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A new species of *Chirixalus* Boulenger, 1893 (Anura: Rhacophoridae) from the lowland forests of Java

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Abstract. The Old World tree frog genus *Chirixalus* is distributed from northeastern India, southern China, continental Southeast Asia to Sumatra and Java. The species of this genus were previously assigned to the genera *Chiromantis* or *Philautus*. Here, we describe a newly discovered species of *Chirixalus* from Java. *Chirixalus pantaiselatan*, new species, is a small rhacophorid frog (male snout-vent length = 25.3–28.9 mm) that can be distinguished from all congeners using a combination of morphological, molecular, and advertisement call characteristics.

Key words. bioacoustics, *Chirixalus*, citizen science, taxonomy

INTRODUCTION

The Old World tree frog genus *Chirixalus* Boulenger, 1893, ranges from northeastern India, southern China, and continental Southeast Asia to Sumatra and Java (Frost, 2021). The generic taxonomy of *Chirixalus* has been controversial. The genus was first proposed by Boulenger (1893), with *Chirixalus doriae* Boulenger, 1893, as the type species. Later, Frost et al. (2006) synonymised this genus with *Chiromantis* Peters, 1854, which is distributed in tropical Africa, and transferred all *Chirixalus* members to *Chiromantis*, which contains African and Asian rhacophrid frogs that were previously classified as *Rhacophorus* Kuhl & Van Hasselt, 1822, *Philautus* Gitsel, 1848, or *Chirixalus*. Li et al. (2013) reassigned *Chiromantis vittata* (Boulenger, 1887), sensu Frost et al. (2006), to the genus *Feihyla* Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green & Wheeler, 2006. Based on the results of Aowphol et al. (2013), Frost (2014) transferred *Chiromantis hansenae* (Cochran, 1927) to *Feihyla*. Subsequently, Chan et al. (2018) transferred *Chiromantis inexpectata* Matsui, Shimada & Sudin, 2014, from Borneo to *Feihyla*. The taxonomic decision by Frost et al. (2006) to synonymise *Chirixalus* with *Chiromantis* has been widely accepted (Yu et al., 2008; Li et al., 2008, 2009, 2013; Pyron & Wiens, 2011; Hertwig et al., 2013; Chan et al., 2018, 2020), but it was named an independent genus by Chen et al. (2020), followed by Frost (2020) and Dubois et al. (2021). Frost (2020) adopted this rearrangement of *Chirixalus* by Chen et al. (2020) and transferred all Asian *Chiromantis* to *Chirixalus* without further explanation. Recently, Biju et al. (2020) rearranged the genus-level name of this group and recognised the new genus *Rohanixalus*, which was rejected by Dubois et al. (2021), who considered *Rohanixalus* to be a junior synonym of *Feihyla*. Currently, five species are recognised within *Chirixalus*: *Chirixalus doriae*; *Chirixalus simus* Annandale, 1915; *Chirixalus nongkhorensis* (Cochran, 1927); *Chirixalus dudhwaensis* Ray, 1992; and *Chirixalus trilaksonoi* (Riyanto & Kurniati, 2014) (Frost, 2021).

In April 2017, the Indonesian Herpetological Society (Penggalang Herpetologi Indonesia) conducted a citizen science activity called Gerakan Observasi Amfibi Reptil Kita (Go ARK) in the Indonesian language, as an initiative to raise awareness of Indonesian amphibian and reptile research and conservation (Kusrini et al., 2019). Participants of Go ARK included students and research communities in Sumatra, Borneo, Java, Bali, and Sulawesi, who conducted field observations of amphibians and reptiles and reported their results via the iNaturalist platform. During observations in the lowland forest in the southern part of West Java, four of the authors (UFK, MAR, DIQ and RR) discovered and collected five individuals of rhacophorid frogs that resembled the genus *Chirixalus* based on a combination of external characters including horizontal pupils, free and deeply notched tongue, distinct tympanum, opposed fingers,

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webbed toes, tips of fingers and toes dilated into disks, outer metatarsal separated by webbing, and obtuse terminal phalanges. These specimens did not match any described species of the genus. Therefore, supported by morphological, molecular, and acoustic evidence, we describe it as a new species in this work.

MATERIAL AND METHODS

Sampling. We (UFK, MAR, DIQ and RR) conducted fieldwork on 24 April 2017 in the lowland forest of the Leuweng Sancang Nature Reserve, Garut Regency, West Java. Five live frogs were collected and transported to the laboratory. After recording their advertisement calls, we euthanised the frogs and collected tissue samples, which were stored in a freezer until subsequent molecular analyses. The specimens were fixed in 10% formalin and later preserved in 70% ethanol and stored in the Museum Zoologicum Bogoriense (MZB) as voucher specimens.

Bioacoustics. We housed the frogs individually in terrariums and recorded advertisement calls using digital pulse-code modulation (PCM) recorders (LS-11; Olympus, Tokyo, Japan) using the WAV format, at a sampling frequency of 44.1 kHz and a rate of 16 bits. During recording, the air temperature was 21–22°C. We analysed advertisement calls using the Raven Pro v1.5 software, with a Hanning window and discrete Fourier transform window size of 256 points (Bioacoustics Research Program, 2014). The note-centred terminology used in this analysis follows Köhler et al. (2017).

Phylogenetic analyses. Total genomic DNA was extracted from a small amount of frozen tissue. Mitochondrial 16S rRNA (16S) gene fragments of ca. 540 bp were assembled and checked manually using the Chromas Pro v1.34 software (Technelysium Pty Ltd., Tewantin, Australia). The detailed protocols, reagents, polymerase chain reaction (PCR) conditions, and sequencing primers used in this study were described previously (Hamidy et al., 2018; Munir et al., 2018). We used additional GenBank 16S sequences from related species (Wilkinson et al., 2002; Frost et al., 2006; Li et al., 2008, 2009, 2013; Meegaskumbura et al., 2010; Aowphol et al., 2013; Matsui et al., 2014; Yodthong et al., 2014; Biju et al., 2020) for phylogenetic tree reconstruction. The sequences were aligned using the MUSCLE alignment programme integrated within the MEGA v6.06 software (Tamura et al., 2013). The resulting aligned sequences are listed in Appendix 1. Next, we used the MEGA v6.06 software to calculate the genetic divergence (uncorrected *p* distance) between species with complete deletion to eliminate gaps. New sequences were deposited in GenBank (accession nos. MT155986–155995). The mitochondrial genealogies were reconstructed based on maximum likelihood (ML) and Bayesian inference (BI) analyses using optimum substitution rates and evolution model selected using the Kakusan 4 software (Tanabe, 2011), based on the Akaike information criterion (AIC) and the GTR+Gamma optimal substitution model. ML analyses were performed with 1,000 bootstrap replicates using the RAxML v8.2.12 software (Stamatakis, 2014) on the CIPRES science gateway platform (Miller et al., 2010). BI analyses were conducted using four Metropolis coupled Markov chain Monte Carlo chains for 10 million generations, sampled every 1,000 generations and discarding the first 25% trees as burn-in, using the Mr. Bayes v3.2.6 software (Ronquist & Huelsenbeck, 2003). Run convergence was evaluated at a split frequency of <0.01 standard deviations and potential scale reduction factors of ~1.0. Tree nodes were considered strongly supported at bootstrap values of ≥70% for ML (Hillis & Bull, 1993) and ≥0.95 or greater for BI (Leaché & Reeder, 2002).

Morphometrics. Body measurements were taken to the nearest 0.1 mm under a binocular stereo microscope using a dial calliper following Grismer et al. (2007a) and Matsui et al. (2014). Abbreviations are as follows (Watters et al., 2016): (1) snout–vent length (SVL), distance from the tip of the snout to the posterior end of the vent; (2) head length (HL), distance from the tip of the snout to the posterior jaw angle; (3) head width (HW), distance between the posterior corners of the eyes; (4) snout length (SL), distance from the tip of the snout to the anterior corner of the eye; (5) eye to nostril distance (EN), from the posterior edge of the nostril to anterior corner of the eye; (6) eye diameter (ED), distance from the anterior to posterior corners of the eye; (7) eye to tympanum distance (ETD), measured from the posterior corner of the eye to the anterior border of the tympanum; (8) tympanum diameter (TD), distance from the anterior to posterior borders of the tympanum; (9) internarial distance (IND), distance between the nostrils; (10) interorbital distance (IOD), distance across the top of the head between the medial margins of the orbits at their closest point; (11) lower arm length (LAL), distance from the elbow to the tip of the third finger; (12) third finger length (Fin3L), distance from the base of the first sub articular tubercle to the tip of the third finger; (13) third finger disk width (Fin3DW), measured at the widest point on the finger III disk; (14) inner palmar tubercle length (IPTL), maximum length of the inner palmar tubercle; (15) thigh length (THL), measured from the centre of the hind limb insertion to the knee; (16) tibia length (TL), measured from the knee to heel; (17) foot length (FL), measured from the proximal edge of the inner metatarsal tubercle to the tip of the fourth toe; (18) inner metatarsal tubercle length (IMTL), greatest length of the inner metatarsal tubercle; (19) fourth toe length (Toe4L), measured from the base of the first sub articular tubercle to the tip of the toe; (20) disk width of the fourth toe (Toe4DW), measured at the widest point of the toe IV disk. The digital webbing formula follows Savage & Heyer (1997). Males were identified by the presence of a vocal sac or vocal slits, and females were confirmed by the gonads via dissection. We performed Student's *t*-test and principal component analyses (PCAs) using the Past v4.01 software (Hammer et al., 2001); we compared only adult male specimens due to the limited number of female samples in our collection. To reduce allometric bias due to ontogeny, the characters of each species were scaled using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} is the adjusted value, X is the measured value, β is the unstandardised regression coefficient of each population, and

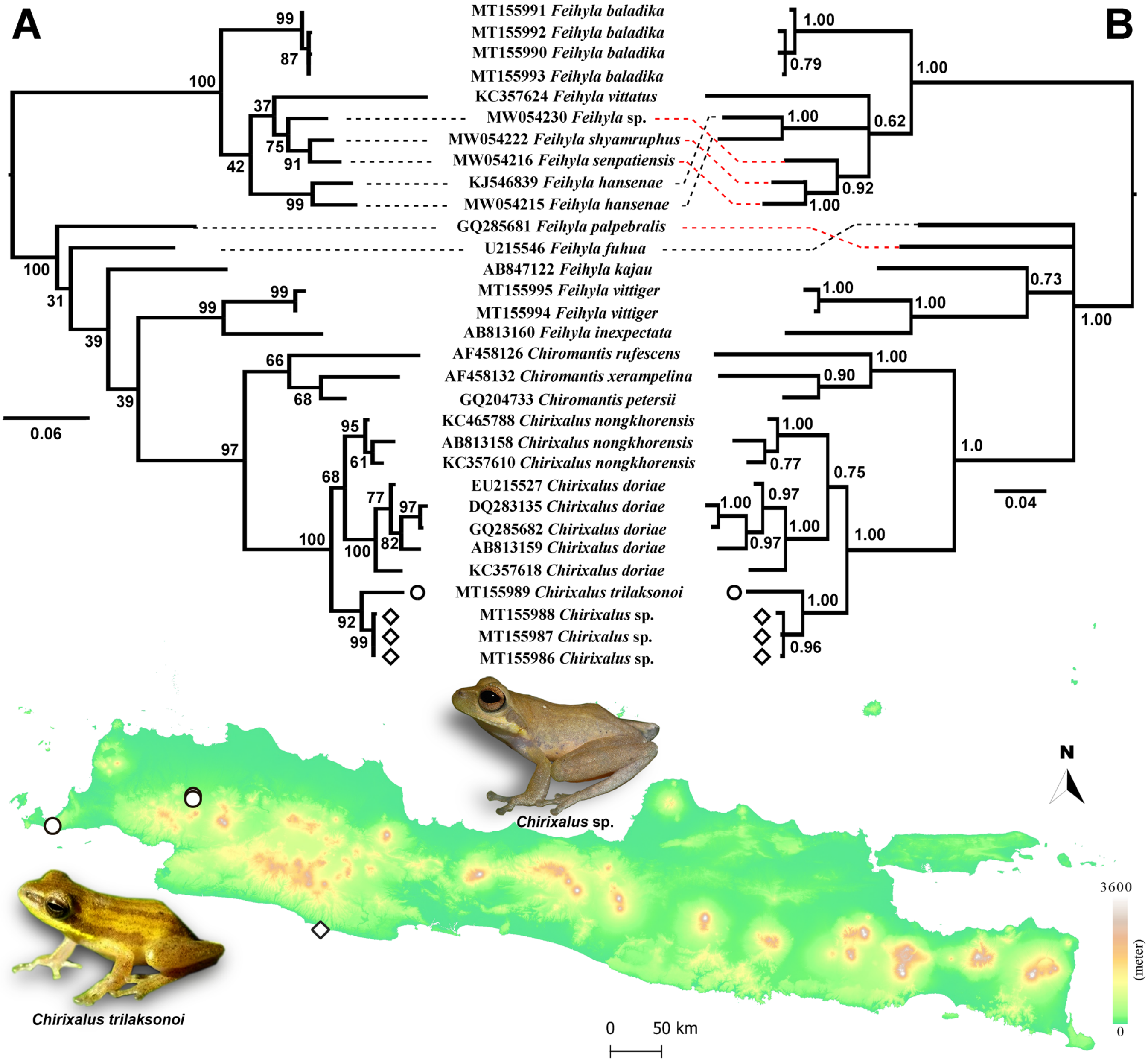

Fig. 1. Phylogenetic tree (A) Maximum likelihood (ML), (B) Bayesian Inference (BI) from ~483 bp of 16S rRNA mtDNA of *Chirixalus* spp., values above or below nodes indicate the Maximum Likelihood Bootstrap Proportion (MLBP) and Bayesian Posterior Probability (BPP) with the current distribution map of *Chirixalus* sp. (open diamond) and *Chirixalus trilaksonoi* (open circle). The distribution map was generated based on voucher material stored at the Museum Zooloogicum Bogoriense and sightings recorded from the ARK project on iNaturalist. Living specimen of *Chirixalus trilaksonoi* photographed by Wahyu Trilaksono.

SVL_{mean} is the overall average SVL of all samples (Thorpe, 1983; Lleonart et al., 2000). We measured five specimens of the newly collected *Chirixalus* sp. and seven specimens of *Chirixalus trilaksonoi* Riyanto & Kurniati, 2014 (Appendix 2). In our comparisons, we used the information in the original descriptions for species that we could not examine directly. Additional characters used for the comparison of *Chirixalus* were modified from Grismer et al. (2007a).

RESULTS

Phylogenetic analyses employing ML and BI methods produced nearly identical topologies (Fig. 1A, B; Appendices 3, 4), different only in the taxonomic position of the *Feihyla* group. The BI analyses results showed that *F. palpebralis* (Smith, 1924), *F. fuhua* Fei, Ye & Jiang, 2010, *F. vittatus* (Boulenger, 1887), *F. kajau* (Dring, 1983), *F. inexpectata*, and *F. vittiger* formed a polytomy against other members of *Feihyla*. In the obtained phylogenetic trees, the Javanese *Chirixalus trilaksonoi*, *Chirixalus* sp., and Indochina *Chirixalus doriae*, *Chirixalus nongkhorensis*, formed a strongly supported clade (ML = 100, BI = 1.00) with respect to the genus *Chiromantis* from Africa (ML = 97, BI = 1.00). Uncorrected sequence divergence of the 16S rRNA gene fragment among and within *Chirixalus* species indicates that *Chirixalus* sp. diverged from known Asian species, with interspecific genetic distances of 3.0–3.2% from its sister taxon *Chirixalus trilaksonoi*, 4.6–6.4% from *Chirixalus doriae*, and 4.1–5.3% from *Chirixalus nongkhorensis*.

Table 1. Inter and intraspecific uncorrected p-distances (in per cent) in the genus *Chirixalus* based on the ~483 bp mitochondrial 16S rRNA gene sequences.

	Taxa	1	2	3	4
1	*Chirixalus* sp.	0.0–0.2			
2	*Chirixalus trilaksonoi*	3.0–3.2	–		
3	*Chirixalus nongkhorensis*	4.1–5.3	5.7–6.0	1.4–2.1	
4	*Chirixalus doriae*	4.6–6.4	5.0–6.4	3.7–6.4	2.3–3.4

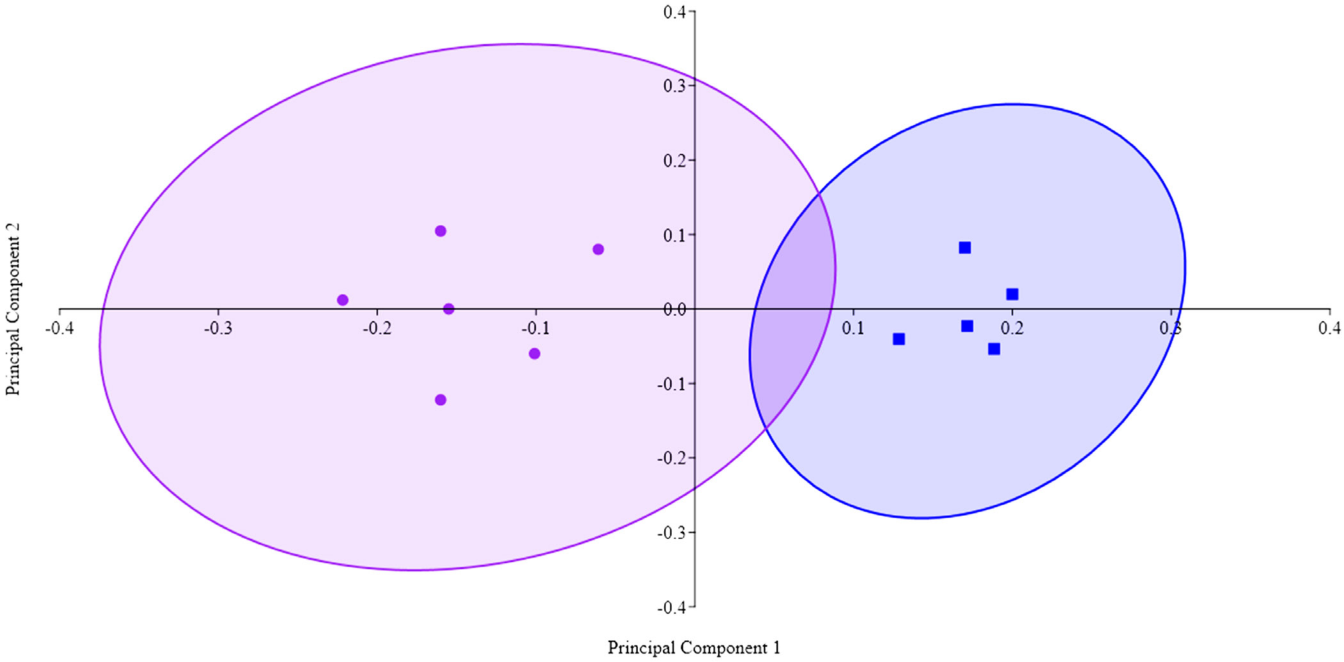

Fig. 2. The plot of the first two principal components with 95% confidence of ellipses within two populations of adult male *Chirixalus trilaksonoi* (violet) and *Chirixalus* sp. (blue) based on the size-corrected morphometric variables (loading scores of the characters, see appendix 5).

Chirixalus doriae from Indochina has an intraspecific genetic distance of 2.3–3.4%, but it may be a species complex. The *Chirixalus doriae* sample from Hua Hin, Prachuap Khiri Khan, Thailand (KC357618) differed from other populations of *Chirixalus doriae* at a heterospecific level (Table 1).

Morphological comparisons of male individuals of the two most closely related species, *Chirixalus trilaksonoi* (n = 6) and *Chirixalus* sp. (n = 5) showed significant differences as visualised in the PCA (Fig. 2). Student's *t*-test detected differences between these species in combinations of several mensural characters: HL, HW, SL, NEL, ED, ETD, TD, IND, IOD, LAL, THL, TL, FL, and Toe4L (Table 2). PCA analyses recovered the first two components with significant eigenvalues and cumulative variance of ~76.99%, with eigenvalues of the first (PC1) and second (PC2) axes accounting for 0.0289 and 0.0048 of the total variation, respectively. The first five highest standardised principal component coefficients were TD, ED, IOD, HW, and LAL for PC1 and ETD, Fin3DW, Toe4L, THL, and Fin3L for PC2 (Appendix 5). Based on these molecular, morphological, and acoustic results, we conclude that the specimens collected from the southern coast of West Java represent a new, distinct species, which we describe below.

SYSTEMATICS AND TAXONOMY

Family Rhacophoridae Hoffman, 1932

Chirixalus Boulenger, 1893

Chirixalus pantaiselatan, new species

(Figs. 3, 4, 5A, B)

Holotype. MZB. Amph 30547 (Figs. 3, 4, 5A; GenBank accession no. MT155987), an adult male collected on 24 April 2017 from Leuweung Sancang Nature Reserve, Sancang, Cibalong District, Garut Regency, Jawa Barat Province (7°43.73′S, 107°54.08′E; 32 m a.s.l.) by Umar Fhadli Kennedi, Mohammad Ali Ridha, Dzikri Ibnul Qayyim, and Rizky Rafsanzani.

Paratype. Four adult males, MZB. Amph 30548 (Fig. 5B, GenBank accession no. MT155986); MZB. Amph 30549;

Table 2. Measurement of adult *Chirixalus pantaiselatan*, new species, and *Chirixalus trilaksonoi* (in mm) with P-values of the Student t-test. Asterisks (*) denote characters that were found to be significantly different based on α=0.05.

Characters	***Chirixalus pantaiselatan*, new species**					***Chirixalus trilaksonoi***							P-values
	MZB. Amph 30547	**MZB. Amph 30548**	**MZB. Amph 30549**	**MZB. Amph 30550**	**MZB. Amph 30551**	**MZB. Amph 17932**	**MZB. Amph 17933**	**MZB. Amph 17934**	**MZB. Amph 28441**	**MZB. Amph 28440**	**MZB. Amph 29165**	**MZB. Amph 27237**	
	Holotype	**Paratype**	**Paratype**	**Paratype**	**Paratype**	**Holotype**	**Paratype**	**Paratype**	–	–	–	–	
	adult male	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult male**	**adult female**	
SVL	28.9	25.3	26.6	26.9	25.9	25.4	26.6	26.0	26.8	25.0	26.8	30.3	0.37216
HL	9.4	8.4	9.2	8.9	8.8	7.5	8.4	8.2	8.9	7.5	8.8	8.8	0.00500*
HW	10.0	9.3	8.4	8.8	9.2	7.1	7.8	7.7	8.8	7.2	8.3	9.4	0.00195*
SL	3.8	3.9	3.7	3.6	4.1	3.4	3.1	3.3	3.6	3.4	3.6	3.6	0.00502*
NEL	2.4	2.5	2.5	2.6	2.1	2.2	2.1	1.9	2.3	2.2	2.2	2.6	0.01534*
ED	4.5	4.4	4.4	4.3	4.8	3.5	3.5	3.1	3.5	3.7	3.2	4.3	1.36E-05*
ETD	1.1	1.2	1.3	1.2	1.4	0.6	0.6	0.6	0.6	0.4	0.5	0.7	0.00211*
TD	2.1	2.0	2.2	2.4	2.0	1.6	1.4	1.4	1.6	1.6	1.5	1.9	1.85E-05*
IND	2.3	2.4	2.4	2.4	2.4	2.1	2.1	1.8	2.2	1.9	2.2	2.0	0.00408*
IOD	3.5	3.4	3.6	3.5	4.1	2.7	3.1	3.1	3.1	2.9	3.0	3.6	0.00045*
LAL	12.7	11.6	11.4	12.0	12.7	10.6	9.9	9.9	11.5	9.7	11.3	12.8	0.00205*
Fin3L	4.0	3.6	3.4	3.7	3.9	3.9	3.3	3.7	4.1	3.2	3.8	4.1	0.76324
Fin3DW	1.3	1.2	1.1	1.0	1.2	0.9	1.0	0.8	1.3	1.1	1.2	1.0	0.91283
IPTL	1.2	1.1	1.4	1.1	1.3	0.7	0.7	0.8	0.9	0.7	0.9	0.8	0.05143
THL	15.3	12.6	12.9	13.0	14.3	11.9	10.8	12.4	12.8	11.6	12.8	14.4	0.00958*
TL	15.0	13.2	13.2	14.0	15.2	12.8	13.1	12.9	13.0	12.6	13.9	15.7	0.01888*
FL	11.1	10.8	10.8	9.8	10.3	9.3	9.5	9.1	10.1	8.7	10.1	11.2	0.00257*
IMTL	1.2	1.1	1.4	1.3	1.4	0.8	0.8	0.7	0.8	0.9	0.8	0.9	0.61948
Toe4L	6.0	5.4	5.6	5.3	5.4	4.8	4.4	5.1	5.4	5.2	5.4	6.3	0.03740*
Toe4DW	1.0	1.0	1.1	1.0	1.0	0.9	0.9	0.9	1.0	0.8	1.0	0.9	0.09094

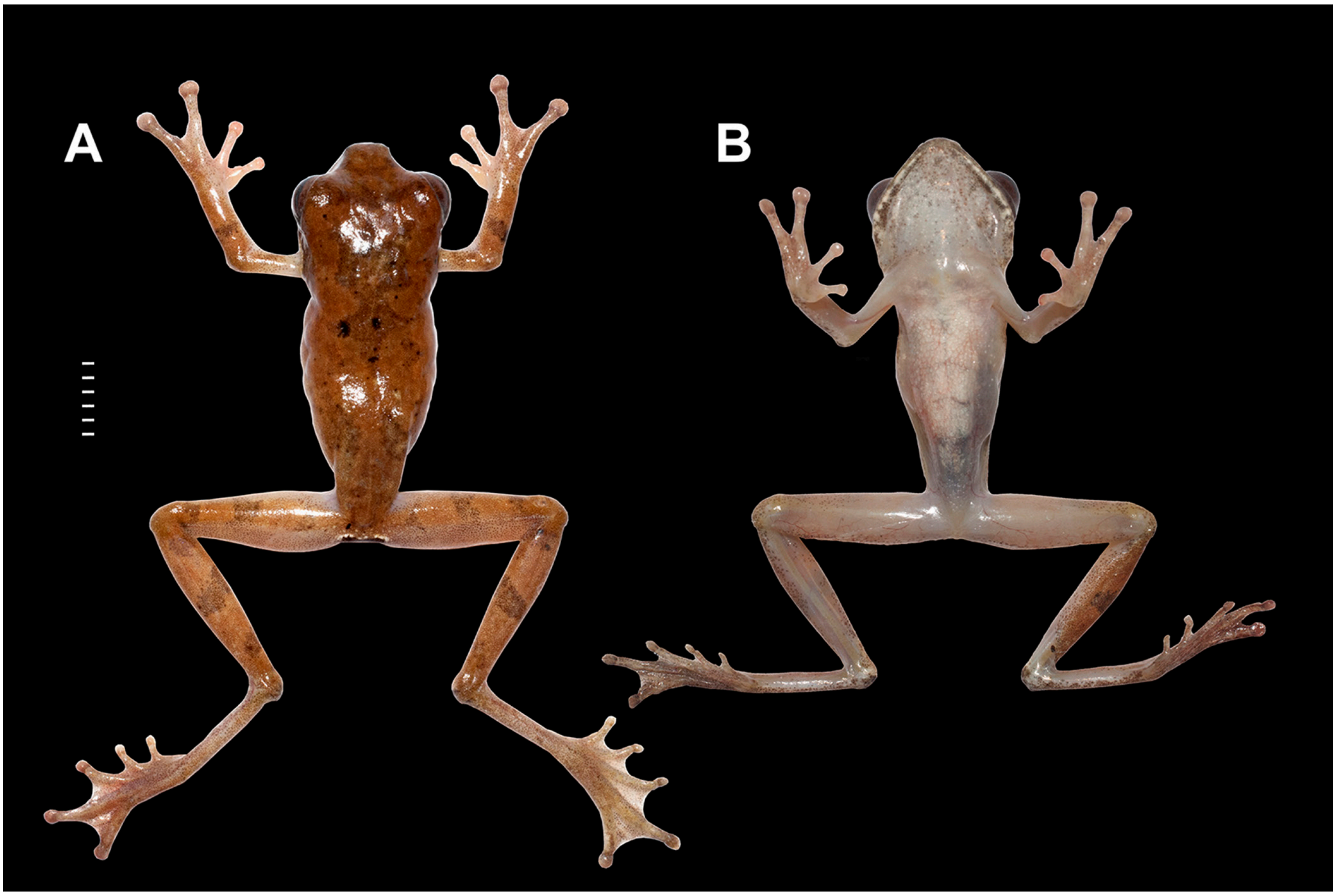

Fig. 3. Dorsal (A) and ventral (B) views of the holotype *Chirixalus pantaiselatan*, new species, MZB. Amph 30547. Scale = 5 mm.

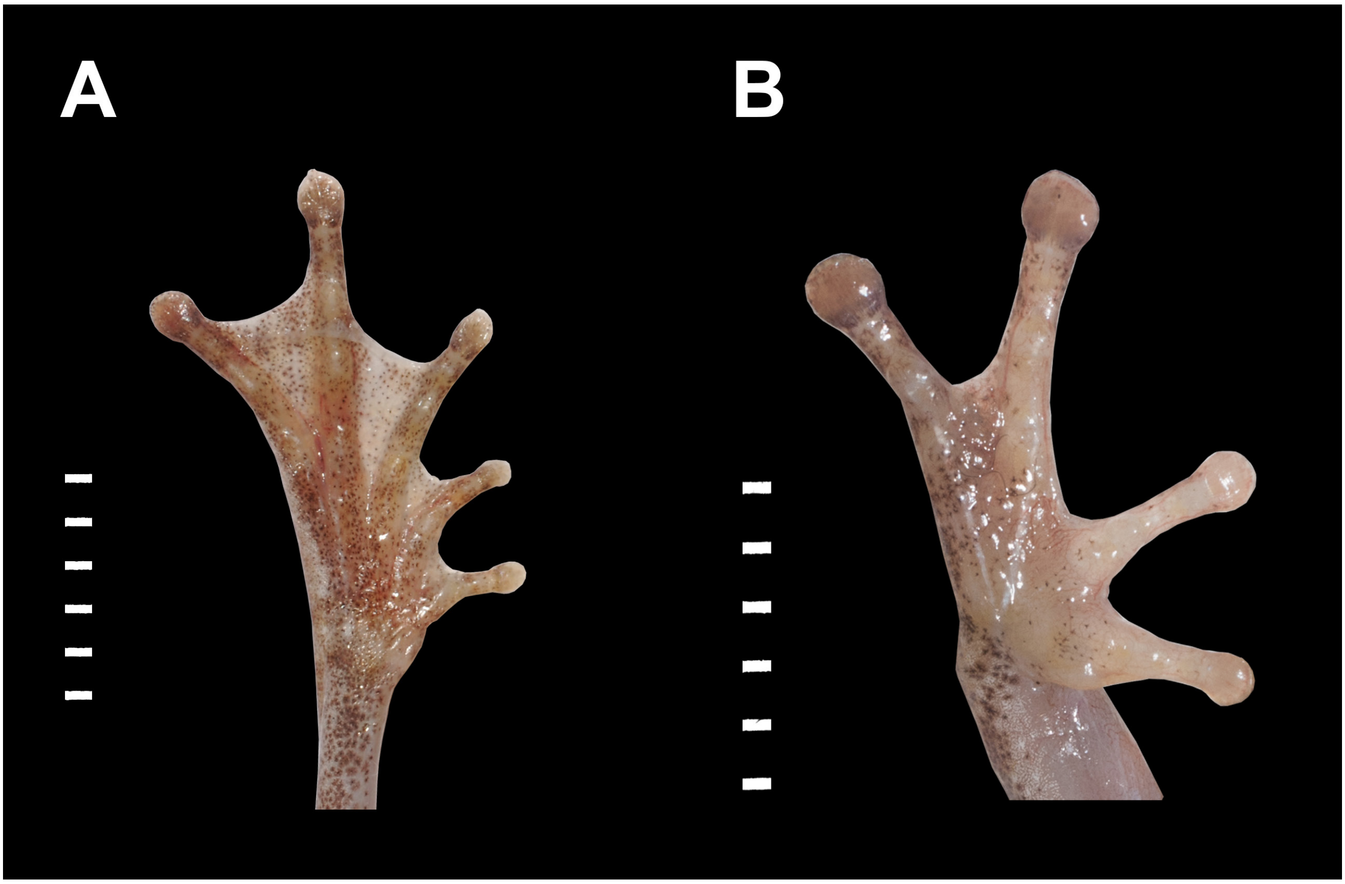

Fig. 4. Ventral of right foot (A) and right hand (B) views of the holotype *Chirixalus pantaiselatan*, new species, MZB. Amph MZB. Amph 30547. Scales = 5 mm.

Fig. 5. *Chirixalus pantaiselatan*, new species, MZB. Amph 30547 in night-time (A) and MZB. Amph 30548 in the daytime (B), uncollected *Chiromantis trilaksonoi* (C), and *Feihyla vittiger*, MZB. Amph 27238 (D). C & D photographed by Farits Alhadi.

MZB. Amph 30550; MZB. Amph 30551 (GenBank accession no. MT155988) from the same locality as the holotype and bearing the same collection data.

Diagnosis. The new species was assigned to the genus *Chirixalus* based on the following external characters: horizontal pupil, tongue free and deeply notched, distinct tympanum, opposed fingers, toes webbed, tips of fingers and toes dilated into disks, outer metatarsal separated by web, terminal phalanges obtuse (Boulenger, 1893). The new species can be distinguished from its congeners by the combination of the following characters: snout truncate; SVL 25.3–28.9 mm in males; uniform lateral body colouration, without a light dorsolateral stripe from canthus rostralis through upper orbital to the body or a light lateral stripe from under orbital to mid-body; brown dorsal colouration, with an indistinct transverse dark brown patch on intercanthal and upper eyelid to interorbital area continued by an indistinct irregular hexagon-like shape covering the parietoscapular region, and a diamond-like shape on suprascapular region to mid-body; distinct dark brown tympanum; third finger disk diameter about half that of tympanum and unique advertisement call consisting of short (2–9 notes), medium (11–17 notes), and long calls (22–46 notes). Calls are 185.71–1,644.28, 1,420.78–2,708.46, and 3,292.29–7,055.79 ms in duration, respectively, with note durations of 4.14–18.03, 4.82–15.19, and 4.78–24.88 ms, respectively. Dominant frequencies ranging from 2.34–3.94, 2.53–3.75, and 2.72–3.94 kHz for calls of short, medium, and long duration.

Description of holotype. An adult male; SVL 28.9 mm; head relatively flat and wider (HW = 34.6% of SVL) than long (HL = 32.5% of SVL); snout truncate in lateral view, sloping antero-ventrally, projecting beyond lower jaw, shorter (SL = 13.0% of SVL) than eye diameter (ED = 15.5% of SVL); canthus rostralis rounded; loreal region concave vertically; nostril oval, positioned laterally, closer to tip of snout than to eye (NEL = 63.1% of SL); internarial distance (IND = 7.9% of SVL) about more than half of interorbital distance (IOD = 12.1% of SVL); eyes relatively large (ED = 15.5% of SVL), twice as large as tympanum diameter (TD = 7.2% of SVL), nearly half of head length (ED = 47.9% of HL), protuberant, pupil horizontally elliptical; subcircular, distinct tympanum, nearly twice as large as eye to tympanum distance (ETD = 3.8% of SVL); well-developed rows of vomerine teeth; choana oval shaped; tongue notched posteriorly; single median vocal sac present, vocal slit near commissure of jaws on both sides right and left.

Forelimbs moderate in length, relatively robust, lower arm length nearly half of the snout-vent length (LAL = 43.9% of SVL); a small, rounded inner palmar tubercle (IPTL = 4.1% of SVL), about one-third of third finger length (Fin3L = 13.8% of SVL), outer one absent; indistinct subarticular tubercle between the penultimate and adjoining proximal phalange on third and fourth fingers; finger length formula I < II < IV < III; inner two fingers widely separated from outer two fingers (opposable); no webbing between first and second finger or second and inner third finger, webbing on outer third finger reaching second subarticular and reaching first subarticular on inner fourth finger (III = 1–2 IV); fingers without fringe, tips with a rounded disk, expanded with a circum marginal and indistinct transverse ventral groove; third finger disk diameter about half of the tympanum diameter (Fin3DW = 61.9 % of TD).

Hindlimbs relatively long, slender, tibiotarsal articulation extends to the posterior of nostril when fully stretched leg adpressed to body; thigh (THL = 52.9% of SVL) slightly longer than tibia (TL = 51.9% of SVL), approximately one and one-third of foot (FL = 38.4% of SVL; THL = 137.8% of FL); a well-developed, small, oval inner metatarsal (IMTL = 4.1% of SVL), about one-fifth of fourth toe length (Toe4L = 20.7% of SVL), outer one absent; toe length formula I < II < III < V < IV; webbing formula (I 1–$^{1}/_{2}$ II 0–1$^{1}/_{2}$ III 0–1 IV$^{1}/_{2}$–0 V); toes without fringe, tips with a rounded disk, bearing expanded disks with circum marginal and transverse ventral groove; fourth toe disk (Toe4DW = 3.4% of SVL) much narrower than third finger disk (Fin3DW = 4.5% of SVL).

Dorsal skin surface smooth, scattered with minute tubercles; a distinct supratympanic fold, continuous as a glandular fold to shoulder; skin fold on the corner of jaws, forming a short fold to anterior base of upper arm; lateral forearm, tarsus and foot with minute tubercles; ventral skin surface generally smooth, throat surface composed of small granules, while the abdomen composed of larger granules than those on throat, ventral surface of hand and foot smooth.

Holotype colouration. Body colour changes in living specimens. Specimens captured at night have dark brown colouration on the dorsum and pinkish colouration on the ventral surfaces of limbs and abdomen; dorsum colours change to light yellow or light brown in the morning (Fig. 5A, B); pupil dark, iris dark brown to gold; fine dark brown spots on the entire dorsal surface of the body, forelimbs, and hindlimbs; indistinct transverse dark brown patch on interchantal and upper eyelid to interorbital area continued by an indistinct irregular hexagon-like shape covering the parietoscapular region, and a diamond-like shape on suprascapular region to mid-body and irregular blotches near the inguinal region (Fig. 3A); presence of a dark transverse band on the forearm, three bands on thigh and three on tarsus; dark brown line along the canthus rostralis; light silver-coloured fold from jaw articulation to anterior of upper arm; uniform dark brown tympanum; clear pinkish ventral surfaces, throat with fine dark spots and darker along the edge of lower jaw, ventral surfaces of forelimbs and hindlimbs with fine dark spots. This colour pattern remains in preserved specimens, with the dorsal surfaces fading to beige and the ventral surfaces fading to dull white.

Variation. Individuals of the type series are morphologically relatively similar, although paratypes have smaller body sizes than the holotype (summary of morphometric variation shown in Table 2). Individuals are slightly variable in colouration, with the rather indistinct dark transverse bands on limbs and irregular dark mark on back in paratypes; all paratypes in life had a yellowish to light brown dorsum; preserved specimens are lighter brown than the holotype.

Advertisement call of the holotype. The description of the advertisement call was made based on the male holotype MZB. Amph 30547. The advertisement call of *Chirixalus pantaiselatan*, new species, was ascending, consisting of multiple notes, and a single note contained three to five visible harmonics (Fig. 6). Based on the number of notes in one call, we divided the calls of *Chirixalus pantaiselatan*, new species, into three categories: short (1–10 notes), medium (11–20 notes), and long calls (>20 notes). Advertisement calls differ in call duration and the number of notes in a single call, but their dominant frequencies overlap. Short calls contain 2–9 notes (1 male, n = 34 calls), with a call duration of 185.71–1,644.28 ms (mean ± SD: 703.2 ± 402.75 ms), inter-call interval of 734.7–6,628.5 ms (3,374.41 ± 1,781.6 ms), call period of 1,273.77–7,570.53 ms (4,079.5 ± 1,953.43 ms), note duration of 4.14–18.03 ms (11.0 ± 3.29 ms), inter-note interval of 77.33–394.33 ms (182.5 ± 47.53 ms), note period of 91.99–404.92 ms (192.9 ± 48.37 ms), and dominant frequency of 2.34–3.94 kHz (3.2 ± 0.41 kHz). Medium calls contain 11–17 notes (1 male, n = 4 calls), with a call duration of 1,420.78–2,708.46 ms (1,873.2 ± 570.53 ms), inter-call interval of 1,056.87–1,404.46 ms (1,230.7 ± 245.79 ms), call period of 3,065.46–3,765.33 ms (3,415.4 ± 494.88 ms), note duration of 4.82–15.19 ms (8.4 ± 2.93 ms), inter-note interval of 49.14–313.62 ms (140.9 ± 47.87 ms), note period of 55.79–319.04 ms (149.1 ± 47.98 ms), and dominant frequency of 2.53–3.75 kHz (3.1 ± 0.33 kHz). Long calls contain 22–46 notes (1 male, n = 4 calls), with a call duration of 3,292.29–7,055.79 ms (4,431.2 ± 1,759.7 ms), note duration of 4.78–24.88 ms (11.7 ± 3.55 ms), inter-note interval of 47.91–247.72 ms (145.4 ± 40.31 ms), note period of 56.1–259.44 ms (157.1 ± 41.15 ms), and dominant frequency of 2.72–3.94 kHz (3.5 ± 0.27 kHz).

Etymology. The specific name is an Indonesian adjective incorporating the words “Pantai,” meaning “coast,” and “Selatan,” meaning “south.” This name refers to the locality of this species in southern Java.

Indonesian Name. Katak-pucat pantaiselatan

Comparisons. The new species *Chirixalus pantaiselatan* is distinguished from other closely related species *Chirixalus trilaksonoi*, *Chirixalus doriae*, *Chirixalus dudhwaensis*, and *Chirixalus simus* by the presence of indistinct transversal dark brown patterns on the interchantal and interorbital areas and an indistinct dark mark on the parietoscapular

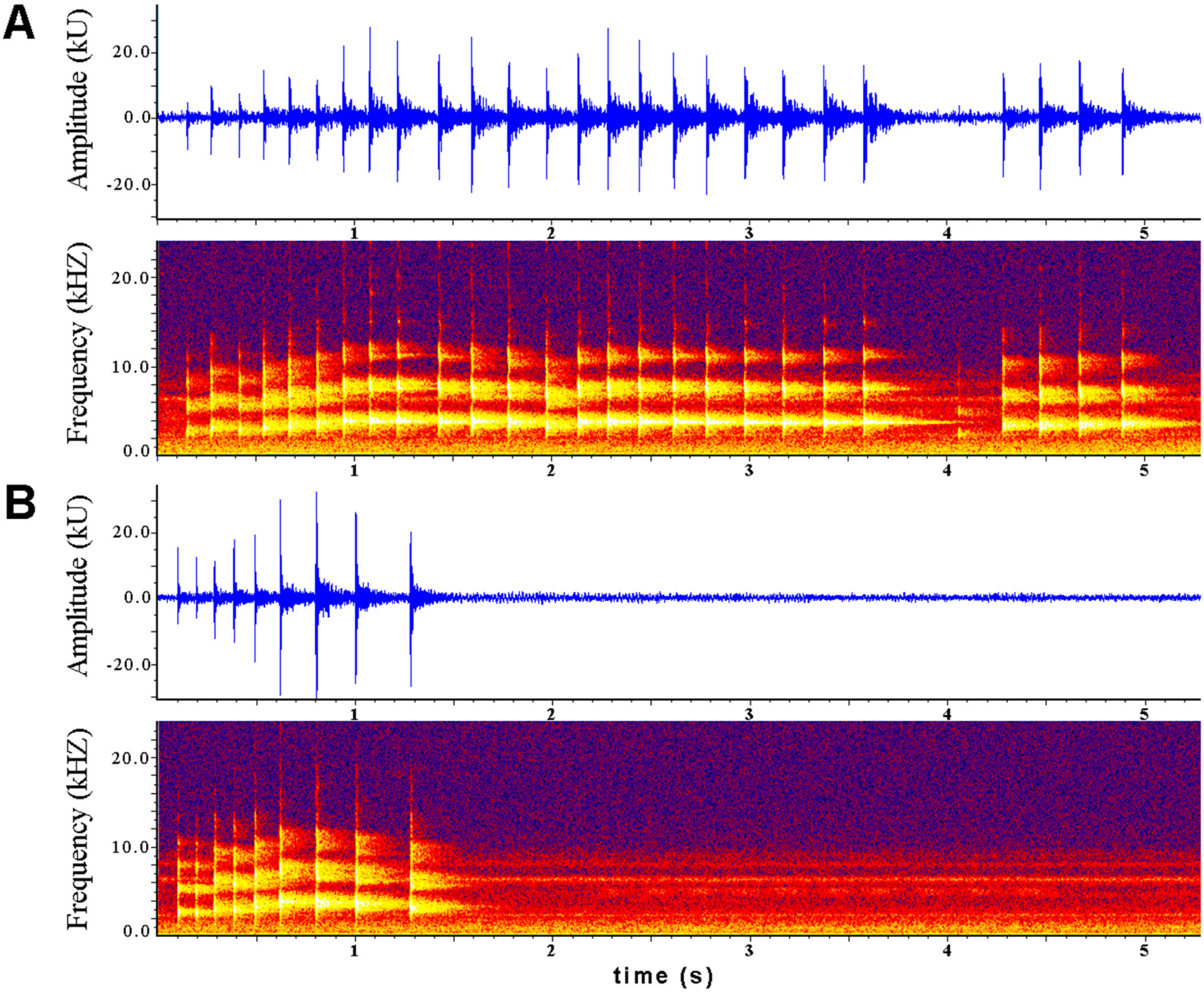

Fig. 6. Oscillogram and spectrogram of *Chirixalus pantaiselatan*, new species, MZB. Amph 30547, long call (A), and short call (B). The samples of advertisement calls are available at https://doi.org/10.6084/m9.figshare.14554179

region to mid-body (vs. distinct dark stripes in *Chirixalus trilaksonoi*, *Chirixalus doriae*, *Chirixalus dudhwaensis*, and indistinct dark stripes with some scattered black spots on *Chirixalus simus*; see Table 3 for external morphological differences in *Chirixalus* species). *Chirixalus pantaiselatan*, new species, differs morphologically from its sister taxon *Chirixalus trilaksonoi* by having truncated snout (vs. obtusely pointed); presence of vomerine teeth (vs. absent); a relatively longer head in males, HL = 8.4–9.4 mm (vs. 7.5–8.9 mm); a wider head in males, HW = 8.4–10.0 mm (vs. 7.1–8.8 mm); a relatively longer snout in males, SL = 3.6–4.1 mm (vs. 3.1–3.6 mm); a slightly longer nostril-eye distance in males, NEL = 2.1–2.6 mm (vs. 1.9–2.3 mm); a relatively larger eye diameter in males, ED = 4.3–4.8 mm (vs. 3.1–3.7 mm); a relatively larger eye-tympanum distance in males, ETD = 1.1–1.4 mm (vs. 0.4–0.6 mm); a larger tympanum diameter in males, TD = 2.0–2.4 mm (vs. 1.4–1.6 mm); a slightly larger internarial distance in males, IND = 2.3–2.4 mm (vs. 1.8–2.2 mm); having a larger interorbital distance in males, IOD = 3.4–4.1 mm (vs. 2.7–3.1 mm); slightly longer lower arm length in males, LAL = 11.4–12.7 mm (vs. 9.7–11.5 mm); a relatively longer hindlimb in males, THL = 12.6–15.3 mm (vs. 10.8–12.8 mm), TL = 13.2–15.2 mm (vs. 12.6–13.9 mm), FL = 9.8–11.1 mm (vs. 8.7–10.1 mm); slightly longer fourth toe in males, Toe4L = 5.3–6.0 mm (vs. 4.4–5.4 mm); wide, distinct transversal bands on limbs (vs. narrow and indistinct); more developed toe webbing, webbing formula = I 1–$^{1}/_{2}$ II 0–1$^{1}/_{2}$ III 0–1 IV $^{1}/_{2}$–0 V (vs. I 1–1$^{1}/_{2}$ II $^{1}/_{2}$–1$^{1}/_{2}$ III 0–1 IV 0–0 V); tibiotarsal articulation reaching posterior of the nostril (vs. tip of the snout). The advertisement call characteristics of these two species vary in the number of notes and call duration; *Chirixalus pantaiselatan*, new species, have short (2–9 notes), medium (11–17 notes), and long calls (22–46 notes) (vs. 2–10 notes: Riyanto & Kurniati, 2014); a more variable call duration, 185.71–1,644.28, 1,420.78–2,708.46, and 3,292.29–7,055.79 ms, in short, medium, and long calls, respectively (vs. 44–370 ms: Kurniati, pers. comm.; incorrectly described in Riyanto & Kurniati, 2014), and lower dominant frequency, ranging from 2.3–3.9 kHz (vs. 3.7–4.8 kHz: Riyanto & Kurniati, 2014).

Chirixalus pantaiselatan, new species, differs from *Chirixalus doriae* by having vomerine teeth (vs. absent: Boulenger, 1893; Taylor, 1962); presence of a white patch on side of

Table 3. Data matrix of the diagnostic characteristic separating the Asian *Chirixalus* species. *character from literature; # character status unknown.

Morphological characters	***C. pantaiselatan***	***C. doriae***	***C. dudhwaensis***	***C. nongkhorensis***	***C. simus***	***C. trilaksonoi***
Sample size	5	*	*	*	*	7
Snout obtusely pointed (1) or truncate (0)	0	0	0	1	0	1
Vomerine teeth present (1) or absent (0)	1	0	#	#	#	0
Canthus rostralis distinct (1) or indistinct (0)	1	1	1	1	0	1
Dark postorbital stripe present (1) or absent (0)	0	1	1	1	0	0
White patch on side of the upper jaw (1) or not (0)	1	0	#	1	0	1
Tympanum distinct (1) or indistinct (0)	1	1	1	1	1	1
Glandular fold between eye and shoulder distinct (1) or faint (0)	1	0	0	1	1	1
External vocal sac present (1) or absent (0)	1	0	1	1	#	1
Dark stripes on dorsum present (1) or absent (0)	0	1	1	0	1	1
Dark markings on dorsum (1) or not (0)	1	0	0	1	0	0
Skin of dorsum smooth (1) with small tubercles (0), or finely granular (x)	1	1	0	x	0/1	1
Banding on dorsal aspect of thighs (1) or not (0)	1	0	0	1	0	1
Third and fourth fingers one-four webbed (1) or less (0)	1	0	0	0	0	1
Disk on third finger as large as tympanum (1) or not (0)	0	1	0	1	0	0
Inner metatarsal tubercle present (1) or absent (0)	1	1	1	1	1	1
More (1) or less (0) than ⅓ webbing on toes	1	1	1	1	1	1

upper jaw (vs. absent: Taylor, 1962; Grismer et al., 2007a); absence of dark postorbital stripe (vs. presence: Grismer et al., 2007a); distinct glandular fold between eye and shoulder (vs. faint: Grismer et al., 2007a); having tympanum diameter about two times that of Fin3DW (vs. equal to that of Fin3DW: Boulenger, 1893; Taylor, 1962; Grismer et al., 2007a); presence of an external vocal sac (vs. absence: Grismer et al., 2007a); third and fourth fingers one-fourth webbed (vs. webbed only at base: Taylor, 1962; Grismer et al., 2007a); tibiotarsal articulation reaching posterior of nostril (vs. reaching eye: Boulenger, 1893; Taylor, 1962); distinct transverse bands on forelimbs and hindlimbs (vs. indistinct to distinct spots: Boulenger, 1893; Taylor, 1962; Aowphol et al., 2013); and more developed webbing on outer margin of third toe (vs. less developed: Taylor, 1962: fig. 88, p. 538). *Chirixalus pantaiselatan*, new species, is distinguished from *Chirixalus dudhwaensis* by the absence of a dark postorbital stripe (vs. presence: Ray, 1992; Grismer et al., 2007a); distinct transverse bands on the forelimbs and hindlimbs (vs. absence of markings: Ray, 1992; Das et al., 2012: fig. 4, p. 2557); third and fourth fingers one-fourth webbed (vs. less webbed: Ray, 1992); smooth dorsal skin (vs. skin with small tubercles; Ray, 1992); a distinct glandular fold between eyes and shoulder (vs. faint: Ray, 1992; Grismer et al., 2007a). *Chirixalus pantaiselatan*, new species, is distinguished from *Chirixalus simus* by having a larger body size, adult male SVL = 25.3–28.9 mm (vs. 22 mm: Annandale, 1915; 20.0–24.0 mm: Deuti, 2013); a distinct canthus rostralis (vs. barely distinguishable: Annandale, 1915); presence of white patch on side of upper jaw (vs. absence; Annandale, 1915; Grismer et al., 2007a); smooth dorsal skin (vs. skin with small tubercles: Annandale, 1915 or smooth: Deuti, 2013); third and fourth fingers one-fourth webbed (vs. rudimentary webbing: Annandale, 1915; Deuti, 2013); distinct transverse bands on the forelimbs and hindlimbs (vs. absence of markings: Annandale, 1915); and tibiotarsal articulation reaching posterior of the nostril (vs. tip of snout: Annandale, 1915).

Chirixalus pantaiselatan, new species, is similar to *Chirixalus nongkhorensis* in dorsal colour pattern, but has a slightly smaller body size, adult male SVL 25.3–28.9 mm (vs. 28 mm: Cochran, 1927; 29–32 mm: Taylor, 1962; 25.6–31.1 mm: Aowphol et al., 2013); truncated snout (vs. pointed: Cochran, 1927; Grismer et al., 2007a); larger eye diameter, ED/SVL = 16.8 ± 1.09, 15.7–18.4% of SVL (vs. 12.2 ± 0.8, 10.6–14.3% of SVL: Aowphol et al., 2013); smaller interorbital distance, IND/SVL 13.6 ± 1.38, 12.1–15.8% of SVL (vs. 19.7 ± 1.4, 11.3–22.1% of SVL: Aowphol et al., 2013); absence of dark postorbital stripe (vs. presence: Grismer et al., 2007a); throat with dark blotches along the ventral edges of the lower jaw (vs. immaculate white: Cochran, 1927; Taylor, 1962); fingers not fringed (vs. fringes along fingers to disks: Cochran, 1927); third finger disk diameter nearly half that of the tympanum (vs. same size as tympanum; Cochran, 1927; Grismer et al., 2007a); outer edge of third finger webbed at base (vs. two-thirds webbed: Cochran, 1927; Taylor, 1962; or one-fourth to one-half webbed: Grismer et al., 2007b); inner edge of the third toes webbed at base (vs. two-thirds webbed; Cochran, 1927); tibiotarsal articulation reaches posterior of nostril (vs. tip of snout; Cochran, 1927). *Chirixalus pantaiselatan*, new species, also differs from *Chirixalus nongkhorensis* acoustically, with its advertisement call more variable in duration; means ± SD are 703.2 ± 402.75, 1,873.2 ± 570.53, and 4,431.2 ± 1,759.7 ms for short, medium, and long calls, respectively (vs. 497.8 ± 239.3 ms: Aowphol et al., 2013) and have more notes per call, at 2–9, 11–17, and 22–46 notes per short, medium, and long call, respectively (vs. 2–4 notes: Aowphol et al., 2013) and a slightly lower dominant frequency, ranging from 2.3–3.9 kHz (vs. 3.6–4.3 kHz: Aowphol et al., 2013).

Natural history. During a clear night between 2000–2100 hours, the frogs were found perched on a shrub, approximately 50 cm above the ground near a small pond in an old secondary forest. The egg, larval, and ecological characteristics of this new species are unknown. The following amphibian species were found sympatrically with the new species: *Chalcorana chalconota* Schlegel, *Fejervarya limnocharis* Gravenhorst, *Ingerophrynus biporcatus* Gravenhorst, *Kalophrynus pleurostigma* Tschudi, *Kaloula baleata* Müller, *Microhyla achatina* Tschudi, *Occidozyga lima* Gravenhorst, *Polypedates leucomystax* Gravenhorst, and *Polypedates macrotis* Boulenger. The *Polypedates macrotis* reported here is the first record of the species occurring in Java (referred specimens MZB. Amph 30420 and MZB. Amph 30421).

Distribution. The new species is known only from the type locality, which is a 21.6 km^2 degraded forest in the Leuweung Sancang Nature Reserve, Garut Regency, Jawa Barat.

DISCUSSION

Our phylogenetic tree results identified five lineages within *Feihyla*, separated by relatively long branches, possibly due to the condition of the short sequences used in our phylogenetic analyses. Previous studies that investigated the relationships among *Feihyla* species concluded that it was monophyletic at the genus level, although only a few selected species were used for these analyses (Li et al., 2009, 2013; Hertwig et al., 2013; Chan et al., 2018, 2020; Dubois et al., 2021). However, several studies have reported that *Feihyla* is paraphyletic (Wilkinson et al., 2002; Yu et al., 2008; Meegaskumbura et al., 2015; Poyarkov et al., 2015; Biju et al., 2016). Biju et al. (2020) proposed the new genus *Rohanixalus* to resolve the phylogenetic position of *Feihyla.* However, the position of the new genus was weakly supported and its relationships remain unresolved. Of interest as well, is the relationship of *F. kajau* from Borneo with other members of *Feihyla*. Li et al. (2013) and Hertwig et al. (2013) showed that *F. kajau* is more closely related to *F. palprebalis* + *F. vittatus*, whereas Poyarkov et al. (2015) argued that it is more closely related to *Polypedates* than to *Feihyla*. Chan et al. (2018) and Biju et al. (2020) showed that *F. kajau* is more closely related to the other Bornean species *F. inexpectata* and the Javanese species *F. vittiger*, which is consistent with our findings. In contrast, Dubois et al. (2021) showed that *F. kajau* is more closely related to *F. palpebralis* + *F. inexpectata* + *F. hansenae* and *F. vittatus*. The unstable phylogenetic position of *F. kajau* and other *Feihyla* species is likely due to the limited numbers of samples from this taxon used in their study (Biju et al., 2020). By increasing the taxa sample within *Feihyla*, it could further resolve the phylogenetic position of this genus.

Our preliminary examination identified some characters that may be useful for defining and investigating species groups among *Feihyla*. The diagnostic characters of *Feihyla* sensu Frost et al. (2006), which are based on Fei (1999), include "the presence of X or a ")(" marking on the dorsum and lacking vomerine teeth," which can only be applied to characterise Chinese and Indochinese *Feihyla* (i.e., *F. palpebralis* and *F. fuhua*). According to Biju et al. (2020), characters that may be useful for distinguishing *Feihyla* group include combinations of the presence of X or a ")(" marking on the dorsum and white streak along upper lip margins, extending from snout tip or below eye to shoulder for *F. palprebalis* group; a narrow light streak starting from snout tip extending laterally along head from below eye to groin, clearly separating dorsal and lateral body colouration (Fig. 5D) for *F. vittiger* group, but this light streak from snout to eye appears to be absent in *F. kajau* (pers. observation); and a light-coloured stripe from snout tip extending over upper eyelid margins to near vent for *F. vittatus* group or *Rohanixalus* sensu Biju et al. (2020). Furthermore, *F. palpebralis* group was previously observed to have laid freshly pigmented eggs in jelly nests (Li et al., 2009; Biju et al., 2020), whereas *F. vittatus* group laid freshly unpigmented eggs in bubble nests (Sheridan & Ocock, 2008; Fei et al., 2009; Wan et al., 2012; Poo & Brickfoord, 2013; Matsui et al., 2014; Biju et al., 2020). The *F. vittiger* group laid freshly unpigmented eggs in bubble nests (Darmawan, 2010; Kusrini et al., 2017), not jelly nests as described by Biju et al. (2020), and *F. kajau* laid eggs in a jelly nest (Das et al., 2016; Sorokin & Steigerwald, 2018). A further comprehensive study of this interesting breeding behaviour will provide evolutionary insight into this genus compared to other genera of the subfamily Rhacophorinae.

Chirixalus pantaiselatan, new species, from western Java is most similar to *Chirixalus nongkhorensis* from Chonburi, Thailand in its dorsal colour pattern, but it is most similar genetically to *Chirixalus trilaksonoi*, which is also from western Java. These two species are distributed in lowland areas; *Chirixalus trilaksonoi* is distributed in the central (Riyanto & Kurniati, 2014) and southwestern coast of West Java (Kaprawi, 2020), whereas *Chirixalus pantaiselatan*, new species, are distributed in the southern coast. Biogeographically, it is interesting that the genus *Chirixalus* is distributed from southern China (Fei, 1999; Fei et al., 2012), northeastern India (Annandale, 1915; Ray, 1992; Deuti et al., 2000; Dinesh et al., 2009; Hasan et al., 2010; Mathew & Sen, 2010; Das et al., 2012; Deuti, 2013), Indochina (Taylor, 1962; Inger et al., 1999; Ohler et al., 2002; Teynié et al., 2004; Stuart et al., 2006; Stuart & Emmett, 2006; Grismer et al., 2007b, 2008; Aowphol et al., 2013; Nguyen et al., 2020) to Peninsular Malaysia (Leong & Lim, 2003; Chan et al., 2011; Quah & Shahrul Anuar, 2018) and Java (Riyanto & Kurniati, 2014), but are absent from Borneo and Sumatra. The lack of *Chirixalus* records in Sumatra and Borneo may be due to the lack of intensive surveys. These small tree frogs are difficult to detect in the field, and usually spend most of their time on trees, sometimes in the high crowns. They are mainly detected by their calls or during their breeding season when they approach water bodies (Deuti, 2001). The egg clutch of *Chirixalus pantaiselatan*, new species, is unknown, it may lay eggs in foam nests, because its sister taxon *Chirixalus trilaksonoi* leaves egg masses hanging in foam nests on leaves at heights of up to two metres above the ground (Novita, 2020: ARK iNaturlist, https://www.inaturalist.org/observations/65843273). *Chirixalus* species reportedly have foamy egg masses hanging on leaves or small branches (e.g., *Chirixalus doriae*: Taylor, 1962; Fei et al., 2009; Matsui et al., 2014; *Chirixalus dudhwaensis*: Biswas, 2000; and *Chirixalus nongkhorensis*: Teynié et al., 2004; Fei et al., 2009; Matsui et al., 2014; *Chirixalus simus*: Deuti, 2001; Banerjee, 2014; Biju et al., 2020; and *Chirixalus trilaksonoi*: Novita, 2020). However, Taylor (1962) reported female *Chirixalus nongkhorensis* depositing foamy egg masses on the water surface. Thus, the accumulation of call and breeding behaviour information is important for detecting these cryptic small frogs.

Chirixalus pantaiselatan, new species, is known only from its type locality, the Leuweung Sancang Nature Reserve which is under pressure due to land cover changes, and most of the area has been logged and turned into open areas and patchy forests. This new species probably occurs in lowland forests along the southern coast of Java. Suitably forested regions may include Ujung Kulon National Park (786.19 km^2; Kementrian Lingkungan Hidup dan Kehutanan, 2016), Pangandaran Nature Reserve (517 km^2; Kementrian Lingkungan Hidup dan Kehutanan, 2016), and Nusakambangan Island (121 km^2 and includes nature reserves; Kementrian Lingkungan Hidup dan Kehutanan, 2016). According to IUCN Standards and Petitions Committee (2019), *Chirixalus pantaiselatan*, new species, is likely to qualify as a critically endangered species following the International Union for Conservation of Nature (IUCN) Red List of Threatened species criterion B1B2ab (iii) because the extent of its occurrence is <100 km^2, its area of occupancy is <10 km^2, and it has been found in only one location, which is declining in habitat quality. This proposal of IUCN Red List status for this new species is based on our limited data, and requires further, more intensive surveys for more robust justification. Our discovery of *Chirixalus pantaiselatan*, new species, and *Polypedates macrotis*, which have never been reported from Java, highlights the importance of public participation and professional scientific engagement in biodiversity monitoring. Citizen science can provide empirical data on an unprecedented spatial scale, and the findings can provide new information on the distribution of some species (Rowley et al., 2018; Kusrini et al., 2019), or even new species from a common area (Priti et al., 2016; Schilthuizen et al., 2017; Freitag et al., 2018). The lack of biodiversity information (e.g., distribution, population, and habitat requirements of a species) is a serious issue in biodiversity conservation programmes in developing countries such as Indonesia (Alford & Richard, 1999; Sodhi et al., 2004; Rowley et al., 2010). Well-managed public participation will help resolve these issues in the future (Ganzevoort et al., 2017; Rowley et al., 2018).

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LITERATURE CITED

Alford RA & Richards SJ (1999) Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics, 30: 133–165.

Annandale N (1915) Herpetological notes and descriptions. Records of the Indian Museum, 11: 341–357.

Aowphol A, Rujirawan A, Taksintum W, Arsirapot S & McLeod DS (2013) Re-evaluating the taxonomic status of *Chiromantis* in Thailand using multiple lines of evidence (Amphibia: Anura: Rhacophoridae). Zootaxa, 3702: 101–123.

Banerjee A (2014) Jelly secretion by a foam-nesting tree frog *Chiromantis simus* (Anura: Rhacophoridae): an unreported behaviour. Alytes, 31: 77–82.

Biju SD, Senevirathne G, Garg S, Mahony S, Kamei RG, Thomas A, Shouche Y, Raxworthy CJ, Meegaskumbura M & Van Bocxlaer I (2016) *Frankixalus*, a new rhacophorid genus of tree hole breeding frogs with oophagous tadpoles. PLoS ONE, 11: e0145727.

Biju SD, Garg S, Gokulakhrisan G, Chandrakasan S, Thammachoti P, Ren J, Gopika C, Bisht K, Hamidy A & Shouche Y (2020) New insights on the systematics and reproductive behaviour in tree frogs of the genus *Feihyla*, with description of a new related genus from Asia (Anura, Rhacophoridae). Zootaxa, 4878: 1–55.

Bioacoustics Research Program (2014) Raven Pro: Interactive Sound Analysis Software. Version 1.5 [Computer Software]. The Cornell Lab of Ornithology, Ithaca, New York. Available from http://ravensoundsoftware.com/.

Biswas S (2000) Notes on the breeding habits of *Chirixalus dudhwaensis* Ray 1992, from Uttar Pradesh, north India. Hamadryad, 25: 200–203.

Boulenger GA (1887) An account of the batrachians obtained in Burma by M.L. Fea of the Genoa Civic Museum. Annali del Museo Civico di Storia Naturale di Genova, 5: 418–424.

Boulenger GA (1893) Concluding report on the reptiles and batrachians obtained in Burma by Signor L Fea dealing with the collection made in Pegu and the Karin Hills in 1887–88. Annali del Museo Civico di Storia Naturale Giacomo Doria, 13: 304–347.

Chan KO, Grismer LL & Brown RM (2018) Comprehensive multi-locus phylogeny of old world tree frogs (Anura: Rhacophoridae) reveals taxonomic uncertainties and potential cases of over and underestimation of species diversity. Molecular Phylogenetics and Evolution, 127: 1010–1019.

Chan KO, Grismer LL, Shahrul AMS, Quah E, Grismer JL, Wood PL Jr, Muin M & Ahmad N (2011) A new species of *Chiromantis* Peters 1854 (Anura: Rhacophoridae) from Perlis State Park in extreme northern peninsular Malaysia with additional herpetofaunal records for the park. Russian Journal of Herpetology, 18: 253–259.

Chan KO, Hutter CR, Wood PLJr, Grismer LL & Brown RM (2020) Target-capture phylogenomics provide insights on gene and species tree discordances in Old World treefrogs (Anura: Rhacophoridae). Proceeding of The Royal Society B, 287: 1–9.

Chen JM, Prendini E, Wu YH, Zhang BL, Suwannapoom C, Chen HM, Jin JQ, Lemmon EM, Lemmon AR, Stuart BL, Raxworthy CJ, Murphy RW, Yuan ZY & Che J (2020) An integrative phylogenomic approach illuminates the evolutionary history of Old World tree frogs (Anura: Rhacophoridae). Molecular Phylogenetics and Evolution, 145: 106724.

Cochran DM (1927) New reptiles and batrachians collected by Dr. Hugh M Smith in Siam. Proceedings of the Biological Society of Washington, 40: 179–192.

Darmawan B (2010) *Philautus vittiger* ko ada di Kalimantan ???. Warta Herpetofauna, 4: 15. [In Indonesian]

Das A, Basu D, Converse L & Choudhury SC (2012) Herpetofauna of Katerniaghat Wildlife Sanctuary, Uttar Pradesh, India. Journal of Threatened Taxa, 4: 2553–2568.

Das I, Hedeir H, Pui YM, Hertwig ST & Haas A (2016) Larval external morphology and development in *Feihyla kajau* (Dring, 1983) (Amphibia: Anura: Rhacophoridae). Raffles Bulletin of Zoology, 64: 319–328.

Deuti K (2001) Breeding ecology of Annandale's tree frog *Chirixalus simus* (Anura: Rhacophoridae) near Kolkata, West Bengal. Journal of the Bombay Natural History Society, 98: 341–346.

Deuti K (2013) Amphibia. In: Venkataraman K, Chattopadhyay A & Subramanian KA (eds.) Endemic Animals of India (Vertebrates). Zoological Survey of India, Kolkata, pp. 67–137.

Deuti K, Biswas S, Ahmed MF & Dutta SK (2000) Rediscovery of *Chirixalus simus* Annandale, 1915 (Anura: Rhacophoridae) from Assam and West Bengal, eastern India. Hamadryad, 25: 215–217.

Dinesh KP, Radhakrishnan C, Gururaja KV & Bhatta GK (2009) An annotated checklist of Amphibia of India with some insight into the patterns of species discoveries, distribution and endemism. Record of Zoological Survey of India, Occasional paper, 302: 1–153.

Dring JCM (1983) Some new frogs from Sarawak. Amphibia-Reptilia, 4: 103–115.

Dubois A, Ohler A & Pyron RA (2021) New concepts and methods for phylogenetic taxonomy and nomenclature in zoology, exemplified by a new ranked cladonomy of recent amphibians (Lissamphibia). Megataxa, 5: 1–738.

Fei L (1999) Atlas of Amphibians of China. Henan Press of Science and Technology, Zhengzhou, 432 pp. [in Chinese]

Fei L, Hu SQ, Ye CY & Huang YZ (2009) Fauna Sinica. Amphibia Vol. 2 Anura. Science Press, Beijing, 957 pp.

Fei L, Ye CY & Jiang JP (2010) A new species of Rhacophoridae from Yunnan, China (Amphibia, Anura). Acta Zootaxonomica Sinica, 35: 413–417.

Fei L, Ye CY & Jiang JP (2012) Colored atlas of Chinese amphibian and their distribution. Sichuan Publishing House of Science and Technology, Sichuan, 620 pp. [in Chinese]

Freitag H, Pangantihon CV & Njunjic I (2018) Three new species of *Grouvellinus* Champion, 1923 from Maliau Basin, Sabah, Borneo, discovered by citizen scientists during the first Taxon Expedition (Insecta, Coleoptera, Elmidae). ZooKeys, 754: 1–21.

Frost DR (2014). Amphibian Species of the World: An Online Resource Version 6.0. American Museum of Natural History, New York, USA. https://amphibiansoftheworld.amnh.org/index.php (Accessed 01 May 2020).

Frost DR (2020) Amphibian Species of the World: an Online Reference Version 6.1. Electronic Database American Museum of Natural History, New York, USA. https://amphibiansoftheworld.amnh.org/index.php (Accessed 29 December 2020).

Frost DR (2021) Amphibian Species of the World: an Online Reference Version 6.1. Electronic Database American Museum of Natural History, New York, USA. https://amphibiansoftheworld.amnh.org/index.php (Accessed 31 March 2021).

Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sa RO, Chaning A, Wilkinson M, Donellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler PE, Drewes RC, Nussbaum RA, Lynch JD, Green DM & Wheeler W (2006) The amphibian tree of life. Bulletin of the American Museum of Natural History, 297: 1–370.

Ganzevoort W, van den Born RJ, Halffman W & Turnhout S (2017) Sharing biodiversity data: citizen scientists' concerns and motivations. Biodiversity and Conservation, 26: 2821–2837.

Gistel J (1848) Naturgeschichte des Thierreichs für höhere Schulen. Hoffmann, Stuttgart, xi + 216 + iv pp., 32 figs. [in German]

Grismer LL, Chav T, Neang T, Wood PL Jr, Grismer JL, Youmans TM, Ponce A, Daltry JC & Kaiser H (2007b) The herpetofauna of the Phnom Aural wildlife sanctuary and checklist of the herpetofauna of the Cardamom Mountains, Cambodia. Hamadryad, 31: 216–241.

Grismer LL, Neang T, Thou C, Wood PL Jr, Oaks JR, Holden J, Grismer JL, Scutz TR & Youmans TM (2008) Additional amphibians and reptiles from the Phnom Samkos Wildlife Sanctuary in Northwestern Cardamom Mountains, Cambodia with comment on their taxonomy and discovery of three new species. Raffles Bulletin of Zoology, 56: 161–175.

Grismer LL, Thy N, Chav T & Holden J (2007a) A new species of *Chiromantis* Peters 1854 (Anura: Rhacophoridae) from Phnom Samkos in the northwestern Cardomom mountains, Cambodia. Herpetologica, 63: 392–400.

Hamidy A, Munir M, Mumpuni, Rahmania M & Kholik AA (2018) Detection of cryptic taxa in the genus *Leptophryne* (Fitzinger, 1843) (Amphibia; Bufonidae) and the description of a new species from Java, Indonesia. Zootaxa, 4450: 427–444.

Hammer O, Harper DAT & Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica, 4: 1–9.

Hasan MK, Hossain MK, Kabir MM & Hassan F (2010) Geographic distribution: *Chiromantis simus*. Herpetological Review, 41: 506.

Hertwig ST, Schweizer M, Das I & Haas A (2013) Diversification in a biodiversity hotspot– The evolution of southeast Asian rhacophorid tree frogs on Borneo (Amphibia: Anura: Rhacophoridae). Molecular Phylogenetics and Evolution, 68: 567–581.

Hillis DM & Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology, 42: 182–192.

Hoffman AC (1932) Researches relating to the validity of the South African Polypedatidae (Rhacophoridae) as an autonomous family of the Anura. South African Journal of Science, 29: 562–583.

Inger RF, Orlov NL & Darevsky IS (1999) Frogs of Vietnam: A report on new collections. Fieldiana Zoology, 92: 1–46.

International Union for Conservation of Nature Standards and Petitions Committee (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14 August 2019. http://www.iucnredlist.org/documents/RedListGuidelines.pdf (Accessed 28 December 2020).

Kaprawi F (2020) ARK iNaturalist: *Chirixalus trilaksonoi*. https://www.inaturalist.org/observations/38026590 (Accessed 31 March 2021).

Kementrian Lingkungan Hidup dan Kehutanan (2016) Statistik Konservasi Sumber Daya Alam dan Ekosistem Statistik Direktorat KSDAE. Kementrian Lingkungan Hidup dan Kehutanan Republik Indonesia, Jakarta, 139 pp. [In Indonesian]

Köhler J, Jansen M, Rodriguez A, Kok PJR, Toledo LP, Emmrich M, Glaw F, Haddad CFB, Rödel MO & Vences M (2017) The use of bioacoustics in anuran taxonomy: theory, terminology, methods, and recommendations for best practice. Zootaxa, 4251: 1–124.

Kuhl H & van Hasselt JC (1822) Uittreksels uit brieven van de Heeren Kuhl en Van Hasselt, aan de Heeren C.J. Temminck, Th. van Swinderen en W. de Haan. Algemeene Konst-en Letterbode, 7: 99–104. [in Dutch]

Kusrini MD, Hamidy A, Prasetyo LB, Nugraha R, Munir M, Arida E, Rahmania M, Riyanto A, Eprilurahman R, Satria D & Janiawati IA (2019) Mobilizing citizen to document herpetofauna diversity of Indonesia. In: Fernandes JC & Wibowo C (eds.) Proceeding of SEAMEO Biotrop Third International Conference on Tropical Biology, Conservation, enhancement and sustainable use of indigenous tropical flora and fauna, September 2018. Seameo Biotrop, Bogor, pp. 26–35.

Kusrini MD, Lubis MI, Darmawan B & Nuraini L (2017) Morphological and ecological observation on *Chiromantis vittiger* (Anura: Rhacophoridae) in mount Halimun-Salak National Park. Treubia, 44: 47–66.

Leaché AD & Reeder TW (2002) Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. Systematic Biology, 51: 44–68.

Leong TM & Lim BL (2003) Geographic distribution: *Chirixalus nongkhorensis*. Herpetological Review, 34: 380.

Li JT, Che J, Bain RH, Zhao EM & Zhang YP (2008) Molecular phylogeny of Rhacophoridae (Anura): a framework of taxonomic reassignment of species within the genera *Aquixalus*, *Chiromantis*, *Rhacophorus* and *Philautus*. Molecular Phylogenetics and Evolution, 48: 302–312.

Li JT, Che J, Murphy RW, Zhao H, Zhao EM, Rao DQ & Zhang YP (2009) New insights to the molecular phylogenetics and generic assessment in the Rhacophoridae (Amphibia: Anura) based on five nuclear and three mitochondrial genes, with comments on the evolution of reproduction. Molecular Phylogenetics and Evolution, 53: 509–522.

Li JT, Li Y, Klaus S, Rao DQ, Hillis DM & Zhang YP (2013) Diversification of rhacophorid frogs provides evidence for accelerated faunal exchange between India and Eurasia during the Oligocene. Proceedings of the National Academy of Sciences of the United States of America, 110: 3441–3446.

Lleonart J, Salat J & Torres GJ (2000) Removing allometric effects of body size in morphological analysis. Journal of Theoretical Biology, 205: 85–93.

Mathew R & Sen N (2010) Pictorial guide of amphibians of northeast India. Zoological Survey of India, Kolkata, 144 pp.

Matsui M, Shimada T & Sudin A (2014) First record of the tree-frog genus *Chiromantis* from Borneo with the description of a new species (Amphibia: Rhacophoridae). Zoological Science, 31: 45–51.

Meegaskumbura M, Meegaskumbura S, Bowatte G, Manamendra-Arachchi K, Pethiyagoda R, Hanken J & Schneider CJ (2010) *Taruga* (Anura: Rhachophoridae), a new genus of foam-nesting tree frog endemic to Sri Lanka. Ceylon Journal of Science (Biological Sciences), 39: 75–94.

Meegaskumbura M, Senevirathne G, Biju SD, Garg S, Meegaskumbura S, Pethiyagoda R, Hanken J & Schneider CJ (2015) Patterns of reproductive mode evolution in Old World tree frogs (Anura, Rhacophoridae). Zoologica Scripta, 44: 509–522.

Miller MA, Pfeiffer W & Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), November 2010. Curran Associates, New Orleans, pp. 1–8.

Munir M, Hamidy A, Farajallah A & Smith EN (2018) A new *Megophrys* Kuhl and Van Hasselt (Amphibia: Megophryidae) from south-western Sumatra, Indonesia. Zootaxa, 4442: 389–412.

Nguyen TV, Brakels P, Maury N, Sudavanh S, Pawangkhanant P, Idiiatullina S, Lorphengsy S, Inkhavilay K, Suwannapoom C & Poyarkov NA Jr (2020) New herpetofauna observations from Laos based on photo records. Amphibian and Reptile Conservation, 14: 218–249.

Novita (2020) ARK iNaturalist: *Chirixalus trilaksonoi* observation. https://www.inaturalist.org/observations/65843273 (Accessed 28 January 2021).

Ohler A, Swan SR & Daltry JC (2002) A recent survey of the amphibian fauna of the Cardamon Mountains, Southwest

Cambodia with descriptions of three new species. Raffles Bulletin of Zoology, 50: 465–481.

Peters WCH (1854) Diagnosen neuer Batrachier, welche zusammen met dir früher (24 July und 17 August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preußischen Akademie der Wissenschaften zu Berlin: 614–628. [in German]

Poo S & Bickford DP (2013) The Adaptive significance of egg attendance in a southeast Asian tree frog. Ethology, 119: 671–679.

Poyarkov NA, Orlov NL, Moiseeva AV, Galoyan EA, Nguyen TT & Gogoleva SS (2015) Sorting out moss frogs: mtDNA data on taxonomic diversity and phylogenetic relationships of the Indochinese species of the genus *Theloderma* (Anura, Rhacophoridae). Russian Journal of Herpetology, 22: 241–280.

Priti H, Naik CR, Seshadri KS, Singal R, Vidisha MK, Ravikanth G & Gururaja KV (2016) A new species of *Euphlyctis* (Amphibia, Anura, Dicroglossidae) from the West Coastal Pains of India. Asian Herpetological Research, 7: 229–241.

Pyron RA & Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of advanced frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution, 61: 543–583.

Quah ESH & Shahrul Anuar MS (2018) Herpetofauna of the northern corridor: A review of recent herpetological discoveries around the Malaysia-Thai border regions. Journal of Wildlife and Parks, 33: 15–29.

Ray P (1992) Description of a new rhacophorid, *Chirixalus dudhwaensis* (Anura: Rhacophoridae) from Dudhwa National Park, District Lakhimpur Kheri, Uttar Pradesh, India. Indian Journal of Forestry, 15: 260–265.

Riyanto A & Kurniati H (2014) Three new species of *Chiromantis* Peters 1854 (Anura: Rhacophoridae). Russian Journal of Herpetology, 21: 65–73.

Ronquist F & Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics, 19: 1572–1574.

Rowley JJL, Brown R, Bain R, Kusrini M, Inger R, Stuart B, Wogan G, Thy N, Chan-ard T, Trung CT, Diesmos A, Iskandar DT, Lau M, Ming LT, Makchai S, Truong NQ & Phimmachak S (2010) Impending conservation crisis for Southeast Asian Amphibians. Biology Letters, 6: 336–338.

Rowley JJL, Callaghan CT, Cutajar T, Portway C, Potter K, Mahony S, Trembath DF, Flemons DF & Woods A (2018) FrogID: citizen scientist provide validated biodiversity data on frogs of Australia. Herpetological Conservation and Biology, 14: 155–170.

Savage JM & Heyer WR (1997) Digital webbing formulae for anurans: a refinement. Herpetological Review, 28: 131.

Schilthuizen M, Seip LA, Otani S, Suhaimi J & Njunjic I (2017) Three new minute leaf litter beetles discovered by citizen scientists in Maliau Basin, Malaysian Borneo (Coleoptera: Leiodidae, Chrysomelidae). Biodiversity Data Journal, 5: e21947.

Sheridan JA & Ocock JF (2008) Parental care in *Chiromantis hansenae* (Anura; Rhacophoridae). Copeia, 2008: 733–736.

Smith MA (1924) New tree-frogs from Indo-China and the Malay Peninsula. Proceedings of the Zoological Society of London, 94: 225–234.

Sodhi NS, Koh LP, Brook BW & Ng PKL (2004) Southeast Asia biodiversity: an in impending disaster. Trends in Ecology and Evolution, 19: 654–660.

Sorokin A & Steigerwald EC (2018) Evidence for parental care in *Feihyla kajau* (Anura: Rhacophoridae). Phyllomedusa, 17: 127–130.

Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics, 30: 1312–1313.

Stuart BL & Emmett DA (2006) A collections of amphibians and reptiles from the Cardomom Mountains, southwestern Cambodia. Fieldiana Zoology, 109: 1–27.

Stuart BL, Sok K & Neang T (2006) A collection of amphibians and reptiles from hilly Eastern Cambodia. Raffles Bulletin of Zoology, 54: 129–155.

Tamura K, Stecher G, Peterson D, Filipski A & Kumar S (2013) MEGA6, Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution, 30: 2725–2729.

Tanabe AS (2011) Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. Molecular Ecology Resources, 11: 914–921.

Taylor EH (1962) The amphibian fauna of Thailand. The University of Kansas Science Bulletin, 43: 265–599.

Teynié A, David P, Ohler A & Luanglath K (2004) Notes on a collection of amphibians and reptiles from southern Laos, with a discussion of the occurrence of Indo-Malayan species. Hamadryad, 29: 33–62.

Thorpe RS (1983) A review of the numerical methods for recognizing and analyzing racial di-erentiation. In: Felsenstein J (ed.) Numerical Taxonomy: NATO Advanced Studies Institute Series, Series G, Ecological sciences, no. 1. Springer Verlag, Berlin, Heidelberg, pp. 404–423.

Wan JPH, Sung YH, Chan BPL & Lu G (2012) *Chiromantis vittatus* (two-striped pigmy tree frog) parental care. Herpetological Review, 43: 630–631.

Watters JL, Cummings ST, Flanagan RL & Siler CD (2016) Review of morphometric measurements used in anuran species descriptions and recommendations for a standardized approach. Zootaxa, 4072: 477–495.

Wilkinson JA, Drewes RC & Tatum OL (2002) A molecular phylogenetic analysis of the family Rhacophoridae with an emphasis on the Asian and African genera. Molecular Phylogenetics and Evolution, 24: 265–273.

Yodthong S, Siler C, Prasankok P & Aowphol A (2014) Phylogenetic Patterns of the Southeast Asian Tree Frog *Chiromantis hansenae* in Thailand. Asian Herpetological Research, 5: 179–196.

Yu GH, Rao DQ, Yang JX & Zhang MW (2008) Phylogenetic relationships among Rhacophorinae (Rhacophoridae, Anura, Amphibia), with an emphasis on the Chinese species. Zoological Journal of Linnean Society, 153: 733–749.

SUPPLEMENTARY MATERIAL

(Appendices 1, 3, 4: https://doi.org/10.6084/m9.figshare.14554179)

Appendix 1. Aligned Sequences used in this study.

Appendix 2. Specimens examined in this study: ***Chirixalus pantaiselatan*, new species** (n=5), see species description. ***Chirixalus trilaksonoi*** (n=7), INDONESIA: Jawa: Jawa Barat: Bogor: Bancar Bungur, Bantar Jaya, MZB. Amph 17932–34 (male), holotype and paratype; Ciampea, Cihideung Udik, MZB. Amph 28440–41 (male); Jasinga, MZB. Amph 29165 (male), MZB. Amph 27237 (female).

Appendix 3. Maximum likelihood phylogenetic tree result (Newick format).

Appendix 4. Bayesian inference phylogenetic tree result (Newick format).

Appendix 5. Summary statistics and loading scores of morphological characters on the first-ten principal component analysis of *Chirixalus pantaiselatan*, new species, and *Chrixalus trilaksonoi* populations. Abbreviations are listed in Material and Methods.

Characters	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10
SVL	0.03921	0.02735	-0.04630	-0.04673	-0.03574	0.09869	0.24729	-0.36496	0.67853	0.24649
HL	0.11257	0.08835	0.00384	0.06442	0.06324	-0.17143	0.30877	-0.36051	-0.30252	0.02743
HW	0.22104	0.20564	-0.02051	-0.14461	-0.29228	-0.16065	0.01812	-0.26929	-0.13428	0.18930
SL	0.15375	0.25962	0.04786	0.05293	-0.02993	0.08224	0.04865	0.22382	-0.00980	-0.21013
NEL	0.16540	-0.09944	0.25826	-0.41238	0.19711	-0.08583	0.13931	0.02159	-0.03405	0.08108
ED	0.35396	-0.03045	0.34509	0.19473	-0.24960	0.06442	-0.16377	0.10212	-0.10558	0.23641
ETD	-0.56477	0.50591	0.58523	-0.01099	0.13974	0.05460	-0.07211	-0.14274	-0.05547	0.05075
TD	0.45404	-0.06317	0.35679	-0.02272	0.51337	-0.13925	-0.18250	0.11957	0.13962	0.10850
IND	0.19338	0.02640	0.17222	-0.15621	0.02363	0.47768	0.32464	-0.27995	0.07134	-0.00739
IOD	0.24151	0.12359	0.04774	0.46346	-0.08903	-0.19124	-0.17264	-0.34339	-0.11391	0.10964
LAL	0.20677	0.21968	0.02267	-0.03412	0.05491	0.31858	-0.05670	0.00437	-0.22447	-0.10461
Fin3L	0.06356	0.27577	-0.31434	-0.17479	0.13424	0.43631	-0.14703	0.23681	-0.14930	0.44975
Fin3DW	0.00326	0.39301	-0.11048	0.01294	-0.27554	-0.23733	0.10405	0.21055	0.09059	0.37441
IPTL	-0.07639	-0.23498	0.27984	0.44006	-0.18807	0.30247	0.31891	0.28201	-0.02626	0.17096
THL	0.17320	0.30265	-0.06431	0.11258	-0.05385	0.06638	-0.03765	0.17617	0.39624	-0.17779
TL	0.09847	0.12805	0.02210	0.16890	-0.12493	0.24394	-0.30854	-0.15495	0.18067	-0.44554
FL	0.14900	0.08704	0.01817	-0.07930	-0.16355	0.04152	0.48798	0.09809	-0.23207	-0.29953
IMT	-0.03106	0.14255	-0.28241	0.48274	0.57546	0.00998	0.27047	-0.03829	-0.04986	0.05587
Toe4L	0.12067	0.30443	0.07015	-0.04956	0.04801	-0.34336	0.24656	0.29598	0.14504	-0.21513
Toe4DW	-0.09876	-0.18026	0.16777	0.11668	-0.06812	-0.07973	0.12180	0.19666	0.16858	0.13323
Eigenvalue	0.02888	0.00482	0.00419	0.00220	0.00128	0.00079	0.00064	0.00057	0.00023	0.00017
% variance	65.97	11.02	9.58	5.03	2.93	1.81	1.45	1.31	0.52	0.38