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A REASSESSMENT OF THE SYSTEMATIC POSITION OF THE ASIAN RANID FROG *Hylorana nicobariensis* STOLICZKA, 1870 (AMPHIBIA: ANURA) WITH THE DESCRIPTION OF A NEW GENUS

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Abstract
We reassessed the systematic position of the ranid frog *Hylorana* (=*Hylarana*) *nicobariensis* that, owing to its uncertain phylogenetic position and lack of clear morphological characterisation, has lately been allocated to various Asian and African frog genera such as *Rana*, *Sylvirana*, *Hylarana*, *Amnirana*, and most recently to *Indosylvirana*. Based on an integrative approach of both phylogenetic and morphological affinities, we describe a new genus to accommodate *Hylorana* (=*Hylarana*) *nicobariensis* and redescribe the species based on new topotypic material from the Nicobar Islands.

***Key words*:** *Amnirana*, *Indosylvirana*, phylogeny, Southeast Asia, Sundaland, taxonomy

Introduction

The cosmopolitan frog family Ranidae Batsch, 1796 currently comprises 26 genera and ranges in distribution from North and Central America, Europe, Asia and Africa excluding the southern parts of South America, South Africa and Australia (Frost 2020). Among these 15 genera, namely *Abavorana*, *Amolops*, *Chalcorana*, *Clinotarsus*, *Huia*, *Humerana*, *Hydrophylax*, *Hylarana*, *Indosylvirana*, *Merystogenis*, *Nidirana*, *Odorrana*, *Papurana*, *Pseudorana* and *Pterorana*, occur in the Oriental realm (Frost 2020, Chan *et al*. 2020). The incorrect spelling of the original description of *Hylarana* Tschudi, 1838 made by Günther (1864) was corrected by Van Kampen (1923) in the account of *nicobariensis*. The Sundaic frog *Hylorana* (= *Hylarana*) *nicobariensis* was firstly moved to the genus *Rana* by Boulenger (1884).

A systematic classification of true frogs of the genus *Rana* Linnaeus, 1758 was carried out by Dubois (1992) who divided the genus into six

genera comprising several new subgenera including *Chalcorana*, *Humerana*, *Papurana*, *Sylvirana* and *Amnirana*. Dubois (1992) placed the sub-Saharan African ranid frogs into *Amnirana*, with *Rana amnicola* Perret, 1977 as the type species, and assigned the Nicobarese species, *Hylorana nicobariensis* Stoliczka, 1870 to a South and Southeast Asian genus, *Sylvirana*, which was considered as the most appropriate placement for this species at that time. Frost *et al*. (2006) followed Dubois (1992) and placed *Rana* (*Sylvirana*) *nicobariensis* under *Sylvirana* while raising the subgenus to a distinct generic level. However, Che *et al*. (2007) included *Sylvirana* members within *Hylarana*. Based on phylogenetic evidence, Oliver *et al*. (2015) later reassigned *H. nicobariensis* to *Amnirana*. Furthermore, in their study on ranid frogs, they elevated several of the sub-genera defined by Dubois (1992) into distinct genera.

The subsequent allocation of this species to an African genus *Amnirana* by Oliver *et al*. (2015) was disputed by Chan & Brown (2017) who showed that the Asian species '*Amnirana*' *nicobariensis* is not sister to the African *Amnirana* but possibly more closely related to the Asian genera such as *Hydrophylax, Indosylvirana, Pulchrana* and *Sylvirana*. Chan *et al*. (2020) provisionally allocated this species to the largely south Asian genus *Indosylvirana*, although with some caution, owing to the inconsistency of its phylogenetic position. Although several of the above studies have discussed the generic placement of *Hylorana nicobariensis*, an unequivocal consensus on its generic placement has not been arrived at. Additionally, most of these studies were based solely on phylogenetic clues and not many of the above studies have backed-up their conclusions with support from morphological or other evidence.

Currently this Asian species (*sensu lato*) is distributed in the Nicobar Islands, Greater Sunda Islands, Philippines, as well as Islands in the Sulu Archipelago (Oliver *et al*. 2015). Herein, we reassess the available phylogenetic evidence concerning *Hylorana nicobariensis* and resolve the problem of its inconsistent generic placement by erecting a new genus for this Southeast Asian species.

Material and methods

***Field survey and specimen collection*:** Adult specimens were observed at night, mostly by locating calling males, and sometimes by opportunistic surveys during both day and night. Live frogs were photographed in the wild. Topotypic specimens collected from the Nicobar Islands are deposited in the Department of Ocean Studies and Marine Biology, Pondicherry University campus at Port Blair (DOSMB), India. The specimens collected from West Java are deposited in the Museum of Zoology, Research Center for Climate Change, University of Indonesia (UIMZ). Comparative materials are given in Appendix I. A Garmin GPSMAP 78s was used to record GPS coordinates in the field. Calls were recorded with a Samsung Galaxy mobile phone using the audio recorder application and analysed with Adobe Soundbooth CS3.

***Phylogenetic analysis*:** For the phylogenetic study, DNA sequences from previously published studies were retrieved for four genes (two mitochondrial: 16S rRNA and Cytb; two nuclear: Rag1 and Tyrosinase) representing the type species of all of the presently recognised 26 ranid genera (except *Pterorana*), including a population of "*Amnirana*" *nicobariensis* from Sumatra, with *Limnonectes laticeps* as the outgroup taxon (Table 1). The individual gene sequences were retrieved and aligned using ClustalW in MEGA 6.06 (Tamura *et al*. 2013). The best fitting DNA substitution model for each gene was determined by using Akaike Information criterion (AIC), as implemented in JModelTest3.5 (Posada & Crandall 1998). The alignments were concatenated to get a final single dataset of 2132 bp and subjected to phylogenetic analysis in the Bayesian framework, conducted using the inferred GTR+G+I base substitution model for each gene partition.

The Bayesian inference (BI) was implemented in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) using the following parameters: GTR+G+I model of DNA substitution, Nst as 6 (all different substitution rates subjected to GTR), 10,000,000 MCMC iterations in two runs and four chains; with sampling at every 1000 iterations; stationarity of the runs determined by minimum standard deviation of the split frequencies 0.01; and burn-in of initial 25% of stored trees. The output trees were visualized using Figtree (http://tree.bio.ed.ac.uk/software/figtree/). For comparison based on genetic distances between all the ranid genera, uncorrected pairwise distances were calculated for the partial 16S rRNA gene in MEGA 6.06 (Tamura *et al*. 2013).

Table 1. Genbank accession numbers of the type species of each ranid genera used in the comparative analysis; "NP", National Park. "NA", Not Available.

Species name	Voucher no	Gene				Locality	Reference
		16S	RAG1	TYR	CYTB		
Abavorana luctuosa	FMNH 45046	KF477635	NA	NA	NA	Sabah, Borneo Island, Malaysia	Brown & Siler (2014)
Amnirana amnicola	A117606	KR264034	KR264359	KR264437	KR264124	Southwest Prov., Cameroon	Oliver *et al*. (2015)
Amolops marmoratus	CAS 221675	MG909572	MG909611	MG909684	NA	Kalaw, Shan, Myanmar	Arifin *et al*. (2018)
Babina holsti	NA	AB761264	NA	NA	AB761264	Okinawa, Japan	Kakehashi *et al*. (2013)
Hylorana nicobariensis	MVZ 239177	KR264094	KR264412	KR264488	KR264186	Sumatra, Indonesia	Oliver *et al*. (2015)
Chalcorana chalconota	MVZ 239431	KR264095	KR264413	KR264489	KR264187	Sumatra, Indonesia	Oliver *et al*. (2015)
Clinotarsus curtipes	SDBDU 2011.42	KM069013	KM069261	NA	KM069226	Karnataka, India	Biju *et al*. (2014)
Glandirana minima	NA	AF315153	NA	NA	NA	China	Jiang & Zhou (2000)
Huia cavitympanum	RMBR 2283	MG909602	MG909632	MG909710	NA	Bukit Baka NP Kalimantan, Indonesia	Arifin *et al*. (2018)
Humerana humeralis	USNM 583171	MG935823	NA	NA	NA	Bago, Myanmar	Mulcahy *et al*. (2018)
Hydrophylax malabarica	BNHS 5880	KM068968	KM069242	NA	KM069182	Amboli, Maharashtra, India	Biju *et al*. (2014)
Hylarana erythraea	MZB 29423	MG909597	MG909639	MG909689	NA	G. Leuser NP, Aceh, Indonesia	Arifin *et al*. (2018)
Indosylvirana flavescens	BNHS 5844	KM068930	KM069230	NA	KM069145	Settukunnu, Kerala, India	Biju *et al*. (2014)
Lithobates palmipes	isolate 1008	DQ347321	DQ347263	DQ347170	NA	South America	Bossuyt *et al*. (2006)
Meristogenys jerboa	KUHE 12028	AB211493	AB526662	NA	AB526620	Sarawak, Malaysia	Matsui *et al*. (2006), Shimada *et al*. (2008)
Nidirana okinavana	Isolate oki. J	AB058879	NA	NA	NA	Okinawa, Japan	Sumida *et al*. (2003)
Odorrana margaritae	603	KU840594	KU840728	KU840789	NA	Emei Shan, Sichuan, China	Goutte *et al*. (2016)
Papurana papua	LSUMZ 97639	KR264091	KR264410	KR264485	KR264183	Madang, Papua New Guinea	Oliver *et al*. (2015)
Pelophylax lessonae	F59	MH410480	NA	NA	MH410420	Croatia	Jelic *et al.* (2018)
Pseudorana weiningensis	SCUM 0405171	KX269217	KX269582	KX269808	KX269362	Weining, Sichuan, China	Yuan *et al.* (2016)
Pulchrana signata	FMNH 273117	KR264086	KR264406	KR264480	KR264178	Sarawak, Malaysia	Oliver *et al*. (2015)
Rana temporaria	ZMMU 4288-1	KX269196	KX269561	KX269788	KX269343	Uzhgorod, Zakarpatska, Ukraine	Yuan *et al.* (2016)
Sanguirana sanguinea	KU 309573	KT881807	KT881675	KT881866	NA	Palawan, Philippines	Brown *et al*. 2016
Staurois natator	CMNH 1626	DQ347312	DQ347250	DQ347155	NA	Mindanao Is., Philippines	Bossuyt *et al*. (2006)
Sumaterana crassiovis	MZB Amp22339	MG909579	MG909621	MG909694	NA	G. Kunyit, Kerinci NP, Indonesia	Arifin *et al*. (2018)
Sylvirana nigrovittata	USNM 583178	KR264114	KR264425	KR264510	NA	Myanmar	Oliver *et al*. (2015)
Limnonectes laticeps	NA	AB277306	AB488960	AB277359	AB488856	Malaysia	Kotaki *et al*. (2008, 2010)

***Morphology and recognition of new genus*:** Our study adopted an integrative approach in recognizing a new genus based on molecular and morphological data. The candidate genus was compared with all available types of type species, recently collected specimens or original descriptions of other Asian ranid genera (Table 2). Museum acronyms are those of Uetz *et al*. (2019). Sex and maturity were determined by examining gonads through a small ventral incision and based on secondary sexual characters such as presence or absence of nuptial pads on the first finger. Only mature (adult) animals were used for morphological analysis, species comparisons. Webbing formula follows Savage & Heyer (1967). The syntypes (ZSIC 2783, 2785–86, 3562–63, 3565–70) of *Hylorana nicobariensis* were studied at the Zoological Survey of India, Kolkata. Measurements of Indian (Nicobarese) specimens were taken by SRC and Indonesian specimens were taken by AATA. Under an AmScope SM-1BZ-RL dissecting microscope, with a Mitutoyo digital caliper to the nearest 0.1 mm, we measured snout–vent length (SVL, from the tip of the snout to the anterior margin of the cloaca), axilla–groin length (AG, from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body), head length (HL, from the posterior edge of the mandible to the tip of the snout), head width (HW, the maximum width of the head at the angle of the jaws), head depth (HD, the maximum depth of the head), eye diameter (ED, the greatest horizontal diameter of the orbit), eye–nostril length (EN, from the anterior border of the orbit to the middle of the nostril), snout length (ES, from the anterior border of the orbit to the tip of the snout), tympanum–eye length (TYE, from the posterior border of the orbit to the anterior border of the tympanum), upper eyelid width (UEW, the maximum width of the upper eyelid), inter-orbital distance (IO, distance between the upper eyelids), inter-narial distance (IN, distance between the nostrils), tympanum diameter (TYD, the greatest horizontal diameter of the tympanum), upper arm length (UAL, from the axilla to elbow), lower arm length (LAL, from the posterior margin of the elbow to the base of the outer metacarpal tubercle), palm length (PAL, from the posterior border of the outer metacarpal tubercle to tip of the 3rd finger), femur length (FEL, from the cloaca to the knee), tibia length (TBL, from knee to heel), tarsus length (TSL, from heel to inner metatarsal tubercle), foot length (FOL, from inner metatarsal tubercle to the tip of the 4th toe). Digit number is represented by roman numerals I–V.

Table 2. Character comparisons across Asian and African ranid genera highlighting the distinction of the new genus (modified after Oliver *et al*. 2015).

Character	*Hylorana nicobariensis*	*Indosylvirana*	*Amnirana*	*Chalcorana*	*Hylarana*	*Sylvirana*	*Humerana*	*Papurana*	*Pterorana*
Posterior part of abdominal skin smooth (0), wrinkled (1), granular (2)	0	1, 2	0, 2	2	0, 1	0, 2	0, 1	0	2
Length comparison: finger I and II	I>II	I>II	I≥II	I<II	I=II	I>II	I>II	I>II	I>II
Dorsolateral fold indistinct (0), weakly distinct (1), markedly-distinct (2)	2	1, 2	0, 1, 2	0	1	0, 1, 2	2	1, 2	2
Dorsolateral fold colour paler than dorsal colour (0), uniform with dorsum (1)	1	0	1	1	0	1	1	1	1
Outer metatarsal tubercle absent (0), present (1)	1	1	0, 1	0, 1	1	1	0, 1	1	1
If present, outer metatarsal tubercle small (0), medium (1), large (2) in size	1	2	0, 1	0	1	1	0	0,1	1
Digital disc shape ovoid (0), rhomboid (1)	0	0	0	1	0	0	0	0	0
Flank colouration uniform with dorsum (0), darker (1), mottled (2), bicoloured (3)	0	0	2	0	1, 2, 3	1	0, 1, 2	0, 2	1
Thigh colour pattern uniform with dorsum (0), banded (1), mottled (2), bicoloured (3)	1	1	2	0	0, 2, 3	2	0, 2	0, 2	1
Hind limb colour pattern uniform with dorsum (0), banded (1), mottled (2), bicoloured (3)	1	1	2	0	0, 2, 3	1	0, 2	0, 1	1
Rictal ridge broken (0), continuous (1)	1	1	1	1	1	1	0, 1	0, 1	1
If continuous, rictal ridge weakly or moderately developed (0), well-developed (1)	1	0	1	0	1	0	1	0	1

Results

***Phylogenetic analysis*:** The phylogenetic analysis based on four genes shows the distinctiveness and unique taxonomic position of *Hylorana nicobariensis* within the family Ranidae. Our Bayesian analysis recovered *Hylorana nicobariensis* as a sister taxon to the southeast Asian clade comprising the genera *Sylvirana* + (*Hylarana* + *Humerana*) with moderate support (0.78 BPP), rather than the African genus *Amnirana* or south Asian genus *Indosylvirana* as proposed by Oliver *et al*. (2015) and Chan *et al*. (2020), respectively. For the mitochondrial 16S, *Hylorana nicobariensis* also showed the least genetic divergence from *Sylvirana nigrovittata* (13.64%) than the other ranid genera (Table 3). Specifically, from *Indosylvirana*, under which Chan *et al*. (2020) provisionally attributed this taxon, it showed a comparatively much higher genetic divergence (19.31%), which was almost at the higher end of the range within Ranidae (13.64–24.03%; Table 3; Figs. 1, 2). The Bayesian analysis also recovered the genus *Amnirana* as the sister group to *Indosylvirana*, with weak support. The sister relationship between *Amnirana* and *Indosylvirana* presented here is consistent with that of Chan & Brown (2017) but deviates from the relationship shown by Chan *et al*. (2020) and Oliver *et al*. (2015). Likewise, the sister relationship between the genera *Hylarana* and *Humerana* observed in our study is largely consistent with most of the recently published ranid phylogenies (Oliver *et al*. 2015; Chan & Brown 2017; Chan *et al*. 2020). However, the relationships of the focal taxon *Hylorana nicobariensis* with other ranid genera have not been consistent. Altogether, our phylogenetic analysis clearly shows that *Hylorana nicobariensis* is not closely related to either *Indosylvirana* as implied by Chan *et al*. (2020) or *Amnirana* as suggested by Oliver *et al*. (2015), necessitating the erection of a new monotypic genus to accommodate *Hylorana nicobariensis* and stabilize its taxonomic status.

Taxonomy

Ranidae Batsch, 1796

The generic names *Calamita* Oken, 1816 (now a synonym of *Epidalea* Cope, 1864: type species: *Bufo calamita* Laurenti, 1768) and *Auletris* Wagler, 1830 (now a synonym of *Boana* Gray, 1825, type species: *Rana boans* Linnaeus, 1758) under which, *Hyla bilineata* Van Ernest in Daudin, 1800, a senior synonym of *Hylorana nicobariensis* Stoliczka, 1870 was once attributed (*fide* Frost, 2020) are now currently allocated to Hylidae Rafinesque, 1815 hence, unavailable for allocation (*vide* Art. 23 of the ICZN 1999). All the specimens of the syntypes series (11 specimens) of *Hylorana nicobariensis* consisting of adult and larval specimens belong to the same species. Therefore, we measured only one syntype (ZSI 2783; see Table 4). Among the type series only few specimens (including the one measured) are in a relatively good condition. The rest have broken limbs. The fresh topotypes used in this study were compared carefully with all the syntypes and confirmed alike. Therefore, here we use fresh topotypes for the redescription.

Table 3. Genetic divergence (in %) of *Hylorana nicobariensis* from the type species of other ranid genera based on 16s rRNA gene.

Type species	Genetic divergence (%)	Type species	Genetic divergence (%)	Type species	Genetic divergence (%)
Sylvirana nigrovittata	13.64	*Huia cavitympanum*	15.50	*Rana temporaria*	17.75
Lithobates palmipes	13.64	*Sumaterana crassiovis*	16.00	*Amnirana amnicola*	17.96
Papurana papua	13.85	*Odorrana margaretae*	16.00	*Sylvirana nigrovittata*	18.10
Pseudorana weiningensis	13.85	*Abavorana luctuosa*	16.74	*Papurana papua*	18.12
Humerana humeralis	14.90	*Amolops marmoratus*	16.74	*Humerana humeralis*	18.42
Chalcorana chalconota	14.90	*Lithobates palmipes*	16.95	*Babina holsti*	18.54
Babina holsti	15.16	*Indosylvirana flavescens*	16.95	*Hylarana erythraea*	18.74
Pelophylax lessonae	15.16	*Pseudorana weiningensis*	17.12	*Hydrophylax malabarica*	19.16
Hylarana erythraea	15.26	*Limnonectes laticeps*	17.12	*Meristogenys jerboa*	19.19
Nidirana okinavana	15.26	*Glandirana minima*	17.37	*Sumaterana crassiovis*	19.31
Hydrophylax malabarica	15.30	*Staurois natator*	17.37	*Abavorana luctuosa*	20.95
Sanguirana sanguinea	15.30	*Clinotarsus curtipes*	17.50		
Meristogenys jerboa	15.50	*Pulchrana signata*	17.54		

***Bijurana* gen. nov.**

[urn:lsid:zoobank.org:act:5515C691-3EBB-4B95-8F76-051C01A2FDB5]

Type species: *Hylorana nicobariensis* Stoliczka, 1870 by present designation

Content: *Bijurana nicobariensis* (Stoliczka, 1870) **comb. nov.**

Syntypes (*n*=11): ZSIC 2783, 2785–86, 3562–63, 3565–70 collected from "Nicobar Is.", India.

Etymology. The generic epithet is a patronym honoring Prof. Sathyabhama Das Biju (University of Delhi, India), for his enormous contributions to amphibian research and conservation in the Indian subcontinent. Prof. Biju is renowned as "the frogman of India" for bringing fresh fascination for Indian amphibians.

Diagnosis and definition. (Figs. 1, 3, 6, 7; Table 2). In a phylogenetic framework, the new genus described below is currently monotypic in the family Ranidae that includes the species *Hylorana nicobariensis*, but not the type species of any of the currently recognised, closely related ranid genera *Sylvirana*, *Humerana*, *Hylarana*, *Indosylvirana*, *Amnirana*, *Hydrophylax*, *Papurana*, *Chalcorana*, or *Pulchrana*.

Morphologically, the new genus *Bijurana* is characterized by the following combination of characters: medium to large body size (SVL 37.0–53.0 mm); smooth abdominal skin; finger I>II; thighs with banded pattern and longitudinal skin folds; pronounced dorsolateral folds; presence of eight presacral vertebrae with horizontally elongated hypapophyses; firmisternal pectoral girdle; sacral diapophysis not flattened or expanded laterally; urostyle lacking lateral dilations; presence of vomerine teeth; presence of large and exposed tympanum; presence of rictal glands; absence of elongated ventrolateral glands; digit tips mildly dilated with expanded, ovoid terminal discs; presence of two dark lateral bands along the sides of the head till the tympanum; flanks the same colour as the dorsum; bronze brown dorsal colouration and a pale white venter.

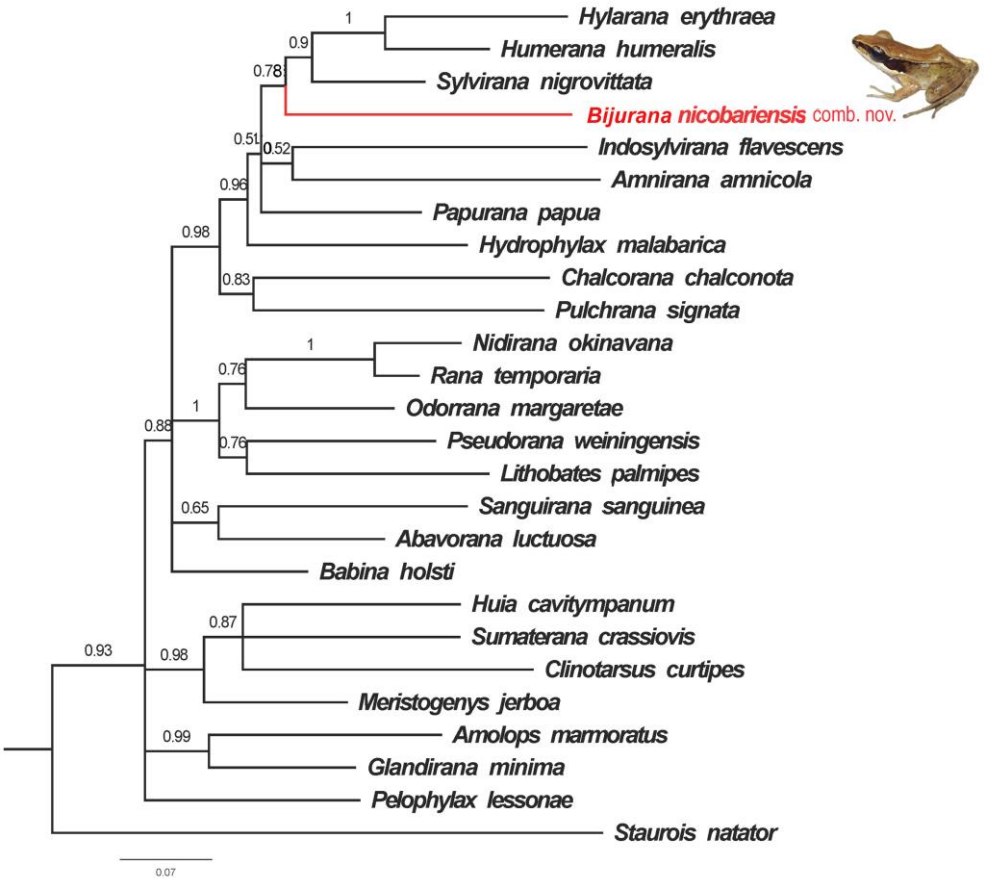

Figure 1. Bayesian phylogram showing the phylogenetic position of the new genus with respect to the type species of other recognised ranid genera (rooted with *Limnonectes laticeps* as the outgroup; not shown).

Comparison. The new genus *Bijurana* can be distinguished from other Asian and African ranid genera by having posterior part of the abdominal skin smooth (*vs* granular or wrinkled in *Indosylvirana*, *Humerana* and *Hylarana*; smooth to granular in *Amnirana*, *Chalcorana* and *Sylvirana*; ventral parts of head, body and limbs: throat with indistinct glandular warts in *Pterorana* fide Ao *et al*. 2006); finger length I>II (*vs* I≥II in *Amnirana*, I<II in *Chalcorana*, I=II in *Hylarana*); thighs with banded pattern (*vs* mottled/plain in *Amnirana*, *Humerana* and *Papurana*; plain in *Hylarana* and *Chalcorana*); thighs with longitudinal ridge-like skin-folds (*vs* smooth in *Amnirana*, *Chalcorana*, *Humerana*, *Hylarana* and *Papurana*); digital terminal disc ovoid (*vs* rhomboidal in *Chalcorana*); rictal glands on the lips well-developed (*vs* moderate in *Indosylvirana* and *Sylvirana*; and poorly developed in *Chalcorana*); pronounced dorsolateral folds (*vs* relatively thin in *Indosylvirana*); flanks of the same colour as the dorsum (*vs* lighter than the dorsum in *Indosylvirana*).

Furthermore, the larvae of *Bijurana* gen. nov. differ from other ranid genera *Chalcorana*, *Hylarana* and also *Indosylvirana* by having a sparsely pigmented body (*vs* dark and densely pigmented in *Hylarana*; yellowish brown with black markings in *Chalcorana*); oral keratodont formula 1//1+1/2 [*vs* 1/3+3//1+1 or 1/4+4//1+1 in *Chalcorana fide* Inger (1985); 1+1//1+1+1 in *Hylarana*; 1/1+1//1+1/1/1 in *Indosylvirana fide* Hiragond & Saidapur (1999)]; and large glandular patches absent on the larval body (*vs* present in *Chalcorana*).

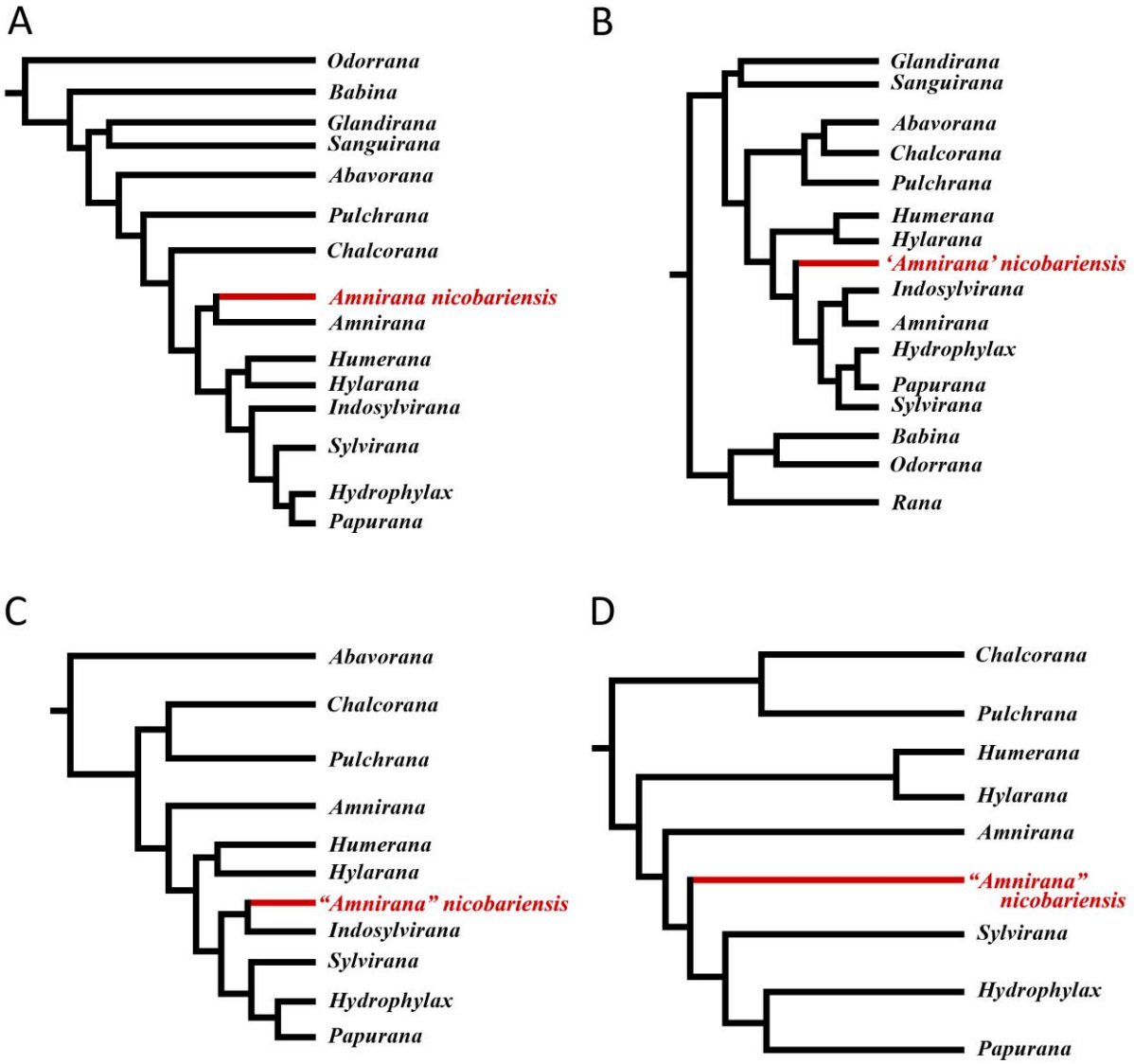

Figure 2. Tree topologies showing the phylogenetic position of *Bijurana nicobariensis* comb. nov. in previous studies **(A)** Oliver *et al*. (2015), **(B)** Chan & Brown (2017), **(C & D)** Chan *et al*. (2020)

***Bijurana nicobariensis* comb. nov.**
(Tables 1–4; Figs. 1–6)

Hylorana nicobariensis Stoliczka, 1870
Rana nicobariensis — Boulenger 1885
Rana (*Hylorana*) *nicobariensis* — Boulenger 1920
Rana (*Hylarana*) *nicobariensis* — van Kampen 1923
Rana (*Sylvirana*) *nicobariensis* — Dubois 1992
Sylvirana nicobariensis — Frost *et al*. 2006
Hylarana nicobariensis — Che *et al*. 2007
Amnirana nicobariensis — Oliver *et al*. 2015
Amnirana (*inc. sed.*) *nicobariensis* — Chan & Brown 2017
Indosylvirana nicobariensis — Chan *et al*. 2020

Syntypes (*n*=11). ZSIC 2783, 2785–86, 3562–63, 3565–70 (Fig. 5); for morphometrics of ZSIC 2783 see Table 4.

Other specimens (*n*=6). Nicobar Archipelago, India: DOSMB 05004, 05010, 05014, 05050, 05077, 05094.

Description of a topotype. Based on DOSMB 05010 from Great Nicobar. An adult female, in a good state of preservation.

Body fairly large (SVL 52.7 mm) with a relatively slender habitus; trunk a little less than half the length of the body (AG:SVL 0.42). Head large and slender (HL:SVL 0.36); longer than broad (HL:HW 1.34) with an obtusely pointed snout, slightly projecting beyond the mandible. Nostrils situated much closer to the snout tip than to the eye (EN:ES 0.61); tympanum fairly large, slightly smaller than the eye (TYD:ED 0.86). A pair of horizontally elongated, ovoid rictal glands present posterior to the jaw angle on either sides of the mandible. Upper eyelids narrower than the inter-orbital space (UEW:IO 0.82); inter-narial space wider than inter-orbital space (IO:IN 0.86).

Upper arms short (UAL:SVL 0.22); lower arms slightly longer than upper arms (LAL:SVL 0.23); palm slightly longer than the lower arm (PAL:LAL 1.07). Relative length of fingers: III>IV>I>II. Thighs long, nearly half as long as the body (FEL:SVL 0.5) and slightly shorter than the tibia (FEL:TBL 0.85). Tarsus short; feet slightly longer than thighs (FEL:FOL 0.98). Toes partially webbed; webbing formula: $I_{0–0.5}II_{0.5–2}III_{1–2}IV_{2–0.5}V$. Inner metatarsal tubercle elongated and ovoid; outer metatarsal tubercle relatively smaller. Relative lengths of toes: IV>V>III>II>I. Digit tips with ovoid and slightly expanded terminal discs with distinct circum-marginal grooves.

Dorsal skin smooth with longitudinal ridge-like skin folds on the hind-limbs; abdominal skin smooth; rectal glands well-developed near the gape and dorsolateral skin folds pronounced.

Colouration. In preservative, dorsum bronze brown without any distinct pattern; two dark brown lateral stripes commencing from the nostril till the tympanum; flanks the same colour as the dorsum; anterior ventral body and head with small brown spots on a cream coloured background; belly un-patterned, cream; under surface of the hind-limbs brownish; hind-limbs, especially thighs bear a feeble banded pattern; ventral surface of the feet dark brown.

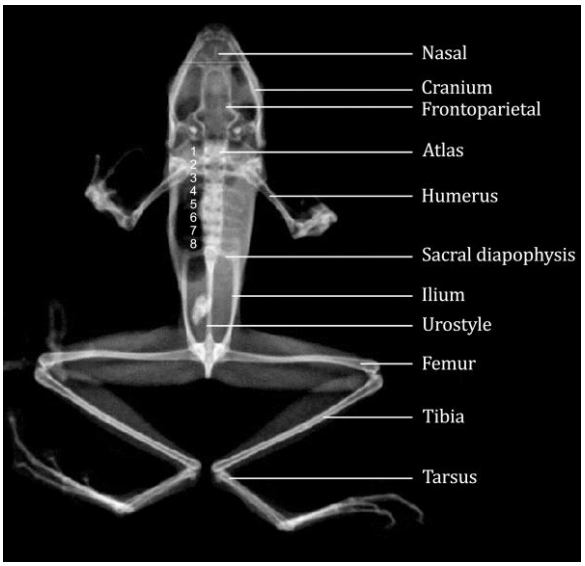

Figure 3. Osteology of an adult *Bijurana nicobariensis* comb. nov. (DOSMB 05050) from Little Nicobar, India.

Call description. Three calls of topotypical *Bijurana nicobariensis* comb. nov. were recorded (Fig. 8) from adult males at Campbell Bay and Govind Nagar, Great Nicobar during November and December in 2016 at a distance of about 1.5–2 m from the calling individuals (SVL ~40–50 mm; not collected).

The calls comprise a series of multi-pulsed notes uttered in succession within short intervals of time. The calls recorded and described here consist of four notes. The notes lasted for a mean duration of 1.65±0.042 s (range 1.526–1.67 s), with a mean interval of 19.43 s (range 18.15–21.3 s) between two consecutive notes. Each note consisted of eight pulses, each of which lasted for a mean duration of 0.12±0.005 s (range 0.11–0.16 s). Dominant frequency of the calls was at 3 kHz.

Plate 43

Figure 4. An adult of *Bijurana nicobariensis* comb. nov. (not collected) from Great Nicobar Island, India

Figure 5. Part of the syntypes series (ZSIC 2783, 2785–86, 3562–63, 3565–70) of *Hylorana nicobariensis* Stoliczka, 1870 from "Nicobar" Island, India (not to scale).

Plate 44

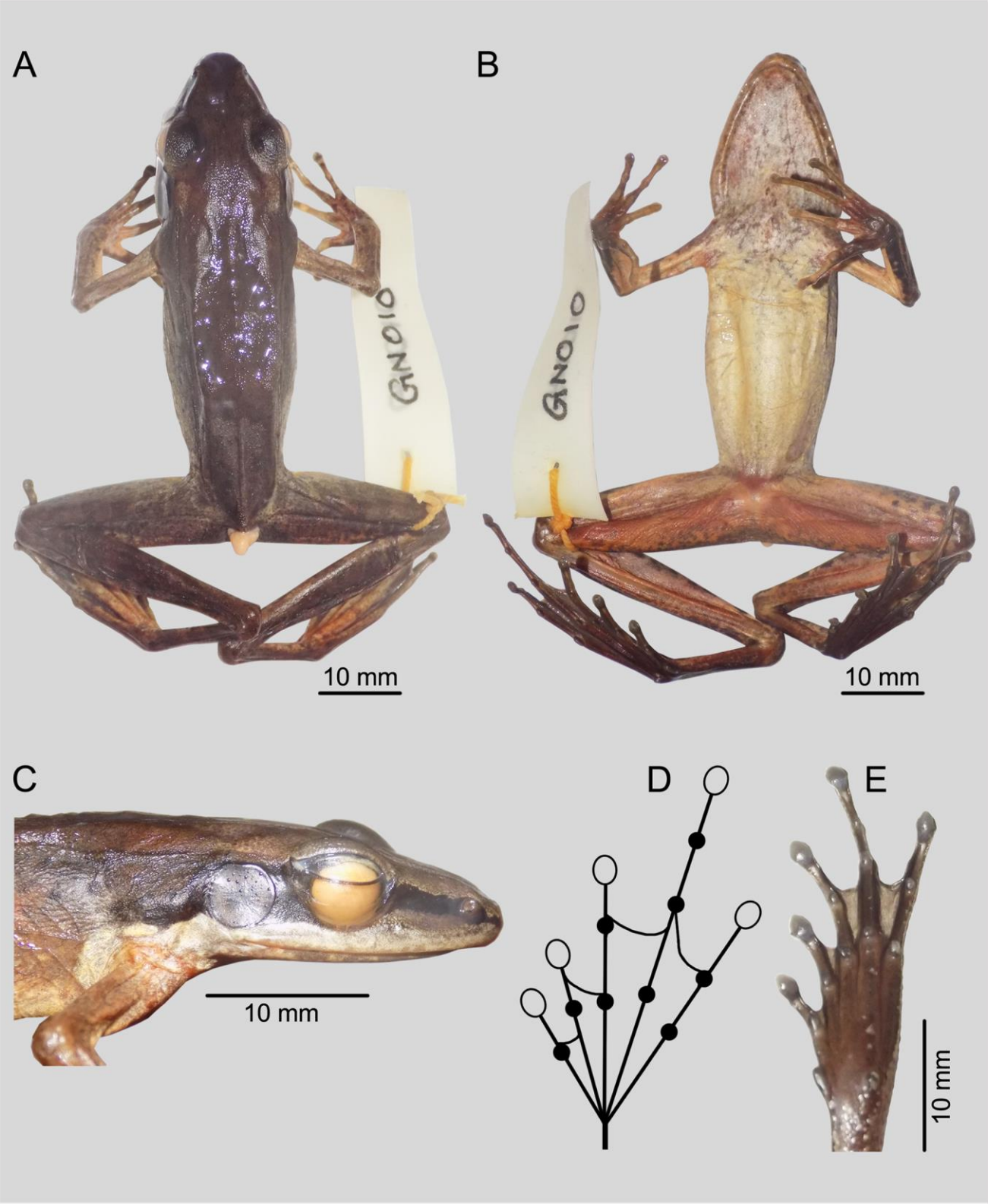

Figure 6. An adult female topotype (DOSMB 05010) of *Bijurana nicobariensis* comb. nov. from Great Nicobar Island, India; **(A)** dorsal and **(B)** ventral views of the body; **(C)** lateral view of the anterior part of the body; **(D)** schematic illustration of webbing of foot and **(E)** ventral view of the foot.

Plate 45

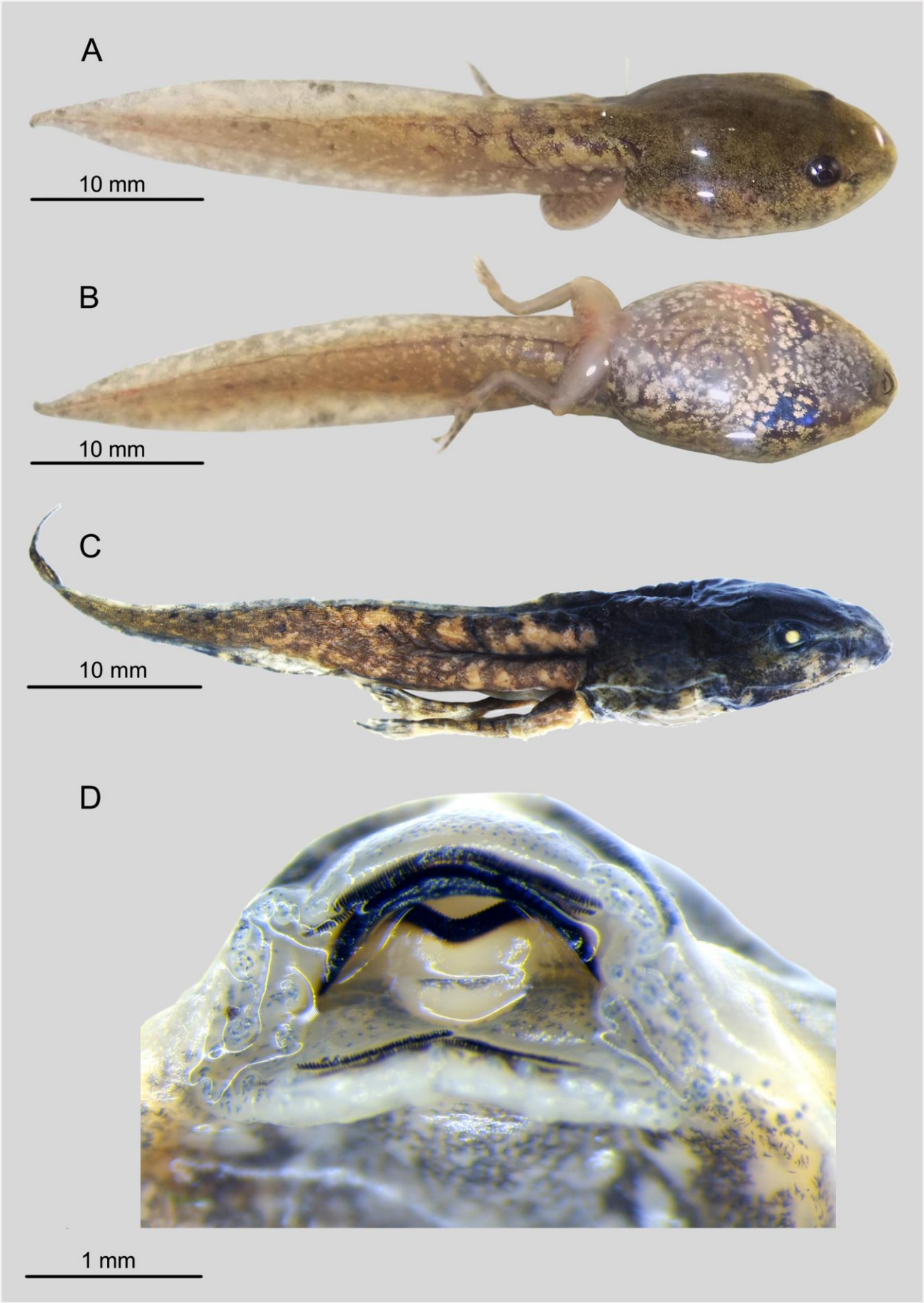

Figure 7. Tadpole of *Bijurana nicobariensis* comb. nov. **(A)** dorsal view and **(B)** ventral view of a live specimen (not collected); **(C)** lateral view of DOSMB 05079; **(D)** ventral view of the mouth parts.

Table 4. Measurements (in mm) of *Bijurana nicobariensis* comb. nov. from the Nicobar Islands and West Java; "—" not measured.

Character	*Bijurana nicobariensis* (Stoliczka, 1870) comb. nov.								
	males			females			Syntype	males	
	DOSMB 05004	DOSMB 05077	DOSMB 05094	DOSMB 05010	DOSMB 05050	DOSMB 05014	ZSI 2783	UIMZ 0160	UIMZ 0161
Location	Great Nicobar	Katchall	Car Nicobar	Great Nicobar	Little Nicobar	Great Nicobar	Nicobar	West Java	
SVL	38.15	37.53	42.70	52.70	42.02	43.16	47.22	34.26	33.55
Axilla–Groin length	12.05	12.82	16.22	21.98	14.46	15.95	16.89	14.69	13.60
Head length	14.06	13.54	15.90	19.00	14.88	15.07	17.59	11.88	12.20
Head width	10.04	10.17	11.55	14.23	11.72	12.50	13.62	8.35	8.22
Head depth	6.05	4.17	6.21	7.98	6.82	8.26	5.90	4.80	4.47
Eye diameter	4.03	4.04	3.73	4.67	4.62	5.04	5.04	3.72	3.84
Eye–nostril length	3.02	4.32	4.26	5.33	4.06	4.26	5.35	3.39	3.23
Eye–snout length	5.04	6.02	7.10	8.73	7.48	6.10	8.72	5.79	5.53
Tympanum diameter	2.02	2.73	3.30	4.03	3.48	3.56	3.53	2.56	2.67
Tympanum–eye	0.98	1.05	1.84	1.47	0.93	1.00	1.24	0.79	0.96
Upper eyelid Width	2.01	2.68	2.81	3.34	2.48	2.67	—	2.15	2.35
Inter orbital distance	2.64	3.00	4.26	4.07	3.47	3.00	5.12	7.85	7.74
Internarial distance	3.15	2.82	3.09	4.71	4.10	3.24	4.27	2.94	3.08
Upper arm length	8.11	7.98	9.38	11.70	8.77	9.03	9.41	5.68	5.31
Lower arm length	8.12	6.70	7.91	12.09	9.53	9.12	9.97	5.99	5.51
Palm length	9.02	10.60	11.03	12.98	10.83	11.06	—	8.88	8.84
Femur length	16.07	17.57	19.73	26.15	20.62	20.95	21.98	17.00	16.78
Tibia length	21.26	20.36	23.17	30.82	24.22	23.09	24.87	19.88	18.66
Tarsus length	11.21	9.72	11.68	16.11	11.38	12.50	10.98	11.46	10.85
Foot length	17.95	19.33	20.91	26.78	22.02	21.08	22.09	17.60	16.53
F1	3.06	4.98	5.44	7.20	5.30	6.01	—	3.29	3.19
F2	2.97	4.62	4.90	5.71	5.09	5.21	—	2.99	3.10
F3	4.68	6.24	7.13	9.79	8.16	6.57	—	5.24	5.33
F4	5.01	4.00	5.01	5.93	4.45	5.04	—	3.53	4.26
T1	3.02	2.30	3.04	3.89	3.12	3.53	—	2.37	2.72
T2	4.13	3.89	4.44	5.74	4.82	4.16	—	3.37	3.81
T3	6.12	6.00	6.64	9.25	7.25	6.57	—	5.52	7.02
T4	10.64	11.05	12.98	15.66	13.71	11.50	—	10.71	10.29
T5	7.06	5.73	7.53	10.16	8.10	7.06	—	6.07	7.07

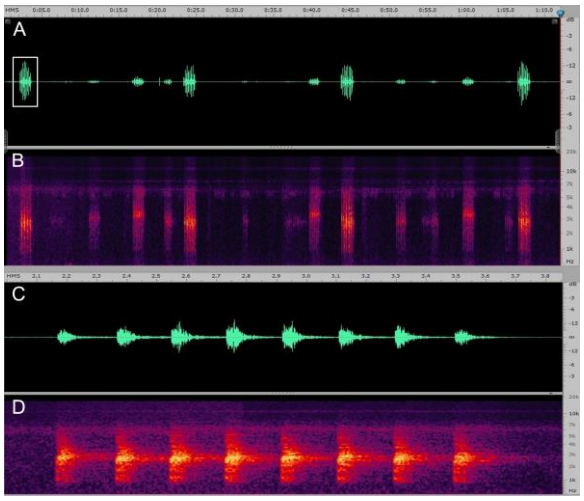

Figure 8. The call of *Bijurana nicobariensis* comb. nov. **(A)** Oscillogram and **(B)** spectrogram; **(C & D)** magnified view of a single note composed of eight pulses.

Discussion

The generic level classification of Ranidae has undergone extensive revisions during the last few decades, with recognition of several new genera as well as new families, which were classically lumped under the cosmopolitan frog family Ranidae (Dubois 1992, Che *et al*. 2007, Oliver *et al*. 2015, Frost 2020). The systematic position of the Southeast Asian species *Hylorana nicobariensis* had remained uncertain, and the constantly conflicting tree topologies have been debated (Fig. 2) due to the lack of concordance (summarized by Chan *et al*. 2020). Although previous authors suggested various generic assignments for this taxon under *Sylvirana*, *Hylarana*, *Amnirana* and *Indosylvirana* (Frost *et al*. 2006; Che *et al*. 2007; Oliver *et al*. 2015; Chan *et al*. 2020, respectively) an unequivocal consensus still does not seem to have been reached. Perhaps it might be due to the reliance solely on genetic data in some of these studies rather than implementing integrative approaches (e.g. see Biju *et al*. 2016, Chandramouli *et al*. 2016, Garg & Biju 2019). The allocations of *Hylorana nicobariensis* to each of the genera mentioned above have

constantly been refuted by the subsequent researchers within a relatively short period of time due to the lack of concordance in their results with the earlier studies (see Introduction).

The present study has addressed this taxonomic issue within an integrated framework using a molecular phylogeny based on four genes (two nuclear and two mitochondrial) backed by morphological characters. Hence, we resorted to erecting a new generic name for *Hylorana nicobariensis* (=*Bijurana nicobariensis* comb. nov.) as a solution to this issue. We believe that this taxonomic action is the most reasonable solution considering its distinct phylogenetic position and morphological affinities, as well as the lack of an unequivocal consensus over its generic reallocations during the last few decades, resulting in non-monophyly of those genera due to its inclusion. Similar taxonomic actions have been implemented to stabilize several cases of either non-monophyletic or uncertain generic allocations, for example, in *Ansonia* and *Bufo* (Biju *et al*. 2009), *Philautus* (Biju *et al*. 2010), and *Pedostibes* (Chan *et al*. 2016). Apart from its distribution on the Islands of the Nicobar archipelago, *Bijurana nicobariensis* comb. nov. extends further northwards and eastwards in several continental as well as insular regions of Southeast Asia, such as Sundaland and the Philippines (Malkmus *et al*. 2002). The complexity and cryptic diversity within the species *Bijurana nicobariensis* com. nov. has been indicated by some of the previous studies (Chan *et al*. 2020). Currently, there are several subjective synonyms for *Bijurana nicobariensis* comb. nov. (summarized by Frost 2020) that originate from regions far from the original type locality (Nicobars). Therefore, a critical integrative assessment is required to understand the cryptic diversity within this new genus of ranid frogs.

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Appendix I. Other specimens examined

***Bijurana nicobariensis* (2 ex.):** Indonesia: Java: UIMZ 0160, 0161.

***Chalcorana chalconota* (2 ex.):** Indonesia: Bali: UIMZ 0052, 0168.

***Chalcorana* sp. (2 ex.):** India: Great Nicobar: DOSMB 05013, 05014.

***Hylarana erythraea* (4 ex.):** Nicobar Islands: DOSMB 05005, 05006, 05076, 05095.

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