Dermal ridge originates from proximal subarticular tubercle on post-axial side of Toe V and terminates at post-axial side of the foot. Inner metatarsal tubercle prominent and elongate; outer metatarsal tubercle absent. Tarsal tubercles and supernumerary tubercles absent.

Colouration (in preservative)

Dorsum dark brown with dark pigmented blotches around raised furrows. Ventrums colour variable, ranging from off white to dark brown. Sides lightly stippled with dark brown reticulations. Labial region light brown, interspersed with wide dark brown bars extending to margin of lower jaw. Forearms with dark blotches tending to occur in longitudinal rows. Inside of thigh is marbled, pale brown on dark brown. Thighs and tibia with transverse round dark ovoid spots.

Variation

Females markedly larger than males. Sexually mature males with paired large triangular blotches on posterior side of each lower jaw. Gular coloration ranges from brown to off-white with dark brown stippling present in most individuals. One individual possessed a wide vertebral stripe (of 36 individuals examined).

DISTRIBUTION AND ECOLOGY

Restricted to the Banda Arcs. This species is found on the islands of Rote, Sumba, Pantar, Alor, Timor and Wetar (Figure 2A,C). Unlike its Lesser Sunda congeners, *F. verruculosa* is rarely found near human habitation and appears to be restricted to freshwater rivers and streams.

Fejervarya iskandari

Veith, Kosuch, Ohler & Dubois, 2001

Iskandar's grass frog

Figures 10–11

MATERIAL EXAMINED

Western Australian Museum specimens collected from Sumbawa (WAM R99850, R99849, R99642), Flores (R105393, R105394), and Bali (R109135, R109324, R109313, R109319, R109326, R109317, R109335, R109047, R109066, R109062, R109011) (see Appendix 1 for collection details).

Holotype

Indonesia: West Java: MNHN 1997.4916 (Muséum National d'histoire Naturelle, Paris, France) from Cianjur.

DIAGNOSIS

A small-bodied species of genus *Fejervarya* identified by the following characters: maximum male SVL 49 mm; maximum female SVL 51 mm; head short, rHL 0.20 in females, 0.22 in males; tympanum-ear distance short, rTED 0.04; dorsal furrows continuous, transitioning to raised oblong patches towards the posterior end of the dorsum; forelimbs short, gracile, rFLL 0.45 in females, 0.48 in males; hindlimbs gracile, rHLL 0.96 for females, 0.98 for males; inner metatarsal tubercle prominent and elongate; outer metatarsal tubercle reduced to a small circular knob (Figure 11B); foot webbing formula I (1–2) II (1–2) III (1–3) IV (2.5–1) V.

Fejervarya iskandari differs from both *F. cancrivora* and *F. verruculosa* by its smaller size, reduced sexual size dimorphism, presence of a reduced outer metatarsal tubercle, inner metatarsal line extending slightly diagonally down the tarsus (as opposed to straight in *F. cancrivora* and *F. verruculosa*), longer tibia (rTIL 0.51 in females, 0.53 in males for *iskandari*; ≤ 0.49 in *F. cancrivora* and *F. verruculosa*) and longer hindlimbs (rHLL ≤ 0.94 in *F. cancrivora* and *F. verruculosa*).

DESCRIPTION

Male SVL 31–49 mm; female SVL 42–51 mm. Dorsum with furrows of variable lengths, irregularly arranged anteriorly and transitioning to raised oblong patches posteriorly. Ventral surface smooth. Head small

and wide. Nares ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length. A distinct fold present at anterior edge of eye. Tympanum circular, annulus weakly developed. Supratympanic fold begins at posterior edge of eye extending to axillary region, terminating before shoulder. Forelimbs slender. Forearm longer than upper arm. Hands shorter in females (rHAL 0.19) than males (rHAL 0.24). Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles medium and conical. Relative finger length $I < II < IV < III$. Prominent prepollax present on base of Finger I. Palmar tubercles circular on Finger II and merged to ovoid on Fingers III + IV. Hindlimbs slender. Thighs and tibia gracile; tibia longer than thigh. Tarsus and foot long and thin. Toes long, thin, with moderate webbing not deeply excised between digits. Relative toe length $I < II < V < III < IV$. Subarticular tubercles small and blade-like. Toe I webbed to the midpoint of the distal subarticular tubercle. Webbing of pre-axial side of Toe II reaches proximal point of distal subarticular tubercle; webbing of post-axial side of Toe II reaches distal point of distal subarticular tubercle. Pre-axial side of Toe III webbed to the distal subarticular tubercle and extends as thin lateral fringe reaching digit terminus (Figure 11B). Post-axial side of Toe III webbed to distal subarticular tubercle. Webbing on pre-axial and post-axial sides of Toe IV ends at third subarticular tubercle from digit terminus, extending to thin fringe merged between second and third subarticular tubercle



FIGURE 10 *Fejervarya iskandari*, Flores, Indonesia (Photos: Sean Reilly).

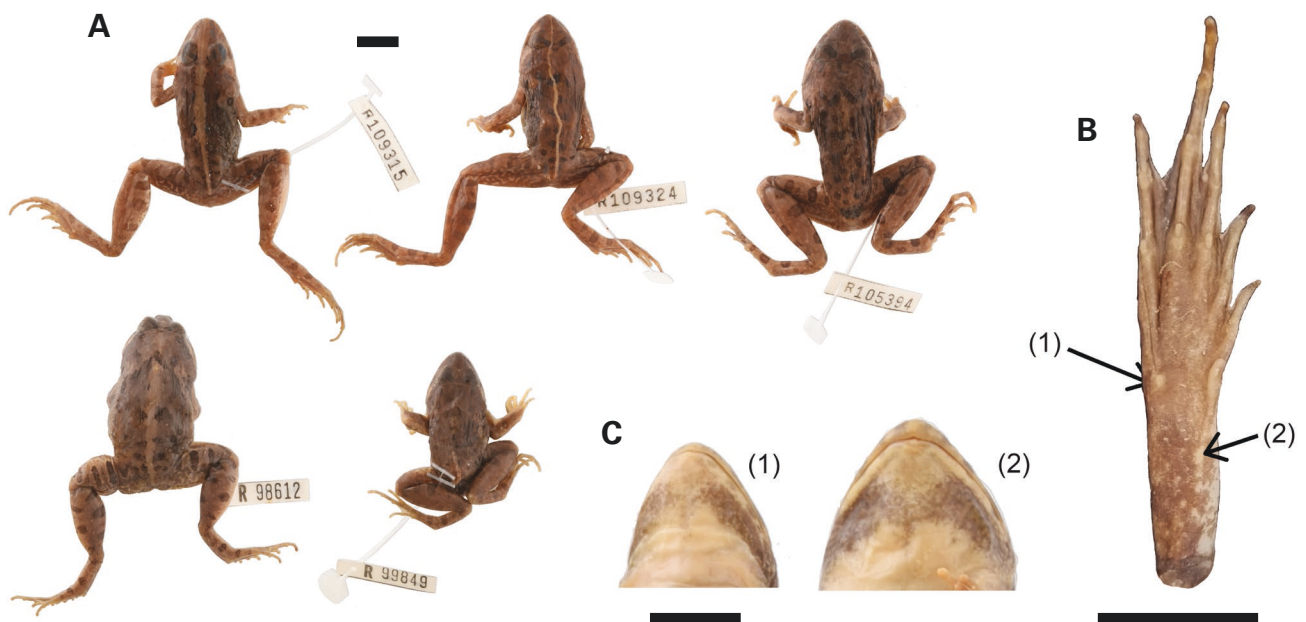


FIGURE 11 Preserved specimens of *Fejervarya iskandari*. A) top row (WAM R109315, R109324 [Bali], R105394 [Flores]), bottom row (WAM R98612; R99849); B) Hindlimb of *F. iskandari* (WAM R109066), arrows indicate: (1) outer metatarsal tubercle, and (2) inner metatarsal ridge; C) ontogeny of males: (1) subadult (WAM R99849); (2) mature adult (R98612). Scale bars = 10 mm.

on both sides of digit. Toe V webbed to the distal subarticulate tubercle extending into a lateral fringe reaching the end of the digit. Dermal ridge present; originates from post-axial side of Toe V terminus and extends to proximal end of basal phalange of Toe V. Inner metatarsal tubercle prominent, elongated; outer metatarsal tubercle reduced to small knob. Dermal line extends from proximal end of inner metatarsal tubercle, extending on angle to base of tarsus. Tarsal tubercles and supernumerary tubercles absent.

Colouration (in preservative)

Light brown dorsum. Dark brown pigmented spots around raised furrows. Ventrums off-white. Sides lightly stippled. Bold brown canthal stripe usually present. Labial region light brown, interspersed with narrow dark brown bars extending to margin of lower jaw. Forearms with narrow dark oval blotches tending to form longitudinal rows. Inside of the thigh is marbled, pale brown on dark brown. Thighs and tibia also with narrow dark blotches tending to form longitudinal rows.

Variation

Males and females show overlap in body size. Sexually mature males can be distinguished by: light grey vocal sacs forming an 'M' shape on throat; and patches of fine spines on the throat, prepollax and Finger I. Gular region off-white; light brown gular stippling variably expressed. Individuals exhibit either a wide dorsal vertebral stripe (2 of 12 individuals examined), a thin vertebral stripe with small exterior spots (three individuals) or no vertebral stripe (seven individuals).

DISTRIBUTION AND ECOLOGY

Fejervarya iskandari is endemic to Java, Bali and the Lesser Sundas. In the Lesser Sundas, the range includes the islands of Flores, Sumbawa and Timor (Figure 2B,D). *Fejervarya iskandari* are known to reside around human habitation, but may be found around natural streams as well (Sean Reilly and Jimmy McGuire, pers. obs.).

DISCUSSION

SYSTEMATICS

The natural history and taxonomy of Lesser Sunda *Fejervarya* remain poorly understood for several reasons. Fieldwork in the LS region is challenging owing to costs and logistical coordination, resulting in limited sampling for most islands. This makes the existing specimens available very valuable to understand biogeographic patterns and systematic relationships. The shallow phylogeographic structure and clear pattern of human-mediated dispersal of *F. cancrivora* suggests ongoing gene flow between populations, supporting their current taxonomic status as a single species across the Malay Peninsula and Indonesia. In contrast, mitochondrial DNA data from *F. iskandari*

and *F. verruculosa* shows geographic sorting into highly divergent clades. Multi-locus or genomic-level analyses assessing gene flow between mtDNA clades/populations within *F. iskandari* and *F. verruculosa* are required to determine if apparently distinct populations represent separate species despite morphological stasis (unified species concept sensu De Quiroz 2007). Determining the specific status of constituent *F. iskandari* and *F. verruculosa* populations will help to resolve the systematic conundrums of *Fejervarya* and further our understanding of how the unique LS herpetofaunal assemblage formed.

Our study clarifies the phylogenetic position of *Fejervarya verruculosa*, placing it as a sister species to *F. cancrivora* and forming a species complex comprising *F. cancrivora* + *F. verruculosa* + Sulawesi *F. cf. cancrivora*. Morphological similarities between *F. cancrivora* and *F. verruculosa* have been noted since their initial description, which is further demonstrated in this study and accurately reflects their close affinity to one another. Early work on *Fejervarya* primarily distinguished *F. verruculosa* from *F. cancrivora* based on the extent of the dermal flap on the post-axial side of Toe V (a 'fringe' in *cancrivora*; a 'ridge' in *verruculosa*) and furrow lengths on the dorsum (Roux 1911; van Kampen 1923). Interestingly, some *F. cancrivora* individuals lack a prominent dermal fringe on the post-axial side of Toe V entirely. These appear to vary between islands, with some private haplotypes retaining the dermal fringe outside of Toe V (e.g. in Nusa Penida) while others completely lack it (e.g. in Sumbawa). *Fejervarya cancrivora* from west of Wallace's Line exhibit this dermal fringe (van Kampen 1923; Dubois and Ohler 2000; Yodthong et al. 2019a). Understanding patterns of dermal fringe expression between different *F. cancrivora* populations requires more comprehensive morphometric and genomic analyses from both mainland Asian and LS Archipelago.

While our results strongly support the sister relationship between *F. cancrivora* + *F. verruculosa*, vouchers labelled '*F. verruculosa*' have been previously recovered as a sister lineage to *F. iskandari* in mtDNA phylogenies (Köhler et al. 2019; Hasan et al. 2022). We believe that these studies had actually sampled the divergent *F. iskandari* Flores lineage and misattributed them to *F. verruculosa*. This study includes *F. verruculosa* from the type locality of Ilwaki, Wetar Island (Roux 1911) so we are confident in our designation of the *F. verruculosa* and its distribution. Conflicting results in this vein are not unexpected in studies of Indonesian *Fejervarya* (e.g. Djong et al. 2007), highlighting the challenges of species delimitation in this genus.

All three species of *Fejervarya* in the Lesser Sundas and insular populations within *F. iskandari* and *F. verruculosa* show modest to high levels of mtDNA diversity while showing very little morphological

variation between them. Conserved morphologies accompanied by high genetic diversity often occur where allopatric populations assume identical environmental niches, limiting ecological competition and rendering morphological divergence selectively neutral (Pyrone et al. 2015; Fišer et al. 2018). Since islands in the LS Archipelago share similar climatic and environmental conditions (Lohman 2011), we hypothesise that this is the likeliest cause for morphological stasis between genetically divergent lineages of Lesser Sunda *Fejervarya*; this has previously been documented in other anurans living in archipelagos (Flury et al. 2021; Ellepolla et al. 2022). Interestingly, patterns of morphological divergence vary in LS herpetofauna. Similar to our *Fejervarya* dataset, some taxa have deeply divergent populations that look nearly identical (e.g. *Sphenomorphus* skinks; Reilly et al. 2022b), while other taxa have very closely related populations which look strikingly different (e.g. emerald tree skinks *Lamprolepis*; Reilly et al. unpublished data).

BIOGEOGRAPHICAL INFERENCES

Interpreting phylogenetic results in a biogeographical context provides an independent line of evidence to understand population divergence and species formation, especially against a backdrop of complex historical biogeography (Arbogast and Kenagy 2001; Fišer et al. 2018) such as in the LS Archipelago. It has been assumed that LS *Fejervarya* frogs are mostly recently introduced due to human activity and therefore less interesting for evolutionary or biogeographic study (Jimmy McGuire, pers. obs.). Here, we present a coarse hypothesis explaining how natural and anthropogenic dispersal of LS *Fejervarya* explain aspects of their contemporary distribution and phylogeographic structures.

The ranges of the three LS *Fejervarya* species roughly correspond to portions of the major tectonic formations in the region, which broadly mirrors the phylogeographic divisions shown in other taxa (Schmitt et al. 2010; Mariyanto et al. 2021). *Fejervarya cancrivora* corresponds to the Sunda Arc, while *F. verruculosa* and *F. iskandari* correspond to the Inner and Outer Banda Arcs, respectively. The shallow phylogenetic structure across Java and the Sunda Arc Islands in *F. cancrivora* is similar to other large-bodied anurans such as *Duttaphrynus melanostictus* and *Polypedates leucomystax*, which was inferred to be a result of human-mediated movement into the LS Archipelago (Brown et al. 2010; Reilly et al. 2017, 2019b). Like *P. leucomystax*, we hypothesise that the lack of phylogenetic structure in LS *F. cancrivora* can be explained by recent human-mediated colonisation in the region, mirroring the spread of agriculture and the movement of *F. cancrivora* as a source of food between communities and islands. Frog meat is consumed in rural areas of Indonesia, and *F. cancrivora* is one of the main species harvested for food (Ohler and

Nicolas 2017). Unlike most farmed food sources, *F. cancrivora* are hand-caught adjacent to paddy fields (Kusrini and Alford 2006), presenting a greater chance of individuals escaping into the wild and forming new populations. Alternatively, populations of *F. cancrivora* may have existed in the region but have been highly introgressed with the new colonists, obscuring evidence of phylogeographic structure. The private *F. cancrivora* island haplotypes in Nusa Penida and Sumbawa could have arisen from natural colonisation of those islands, or they could be introduced from populations that are missing in our phylogeny. Presence or absence of gene flow between the haplogroups and introduced populations should be assessed once nuclear genetic data are available for those populations

Fejervarya verruculosa occurs on Sumba and the Banda Arcs. Their phylogenetic position implies that they diverged from naturally dispersing populations of an *F. cancrivora* ancestor moving eastward prior to introgression by human-mediated colonists. Our estimate of the age of the Rote population is enigmatic as this lineage appears much older than the island itself. The common ancestor of *F. verruculosa* diverged from *F. cancrivora* over 6 Ma, even though the islands that *F. verruculosa* occurs on are estimated to be younger than this, especially Rote which is only estimated to have been emergent for ~1 Ma (Roosmawati and Harris 2009). This pattern of old lineages on young islands is well documented, with Christmas Island lizards being a notable example (Oliver et al. 2018; Dodge et al. 2023). Heads (2011) outlined various global examples and possible biogeographic explanations for this pattern. Sumba and Banda Arc Island (minus Rote) clades of *F. verruculosa* are sister to each other, a pattern also found in ranid frogs (Reilly et al. 2022a), *Sphenomorphus* forest skinks (Reilly et al. 2022b), *Draco* flying lizards (Reilly et al. 2022c) and *Cyrtodactylus* bent-toed geckos (Reilly et al. 2023). The divergence estimate of the Sumba lineage is similar to the estimated time at which that island emerged (~3 Ma; Fortuin 1997), and the remaining lineages (Timor, Semau, Alor, Pantar and Wetar) are estimated to be significantly younger than the islands they occupy. The highly nested topology of the tree, with Semau, Alor, Pantar, and Wetar samples nested within Timor samples, suggests that Timor served as the source of dispersal to these neighbouring islands. Pantar and Alor have a shared haplotype suggesting Pantar may have been recently colonised from Alor. As far as we know, *F. verruculosa* is the only known frog species on Pantar Island, which is very hot and dry.

Fejervarya iskandari occurs on the Sunda Arc (Java, Bali, Sumbawa, Flores) and Timor, confirming that their distribution is not restricted to Java. Phylogenetically, *F. iskandari* from Sunda Arc + Timor form a shallow monophyletic clade, like *Polypedates leucomystax*. Timor *F. iskandari* appears to be a recent, human-mediated introduction from Bali and/or Java, which

has also been suggested in *P. leucomystax* (Reilly et al. 2019b). However, the circumstances surrounding the introduction of *F. iskandari* into the Banda Arc remains unclear. Within *F. iskandari*, populations in Sumbawa and Flores naturally diverged from the Sunda Shelf populations approximately 5 Ma, when the archipelago's landscape and geography was significantly different than the present day. Our dataset lacks morphological data from Timor *F. iskandari*, which is worth including in future studies to contextualise this unusual range expansion. Another interesting find is that *F. iskandari* has not yet been confirmed from Lombok though we speculate that *F. iskandari* occurs on the island due to the volume of people and goods moving between Lombok and Bali. However, continued survey efforts are needed to confirm this.

We note that *F. cancrivora* occurs on many of the islands that the dicroglossid frogs of the genus *Limnectes* occur on, such as Bali, Lombok and Sumbawa. On these islands, *F. cancrivora* is found primarily in rice paddies and human-modified habitats whereas *Limnectes* occupies more natural mountain streams. In contrast, *F. verruculosa* occurs on islands that do not have any *Limnectes* frogs, and they tend to be found both in rice paddies and in mountain streams. This suggests that *F. verruculosa* may be occupying a vacant 'stream' niche when *Limnectes* is absent. The smaller-bodied *F. iskandari* appears to be able to co-occur with larger-bodied *Fejervarya* species, suggesting that they are sufficiently ecologically distinct to limit interspecific competition.

From the combined mitochondrial and morphometric data, we envision a scenario where the common ancestor of both *F. cancrivora* and *F. verruculosa* colonised the Sunda Arc islands of the Lesser Sundas by way of Java, then dispersed out to Sumba and the Banda Arcs where they adopted a stream-living niche and diverged into *F. verruculosa*. Parallel to this, *F. iskandari* colonised the Inner Banda Island arc where they evolved in sympatry with large-bodied dicroglossid frogs in the genus *Limnectes*.

CONCLUSIONS AND FUTURE DIRECTIONS

We have clarified the phylogenetic relationships of LS *Fejervarya*, placing *F. cancrivora* and *F. verruculosa* as a pair of allopatric sister taxa and confirming the presence of divergent populations of *F. iskandari* in the LS Archipelago. The inclusion of mtDNA topotypes (vouchers from the locality where the type specimen was collected) for all three species allows us to confidently assign vouchers to species, providing updated accounts based on modern systematic techniques and determine the range of all three species with greater precision. While molecular data for *F. cancrivora* indicates a single panmictic population across South-East Asia, data for *F. iskandari* and *F. verruculosa* comprises of several well-diverged

populations which roughly corresponds to different LS islands. Gene flow between divergent populations should be assessed to help determine if each clade constitutes a separate species.

A two-pronged hypothesis of dispersal (one by *F. iskandari* and one by *F. cancrivora* + *F. verruculosa*) largely explains the current distribution of Lesser Sundas *Fejervarya*. However, there are several peculiar biogeographical patterns that are difficult to explain. The early diverging *F. verruculosa* lineage on Rote is particularly perplexing. Assuming a direct eastward path from the Sunda Arc into the Banda Arc, this ancestral *Fejervarya* somehow bypassed Sumba through means unknown. The Rote *F. verruculosa* lineage is six times as old as the island itself, indicating this lineage came from somewhere else.

Bioacoustics has been previously applied to delineate *Fejervarya* species (e.g. Köhler et al. 2019), and our study suffered from lack of such calls. It is clear that future studies on Lesser Sunda frogs need to integrate bioacoustics alongside morphological and genomic data. While surveys by WAM, MZB, MVZ and ITB have refined our knowledge of Lesser Sunda *Fejervarya* distributions and diversity, it is likely that more comprehensive surveys will reveal new populations and lineages.

CONTRIBUTIONS

Alen Tanoyo and Sean Reilly jointly drafted the manuscript. Alen Tanoyo measured specimens and performed morphometric analyses. Sean Reilly, Evy Arida, Djoko Iskandar and Jimmy McGuire collected MVZ specimens, Alen Tanoyo and Sean Reilly conducted molecular lab work and analyses. Djoko Iskandar provided systematic and taxonomic clarification, as well as final edits. Paul Doughty and Jimmy McGuire jointly guided experimental design and provided final edits.

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REFERENCES

- Abdullah, C.I., Rampnoux, J.-P., Bellon, H., Maury, R.C., and Soeria-Atmadja, R. (2000). The evolution of Sumba Island (Indonesia) revisited in the light of new data on the geochronology and geochemistry of the magmatic rocks. *Journal of Asian Earth Sciences* **18**: 533–546.
- Alam, M.S., Kurabayashi, A., Hayashi, Y., Sano, N., Khan, M.M.R., Fujii, T., and Sumida, M. (2010). Complete mitochondrial genomes and novel gene rearrangements in two dicroglossid frogs, *Hoplobatrachus tigerinus* and *Euphylyctis hexadactylus*, from Bangladesh. *Genes and Genetic Systems* **85**(3): 219–232. doi: 10.1266/ggs.85.219
- Ali, J.R., and Heaney, L.R. (2021). Wallace's line, Wallacea, and associated divides and areas: history of a tortuous tangle of ideas and labels. *Biological Reviews* **96**(3): 922–942. doi: 10.1111/brv.12683
- Arbogast, B.S., and Kenagy, G.J. (2001). Comparative phylogeography as an integrative approach to historical biogeography. *Journal of Biogeography* **28**(7): 819–825. doi: 10.1046/j.1365-2699.2001.00594.x
- Bolkay, S. J. (1915). Beiträge zur Osteologie einiger exotischer Raniden. *Anatomischer Anzeiger* **48**: 172–183.
- Bouckaert R., Vaughan T.G., Barido-Sottani J., Duchêne S., Fourment M., Gavryushkina A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F., Ogilvie, H.A., du Plessis, L., Poppinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C.H., Xie, D., Zhang, C., Stadler, T., and Drummond, A. (2019). BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **15**(4): e1006650. doi: 10.1371/journal.pcbi.1006650
- Brown, R.M., Linkem, C.W., Siler, C.D., Sukumaran, J., Esselstyn, J.A., Diesmos, A.C., Iskandar, D.T., Bickford, D., Evans, B.J., McGuire, J.M., Grismer, L., Supratina, J.S., and Andayani, N. (2010). Phylogeography and historical demography of *Polypedates leucomystax* in the islands of Indonesia and the Philippines: evidence for recent human-mediated range expansion? *Molecular Phylogenetics and Evolution* **57**(2): 598–619. doi: 10.1016/j.ympev.2010.06.015
- Che, J., Pang, J., Zhao, H., Wu, G.F., Zhao, E.M., and Zhang Y.P. (2007). Molecular phylogeny of the Chinese ranids inferred from nuclear and mitochondrial DNA sequences. *Biochemical Systematics and Ecology* **35**: 29–35. doi: 10.1016/j.bse.2006.09.003
- Che, J., Hu, J.S., Zhou, W.W., Murphy, R.W., Papenfuss, T.J., Chen, M.Y., Rao, D.Q. Li, P.P., and Zhang, Y.P. (2009). Phylogeny of the Asian spiny frog tribe Paini (Family Dicroglossidae) sensu Dubois. *Molecular Phylogenetics and Evolution* **50**(1): 59–73. doi: 10.1016/j.ympev.2008.10.007
- Chen, L.Q., Murphy, R.W., Lathrop, A., Ngo, A., Orlov, N.L., Ho, C.T., and Somorja, I.L.M. (2005). Taxonomic chaos in Asian ranid frogs: an initial phylogenetic resolution. *Herpetological Journal* **15**: 231–243.
- Cheng, J.X., Cai, Y.T., Zheng, Y.J., Zhang, J.Y., Storey, K.B., Bao, Y.X., and Yu, D.N. (2018). The complete mitochondrial genome of *Fejervarya kawamurai* (Anura: Dicroglossidae) and its phylogeny. *Mitochondrial DNA Part B, Resources* **3**(2): 551–553. doi: 10.1080/23802359.2018.1467219
- Daudin, F.M. (1802). *Histoire naturelle des rainettes, des grenouilles et des crapauds*. Levrault, Paris.
- De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology* **56**(6): 879–886. doi: 10.1080/10635150701701083
- Deng, W., Maust, B.S., Nickle, D.C., Learn, G.H., Liu, Y., Heath, L., Kosakovsky-Pond, S.L., and Mullins, J.I. (2010). DIVEIN: a web server to analyze phylogenies, sequence divergence, diversity, and informative sites. *BioTechniques* **48**(5): 405–408. doi: 10.2144/000113370
- Djong, T.H., Matsui, M., Kuramoto, M., Belabut, D.M., Sen, Y.H., Nishioka, M., and Sumida, M. (2007). Morphological divergence, reproductive isolating mechanism, and molecular phylogenetic relationships among Indonesia, Malaysia, and Japan populations of the *Fejervarya limnocharis* complex (Anura, Ranidae). *Zoological Science* **24**(12): 1197–1212. doi: 10.2108/zsj.24.1197
- Djong, H.T., Matsui, M., Kuramoto, M., Nishioka, M., and Sumida, M. (2011). A new species of the *Fejervarya limnocharis* complex from Japan (Anura, Dicroglossidae). *Zoological Science* **28**(12): 922–929. doi: 10.2108/zsj.28.922
- Dodge, T.O., Farquharson, K.A., Ford, C., Cavanagh, L., Schubert, K., Schumer, M., Belov, K., and Hogg, C.J. (2023). Genomes of two extinct-in-the-wild reptiles from Christmas Island reveal distinct evolutionary histories and conservation insights. *Molecular Ecology Resources*. doi: 10.1111/1755-0998.13780
- Dubois, A., and Ohler, A. (2000). Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 1. Nomenclatural status and type-specimens of the nominal species *Rana limnocharis* Gravenhorst, 1829. *Alytes* **18**: 15–50.
- Ellepola, G., Pie, M.R., Pethiyagoda, R., Hanken, J., and Meegaskumbura, M. (2022). The role of climate and islands in species diversification and reproductive-mode evolution of Old World tree frogs. *Nature Communications Biology* **5**: 347. doi: 10.1038/s42003-022-03292-1
- Fišer, C., Robinson C.T., and Malard, F. (2018). Cryptic species as a window into the paradigm shift of the species concept. *Molecular Ecology* **27**(3): 613–635. doi: 10.1111/mec.14486
- Flury, J. M., Haas, A., Brown, R.M., Das, I., Pui, Y.M., Boon-Hee, K., Scheidt, U., Iskandar, D.T., Jankowski, A., and Hertwig, S.T. (2021). Unexpectedly high levels of lineage diversity in Sundaland puddle frogs (Dicroglossidae: *Occidozyga* Kuhl and van Hasselt, 1822). *Molecular Phylogenetics and Evolution* **163**: 107210. doi: 10.1016/j.ympev.2021.107210
- Fortuin, A.R., Van der Werff, W., and Wensink, H. (1997). Neogene basin history and paleomagnetism of a rifted and inverted forearc region, on- and offshore Sumba, Eastern Indonesia. *Journal of Asian Earth Sciences* **15**: 61–88.
- Frost, D.R. (2024). Amphibian Species of the World, an Online Reference. American Museum of Natural History. <https://amphibiansoftheworld.amnh.org/index.php> [accessed 15 January 2024].

- Gravenhorst, J.L.C. (1829). *Deliciae Musei Zoologici Vratislaviensis. Fasciculus primus. Chelonios et Batrachia*. Leopold Voss, Leipzig, Germany.
- Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* **59**(3): 307–321. doi: 10.1093/sysbio/syq010
- Hall, R. (2011). Australia-SE Asia collision: plate tectonics and crustal flow. *Geological Society of London Special Publication* **355**: 75–109. doi: 10.1144/SP355.5
- Hallowell, E. (1861). 'Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U.S.N.' *Proceedings of the Academy of Natural Sciences of Philadelphia* **12**: 480–510.
- Hasan, M., Kurniawan, N., Soewondo, A., Nalley, W.M.M., Matsui, M., Igawa, T., and Sumida, M. (2022). Postmating isolation and evolutionary relationships among *Fejervarya* species from Lesser Sunda, Indonesia and other Asian countries revealed by crossing experiments and mtDNA Cytb sequence analyses. *Ecology and Evolution* **12**(10): e9436. doi: 10.1002/ece3.9436
- Heads, M. (2011). Old taxa on young islands: a critique of the use of island age to date island-endemic clades and calibrate phylogenies. *Systematic Biology* **60**(2): 204–218. doi: 10.1093/sysbio/syq075
- Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q., and Vinh, L.S. (2018). UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* **35**(2): 518–522. doi: 10.1093/molbev/msx281
- Huson, F., Lê, S., and Pagès, J. (2017). *Exploratory multivariate analysis by example using R* (second edition). CRC Press, Florida, United States of America.
- Jiang, L., Lü, G., Liu, L., Wu, B., Xu, Z., and Li, Y. (2020). Characterization of the complete mitochondrial genome of the paddy frog *Fejervarya multistriata* (Anura: Dicroglossidae) and its phylogeny. *Mitochondrial DNA Part B, Resources* **5**(2): 1248–1250. doi: 10.1080/23802359.2020.1731359
- Kaiser, H., Venancio, L.C., Ceballos, J., Freed, P., Heacox, S., Lester, B., Richards, S.J., Trainor, C.R., Sanchez, C., and O'Shea, M. (2011). The herpetofauna of Timor-Leste: a first report. *ZooKeys* **109**: 19–86. doi: 10.3897/zookeys.109.1439
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A., and Jermini, L.S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**(6): 587–589. doi: 10.1038/nmeth.4285
- Köhler, G., Mogk, L., Khaing, K.P.P., and Than, N.L. (2019). The genera *Fejervarya* and *Minervarya* in Myanmar: description of a new species, new country records, and taxonomic notes (Amphibia, Anura, Dicroglossidae). *Vertebrate Zoology* **69**(2): 183–126. doi: 10.26049/VZ69-2-2019-05
- Kotaki, M., Kurabayashi, A., Matsui, M., Khonsue, W., Djong, T.H., Tandon, M., and Sumida, M. (2008). Genetic divergence and phylogenetic relationships among the *Fejervarya limnocharis* complex in Thailand and neighboring countries revealed by mitochondrial and nuclear genes. *Zoological Science* **25**: 381–390. doi: 10.2108/zsj.25.381
- Kotaki, M., Kurabayashi, A., Matsui, M., Kuramoto, M., Djong, T.H., and Sumida, M. (2010). Molecular phylogeny of the diversified frogs of genus *Fejervarya* (Anura: Dicroglossidae). *Zoological Science* **27**(5): 386–395. doi: 10.2108/zsj.27.386
- Kurniawan, N., Islam, M.M., Tjong H.D., Igawa, T., Daicus, M.B., Yong, H.S., Wanichanon, R., Khan, M.M.R., Iskandar, D.T., Nishioka, M., and Sumida, M. (2010). Genetic divergence and evolutionary relationship in *Fejervarya cancrivora* from Indonesia and other Asian countries inferred from allozyme and mtDNA sequence analyses. *Zoological Science* **27**(3): 222–233. doi: 10.2108/zsj.27.222
- Kurniawan, N., Djong, T. H., Maideliza, T., Hamidy, A., Hasan, M., Igawa, T., and Sumida, M. (2014). Genetic divergence and geographic distribution of frogs in genus *Fejervarya* from Indonesia inferred from mitochondrial 16S rRNA gene analysis. *Treubia* **41**: 1–16. doi: 10.14203/treubia.v41i0.361
- Kusrini, M. D., and Alford, R. A. (2006). Indonesia's exports of frogs' legs. *Traffic Bulletin* **21**: 13–24.
- Lê, S., Josse, J., and Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* **25**(1): 1–18. doi: 10.18637/jss.v025.i01
- Linkem, C.W., Brown, R.M., Siler, C.D., Evans, B.J., Austin, C.C., Iskandar, D.T., Diesmos, A.C., Supriatna, J., Andayani, N., and McGuire, J.A. (2013). Stochastic faunal exchanges drive diversification in widespread Wallacean and Pacific island lizards (Squamata: Scincidae: *Lamprolepis smaragdina*). *Journal of Biogeography* **40**(3): 507–520. doi: 10.1111/jbi.12022
- Liu, Z.Q., Wang, Y.Q., and Su, B. (2005). The mitochondrial genome organization of the rice frog, *Fejervarya limnocharis* (Amphibia: Anura): a new gene order in the vertebrate mtDNA. *Gene* **346**: 145–151, doi: 10.1016/j.gene.2004.10.013
- Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K.L., Shih, H.T., Carvalho, G.R., and von Rintelen, T. (2011). Biogeography of the Indo-Australian Archipelago. *Annual Review of Ecology, Evolution, and Systematics* **42**(1): 205–226. doi: 10.1146/annurev-ecolsys-102710-145001
- Macey, J.R., Strasburg, J.L., Brisson, J.A., Vredenburg, V.T., Jennings, M., and Larson, A. (2001). Molecular phylogenetics of western North American frogs of the *Rana boylii* species group. *Molecular Phylogenetics and Evolution* **19**(1): 131–143. doi: 10.1006/mpev.2000.0908
- Maryanto, I., Hisheh, S., Maharadatunkamsi, How, R.A., and Schmitt, L.H. (2021). The impact of Pleistocene glaciations on population structure and systematics in five snake species in the Banda Arc islands of southern Wallacea: the views from genes, morphology and species assemblages. *Journal of the Royal Society of Western Australia* **104**: 65–84.
- Matsui, M., Kuraishi, N., Jiang, J. P., Ota, T., Hamidy, A., Orlov, N.L., and Nishikawa, K. (2010). Systematic reassessments of fanged frogs from China and adjacent regions (Anura: Dicroglossidae). *Zootaxa* **2345**(1): 33–42. doi: 10.11646/zootaxa.2345.1.3
- Mertens, R. (1967). Die herpetologische Sektion des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. *Senckenbergiana Biologica* **48**(A): 1–106.
- Muraoka, H., Nasution, A., Simanjuntak, J., Dwipa, S., Takahashi, M., Takahashi, H., Matsuda, K., and Sueyoshi, Y. (2005). 'Geology and geothermal systems in the Bajawa volcanic rift zone, Flores, Eastern Indonesia'. Proceedings of the World Geothermal Congress.

- Nguyen, L.T., Schmidt, H.A., Von Haeseler, A., and Minh, B.Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**(1): 268–274. doi: 10.1093/molbev/msu300
- O'Connor, S., Ono, R., and Clarkson, C. (2011). Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science* **334**: 1117–1121. doi: 10.1126/science.1207703
- Ohler, A., and Nicolas, V. (2017). What frog's leg do froggies eat? The use of DNA barcoding for identification of deep frozen frog legs (Dicroglossidae, Amphibia) commercialized in France. *European Journal of Taxonomy* **271**: 1–19. doi: 10.5852/ejt.2017.271
- Oliver, P.M., Blom, M.P.K., Cogger, H.G., Fisher, R.N., Richmond, J.Q., and Woinarski, J.C. Z. (2018). Insular biogeographic origins and high phylogenetic distinctiveness for a recently depleted lizard fauna from Christmas Island, Australia. *Biology Letters* **14**(6): 20170696. doi: 10.1098/rsbl.2017.0696
- O'Shea, M.T., Sanchez, C., Heacox, S., Kathriner, A., Carvalho V.L., Ribeiro A.V., Soares, Z.A., De Araujo, L.L., and Kaiser, H. (2012). First update to herpetofaunal records from Timor-Leste. *Asian Herpetological Research* **3**(2): 114–126. doi: 10.3724/SP.J.1245.2012.00114
- Palumbi, S.R., Martin, A., Romano, S., McMillan, W.O., Stice, L., and Grabowski, G. (2002). The Simple Fool's Guide to PCR. Technical report by Department of Zoology and Kewalo Marine Laboratory, University of Hawaii. Honolulu, United States of America.
- Pyron, R.A., Costa, G.C., Patten, M.A., and Burbrink, F.T. (2015). Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biological Reviews* **90**(4): 1248–1262. doi: 10.1111/brv.12154
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G., and Suchard, M.A. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**(5): 901–904. doi: 10.1093/sysbio/syy032
- Ratnasingham, S., and Hebert, P.D. (2007). BoLD: The Barcode of Life data system (<http://www.barcodinglife.org>). *Molecular Ecology Notes* **7**(3): 355–364. doi: 10.1111/j.1471-8286.2007.01678.x
- Reilly, S.B., Wogan, G., Stubbs, A.L., Arida, E., Iskandar, D.T., and McGuire, J.A. (2017). Toxic toad invasion of Wallacea: a biodiversity hotspot characterized by extraordinary endemism. *Global Change Biology* **23**(12): 5029–5031. doi: 10.1111/gcb.13877
- Reilly, S.B., Stubbs, A.L., Karin, B.R., Bi, K., Arida, E., Iskandar, D.T., and McGuire, J.A. (2019a). Leap-frog dispersal and mitochondrial introgression: Phylogenomics and biogeography of *Limnectes* fanged frogs in the Lesser Sundas Archipelago of Wallacea. *Journal of Biogeography* **46**(4): 757–769. doi: 10.1111/jbi.13526
- Reilly S.B., Stubbs, A.L., Karin, B.R., Arida, E., Iskandar, D.T., and McGuire, J.A. (2019b). Recent colonization and expansion through the Lesser Sundas by seven amphibian and reptile species. *Zoologica Scripta* **48**: 614–626. doi: 10.1111/zsc.12368
- Reilly, S.B., Arifin, U., Stubbs, A.L., Karin, B.R., Kaiser, H., Frederick, J.H., Arida, E., Iskandar, D.T., and McGuire J.A. (2022a). Phylogenetic relationships of southern Wallacean ranid frogs (Anura: Ranidae: *Hylarana*). *Zootaxa* **5150**(4): 591–599. doi: 10.11646/zootaxa.5150.4.7
- Reilly, S.B., Karin, B.R., Stubbs, A.L., Arifin, U., Arida, E., Kaiser, H., Bi, K., Hamidy, A., Iskandar, D.T., and McGuire, J.A. (2022b). Diverge and conquer: phylogenomics of southern Wallacean forest skinks (Genus: *Sphenomorphus*) and their colonization of the Lesser Sunda Archipelago. *Evolution* **76**(10): 2281–2301. doi: 10.1111/evo.14592
- Reilly, S.B., Stubbs, A.L., Karin, B.R., Arifin, U., Arida, E., Kaiser, H., Bi, K., Iskandar, D.T., and McGuire J.A. (2022c). Phylogenomics reveals dispersal-driven speciation and divergence with gene flow in Lesser Sunda flying lizards (Genus *Draco*). *Systematic Biology* **71**(1): 221–241. doi: 10.1093/sysbio/syab043
- Reilly, S.B., Stubbs, A.L., Karin, B.R., Arida, E., Arifin, U., Hamidy, A., Kaiser, H., Bi, K., Riyanto, A., Iskandar, D. T., and McGuire, J.A. (2023). Bewildering biogeography: waves of dispersal and diversification across southern Wallacea by bent-toed geckos (genus: *Cyrtodactylus*). *Molecular Phylogenetics and Evolution* **186**: 107853. doi: 10.1016/j.ympev.2023.107853
- Reilly, S.B. (2024). *Fejervarya* mtDNA phylogenetics files [Dataset]. Dryad. doi: 10.5061/dryad.0zpc8674w
- Ren, Z.M., Zhu, B., Ma, E.B., Wen, J., Tu, T.Y., Cao, Y., Hasegawa, M., and Zhong, Y. (2009). Complete nucleotide sequence and gene arrangement of the mitochondrial genome of the crab-eating frog *Fejervarya cancrivora* and evolutionary implications. *Gene* **441**(1–2): 148–155. doi: 10.1016/j.gene.2008.09.010
- Roosmawati, N., and Harris, R. (2009). Surface uplift history of the incipient Banda arc-continent collision: geology and synorogenic foraminifera of Rote and Savu Islands, Indonesia. *Tectonophysics* **479**(1–2): 95–110. doi: 10.1016/j.tecto.2009.04.009
- Roux, J. (1911). Elbert-Sunda-Expedition des Frankfurter Vereins für Geographie und Statistik: Reptilien und Amphibien. *Zoologische Jahrbücher* **30**: 495–508.
- RStudio Development Team (2023). RStudio: integrated development for R. Posit PBC. <http://www.rstudio.com>
- Sanchez, E., Biju, S.D., Islam, M.M., Hasan, M., Ohler, A., Vences, M., and Kurabayashi, A. (2018). Phylogeny and classification of fejervaryan frogs (Anura: Dicroglossidae). *Salamandra* **54**(2): 109–116.
- Savage J.M., and Heyer W.R. (1967). Variation and distribution in the tree-frog genus *Phyllomedusa*. *Beiträge zur Neotropischen Fauna* **5**(2): 111–131.
- Schmitt, L., Hisheh, S., Suyanto, A., Maharadatunkamsi, N.V., Newbound, C., Kitchener, D.J., and How, R.A. (2010). Crossing the Line: the impact of contemporary and historical sea barriers on the population structure of bats in Southern Wallacea. In: T.H. Fleming and P.A. Racey (eds), *Island bats: evolution, ecology and conservation*. University of Chicago Press, United States of America.
- Sievers, F., Wilm, A., Dineen, D., Gibson, T.J., Karplus, K., Li, W., Lopez, R., McWilliam, H., Remmert, M., Söding, J., Thompson, J.D., and Higgins, D.G. (2011). Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Molecular Systems Biology* **7**: 539. doi: 10.1038/msb.2011.75
- Sumida, M., Kondo, Y., Kanamori, Y., and Nishioka, M. (2002). Inter- and intraspecific evolutionary relationships of the rice frog *Rana limnocharis* and allied species *R. cancrivora* inferred from crossing experiments and mitochondrial DNA sequences of the 12S and 16S rRNA genes. *Molecular Phylogenetics and Evolution* **25**(2): 293–305. doi: 10.1016/S1055-7903(02)00243-9

- Taylor, E.H. (1920). Philippine amphibia. *Philippine Journal of Science* **16**: 213–359.
- van Kampen, P.N. (1923). *The amphibia of the Indo-Australian archipelago*. E.J. Brill Ltd., Leiden, Netherlands.
- Veith, M., Kosuch, J., Ohler, A., and Dubois, A. (2001). Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 2. Morphological and molecular variation in frogs from the Greater Sunda Islands (Sumatra, Java, Borneo) with the definition of two species. *Alytes* **19**: 5–28.
- White, A.E., Dey, K.K., Stephens, M., and Price, T.D. (2021). Dispersal syndromes drive the formation of biogeographical regions, illustrated by the case of Wallace's Line. *Global Ecology and Biogeography* **30**(3): 685–696. doi: 10.1111/geb.13250
- Whittaker, R.J. and Fernández-Palacios, J.M. (2007). *Island biogeography: ecology, evolution, and conservation* (second edition). Oxford University Press, New York, United States of America.
- Wostl, E., Smith, E.N., and Reed, R.N. (2016). Origin and Identity of *Fejervarya* (Anura: Dicroglossidae) on Guam. *Pacific Science* **70**(2): 233–241. doi: 10.2984/70.2.9
- Yodthong, S., Stuart, B.L., and Aowphol, A. (2019a). Species delimitation of crab-eating frogs (*Fejervarya cancrivora* complex) clarifies taxonomy and geographic distributions in mainland Southeast Asia. *ZooKeys* **883**: 119–153. doi: 10.3897/zookeys.883.37544
- Yodthong, S., Stuart, B.L., and Aowphol, A. (2019b) Corrigenda: Species delimitation of crab-eating frogs (*Fejervarya cancrivora* complex) clarifies taxonomy and geographic distributions in mainland Southeast Asia. *ZooKeys* **883**: 119–153. doi: 10.3897/zookeys.883.37544; and *ZooKeys* **897**: 149–150. doi: 10.3897/zookeys.897.48818
- Zheng, Y., Zhang, S., Lu Q., Zhang, S., Wang, L., Hong, M., Nguyen, T., Zhao, J., and Yao, M. (2021). Population genetic patterns of a mangrove-associated frog reveal its colonization history and habitat connectivity. *Diversity and Distribution* **27**(8): 1584–1600. doi: 10.1111/ddi.13304

APPENDIX 1 Vouchers of *Fejervarya* analysed in this study. Institutional abbreviations: WAM = Western Australian Museum, Perth, Australia. MVZ = Museum of Vertebrate Zoology, Berkeley, CA, USA. ALS = collected by Alexander Stubbs (Integrative Biology, UC Berkeley).

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R109061	<i>F. cancrivora</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	
WAM R109065	<i>F. cancrivora</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	
WAM R109096	<i>F. cancrivora</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	
WAM R109098	<i>F. cancrivora</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	
WAM R109000	<i>F. cancrivora</i>	Ubud, Bali Island	-8.5000	115.2667	•	•	
WAM R109002	<i>F. cancrivora</i>	Ubud, Bali Island	-8.5000	115.2667	•	•	
WAM R109003	<i>F. cancrivora</i>	Ubud, Bali Island	-8.5000	115.2667	•	•	
ALS72	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
ALS73	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274414	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274421	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274422	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274423	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274424	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274425	<i>F. cancrivora</i>	Bali Island	-8.4380	115.4020	•		
WAM R109159	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109193	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109149	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109151	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109152	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109154	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109155	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109185	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R 109188	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R 109189	<i>F. cancrivora</i>	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R98345	<i>F. cancrivora</i>	Kuta, Lombok Island	-8.9166	116.2833		•	•
WAM R98344	<i>F. cancrivora</i>	Kuta, Lombok Island	-8.9166	116.2833		•	
MVZ:Herp.293823	<i>F. cancrivora</i>	Lombok Island	-8.5320	116.3990	•		
MVZ:Herp.293878	<i>F. cancrivora</i>	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp.293879	<i>F. cancrivora</i>	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp.293880	<i>F. cancrivora</i>	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp.293871	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293872	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293873	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293874	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293875	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293876	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293877	<i>F. cancrivora</i>	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp.293900	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293901	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293902	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293903	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293904	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293905	<i>F. cancrivora</i>	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp.293906	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293907	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293908	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293909	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293910	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293911	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293912	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293913	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293914	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp.293915	<i>F. cancrivora</i>	Sumbawa Island	-9.0290	116.8190	•		
WAM R98416	<i>F. cancrivora</i>	Meratan Lebo, Taliwang, Sumbawa Island	-8.6916	116.8500	•	•	•
MVZ:Herp.293884	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp.293885	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp.293886	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp.293887	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp.293888	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp.294026	<i>F. cancrivora</i>	Sumbawa Island	-8.7580	117.3500	•		
WAM R98475	<i>F. cancrivora</i>	Batu Tering, Sumbawa Island	-8.8000	117.3667	•	•	
MVZ:Herp.293889	<i>F. cancrivora</i>	Sumbawa Island	-8.7240	117.3830	•		
WAM R98367	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98374	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5030	117.4333	•	•	
WAM R98375	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98376	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98377	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98379	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98388	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	
WAM R98387	<i>F. cancrivora</i>	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333	•	•	•
WAM R98691	<i>F. cancrivora</i>	Brang Kua, Mojo Island	-8.2375	117.6125	•	•	•
WAM R98647	<i>F. cancrivora</i>	Desa Sebotok, Mojo Island	-8.1583	117.6208	•	•	
MVZ:Herp.293916	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp.293917	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293918	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp.293919	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp.293920	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp.293921	<i>F. cancrivora</i>	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp.293824	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293892	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293893	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293894	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293895	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293896	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293897	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293898	<i>F. cancrivora</i>	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp.293890	<i>F. cancrivora</i>	Sumbawa Island	-8.5510	118.3840	•		
MVZ:Herp.293891	<i>F. cancrivora</i>	Sumbawa Island	-8.5510	118.3840	•		
WAM R98615	<i>F. cancrivora</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333	•	•	
WAM R98611	<i>F. cancrivora</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333	•	•	•
WAM R98616	<i>F. cancrivora</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333	•	•	•
MVZ:Herp.293826	<i>F. cancrivora</i>	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp.293923	<i>F. cancrivora</i>	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp.293924	<i>F. cancrivora</i>	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp.293849	<i>F. cancrivora</i>	Sumbawa Island	-8.7660	118.6050	•		
MVZ:Herp.293827	<i>F. cancrivora</i>	Sumbawa Island	-8.7400	118.6050	•		
MVZ:Herp.293828	<i>F. cancrivora</i>	Sumbawa Island	-8.7400	118.6050	•		
MVZ:Herp.293925	<i>F. cancrivora</i>	Sumbawa Island	-8.7630	118.6070	•		
MVZ:Herp.293984	<i>F. cancrivora</i>	Sumbawa Island	-8.4870	118.6640	•		
MVZ:Herp.293985	<i>F. cancrivora</i>	Sumbawa Island	-8.4870	118.6640	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R98533	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917	•	•	•
WAM R98534	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98535	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98537	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98538	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98539	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98540	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R99843	<i>F. cancrivora</i>	Waworada, Sumbawa Island	-8.7083	118.7920			•
MVZ:Herp.293851	<i>F. cancrivora</i>	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp.293852	<i>F. cancrivora</i>	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp.293853	<i>F. cancrivora</i>	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp.293829	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293830	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293831	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293832	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293833	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293834	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293836	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293838	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293839	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293841	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293842	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293843	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293844	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293845	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293846	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293847	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293848	<i>F. cancrivora</i>	Sumbawa Island	-8.5010	119.0360	•		
WAM R 109315	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109324	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109333	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	
WAM R 109313	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109319	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109320	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109326	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109317	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109335	<i>F. iskandari</i>	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R 109047	<i>F. iskandari</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	•
WAM R 109066	<i>F. iskandari</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	•
WAM R 109048	<i>F. iskandari</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	•
WAM R 109064	<i>F. iskandari</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	•
WAM R 109062	<i>F. iskandari</i>	Banjär, Bali Island	-8.2000	114.9667	•	•	•
WAM R 109011	<i>F. iskandari</i>	Ubud, Bali Island	-8.5000	115.2667	•	•	•
MVZ:Herp:274419	<i>F. iskandari</i>	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274420	<i>F. iskandari</i>	Bali Island	-8.4380	115.4020	•		
WAM R 98397	<i>F. iskandari</i>	Merente, 5km SSE Alas, Sumbawa Island	-8.5527	117.0208	•	•	
MVZ:Herp:293881	<i>F. iskandari</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293882	<i>F. iskandari</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293883	<i>F. iskandari</i>	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293899	<i>F. iskandari</i>	Sumbawa Island	-8.5270	118.3140	•		
WAM R 99850	<i>F. iskandari</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333			•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R99849	<i>F. iskandari</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333			•
WAM R98612	<i>F. iskandari</i>	Desa Daha, Sumbawa Island	-8.7500	118.4333			•
MVZ:Herp.293922	<i>F. iskandari</i>	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp.293850	<i>F. iskandari</i>	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp.293835	<i>F. iskandari</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293837	<i>F. iskandari</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293840	<i>F. iskandari</i>	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp.293856	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293857	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293858	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293859	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293860	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293861	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293862	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293863	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293864	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293865	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293866	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293867	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293868	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293869	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293870	<i>F. iskandari</i>	Flores Island	-8.7230	121.7510	•		
MVZ:Herp.293854	<i>F. iskandari</i>	Flores Island	-8.7060	121.7730	•		
MVZ:Herp.293855	<i>F. iskandari</i>	Flores Island	-8.7060	121.7730	•		
WAM R105393	<i>F. iskandari</i>	Daraloeng Boru, Flores Island	-8.5500	122.6500	•	•	•
WAM R105394	<i>F. iskandari</i>	Daraloeng Boru, Flores Island	-8.5500	122.6500	•	•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293819	<i>F. iskandari</i>	Flores Island	-8.2160	122.9730	•		
MVZ:Herp.293820	<i>F. iskandari</i>	Flores Island	-8.2160	122.9730	•		
MVZ:Herp.293821	<i>F. iskandari</i>	Flores Island	-8.2160	122.9730	•		
MVZ:Herp.293822	<i>F. iskandari</i>	Flores Island	-8.2160	122.9730	•		
MVZ:Herp.293960	<i>F. iskandari</i>	Timor Island	-10.2440	123.6580	•		
MVZ:Herp.293999	<i>F. iskandari</i>	Timor Island	-10.0290	123.8620	•		
MVZ:Herp.294000	<i>F. iskandari</i>	Timor Island	-10.0290	123.8620	•		
MVZ:Herp.294001	<i>F. iskandari</i>	Timor Island	-10.0280	123.8620	•		
MVZ:Herp.294002	<i>F. iskandari</i>	Timor Island	-10.0280	123.8620	•		
MVZ:Herp.293990	<i>F. iskandari</i>	Timor Island	-10.0240	123.8660	•		
MVZ:Herp.293986	<i>F. iskandari</i>	Timor Island	-10.0220	123.8670	•		
MVZ:Herp.293987	<i>F. iskandari</i>	Timor Island	-10.0220	123.8670	•		
MVZ:Herp.293988	<i>F. iskandari</i>	Timor Island	-10.0220	123.8670	•		
MVZ:Herp.293989	<i>F. iskandari</i>	Timor Island	-10.0220	123.8670	•		
MVZ:Herp.293996	<i>F. iskandari</i>	Timor Island	-10.0240	123.8680	•		
MVZ:Herp.293997	<i>F. iskandari</i>	Timor Island	-10.0240	123.8680	•		
MVZ:Herp.293998	<i>F. iskandari</i>	Timor Island	-10.0240	123.8680	•		
MVZ:Herp.293991	<i>F. iskandari</i>	Timor Island	-10.0220	123.8690	•		
MVZ:Herp.293992	<i>F. iskandari</i>	Timor Island	-10.0220	123.8690	•		
MVZ:Herp.293993	<i>F. iskandari</i>	Timor Island	-10.0220	123.8690	•		
MVZ:Herp.293995	<i>F. iskandari</i>	Timor Island	-10.0220	123.8690	•		
MVZ:Herp.294003	<i>F. iskandari</i>	Timor Island	-10.0240	123.8690	•		
MVZ:Herp.294005	<i>F. iskandari</i>	Timor Island	-10.0390	123.9320	•		
MVZ:Herp.294006	<i>F. iskandari</i>	Timor Island	-10.0390	123.9320	•		
MVZ:Herp.293962	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
MVZ:Herp.293963	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293964	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
MVZ:Herp.293965	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
MVZ:Herp.293967	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
MVZ:Herp.293968	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
MVZ:Herp.293969	<i>F. iskandari</i>	Timor Island	-9.8220	124.3100	•		
WAM R 101763	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	•
WAM R 101723	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R 101765	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R 101721	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R 101764	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R 101766	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R 101805	<i>F. verruculosa</i>	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	•
WAM R 101681	<i>F. verruculosa</i>	Waikelosawah, Sumba Island	-9.6000	119.4833	•	•	•
WAM R 101682	<i>F. verruculosa</i>	Waikelosawah, Sumba Island	-9.6000	119.4833	•	•	•
WAM R 101685	<i>F. verruculosa</i>	Waikelosawah, Sumba Island	-9.6000	119.4833	•	•	•
WAM R 101686	<i>F. verruculosa</i>	Waikelosawah, Sumba Island	-9.6000	119.4833	•	•	•
MVZ:Herp.293947	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293948	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293949	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293950	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293951	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293952	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293953	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293954	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293955	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293956	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293957	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp.293958	<i>F. verruculosa</i>	Sumba Island	-10.0070	120.0450	•		
WAM R 101580	<i>F. verruculosa</i>	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R 101581	<i>F. verruculosa</i>	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R 101582	<i>F. verruculosa</i>	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R 101584	<i>F. verruculosa</i>	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R 101589	<i>F. verruculosa</i>	Waingapu, Sumba Island	-9.6500	120.2500		•	•
WAM R 101594	<i>F. verruculosa</i>	Waingapu, Sumba Island	-9.6500	120.2500		•	
WAM R 101593	<i>F. verruculosa</i>	Waingapu, Sumba Island	-9.6500	120.2500		•	•
WAM R 101592	<i>F. verruculosa</i>	Waingapu, Sumba Island	-9.6500	120.2500		•	
MVZ:Herp.293946	<i>F. verruculosa</i>	Sumba Island	-10.0190	120.6590	•		
WAM R 101918	<i>F. verruculosa</i>	Ngallu, Sumba Island	-10.1083	120.6917		•	
WAM R 101919	<i>F. verruculosa</i>	Ngallu, Sumba Island	-10.1083	120.6917		•	
MVZ:Herp.293926	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293927	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293928	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293929	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293930	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293931	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293932	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293933	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293934	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293935	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293936	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293937	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293938	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293939	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293940	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293941	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293942	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293943	<i>F. verruculosa</i>	Rote Island	-10.8880	122.8320	•		
MVZ:Herp.293944	<i>F. verruculosa</i>	Rote Island	-10.7450	123.0540	•		
MVZ:Herp.293945	<i>F. verruculosa</i>	Rote Island	-10.7450	123.0540	•		
WAM R 105671	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105681	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105682	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105684	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105622	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105621	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105623	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105670	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105604	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105611	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105606	<i>F. verruculosa</i>	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R 105000	<i>F. verruculosa</i>	Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 105876	<i>F. verruculosa</i>	Desa Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 105878	<i>F. verruculosa</i>	Desa Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 105001	<i>F. verruculosa</i>	Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 105874	<i>F. verruculosa</i>	Desa Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 105877	<i>F. verruculosa</i>	Desa Uiasa, Semau Island	-10.1666	123.4667	•	•	•
WAM R 108085	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000	•	•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R 108086	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108087	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108088	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108089	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108122	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108124	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108126	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108128	<i>F. verruculosa</i>	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R 108175	<i>F. verruculosa</i>	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R 108176	<i>F. verruculosa</i>	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R 108177	<i>F. verruculosa</i>	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R 108178	<i>F. verruculosa</i>	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R 108179	<i>F. verruculosa</i>	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
MVZ:Herp.294007	<i>F. verruculosa</i>	Timor Island	-10.2660	123.5660	•		
MVZ:Herp.293959	<i>F. verruculosa</i>	Timor Island	-10.2440	123.6580	•		
WAM R 101508	<i>F. verruculosa</i>	Baumata, West Timor, Timor Island	-10.1833	123.7167		•	•
WAM R 101511	<i>F. verruculosa</i>	Baumata, West Timor, Timor Island	-10.1833	123.7167		•	•
WAM R 101535	<i>F. verruculosa</i>	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	•
WAM R 101517	<i>F. verruculosa</i>	Baumata, West Timor, Timor Island	-10.1833	123.7167		•	
WAM R 101534	<i>F. verruculosa</i>	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R 101565	<i>F. verruculosa</i>	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R 101566	<i>F. verruculosa</i>	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R 107045	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•		•
WAM R 107024	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•
WAM R 107027	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•
WAM R 107035	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R107040	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107015	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107017	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107020	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107022	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107025	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107028	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107029	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107030	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107032	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107033	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107037	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107041	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107043	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107044	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107047	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107048	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107049	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107050	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107051	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107052	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107053	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107054	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107058	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107059	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107060	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R 107062	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107063	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107064	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107065	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107066	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107067	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107068	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107069	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107071	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107072	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R 107073	<i>F. verruculosa</i>	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
MVZ:Herp.293994	<i>F. verruculosa</i>	Timor Island	-10.0220	123.8690	•		
MVZ:Herp.294004	<i>F. verruculosa</i>	Timor Island	-10.0390	123.9320	•		
WAM R 101567	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 101568	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 101569	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 101570	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 101571	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 101572	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 107213	<i>F. verruculosa</i>	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R 106470	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167	•	•	
WAM R 106651	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167	•	•	
WAM R 106400	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106402	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106403	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106413	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R 106415	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106637	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106638	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106640	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106641	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106642	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106643	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106645	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106649	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106650	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106654	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106655	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R 106656	<i>F. verruculosa</i>	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
MVZ:Herp.293974	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293975	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293976	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293977	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293978	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293979	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293980	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
MVZ:Herp.293981	<i>F. verruculosa</i>	Timor Island	-9.6570	124.2240	•		
WAM R 107899	<i>F. verruculosa</i>	Kabit, Pantar Island, Alor Archipelago	-8.2166	124.2333		•	•
WAM R 106884	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	•
WAM R 106885	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R 106886	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R 106887	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106888	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106889	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106890	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106892	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106893	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106894	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106895	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106896	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106897	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106898	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106902	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106903	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106904	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106905	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106906	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106907	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106908	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106909	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106911	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106912	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106913	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106914	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106916	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106917	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106918	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R106919	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R 106920	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R 106921	<i>F. verruculosa</i>	Oimoro, West Timor, Timor Island	-10.1333	124.2833	•	•	
WAM R 107861	<i>F. verruculosa</i>	Batu Bakalang, Pantar Island, Alor Archipelago	-8.2333	124.3000	•	•	
MVZ:Herp.293961	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
MVZ:Herp.293966	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
MVZ:Herp.293970	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
MVZ:Herp.293971	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
MVZ:Herp.293972	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
MVZ:Herp.293973	<i>F. verruculosa</i>	Timor Island	-9.8220	124.3100	•	•	
WAM R 106836	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106855	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106787	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106788	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106789	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106790	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106792	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106799	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106801	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106802	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106803	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106811	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106812	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106813	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106814	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106816	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R 106817	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106831	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106832	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106833	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106834	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106835	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106837	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106838	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106846	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106856	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106857	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106861	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106862	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106863	<i>F. verruculosa</i>	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R107708	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	•
WAM R107646	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107651	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107786	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107785	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	•
WAM R107787	<i>F. verruculosa</i>	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	•
MVZ:Herp:293818	<i>F. verruculosa</i>	Alor Island	-8.1640	124.6690		•	
WAM R108075	<i>F. verruculosa</i>	Apui, Alor Island, Alor Archipelago	-8.2500	124.7167		•	
WAM R107987	<i>F. verruculosa</i>	Apui, Alor Island, Alor Archipelago	-8.2500	124.7167		•	•
MVZ:Herp:293809	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220		•	
MVZ:Herp:293810	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220		•	
MVZ:Herp:293811	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220		•	
MVZ:Herp:293812	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293813	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220	•		
MVZ:Herp.293814	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220	•		
MVZ:Herp.293815	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220	•		
MVZ:Herp.293816	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220	•		
MVZ:Herp.293817	<i>F. verruculosa</i>	Alor Island	-8.2740	124.7220	•		
MVZ:Herp.293776	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293777	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293778	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293779	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293780	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293781	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293782	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293783	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293784	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293785	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293786	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293787	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293788	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293789	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293790	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293791	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293792	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293793	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293794	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293795	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293796	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.293797	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293798	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293799	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293800	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293801	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293802	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293803	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293804	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293805	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293806	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293807	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.293808	<i>F. verruculosa</i>	Alor Island	-8.1650	124.7480	•		
MVZ:Herp.294016	<i>F. verruculosa</i>	Wetar Island	-7.9220	126.3990	•		
MVZ:Herp.294009	<i>F. verruculosa</i>	Wetar Island	-7.9300	126.4090	•		
MVZ:Herp.294017	<i>F. verruculosa</i>	Wetar Island	-7.9300	126.4090	•		
MVZ:Herp.294021	<i>F. verruculosa</i>	Wetar Island	-7.9290	126.4100	•		
MVZ:Herp.294010	<i>F. verruculosa</i>	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp.294011	<i>F. verruculosa</i>	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp.294018	<i>F. verruculosa</i>	Wetar Island	-7.9370	126.4120	•		
MVZ:Herp.294019	<i>F. verruculosa</i>	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp.293982	<i>F. verruculosa</i>	Wetar Island	-7.9280	126.4220	•		
MVZ:Herp.294008	<i>F. verruculosa</i>	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp.294012	<i>F. verruculosa</i>	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp.294013	<i>F. verruculosa</i>	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp.294024	<i>F. verruculosa</i>	Wetar Island	-7.9290	126.4230	•		
MVZ:Herp.294022	<i>F. verruculosa</i>	Wetar Island	-7.9320	126.4230	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp.294023	<i>F. verruculosa</i>	Wetar Island	-7.9320	126.4230	•		
MVZ:Herp.294025	<i>F. verruculosa</i>	Wetar Island	-7.9320	126.4230	•		
MVZ:Herp.294020	<i>F. verruculosa</i>	Wetar Island	-7.9290	126.4240	•		
MVZ:Herp.294014	<i>F. verruculosa</i>	Wetar Island			•		
MVZ:Herp.294015	<i>F. verruculosa</i>	Wetar Island			•		

APPENDIX 2 GenBank 16S sequences used as outgroups. Full references provided in the main text.

Genbank accession	Species	Locality	Reference
AP011543	<i>Hoplobatrachus tigrinus</i>	Mymensingh, Bangladesh	Alam et al. (2010)
MH087466	<i>Fejervarya kawamurai</i>	Guizhou, China	Cheng et al. (2018)
MN987553	<i>Fejervarya multistriata</i>	Sichuan, China	Jiang et al. (2020)
AY158705	<i>Fejervarya limnocharis</i>	Yancheng, China	Liu et al. (2005)
NC012647	<i>Fejervarya cancrivora</i>	Guangxi, China	Ren et al. (2009)
AB444693	<i>Fejervarya cf. cancrivora</i> (Sulawesi-type)	Pelabuhan Ratu, Indonesia	Kurniawan et al. (2010); assigned by Kurniawan et al. (2010) and Yodthong et al. (2019)
AB444689	<i>Fejervarya cancrivora</i>	Bogor, Indonesia	Kurniawan et al. (2010)
AB444684	<i>Fejervarya cancrivora</i>	Cianjur, Indonesia	Kurniawan et al. (2010)
AB444690	<i>Fejervarya cancrivora</i>	Banyumas, Indonesia	Kurniawan et al. (2010)
AB444692	<i>Fejervarya moodiei</i>	Trat, Thailand	Kurniawan et al. (2010); re-assigned by inference from Yodthong et al. (2019)
AB444691	<i>Fejervarya moodiei</i>	Trat, Thailand	Kurniawan et al. (2010); re-assigned by inference from Yodthong et al. (2019)
AB444688	<i>Fejervarya cancrivora</i>	Selangor, Malaysia	Kurniawan et al. (2010)

Genbank accession	Species	Locality	Reference
AB444687	<i>Fejervarya cancrivora</i>	Jambi, Indonesia	Kurniawan et al. (2010)
AB444686	<i>Fejervarya cancrivora</i>	Lampung, Indonesia	Kurniawan et al. (2010)
AB444685	<i>Fejervarya cancrivora</i>	Padang, Indonesia	Kurniawan et al. (2010)
MW007342	<i>Fejervarya</i> sp. (Borneo-type)	Sarawak, Malaysia	Flury et al. (2021)
KR816720	<i>Fejervarya cancrivora</i>	Mangliano, Guam	Wostl et al. (2016)
KR816719	<i>Fejervarya cancrivora</i>	Mangliano, Guam	Wostl et al. (2016)
KR816718	<i>Fejervarya cancrivora</i>	Agat, Guam	Wostl et al. (2016)
AB488882	<i>Fejervarya moodiei</i>	Selangor, Malaysia	Kotaki et al. (2010); re-assigned by inference from Yodthong et al. (2019)
EU979849	<i>Fejervarya</i> cf. <i>cancrivora</i> (Sulawesi-type)	South Sulawesi, Indonesia	Che et al. (2007); re-assigned by Yodthong et al. (2019)
EU435303	<i>Fejervarya cancrivora</i>	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435280	<i>Fejervarya cancrivora</i>	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435282	<i>Fejervarya cancrivora</i>	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435279	<i>Fejervarya cancrivora</i>	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
DQ458252	<i>Fejervarya moodiei</i>	Hainan, China	Che et al. (2009); re-assigned by Yodthong et al. (2019b)
AF206473	<i>Fejervarya moodiei</i>	Negros Island, Philippines	Chen et al. (2005); re-assigned by Yodthong et al. (2019)
AB070738	<i>Fejervarya moodiei</i>	Manila, Philippines	Sumida et al. (2002); re-assigned by Yodthong et al. (2019)
KX055955	<i>Fejervarya cancrivora</i>	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)
KX055954	<i>Fejervarya cancrivora</i>	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)
KX055953	<i>Fejervarya cancrivora</i>	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)

Genbank accession	Species	Locality	Reference
MK396095	<i>Fejervarya moodiei</i>	Hainan, China	Zheng et al. (2021), re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396094	<i>Fejervarya moodiei</i>	Guangdong, China	Zheng et al. (2021), re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396093	<i>Fejervarya moodiei</i>	Hainan, China	Zheng et al. (2021), re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396092	<i>Fejervarya moodiei</i>	Guangdong, China	Zheng et al. (2021), re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396091	<i>Fejervarya moodiei</i>	Guangdong, China	Zheng et al. (2021), re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
AB570277	<i>Fejervarya cancrivora</i>	Bali, Indonesia	Kurniawan et al. (2014)
AB570276	<i>Fejervarya cancrivora</i>	Bali, Indonesia	Kurniawan et al. (2014)
AB570275	<i>Fejervarya cancrivora</i>	Bali, Indonesia	Kurniawan et al. (2014)
AB570274	<i>Fejervarya cancrivora</i>	Bali, Indonesia	Kurniawan et al. (2014)
AB570273	<i>Fejervarya cancrivora</i>	Malang, Indonesia	Kurniawan et al. (2014)
AB570272	<i>Fejervarya iskandari</i>	Banyuwangi, Indonesia	Kurniawan et al. (2014)
AB570271	<i>Fejervarya iskandari</i>	Malang, Indonesia	Kurniawan et al. (2014)
AB530613	<i>Fejervarya iskandari</i>	Cianjur, Indonesia	Hasan et al. (2014)
AB277303	<i>Fejervarya iskandari</i>	Cianjur, Indonesia	Kotaki et al. (2008)
AB526324	<i>Fejervarya iskandari</i>	Banyuwangi, Indonesia	Matsui et al. (2010)
AB570270	<i>Fejervarya iskandari</i>	Malang, Indonesia	Kurniawan et al. (2014)
AB570269	<i>Fejervarya iskandari</i>	Malang, Indonesia	Kurniawan et al. (2014)
AB570268	<i>Fejervarya iskandari</i>	Malang, Indonesia	Kurniawan et al. (2014)