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A review of the genus *Cyrtodactylus* Gray 1827 (Squamata: Gekkonidae) of Nepal with descriptions of three new species

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Abstract

We conduct a review of the known species of *Cyrtodactylus* from Nepal based on type and topotypical material, resulting in the synonymization of one species and description of three additional species from Central Nepal. The five species of *Cyrtodactylus* from Nepal are members of the Indo-Burma clade and are at least 11.7 % divergent from known congeners based on the mitochondrial ND2 gene. The results show that *C. nepalensis* and one of the new species are allied to the *C. fasciolatus* group while the other two new species and *C. martinstolli* are members of the mountain subclade within the *khasiensis* group. The new species can be readily distinguished from congeners in the Himalaya by a combination of body size, meristic characters including number of dorsal tubercle rows and mid ventral scales across the belly, the number and arrangement of pores in males and females, and subcaudal condition.

Key words: Bent-toed geckos, Himalaya, Indian subcontinent, integrative taxonomy

Introduction

Nepal hosts rich biodiversity largely due to its extreme topographical range and complexity and associated climatic variation, from the low elevations of the Indo-Gangetic floodplains or Terai (~60–300 m asl.) to the tallest mountains in the world (up to 8848 m asl.). About one third of the Himalaya are within Nepal, including the Central Himalaya and parts of the Western Himalaya (Mani 1974). There is a strong longitudinal gradient in rainfall and seasonality from west to east in the Himalaya; from the drier, more seasonal, and higher latitude Western Himalaya (west of the Kali River) to the Eastern Himalaya (east of the Teesta River) with higher rainfall and lower seasonality, with the transitional Central Himalaya including some of the most southern latitudes within the mountain range (Mani 1974). The challenging terrain and a sparse road network with frequent landslides, as in other regions of the Himalaya, coupled with a general lack of momentum in biodiversity exploration, has left Nepal's biodiversity incompletely surveyed (Amano & Sutherland 2013; Hughes *et al.* 2021).

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Cyrtodactylus Gray is the third most speciose vertebrate genus, with over 350 described species distributed from the Western Himalaya through South and Southeast Asia to the Western Pacific (Wood *et al.* 2012; Grismer *et al.* 2021). However, only three *Cyrtodactylus* species are currently known from Nepal, the syntopic *C. markuscombaii* (Darevsky, Helfenberger, Orlov & Shah) and *C. martinstolli* (Darevsky, Helfenberger, Orlov & Shah) from Ilam District, Koshi Province in the extreme east, and *C. nepalensis* (Schleich & Kästle) from Dadeldhura District, Sudurpashchim Province in the extreme west (Darevsky *et al.* 1998; Schleich & Kästle 1998a, 2002). All three currently known Nepalese species were originally described in the genus *Gonydactylus* Kuhl & van Hasselt, an invalid genus name and senior objective synonym of *Cyrtodactylus* (Kluge 1985). These species have been variously assigned to different genera (Bauer *et al*. 2013) including *Cyrtopodion* (Rösler 2000; Schleich & Kästle 2002; Shah & Tiwari 2004); *Gonydactylus* (Darevsky *et al.* 1998; Shah 1998; Shrestha 2001), *Siwaligekko* (Khan 2003) and finally *Cyrtodactylus* (Mahony *et al.* 2009; Kästle *et al.* 2013; Bhattarai *et al*. 2020; Rai *et al.* 2022; Uetz *et al*. 2022). The three Nepalese *Cyrtodactylus* are listed in regional field guides (see chresonymy for each species below) but have apparently not been collected since their original descriptions, and their phylogenetic affinities are unknown—though they are geographically within the distributional range of the Indo-Burma clade of *Cyrtodactylus* and share similar body size and broad colour pattern (Wood *et al.* 2012; Agarwal *et al.* 2014; Grismer *et al.* 2021).

The Indo-Burma clade of *Cyrtodactylus* (sensu Agarwal *et al.* 2014) was first recognized by Wood *et al.* (2012) as the Myanmar clade and subsequently determined to be made up of the *fasciolatus*, *khasiensis* and *peguensis* species groups (Grismer *et al.* 2021). Just 10 species were known from the region at the turn of the century, but a massive 56 species are currently recognized in the Indo-Burma clade—distributed from < 50—~ 1600 m asl. from the Western Himalaya across northeast India, adjacent Tibet, and areas of Myanmar east of the Salween (Grismer *et al.* 2021; Boruah *et al.* 2024; Uetz *et al.* 2024; Fig. 1; Appendix 1). The highest diversity within the Indo-Burma clade is in northeast India and Myanmar, and only 13 species are distributed in the Himalaya—two in the Western Himalaya of India and Nepal, *Cyrtodactylus fasciolatus* (Blyth) and *C. nepalensis*; eight species from the Eastern Himalaya of India and Nepal—*C. cayuensis* Li, *C. bhupathyi* Agarwal, Mahony, Giri, Chaitanya & Bauer, *C. gubernatoris* (Annandale), *C. himalayicus* (Annandale), *C. kamengensis* Mirza, Bhosale, Thackeray, Phansalkar, Sawant, Gowande & Patel, *C. markuscombaii*, *C. martinstolli, C. siangensis* Boruah, Narayanan, Deepak & Das; and four species from the eastern syntaxis in northeast India, *C. nagalandensis* Agarwal, Mahony, Giri, Chaitanya & Bauer*, C. kiphirae* Boruah, Narayanan, Deepak & Das, *C. namtiram* Mahony & Kamei and *C. ngopensis* Bohra, Zonunsanga, Das, Purkayastha, Biakzuala & Lalremsanga (Agarwal *et al.* 2018a, b; Mahony & Kamei 2021; Mirza *et al.* 2021, 2022; Boruah *et al.* 2024). All these species have been sampled recently and included in phylogenies apart from *C. himalayicus* from India and the three species from Nepal (Grismer *et al.* 2021; Lalremsanga *et al.* 2023; Boruah *et al.* 2024).

Given the recent increase in our understanding of species diversity within the Indo-Burma clade of *Cyrtodactylus* in Myanmar and northeast India, and the vast tracts of suitable habitat in Nepal, it is likely that the low known species diversity in Nepal is a sampling artefact. To address this sampling gap, and lay a baseline for *Cyrtodactylus* systematics in Nepal, we sampled topotypic and type material of the three known Nepalese species and collected *Cyrtodactylus* from four additional localities in central Nepal (Fig. 1). The analysis of the mitochondrial ND2 gene and morphological traits reveal that *C. markuscombaii* and *C. martinstolli* are conspecific and identifies five distinct species-level lineages within Nepal. In this study, we provide redescriptions of *C. nepalensis* and *C. martinstolli*, and synonymize *C. markuscombaii* with *C. martinstolli*. Additionally, we describe three new species belonging to the Indo-Burma clade from central Nepal.

Material and methods

Taxon sampling

Cyrtodactylus were sampled in the Chitwan-Annapurna Landscape in April–September 2023 by SB and team, as part of SB's PhD fieldwork, with the approval of Federation University's Animal Ethics Committee (AEC- 2022-008). These surveys took place after dark, along road-cuttings, boulders, stone walls, trees, and shrubs. *Cyrtodactylus* specimens identified during surveys were hand-collected, photographed in life and later euthanized. Samples of either liver tissue or tail tips were collected during the fieldwork, following euthanasia but prior to preservation, and stored

in 100 % ethanol until they could be transported for subsequent storage at -20°C. Whole, euthanized *Cyrtodactylus* specimens were fixed in 8–14 % formalin for ~12–24 hours, and later transferred to 70 % ethanol after being thoroughly washed. Collection permits for this work were issued by the Nepal Government's Department of National Parks and Wildlife Conservation and Department of Forests and Soil Conservation (see acknowledgements). Specimens are deposited in the Natural History Museum, Kathmandu, Nepal (NHM). Comparative material was examined from the following collections: MHNG (Muséum d'Histoire naturelle, Geneva, Switzerland), SH (private collection Notker Helfenberger, Klong Yai, Trat, Thailand), ZISP (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia), ZMB (Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany), ZSM (Zoologische Staatssammlung München, Munich, Germany).

Preliminary phylogenetic analyses with representatives of all broad *Cyrtodactylus* clades (after Grismer *et al.* 2021; not shown) placed all our samples from Nepal within the Indo-Burma clade (Figs 1, 2). The Indo-Burma clade has over 50 species, of which only *C. feae* (Boulenger), *C. himalayicus*, *C. mandalayensis* Mahony, and *C. tamaiensis* (Smith) have not been genetically sampled (Fig. 2). We restricted morphological comparisons of the new species and previously described Nepal species to regional congeners of the Indo-Burma clade and *lawderanus* group (species from the Western, Central and Eastern Himalaya): *C. bhupathyi*, *C. cayuensis*, *C. chamba* Agarwal, Khandekar & Bauer, *C. fasciolatus*, *C. gubernatoris, C. himalayicus*, *C. kamengensis*, *C. lawderanus* (Stoliczka), *C. markuscombaii*, *C. martinstolli, C. nepalensis, C. siangensis*). Sources of data for the following species are based on material examined (Appendix 1): *C. bhupathyi, C. chamba*, *C. fasciolatus, C. gubernatoris, C. himalayicus, C. markuscombaii*, *C. martinstolli,* and *C. nepalensis*. Data for *C. kamengensis* and *C. siangensis* were taken from the original descriptions (Mirza *et al.* 2022; Boruah *et al.* 2024); and for *C. cayuensis* from Boruah *et al.* (2024) who considered *C. arunachalensis* a synonym of *C. cayuensis* (though the high levels of intraspecific genetic and morphological divergence suggest it constitutes multiple species).

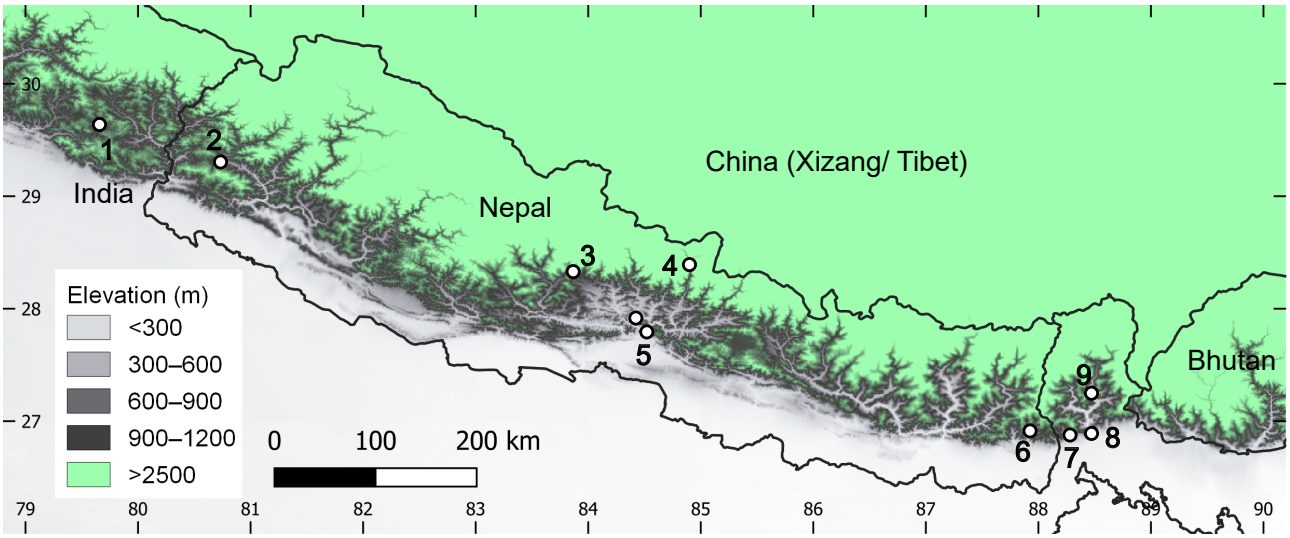

FIGURE 1. Elevation map of the Himalayan region with type localities of Nepal *Cyrtodactylus* and other species from the region shown; 1, *C. lawderanus*; 2, *C. nepalensis*; 3, *C. annapurnaensis* **sp. nov.**; 4, C. *karanshahi* **sp. nov.**; 5, *C. chitwanensis* **sp. nov.** (type and paratype locality); 6, *C. markuscombaii* and *C. martinstolli*; 7, *C. himalayicus*; 8. *C. bhupathyi*; 9, *C. gubernatoris*. Country borders are marked in black.

Morphological data

The morphological dataset comprised of 50 characters from a total of 27 specimens of *Cyrtodactylus* from Nepal, including all type as well as topotypic material of three described species, (material examined listed under respective species accounts), and the three new species. We recorded colour patterns from live photographs of specimens and a single observer (AK; except type material of *C. markuscombaii, C. martinstolli,* and *C. nepalensis* and specimens in the Berlin Museum examined by FT) recorded morphological data under a ZEISS Stereo Discovery V8 dissecting microscope on the left side of the body whenever possible, with bilateral scale counts taken on both sides of each specimen. The following measurements were taken with a Mitutoyo digital caliper (to the nearest 0.1 mm): snout

vent length (SVL, from tip of the snout to cloacal opening); tail length (TL, from cloaca to tail tip); tail width (TW, measured at tail base); lower arm length (LAL, from elbow to distal end of wrist); crus length (CL, from knee to heel); axilla to groin length (AGL, from posterior margin of forelimb insertion to anterior margin of hindlimb insertion); body height (BH, maximum height of body); body width (BW, maximum width of body); head length (HL, distance between retroarticular process of lower jaw and snout tip); head width (HW, maximum width of head); head height (HH, maximum height of head); eye diameter (ED, greatest horizontal diameter of eye); eye to ear distance (EE, distance from anterior edge of ear opening to posterior margin of eye); eye to snout distance (ES, distance between anterior margin of eye and tip of snout); eye to nares distance (EN, distance between anterior margin of eye and posterior edge of nostril); internarial distance (IN, distance between nares measured dorsally from internal margins on snout); interorbital distance (IO, shortest distance between left and right supraciliary scale rows in front of orbit); and ear length (EL, maximum length of ear opening).

The following meristic data were recorded for all specimens: number of internasals (INS, number of scales behind rostral and between supranasals); number of supralabials (SL), and infralabials (IL), from rostral and mental, respectively, to posterior-most enlarged scale at angle of the jaw; supralabials at midorbital position (SL M), and infralabials at midorbital position (IL M), from rostral and mental, respectively, to below the middle of the eye; paravertebral tubercles (PVT, number of enlarged tubercles between limb insertions counted in a straight line immediately left or right of the vertebral column); dorsal tubercle rows (DTR, number of longitudinal rows of enlarged tubercles around the body counted at midbody); mid ventral scale rows (MVSR, counted at midbody between the ventrolateral fold); ventral scales 1 (VS1, counted between forelimb and hindlimb insertions); ventral scales 2 (VS2, counted from posterior of mental to anterior border of cloacal opening); distal subdigital lamellae counted from digital inflection at first phalanx to the claw and including the claw sheath on manus: digit 1 (DLAMF1), digit 4 (DLAMF4), on pes: digit 1 (DLAMT1), digit 4 (DLAMT4), and digit 5 (DLAMT5); basal subdigital lamellae, counted from digital inflection at first phalanx to the base of the digits including all scales that are wider than high; on manus: digit 1 (BLAMF1), digit 4 (BLAMF4), on pes: digit 1 (BLAMT1), digit 4 (BLAMT4), and digit 5 (BLAMT5); total lamellae (TLAMF1, TLAMF4, TLAMT1, TLAMT4, and TLAMT5 are sum of respective basal and distal lamellae); femoral scales (FS, number of enlarged scales on otherwise pore baring femoral row); precloacal-femoral pores (P-F, number of continuous series of precloacal-femoral pore bearing scales); precloacal scales (PCS, number of enlarged scales on otherwise pore baring precloacal row); precloacal pores (PP, number of pore bearing scales on precloacal row); post cloacal tubercles (PCT, number of post cloacal tubercles on either side of the tail base).

Molecular data and phylogenetic analyses

We extracted DNA from thawed liver tissue/tail-tips with the Qiagen DNeasy Blood and Tissue Kit and used the primers L4437 + H5540 (Macey *et al.* 1997) to target the mitochondrial protein coding gene ND2 (NADH dehydrogenase 2; 1038 nucleotides), widely used in *Cyrtodactylus* (Grismer *et al.* 2021). Extractions and Polymerase Chain Reaction (PCR) were carried out at the National Trust for Nature Conservation (NTNC)-Biodiversity Conservation Center, Sauraha, Chitwan District, Bagmati Province, Nepal. PCR and Sanger sequencing was outsourced to Medauxin (Bangalore) and chromatograms were assembled using Chromas 2.6.6 (Technelisium, Australia; http://technelysium.com.au/wp/chromas/). Preliminary analyses placed our new sequences of Nepal *Cyrtodactylus* within the Indo-Burma clade, and thus the final alignment included published sequences for the Indo-Burma clade with the *lawderanus* group used as the outgroup (Table 1; after Wood *et al.* 2012; Grismer *et al.* 2021). Sequences were aligned with default settings using ClustalW (Thompson *et al.* 1994) in MEGA 5.2 (Tamura *et al.* 2011) with translation to amino acid to verify no erroneous stop codons were present. Pairwise uncorrected sequence divergence (p-distance) was calculated in MEGA and phylogenetic relationships were reconstructed using Maximum Likelihood (ML) and Bayesian Inference (BI). A partitioned ML phylogeny was reconstructed using the IQ-TREE webserver (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) with auto substitution models in ModelFinder (Kalyaanamoorthy *et al.* 2017; TVM+F+I+G4 for codon position (cp) 1 and TIM+F+G4 for cp2, cp3) and support assessed with 1000 ultrafast bootstraps (BS). Best-fit models of sequence evolution and partitioning scheme for BI were selected using the Bayesian Inference Criterion (BIC) in PartitionFinder2 (Lanfear *et al.* 2016) which picked GTR+I+G+X for all three codon positions with parameters unlinked across partitions. We carried out the partitioned BI analyses in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003; Ronquist *et al.* 2012) with four chains each (one

cold and three hot) in two parallel runs with 1,000,000 generations sampled every 100 generations, and convergence determined based on a standard deviation of split frequencies (<< 0.01). The sumt function was used to build a consensus tree after removing the first 25% of trees as burn-in.

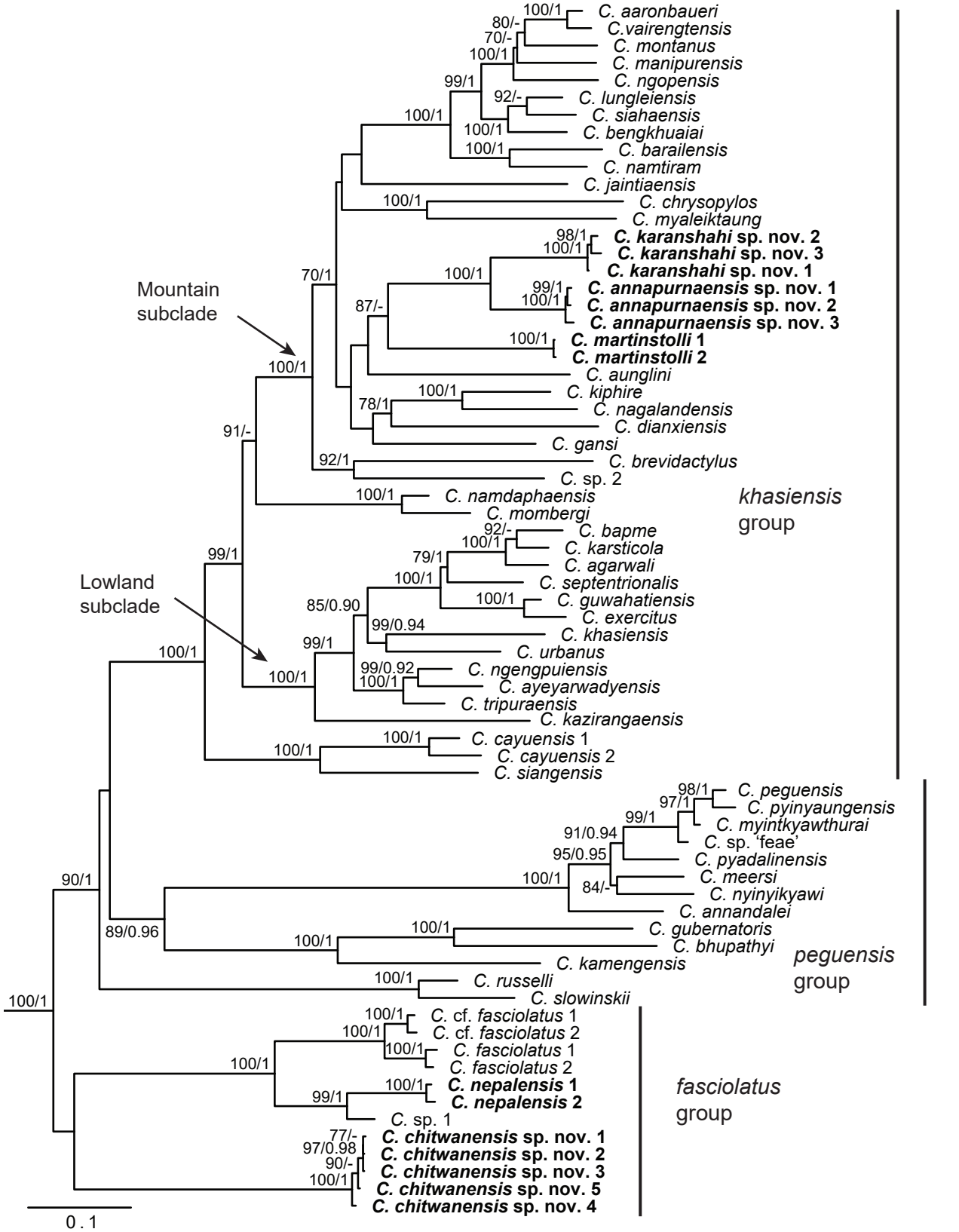

FIGURE 2. Maximum Likelihood phylogeny (ND2, 1038 nucleotides) of the Indo-Burma clade of *Cyrtodactylus*; species from Nepal marked in bold, bootstrap support ≥ 60/ posterior probability ≥ 0.70 shown at nodes, numbers following species name indicate individual specimens for species with multiple samples and outgroups not shown (see Table 1).

TABLE 1. List of ND2 sequences used in this study with accession numbers, voucher and locality details. Newly generated sequences in bold. Museum abbreviations are as follows: BNHS, Bombay Natural History Society, Mumbai; BYU, Brigham Young University, Monte L. Bean Life Science Museum, Provo; CAS, California Academy of Sciences, San Francisco; CES, Centre for Ecological Sciences, Bangalore; CIB, Chengdu Institute of Biology, Chengdu; KIZ; Kunming Institute of Zoology, Kunming; LSUHC, La Sierra University Herpetology Collection, Riverside; MVZ, Museum of Vertebrate Zoology, Berkeley; PMNH, Pakistan Museum of Natural History, Karachi; SB, Santosh Bhattarai field series; USNM, United States National Museum of Natural History, Washington DC; WII, Wildlife Institute of India, Dehradun.

Species	Voucher	Genbank No.	Locality
C. aaronbaueri	MZMU2020	MW596519	India, Mizoram, Tamdil National Wetland
C. agarwali	MZMU2158	MW596515	India, Meghalaya, South Garo Hills, Siju
C. annandalei	CAS215722	JX440524	Myanmar, Sagaing Div., Mon Ywa Dist.
***C. annapurnaensis* sp. nov. 1**	NHM 2023/367 (SB029)	**PV083863**	Nepal, Gandaki Province, Kaski District, Lwang
***C. annapurnaensis* sp. nov. 2**	NHM 2023/368 (SB030)	**PV083864**	Nepal, Gandaki Province, Kaski District, Lwang
***C. annapurnaensis* sp. nov. 3**	NHM 2023/369 (SB031)	**PV083865**	Nepal, Gandaki Province, Kaski District, Lwang
C. aunglini	LSUHC 13948	MH764589	Myanmar, Mandalay Region, Pyin Oo Lwin District
C. ayeyarwadyensis	CAS: 222812	GU550716	Myanmar, Ayeyarwady Division, Myaung Mya Township
C. bapme	BNHS2754	MW367438	India, Meghalaya, West Garo Hills Dist., Jangrapara Village
C. barailensis	WII-ADR971	PQ009374	India, Nagaland, Peren District, Athibung
C. bengkhuaiai	MZMU1985	MW596516	India, Mizoram, Sailam Community Reserved Forest
C. bhupathyi	CES10/1235	KM255204	India, West Bengal, Kalimpong Dist., near Lower Mongpong
C. brevidactylus	CAS214104	JX440527	Myanmar, Mandalay Division: Popa Mountain Park
C. cayuensis 1	YPX1446	MW792058	China
C. cayuensis 2	CES10/1350	KM255193	India, Arunachal Pradesh, Changlang District, Glaw Lake
***C. chitwanensis* sp. nov. 1**	NHM 2023/364 (SB026)	**PV083866**	Nepal, Gandaki Province, Tanahun District, Bandipur
***C. chitwanensis* sp. nov. 2**	NHM 2023/365 (SB027)	**PV083867**	Nepal, Gandaki Province, Tanahun District, Bandipur
***C. chitwanensis* sp. nov. 3**	NHM 2023/366 (SB028)	**PV083868**	Nepal, Bagmati Province, Chitwan District, Kabilas
***C. chitwanensis* sp. nov. 4**	NHM 2023/362 (SB024)	**PV083869**	Nepal, Bagmati Province, Chitwan District, Kabilas
***C. chitwanensis* sp. nov. 5**	NHM 2023/363 (SB025)	**PV083870**	Nepal, Bagmati Province, Chitwan District, Kabilas
C. chrysopylos	CAS 22641	JX440530	Myanmar, Ywnagan Township, Taunggyi District, Shan State, Myanmar.
C. dianxiensis	KIZ059201	MW971927	China, Yunnan
C. exercitus	MZMU2545	OK247680	India, Meghalaya, Umroi
C. fasciolatus 1	CES11/1269	KM255171	India, Himachal Pradesh, Shimla District, Nr. Tattapani
C. fasciolatus 2	CES11/1337	KM255184	Himachal Pradesh State, Shimla Dist., near Subathu, India.

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TABLE 1. (Continued)

Species	Voucher	Genbank No.	Locality
C. cf. *fasciolatus*	CES09/1196	KM255172	India, Uttarakhand, Dehradun District, Mussoorie-Kempty Road
C. cf. *fasciolatus*	CES11/1257	KM255185	India, Himachal Pradesh, Sirmaur District, Nr. Nahan
C. gansi	CAS 222412	JX440537	Myanmar, Chin State, Min Dat Township
C. gubernatoris	CES09/1197	KM255181	India, Sikkim, East District, Singtam
C. guwahatiensis	BNHS 2146	KM255194	India, Assam, Guwahati
C. jaintiaensis	BNHS 2248	KM255195	India, Meghalaya, Jaintia Hills Dist., near Jowai
C. kamengensis	CES10/1464	KM255196	India, Arunachal Pradesh, West Kameng District, Khellong
***C. karanshahi* sp. nov. 1**	NHM 2023/371 (SB033)	**PV083871**	Nepal, Gandaki Province, Gorkha District, Manaslu Conservation Area, Philim
***C. karanshahi* sp. nov. 2**	NHM 2023/372 (SB034)	**PV083872**	Nepal, Gandaki Province, Gorkha District, Manaslu Conservation Area, Philim
***C. karanshahi* sp. nov. 3**	NHM 2023/373 (SB035)	**PV083873**	Nepal, Gandaki Province, Gorkha District, Manaslu Conservation Area, Philim
C. karsticola	MZMU2153	MW596514	India, Meghalaya, South Garo Hills District, Siju
C. kazirangaensis	BNHS 2147	KM255170	India, Assam, Golaghat Dist., Kohora
C. khasiensis	BNHS 2249	KM255188	India, Meghalaya, East Khasi Hills Dist., near Cherrapunjee Resort
C. kiphire	WII-ADR963	PQ009375	India, Nagaland, Kiphire District, Kiphire forest division
C. lungleiensis	MZMU2428	MZ645742	India, Mizoram, Lunglei Dist., outskirts of Lunglei town
C. manipurensis	WII-ADR1596	PQ009373	India, Manipur, Churachandpur District, Lamdan Kabui
***C. martinstolli* 1**	NHM 2023/356 (SB014)	**PV083874**	Nepal, Koshi Province, Ilam District, Dobate
***C. martinstolli* 2**	NHM 2023/359 (SB017)	**PV083875**	Nepal, Koshi Province, Ilam District, Dobate
C. meersi	LSUHC 13455	MH624104	Myanmar, Bago Region, Yangon (north) Dist., Taikkyi Township,
C. mombergi	LSUHC_14656	MN059871	Myanmar, Kachin State, Indawgyi Wildlife Sanctuary
C. montanus	BNHS 2231	KM255200	India, Tripura, North Tripura Dist., Phuldungsei
C. myaleiktaung	LSUHC_13965	MH764598	Myanmar, Mandalay Region, Mandalay District
C. myintkyawthurai	LSUHC_13809	MH624119	Myanmar, Mandalay Region, Kyauk-pa-taung Township
C. nagalandensis	BNHS 2253	KM255199	India, Nagaland, Kohima Dist., Khonoma
C. namdaphaensis	WII-ADR1415	PQ009385	India, Arunachal Pradesh, Changlang District, Namdapha Tiger Reserve
C. namtiram	BNHS2751	MW367433	India, Manipur, Tamenglong District, Namtiram
C. nepalensis	NHM 2023/360 (SB038)	**PV083876**	Nepal, Sudurpaschim Province, Dadeldhura District, Sakayal
C. nepalensis	NHM 2023/361 (SB039)	**PV083877**	Nepal, Sudurpaschim Province, Dadeldhura District, Sakayal

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TABLE 1. (Continued)

Species	Voucher	Genbank No.	Locality
C. ngengpuiensis	WII-ADR1057	PQ009378	India, Mizoram, Lawngtlai District, Ngengpui Wildlife Sanctuary
C. ngopensis	MZMU2360	OM912605	India, Mizoram, Champhai District, Ngoma
C. nyinyikyawi	CAS 226139	MH624118	Myanmar, Magwe Reg., Min Bu Township, Shwe Settaw WLS
C. peguensis	LSUHC 13454	MH756190	Myanmar, Bago Reg., Myin Mo Shwe Taung Pagoda
C. pyadalinensis	LSUHC 13932	MH624105	Myanmar, Shan State, Ywangan Township
C. pyinyaungensis	BYU 52234	MF872307	Myanmar, Mandalay Reg., 5.3 km north of Pyinyaung Village
C. russelli	CAS 226137	JX440555	Myanmar, Sagaing Div., Htamanthi WLS
C. septentrionalis	BNHS 1989	MH971164	India, Assam, Bongaigaon Dist., near Abhayapuri
C. siahaensis	MZMU2445	OK247677	India, Mizoram, Siaha
C. siangensis	WII-ADR1581	PQ009371	India, Arunachal Pradesh, East Siang District, Bodak
C. slowinskii	CAS 210205	JX440559	Myanmar, Sagaing Division, Alaungdaw Kathapa National Park
C. sp. *'feae'*	USNM 559805	JX440536	Myanmar, Mandalay Division, Popa Mountain Park
C. sp. *1*	CES11/1345	KM255169	India, Uttarakhand, Almora District, Almora
C. sp. *2*	HLM0310	MW713970	Myanmar, Sagaing, Ban Mauk
C. tripuraensis	BNHS2238	KM255183	India, Tripura, Sepahijala District, Sepahijala Wildlife Sanctuary
C. urbanus	BNHS 2852	MW367439	India, Meghalaya, Ri Bhoi Dist., Saiden
C. vairengtensis	MZMU2905	OP874796	India, Mizoram, Kolasib District, Vairengte
C. battalensis	PMNH 2303	KC151984	Pakistan, North-West Frontier Prov., Battagram City
C. chamba	CES11/1291	KM255191	India, Himachal Pradesh, Chamba Dist., near Chamba
C. himalayanus	CES11/1317	KM255187	India, Jammu and Kashmir, Kishtwar District, Nr. Kishtwar
C. lawderanus	CES11/1343	KM255190	India, Uttarakhand, Almora Dist., Almora
C. laevis	CIB 121654	PQ140597	China, Xizang, Linzhi, Lang
C. tibetanus	MVZ233251	JX440561	Tibet Autonomous Region, Lhasa
C. zhaoermii	CIB XZ2024100	PQ140609	China, Xizang, Lasa, Nimu

Results

Phylogenetic relationships

We recovered a strongly supported (BS 100, posterior probability 1) Indo-Burma clade, within which a basal divergence separates the *C. fasciolatus* group which includes *C. fasciolatus, C.* sp. 1 and *C. nepalensis* that collectively form the weakly supported (BS < 75, PP < 0.9) sister taxon to a divergent lineage from Chitwan and Bandipur (Fig. 2). Within the subclade containing the remaining species, a basal divergence separates a subclade including *C. russelli* Bauer and *C. slowinskii* Bauer from another subclade. This final subclade is split into two broad subclades, the first approximately corresponding to the *peguensis* group (minus *C. russelli* and *C. slowinskii*) and the second to the *khasiensis* group (sensu Grismer *et al.* 2021). The *peguensis* group includes the Eastern Himalayan subclade (sensu Agarwal *et al.* 2014) as the sister taxon to a largely Myanmarese clade. The *khasiensis* group is the largest of the subclades, and includes two well-supported subclades that correspond to the mountain and lowland clades of Agarwal *et al.* (2014), besides a divergence at the base of *khasiensis* group and at the base of the mountain clade separating species from Arunachal Pradesh/ adjacent Myanmar and China. The remaining samples from Nepal fall within the mountain clade—with *C. markuscombaii* and *C. martinstolli* from eastern Nepal identical in mitochondrial sequence data, forming a moderately supported subclade (87/ < 0.9) along with two divergent lineages from central Nepal.

Uncorrected ND2 sequence divergence within the Nepal samples is as low as 0.1 % between the two 'species' from eastern Nepal and 11.7–25.0 % between the other lineages, and ≥ 14.3 % from previously described species of the Indo-Burma clade (Table S1). The mitochondrial sequence data clearly demonstrates that the syntopic *C. markuscombaii* and *C. martinstolli* from eastern Nepal represent a single species, and that three lineages from central Nepal represent divergent, unnamed lineages. Below, we use morphological data to formally relegate *C. markuscombaii* to the synonymy of *C. martinstolli*, present an expanded morphological dataset for *C. martinstolli* and *C. nepalensis* based on the types and topotypical material, and describe the three divergent lineages from central Nepal as new species.

Systematics

Cyrtodactylus martinstolli (Darevsky, Helfenberger, Orlov & Shah, "1997" 1998)

(Figs 3 & 4; Tables 2 & 3)

Gonydactylus martinstolli Darevsky, Helfenberger, Orlov & Shah "1997" 1998, p. 89; Shah 1998, p. 28; Shrestha 2001, p. 258.
Cyrtopodion martinstollii—Rösler 2000, p. 74; Schleich & Kästle 2002, p. 684; Shah & Tiwari 2004, p. 117.
S.[*iwaligekko*] *martinstollii*—Khan 2003, p. 3.
Cyrtodactylus martinstolli—Mahony *et al.* 2009, p. 245; Rai *et al*. 2022, p. 10.
Gonydactylus markuscombaii Darevsky, Helfenberger, Orlov & Shah "1997" 1998, p. 90; Shah 1998, p. 28; Shrestha 2001, p. 258.
Cyrtopodion markuscombaii—Rösler 2000, p. 74; Schleich & Kästle 2002, p. 682; Shah & Tiwari 2004, p. 116.
S.[*iwaligekko*] *markuscombaii*—Khan 2003, p. 3.
Cyrtodactylus marcuscombaii [sic]—Mahony *et al.* 2009, p. 245.
Cyrtodactylus markuscombaii—Kästle *et al*. 2013, p. 439; Rai *et al*. 2022, p. 10.

Holotype (Fig. 3A, B). MHNG 2590.09, adult male, from the road between Ilam town and Pawakhola [=Puwakhola] village (1200 to 1300 m asl.), Ilam District, Koshi Province, Nepal; collected by K.B. Shah, N. Helfenberger, and N. Orlov, on 1st October 1996.

Paratypes. MHNG 2590.10–33, collected between 1st and 2nd October 1996. Other data as for the holotype.

Referred material (Fig. 4C, D). MHNG 2590.35, adult male and ZISP 20685, adult female (holotype and paratype of *C. markuscombaii* respectively), from the road between Ilam town and Puwakhola village (1200 to 1300 m asl.), Ilam District, Koshi Province, Nepal; collected by K.B. Shah, N. Helfenberger, and N. Orlov, on 2nd October 1996; ZSM 0587/2012 (ex SH 2306), same data as for the holotype of *C. martinstolli*; NHM 2023/356 (SB014), adult male, NHM 2023/357 (SB015), NHM 2023/358 (SB016), NHM 2023/359 (SB017), adult females, from Dobate, between Ilam market and Puwakhola (26.9129°N, 87.9323°E; *ca.* 1180 m asl.), Ilam District, Koshi Province, Nepal; collected by Santosh Bhattarai on 7th July 2023.

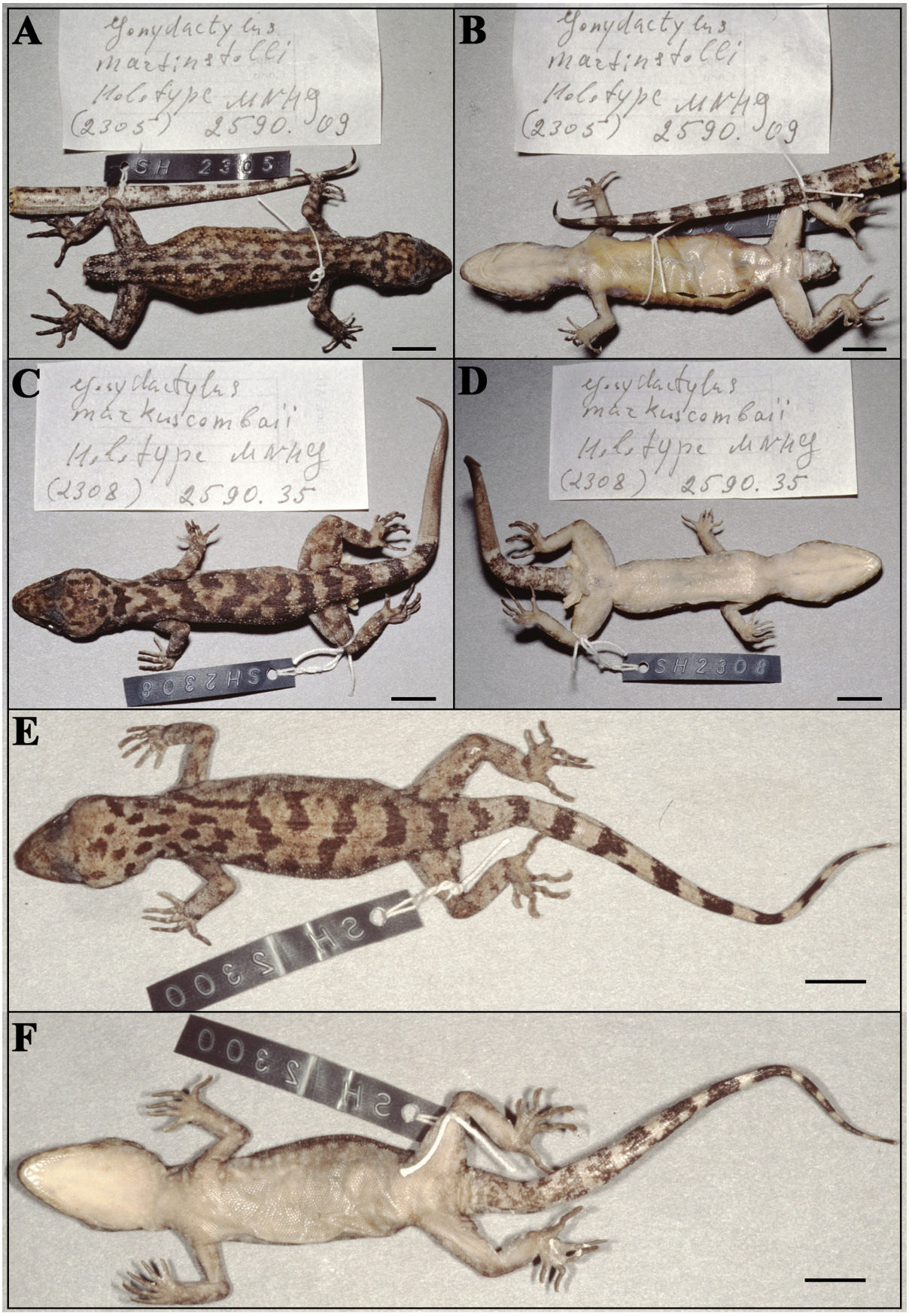

FIGURE 3. Type photos of: *Cyrtodactylus martinstolli* (A) dorsal view, (B) ventral view of the holotype (male, MHNG 259.09); *C. markuscombaii* (C) dorsal view, (D) ventral view of the paratype (male, MHNG 2590.35); and (E) dorsal view, (F) of the paratype (female, ZISP 20685). Scale bars 10 mm; photos by Frank Tillack.

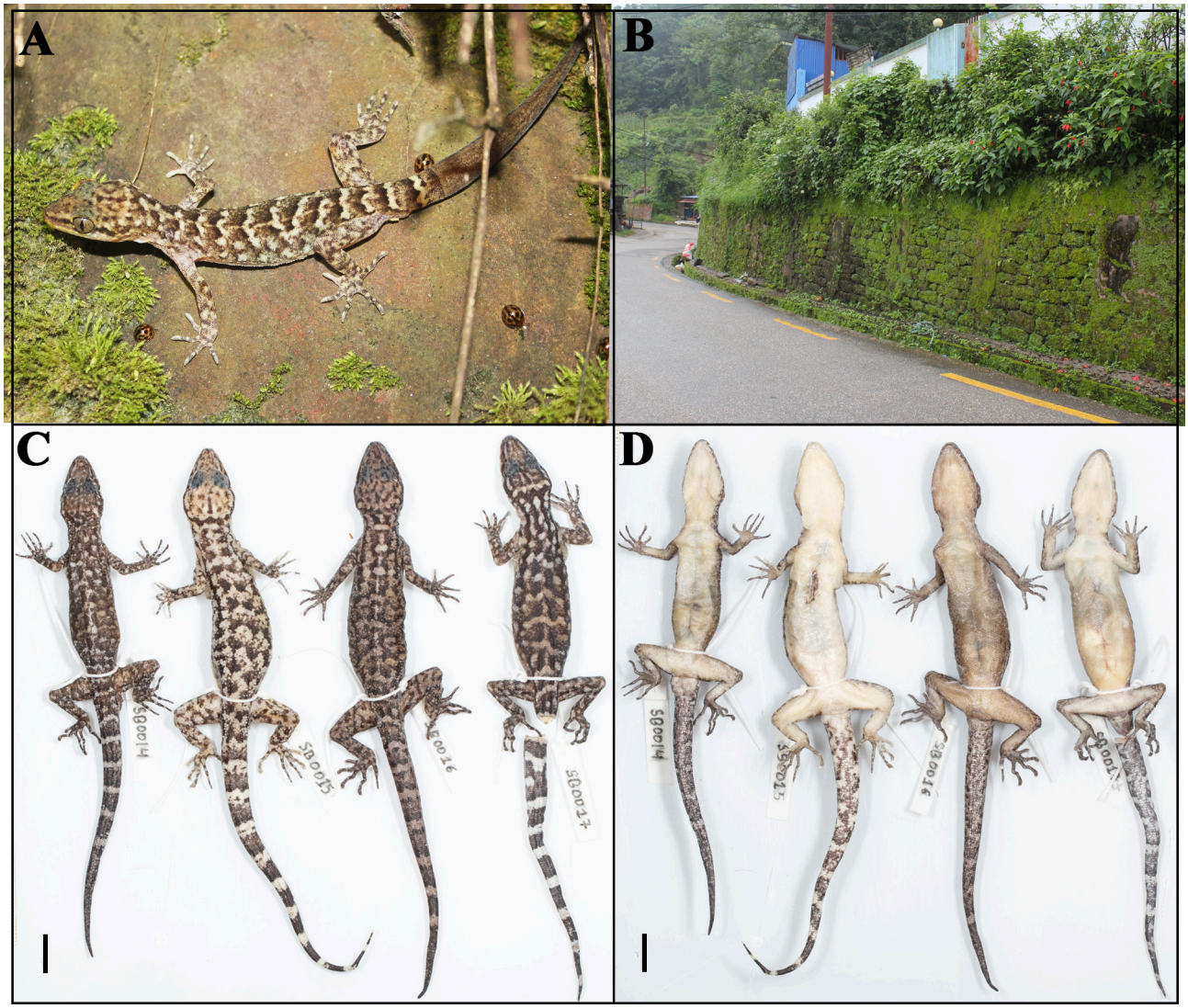

FIGURE 4. (A) Life photo of *Cyrtodactylus martinstolli* in situ (uncollected); (B) microhabitat at the type locality Dobate, Ilam District from where topotypes were collected; topotypes, from left to right, NHM 2023/356–359, (C) dorsal view, and (D) ventral view. Scale bar 10 mm; photos by Santosh Bhattarai (A&B) and Akshay Khandekar (C&D).

Etymology. Patronym for Martin Stoll (b. 1956), who supported the Nepalese-Swiss-Russian Herpetological Expedition to Nepal in 1996 during which the type material was collected.

Suggested common name. Ilam bent-toed gecko.

Diagnosis (Tables 2 & 3). A medium-sized *Cyrtodactylus*, snout to vent length up to 80.4 mm (*n*=7). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled to smooth, weakly pointed tubercles; a ventrolateral fold of skin present on lower flank; 19–23 rows of dorsal tubercles at midbody, 30–37 tubercles in paravertebral rows; ventral scales subequal from chest to vent, smooth, subcircular, and subimbricate with rounded end; 35–40 scales across belly at midbody, 84–91 longitudinal scales between axilla to groin, 184–196 longitudinal scales from mental to cloaca; subdigital scansors smooth, unnotched, and mostly entire; 14 or 15 lamellae under digit I of manus and pes, 18–20 lamellae under digit IV of manus and 19–22 lamellae under digit IV of pes; males with continuous series of seven or eight precloacal pores and 9–12 enlarged precloacal scales on pore bearing scale row (*n*=3); female without pores but having eight or nine pitted scales, and 8–10 enlarged precloacal scales on pit bearing scale row (*n*=4); scales on non-regenerated tail dorsum homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few

TABLE 2. Mensural (mm) data for three previously described species of *Cyrtodactylus*. Abbreviations are listed in Materials and Methods except for: M = male, F = female, and / = data unavailable.

Species	*Cyrtodactylus nepalensis*			*Cyrtodactylus markuscombaii*		*Cyrtodactylus martinstolli*				
Type	Holotype	Topotypes		Holotype	Paratype	Holotype	Topotypes			
Specimen Number	ZSM 0854-212	NHM 2023/360	NHM 2023/361	MHNG 2590.35	ZISP 20685	MHNG 2590.09	NHM 2023/356	NHM 2023/357	NHM 2023/358	NHM 2023/359
Sex	M	M	F	M	F	M	M	F	F	F
SVL	74.2	69.0	74.7	72.5	71.0	80.4	64.6	73.0	74.9	71.4
TL	65.6	97.5	7.2*	60.0	73.8	89.2	69.6	87.1	74.5	76.4
TW	9.3	6.9	7.0	/	/	/	6.8	6.2	5.9	5.4
LAL	11.4	10.6	10.2	/	/	/	9.6	10.6	10.7	10.6
CL	15.1	13.1	13.1	/	/	/	11.8	12.5	12.8	12.4
AGL	34.3	31.0	33.6	31.0	29.1	38.9	27.7	33.5	32.8	36.9
BH	11.5	7.0	7.9	/	/	/	8.0	11.6	9.1	10.7
BW	14.8	11.8	13.1	/	/	/	11.3	15.5	14.5	14.4
HL	20.4	17.7	18.9	20.3	19.8	19.8	16.2	18.7	18.5	17.9
HW	14.0	12.5	13.3	14.6	13.0	13.0	11.0	13.0	12.7	11.9
HD	9.5	7.2	7.5	7.9	7.7	8.4	6.6	7.3	7.3	6.5
ED	4.5	4.0	4.0	4.5	4.0	4.4	4.1	4.3	4.4	3.9
EE	6.1	5.2	5.6	5.9	6.1	6.4	4.7	5.4	5.3	5.2
ES	8.4	8.2	8.9	7.1	7.8	8.2	7.0	7.5	8.1	8.1
EN	6.3	6.2	6.6	/	/	/	5.4	6.0	6.0	6.2
IN	2.6	2.3	2.5	/	/	/	2.0	2.2	2.1	2.5
IO	6.4	4.2	3.9	/	/	/	3.6	4.9	3.9	4.1
EL	1.9	2.0	1.8	0.9	1.1	1.1	1.1	1.7	1.7	1.4

TABLE 3. Meristic data for three previously described species of *Cyrtodactylus*. The values in parentheses are the number of pitted scales in females. Abbreviations are listed in Materials and Methods except for: M = male, F = female, L&R = left & right, / = data unavailable, * = incomplete count, P/A = present/absent, DIST EN = distinctly enlarged, NOT EN = not enlarged; numbers in parentheses for FS indicates number of pitted scales in females.

Species	*Cyrtodactylus nepalensis*			*Cyrtodactylus markuscombaii*		*Cyrtodactylus martinstolli*				
Type	Holotype	Topotypes		Holotype	Paratype	Holotype	Topotypes			
Museum number	ZSM 0854-212	NHM 2023/360	NHM 2023/361	MHNG 2590.35	ZISP 20685	MHNG 2590.09	NHM 2023/356	NHM 2023/357	NHM 2023/358	NHM 2023/359
Sex	M	M	F	M	F	M	M	F	F	F
INS	0	1	1	1	2	1	1	1	2	1
SL L&R	10&10	12&13	13&13	/&11	11&11	11&11	11&10	12&12	11&11	12&12
IL L&R	9&9	9&9	10&9	/&10	10&10	11&11	11&11	10&10	11&10	12&12
SL M L&R	8&8	8&8	9&8	/&7	9&7	8&8	7&7	8&8	8&8	9&9
IL M L&R	7&7	6&6	6&6	/&6	6&6	7&7	7&7	6&6	6&6	8&8
PVT L&R	30&33	31&31	31&30	/	/	30&32	34&34	31&32	35&37	31&32
DTR	17	17	17	19	23	19	22	21	20	20
MVSR	33	33	30	38	39	39	35	39	37	40
VS1	72	71	68	/	/	/	84	91	89	84
VS2	158	163	150	186	188	196	185	188	184	184
DLAMF1 L&R	10&9	11&10	9&10	/	/	/	9&9	9&10	9&9	9&9
BLAMF1 L&R	5&4	6&6	5&6	/	/	/	5&4*	5&5	5&5	5&5
DLAMF4 L&R	12&12	13&13	13&13	/	/	/	12&13	13&13	13&13	12&13
BLAMF4 L&R	8&7	6&6	6&6	/	/	/	6&7	6&6	6&6	6&7
DLAMT1 L&R	11&11	10&10	10&10	/	/	/	11&11	11&11	11&11	11&11
BLAMT1 L&R	4&4	4&6	5&5	/	/	/	4&4	4&4	4&4	3&4
DLAMT4 L&R	*&14	14&15	14&14	/	/	/	13&13	14&13	14&15	13&13
BLAMT4 L&R	5*&7	10&10	10&10	/	/	/	6&6	8&7	7&7	7&6
DLAMT5 L&R	14&14	14&14	15&15	/	/	/	14&13	15&13	14&14	14&13
BLAMT5 L&R	8&8	9&8	9&9	/	/	/	6&6	6&6	6&6	6&6
TLAMF1 L&R	15&13	17&16	14&16	/	/	/	14&13*	14&15	14&14	14&14
TLAMF4 L&R	20&19	19&19	19&19	/	/	/	18&20	19&19	19&19	18&20
TLAMT1 L&R	15&15	14&16	15&15	/	/	/	15&15	15&15	15&15	14&15
TLAMT4 L&R	*&21	24&25	24&24	/	/	/	19&19	22&20	21&22	20&19
TLAMT5 L&R	22&22	23&22	24&24	/	/	/	20&19	21&19	20&20	20&19
FS	39	38	33 (13)	A	A	A	A	A	A	A
P-F	35	38	A	A	A	A	A	A	A	A
PCS	A	A	A	9	8 (/)	10	12	10 (8)	10 (9)	10 (8)
PP	A	A	A	7	A	8	7	A	A	A
PCT L&R	2&2	3&3	3&2	/	3&3	3&3	3&3	3&4	4&3	3&3
Caudal tubercles P/A	/	A	A	/	A	A	A	A	A	A
Subcaudals enlarged or not	/	DIST EN	/	/	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN

scattered enlarged tubercles present on the tail base; subcaudal scales in median series smooth, variable in size and shape, and not enlarged; variegated dorsal pattern with 8–11 dark bands, original tail with 10–12 alternating dark and lighter bands.

Genetic divergence. *C. martinstolli* is 15.8–28.1 % divergent from described members of the Indo-Burma clade and 15.8–16.6 % from the two new species from Central Nepal that it forms the sister taxon to, with only 0.3 % intraspecific divergence (Table S1). The species falls in the mountain subclade of the *khasiensis* group within the Indo-Burma clade (Fig. 2).

Comparisons with regional congeners. *Cyrtodactylus martinstolli* can be differentiated from all regional congeners based on the following differing or non-overlapping characters: no femoral pores and seven or eight precloacal pores in males (*versus* femoral pores present in males of *C. fasciolatus*, *C. gubernatoris*, and *C. nepalensis*; five precloacal pores in *C. chamba*, 7–11 in *C. kamengensis*, 10 in C. *himalayicus*); no precloacal or femoral pores in females (*versus* precloacal and femoral pores present in females in *C. bhupathyi*); length of original tail > SVL (*versus* length of original tail < SVL in *C. lawderanus*); 19–23 rows of dorsal tubercles at midbody and 35–40 scales across belly at midbody (*versus* 15–26 DTR and 28–44 MVSR in *C. cayuensis*, 30–34 MVSR in *C. kamengensis*, and 15 or 16 DTR and 40–45 MVSR in C. *siangensis*).

Colouration in life (Fig. 4A). Dorsal ground colour of head, body, limbs and tail brown; head with dark brown spots, a broken occipital collar sometimes present; labials lighter than head dorsum and with some yellow streaks; dark brown pre and postorbital streaks distinct; dorsum with 8–11 dark, irregular bands that are more or less broken up, sometimes forming a variegated pattern; a fine light mid-vertebral stripe between forelimb insertions and tail base in some specimens; 10–12 dark and light caudal bands on original tail; rest of ventral surfaces immaculate; iris grey with fine reticulations, pupil black.

Synonymy of C. *markuscombaii*. The morphological data of our topotypical specimens as well as type material of both species clearly demonstrate that *C. markuscombaii* and *C. martinstolli* are conspecific. The colour pattern of the types of *C. markuscombaii* and *C. martinstolli* are fairly distinct, and that may have been what drove the authors to recognize two distinct species as there is complete overlap in all other morphological characters in the types and presented in the original description (Darevsky *et al.* 1998). As first revisers, we apply the name *Cyrtodactylus martinstolli* to take precedence over the simultaneously published *C. markuscombaii* (Anonymous 1999).

Distribution and natural history. *Cyrtodactylus martinstolli* is known only from the type locality in Ilam, eastern Nepal at an elevation of 1200–1300 m asl. (Fig. 1). The habitat at the type locality is characterised by roadside walls and embankments and some rocky patches along the road. We surveyed the type locality after dark till night (~1930–2330 hrs). *Cyrtodactylus martinstolli* is nocturnal and locally abundant on the roadside walls and rocky patches along roads. The species was observed along roads at Dobate and Ilam Market, besides roadside walls and rocks along the main highway towards Taplejung from Ilam market up to Puwa Khola. We also observed individuals on the roadside walls of the main market of Ilam. At collection sites, many individuals (*n*=> 20) were observed active during the late evening (1930–2300 hrs) about one or two meters above the ground on roadside walls, even on well exposed walls (Fig. 4B), and a few individuals were seen resting near rock crevices at night (1930–2230 hrs). Some individuals were peeping from holes of the roadside walls, and juveniles were also observed. The only sympatric lizard observed was *Hemidactylus flaviviridis* Rüppell on the roadside walls in Ilam market.

Cyrtodactylus nepalensis (Schleich & Kästle, 1998a)

(Figs 5 & 6; Tables 2 & 3)

Gonydactylus nepalensis Schleich & Kästle 1998a, p. 269; Shah 1998, p. 28; Shrestha 2001, p. 258.
Cyrtopodion nepalensis—Rösler 2000, p. 75; Schleich & Kästle 2002, p. 687.
Cyrtopodion nepalense—Shah & Tiwari 2004, p. 218.
S.[*iwaligekko*] *nepalensis*—Khan 2003, p. 3.
Cyrtodactylus nepalensis—Mahony *et al*. 2009, p. 245; Bhattarai *et al*. 2020, p. 28; Rai *et al*. 2022, p. 10.

Holotype (Fig. 5A, B). ZSM 854/2012 (originally SHHS 1998/33, VW D 94/14 (Fuhlrott-Museum Wuppertal), VW-D 94114, adult male (transferred to ZSM in 2012), from "Sakaye…close to Dipayal" [=Sakayal Village], Dadeldhura District, Sudurpaschim Province, Nepal, 29°18′37.6 N, 80°43′10.6 E, 745 m asl.; collected on 28th April 1994 by H.-H. Schleich and K.B. Shah.

Referred material (Fig. 6B, C). NHM 2023/360 (SB038), adult male, and NHM 2023/361 (SB039), adult female; both from Sakayal (29.3075°N, 80.7269°E; *ca.* 800 m asl.), Dadeldhura District, Sudurpaschim Province, Nepal; collected by Santosh Bhattarai on 27th July 2023.

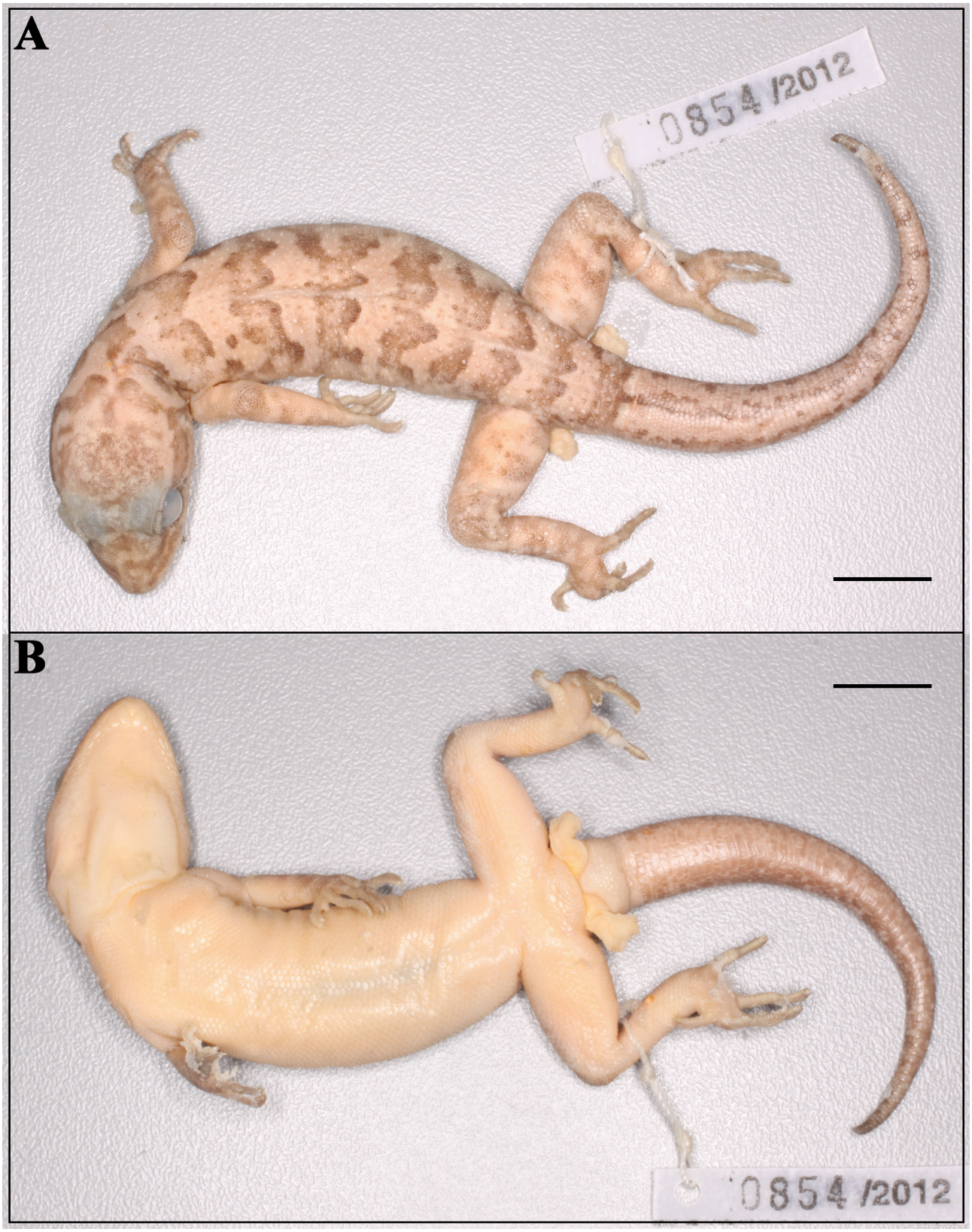

FIGURE 5. Holotype of *Cyrtodactylus nepalensis* (male, ZSM 0854/2012): (A) dorsal view and (B) ventral view. Scale bar 10 mm; photos by Frank Tillack.

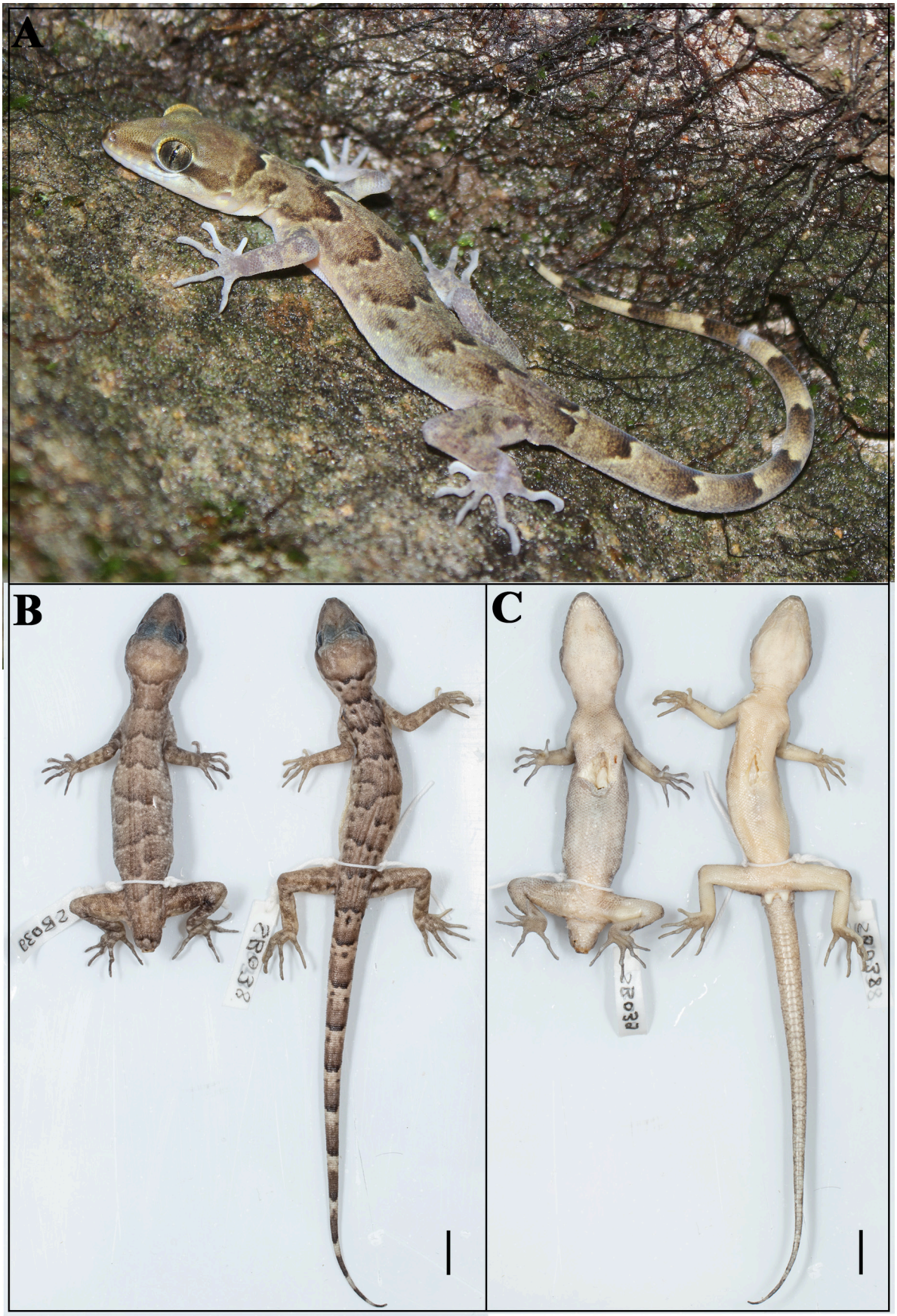

FIGURE 6. *Cyrtodactylus nepalensis*, (A) life photo in situ (uncollected specimen); and topotypes, from left to right, NHM 2023/360 and NHM 2023/361, in (B) dorsal view and (C) ventral view. Scale bar 10 mm; photos by Santosh Bhattarai (A) and Akshay Khandekar (B&C).

Etymology. Toponym for Nepal. .

Suggested common name. Nepal bent-toed gecko.

Diagnosis (Tables 2 & 3). A medium-sized *Cyrtodactylus*, snout to vent length up to 74.7 mm (*n*=3). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled, weakly pointed tubercles; a ventrolateral fold of skin present on lower flank; 17 rows of dorsal tubercles at midbody, 30–33 tubercles in paravertebral rows; Ventral scales subequal from chest to vent, smooth, subcircular, and subimbricate with rounded end; 30–33 scales across belly at midbody, 68–72 longitudinal ventral scales between axilla to groin, 150–163 longitudinal scales from mental to cloaca; subdigital scansors smooth, unnotched, entire; 13–17 lamellae under digit I of manus and 14–16 under digit I of pes, 19 or 20 lamellae under digit IV of manus and 21–25 lamellae under digit IV of pes; males with continuous series of 35–38 precloacal-femoral pores and 38 or 39 enlarged precloacal-femoral scales on pore bearing scale row (*n*=2); females without pores but having 13 pitted scales, 33 enlarged precloacal-femoral scales on pit bearing scale row (*n*=1); scales on non-regenerated tail dorsum homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base; subcaudal scalation of original tail with median series of enlarged plates; dorsal pattern of 6–8 irregular dark bands from neck to tail base and one on occiput, original tail with 11 alternating dark and lighter bands.

Genetic divergence. *C. nepalensis* is 14.3–27.0 % divergent from described members of the Indo-Burma clade and 6.9 % from its sister taxon *C*. sp. 1, with just 1.1 % intraspecific divergence. The species falls in the broader *fasciolatus* group within the Indo-Burma clade (Fig. 2).

Comparisons with regional congeners. *Cyrtodactylus nepalensis* can be differentiated from all regional congeners based on the following differing or non-overlapping characters: a continuous series of 35–38 precloacal-femoral pores in males (*versus* femoral pores absent in males of *C. cayuensis*, *C. chamba*, *C. himalayicus*, *C. kamengensis*, *C. lawderanus*, *C. martinstolli*; femoral pore series separated from precloacal pores in males in *C. gubernatoris* and *C. fasciolatus*); length of original tail > SVL (*versus* length of original tail < SVL in *C. lawderanus*); 17 rows of dorsal tubercles at midbody and 30–33 scales across belly at midbody (*versus* 24 or 25 DTR and 37 or 38 MVSR in *C. bhupathyi*, 13–15 DTR in *C. chamba*, 20 or 21 DTR in *C. gubernatoris*, 20–24 DTR in *C. kamengensis*, 19–21 DTR in *C. himalayicus,* 15 or 16 DTR and 40–45 MVSR in *C. siangensis*); median subcaudal series smooth, distinctly enlarged (*versus* median series of subcaudals not enlarged in *C. bhupathyi*, *C. cayuensis*, *C. chamba*, *C. gubernatoris C. himalayicus*, *C. kamengensis*, *C. martinstolli, C. siangensis*). *Cyrtodactylus nepalensis* is similar to *C. fasciolatus*, from which it can be distinguished by slightly smaller maximum SVL 74.7 mm (*versus* 84.3 mm), a continuous series of 35–38 precloacal-femoral pores in males (*versus* 13–16 femoral pores on each side separated by 1–7 scales (mean 3.7) from 10–12 precloacal pores; 41–43 total pores).

Colouration in life (Fig. 6A). Dorsal ground colour of head, body, limbs and tail brown; head dorsum uniform, with a dark band on the occiput posteriorly outlined by light cream; labials lighter than head dorsum and with some yellow streaks; a brown postorbital streak that extends to the ear opening and just meets occipital band; limbs mottled with grey and light tan spots; 10 or 11 dark and light caudal bands on complete original tail, dark and light bands subequal; rest of ventral surfaces immaculate; iris grey with dark reticulations, pupil black, bordered by much lighter and thin outline.

Distribution and natural history. *Cyrtodactylus nepalensis* is known only from its type locality in Sakayal, Dadeldhura District, Sudurpaschim Province, Nepal from elevations between 445–800 m asl. The habitat at the type locality is characterised by roadside walls and rocky habitats along the Sakayal stream. The holotype was collected at midnight at a village house and another specimen (not preserved) was observed at the Sakayal police station. We surveyed the type locality after dark till night (~1930–2330 hrs). *Cyrtodactylus nepalensis* is nocturnal and uncommon on the roadside walls but common on rocky habitats along the stream. Besides rocks, we also observed some individuals on a large *Ficus religiosa* tree *ca.* two meters above the ground. At collection sites, we observed less than ten individuals active during the late evening (1930–2300 hrs) about one or two meters above the ground on rocks and boulders along the stream. Sympatric lizards observed included *Hemidactylus flaviviridis* during the nocturnal survey and *Calotes versicolor* (Daudin) and *Eutropis carinata* (Schneider) during day light hours.

***Cyrtodactylus chitwanensis* sp. nov.**

http://www.zoobank.org/urn:lsid:zoobank.org:act:73C0B779-2BDA-474C-BBD2-BAED3839EFFA

(Figs 7–11; Tables 4 & 5)

Holotype. NHM 2023/376 (SB052), adult male, from Bandipur (27.9356°N, 84.4143°E; *ca.* 1050 m asl.), Tanahun District, Gandaki Province, Nepal; collected by Santosh Bhattarai 7th July 2024.

Paratypes. NHM 2023/362 (SB024) and NHM 2023/363 (SB025), adult females, from Kabilas (27.7879°N, 84.4999°E; *ca.* 980 m asl.), Chitwan District, Bagmati Province, Nepal; collected by Santosh Bhattarai 23rd September 2023; NHM 2023/364 (SB026), NHM 2023/365 (SB027), and NHM 2023/366 (SB028), adult females, same collection data as holotype except collected on 21st September 2023; NHM 2023/377 (SB053), adult male, and NHM 2023/378 (SB054), subadult male, same collection data as the holotype.

Etymology. The specific epithet is a toponym for the distributional range of the new species, which includes localities in Chitwan District and the Barandabhar Corridor Forest, a part of the Chitwan-Annapurna Landscape connecting to Chitwan National Park (CNP) in the south. CNP is the first protected area in Nepal and one of the major strongholds of the greater one-horned rhinoceros and gharial.

Suggested common name. Chitwan bent-toed gecko.

Diagnosis. A medium-sized *Cyrtodactylus*, snout to vent length up to 86.3 mm (*n*=8). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled, weakly pointed tubercles; a ventrolateral fold of skin present on lower flank; 18–20 (rarely 17, *n*=1/8) rows of dorsal tubercles at midbody, 31–36 tubercles in paravertebral rows; ventral scales subequal from chest to vent, smooth, subcircular, and subimbricate with rounded end; 40–43 scales across belly at midbody, 63–75 longitudinal ventral scales between axilla to groin, 156–183 longitudinal scales from mental to cloaca; subdigital scansors smooth, unnotched, entire; 15–18 lamellae under digit I of manus and 15–17 under digit I of pes, 18–20 lamellae under digit IV of manus and 23–26 (rarely 22, *n*=1/8) lamellae under digit IV of pes; males with continuous series of 28–32 precloacal-femoral pores and 32 or 33 enlarged precloacal-femoral scales on pore bearing scale row (*n*=3); females without pores but having 17–29 pitted scales, 30–33 enlarged precloacal-femoral scales on pit bearing scale row (*n*=3); scales on non-regenerated tail dorsum homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base; subcaudal scalation of original tail with median series of smooth, slightly enlarged plates of which a few are divided on anterior half of tail; dorsal pattern of seven or eight paired blotches or irregular dark bands from neck to tail base and one on occiput, original tail with 9–11 alternating dark and lighter bands.

Genetic divergence. *Cyrtodactylus chitwanensis* **sp. nov.** is 21.1–29.5 % divergent from described members of the Indo-Burma clade and 15.8–16.6 % from the two new species from Central Nepal that it forms the sister taxon to, with only 0.3 % intraspecific divergence (Table S1). The species forms the poorly supported sister taxon to the *fasciolatus* group within the Indo-Burma clade (Fig. 2).

Comparisons with regional congeners. *Cyrtodactylus chitwanensis* **sp. nov.** can be differentiated from all regional congeners based on the following differing or non-overlapping characters: males with continuous series of 28–32 precloacal-femoral (*versus* femoral pores absent in males of *C. cayuensis*, *C. chamba*, *C. himalayicus*, *C. kamengensis*, *C. lawderanus*, *C. martinstolli*; continuous series of 35–38 femoral pores in *C. nepalensis* and a discontinuous series of 13–16 femoral pores on each side separated by 1–7 scales (mean 3.7) from 10–12 precloacal pores; 41–43 total pores in *C. fasciolatus*); length of original tail > SVL (*versus* length of original tail < SVL in *C. lawderanus*); median subcaudal series smooth, distinctly enlarged (*versus* median series of subcaudals not enlarged in *C. bhupathyi*, *C. cayuensis*, *C. chamba*, *C. gubernatoris*, *C. himalayicus*, *C. siangensis*). Moderately large body size SVL up to 86.3 mm (*versus* SVL < 75 mm in *C. bhupathyi, C. chamba, C. gubernatoris, C. lawderanus, C. himalayicus, C. nepalensis, C. siangensis*); 40–43 scales across belly at midbody (*versus* ≤ 38 MVSR in *C. bhupathyi, C. fasciolatus, C. gubernatoris, C. himalayicus, C. kamengensis, C. nepalensis*).

Cyrtodactylus chitwanensis **sp. nov.** shares a large series of precloacal-femoral pores and median enlarged subcaudals with *C. fasciolatus* and *C. nepalensis* but may be distinguished by its body size and MVSR (maximum SVL 86.3 mm and 40–43 MVSR *versus* maximum SVL 74.7 mm and 30–33 MVSR in *C. nepalensis* and 32–36 MVSR in *C. fasciolatus*).

Description of the holotype. Adult male in good state of preservation except tail tip curved towards left, a 4.3 mm long incision in sternal region for tissue collection, and fifth finger on right manus is damaged (Fig. 7A–D).

SVL 72.8 mm, head short (HL/SVL 0.25), wide (HW/HL 0.73), not strongly depressed (HD/HL 0.44), distinct from neck. Loreal region inflated, canthus rostralis indistinct. Snout half of head length (ES/HL 0.43), two times eye diameter (ES/ED 2.03); scales on snout and canthus rostralis circular, subequal, smooth, protrudent, larger than those on forehead and interorbital region; scales on forehead similar to those on snout and canthus rostralis except slightly smaller; scales on interorbital, occipital, and temporal regions heterogeneous, composed of granular scales intermixed with enlarged, feebly keeled, rounded tubercles (Fig. 8A). Eye small (ED/HL 0.21), with vertical pupil having crenulated margins; supraciliaries short, larger anteriorly; 19 interorbital scale rows across narrowest point of frontal; 53 scale rows between left and right supraciliaries at mid-orbit (Fig. 8A, C). Ear-opening small, oval, deep (EL/HL 0.10); eye to ear distance much greater than diameter of eye (EE/ED 1.44) (Fig. 8C). Rostral almost two times wider (3.0 mm) than high (1.7 mm), incompletely divided dorsally by a strongly developed rostral groove for almost half of its height; a single enlarged, roughly rectangular supranasal on each side, more than four or five times the size of upper postnasal, separated from each other behind rostral by two much smaller internasal scales; rostral in contact with supralabial I, nostril and supranasal, and a single internasal on either side; nostrils oval, surrounded by two postnasals, supranasal, rostral, and supralabial I on either side; two subequal postnasals on either side; one or two rows of scales separate orbit from supralabials (Fig. 8C). Mental enlarged, subtriangular, two times wider (3.0 mm) than high (1.5 mm); two pairs of postmentals, inner pair roughly rectangular, much longer (2.2 mm) than mental, in strong contact with each other below mental (1.3 mm); inner pair bordered by mental, infralabial I, outer postmental either side and additionally by five slightly enlarged chin shields; outer postmentals roughly rectangular, much smaller (1.2 mm) than inner pair, bordered by inner postmentals, infralabial I & II, and four chin shields on either side; all chin shields bordering postmentals somewhat protrudent, subequal, subcircular, smooth, and much smaller than outermost postmentals; scales on rest of throat, granular, much smaller, smooth, and subcircular (Fig. 8B). Infralabials bordered below by a row or two of slightly enlarged, much elongated scales, decreasing in size posteriorly. Thirteen supralabials to angle of jaw and 10 at midorbital position on either side; supralabial I largest, gradually decreasing in size posteriorly; 10 infralabials to angle of jaw and six at midorbital position on either side; infralabial I largest, gradually decreasing in size posteriorly (Fig. 8C).

Body relatively slender (BW/AGL 0.42), trunk just less than half of SVL (AGL/SVL 0.45) with ventrolateral fold of skin on lower flank (Fig. 9A–C). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled, weakly pointed tubercles; granular scales gradually increasing in size towards each flank, largest on mid-flank; granular scales on occiput slightly smaller than paravertebral granular scales; enlarged tubercles in approximately 20 longitudinal rows at midbody; 34 tubercles in left paravertebral row and 33 on right (Fig. 9A). Ventral scales much larger than granular scales on dorsum, subequal from chest to vent, and smooth, subcircular and subimbricate with rounded end; scales on precloacal region and pore bearing femoral scale row distinctly enlarged; midbody scale rows across belly 42; 161 scales from mental to anterior border of cloaca and 65 scales between limb insertions (Fig. 9B). A continuous series of 32 precloacal-femoral pores (Fig. 8D).

Scales on palm and soles, smooth, heterogeneous in size and shape, and somewhat protrudent; scales on dorsal aspects of limbs heterogenous; upper arm with slightly smaller scales than body ventrals, smooth and subimbricate; scales on lower arm composed of slightly smaller, smooth, granular scales intermixed with enlarged, smooth, rounded, weakly pointed tubercles; thigh and shank with slightly smaller, weakly keeled, granular scales intermixed with enlarged, smooth, rounded, weakly pointed tubercles which are slightly larger on thigh and shank; scales on ventral aspect of upper arm smooth, granular, slightly smaller than granular scales on body dorsum, scales on ventral aspect of lower arm much larger than those on upper arm, smooth, subcircular, weakly conical to flattened, and subimbricate; ventral aspect of thigh and shank with enlarged, smooth, subcircular, flattened, subimbricate scales, those in precloacal-femoral row much larger than the rest (Fig. 7A, B). Forelimbs and hindlimbs slightly long, slender (LAL/ SVL 0.14; CL/SVL 0.18); digits long, with a strong, recurved claw, distinctly inflected, distal portions laterally compressed conspicuously. Digits with unpaired lamellae, separated into a basal and narrower distal series by a single, much enlarged lamella at inflection; basal lamellae series: (5-5-7-6-7 right manus, 5-6-8-10-6 right pes), (5-5-6-5-7 left manus, Fig. 8E; 5-7-8-10-6 left pes, Fig. 8F); distal lamellae series: (11-11-13-13-12 right manus, 10-12-13-14-14 right pes), (11-11-13-13-12 left manus, Fig. 8E; 10-11-13-14-14 left pes, Fig. 8F). Relative length of digits (measurements in mm in parentheses): IV (7.7) > III (7.6) > II (7.0) > V (6.5) > I (4.7) (left manus); IV (9.2) > V (8.5) = III (8.4) > II (7.4) > I (4.8) (left pes).

Tail original, subcylindrical, slender, entire, slightly longer than body (TL/SVL 1.13) (Fig. 7C, D). Dorsal pholidosis on tail homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and

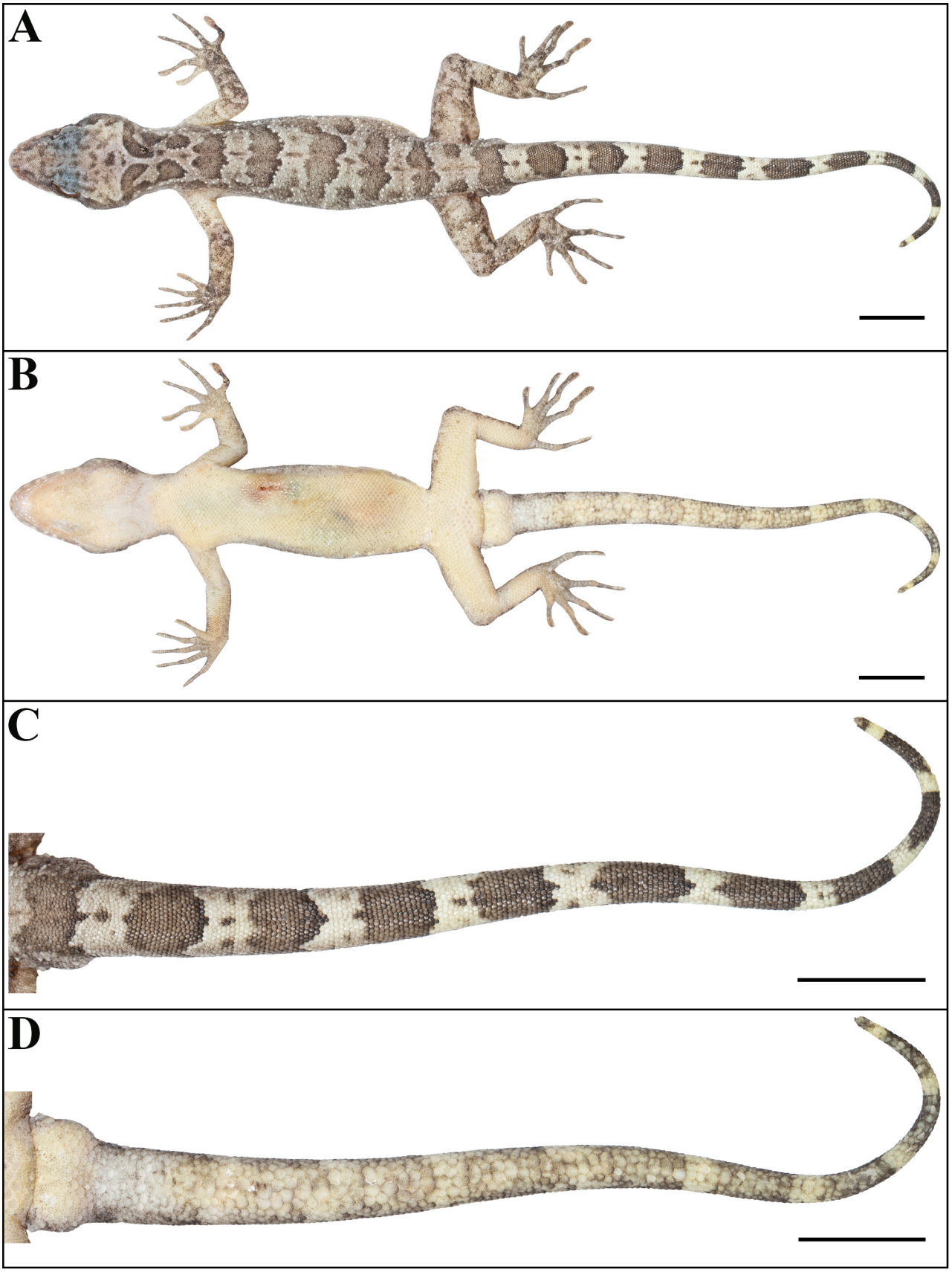

FIGURE 7. Holotype of *Cyrtodactylus chitwanensis* **sp. nov.** (male, NHM 2023/376): (A) dorsal view of body, (B) ventral view of body, (C) dorsal view of tail, and (D) ventral view of tail. Scale bars 10 mm; photos by Akshay Khandekar.

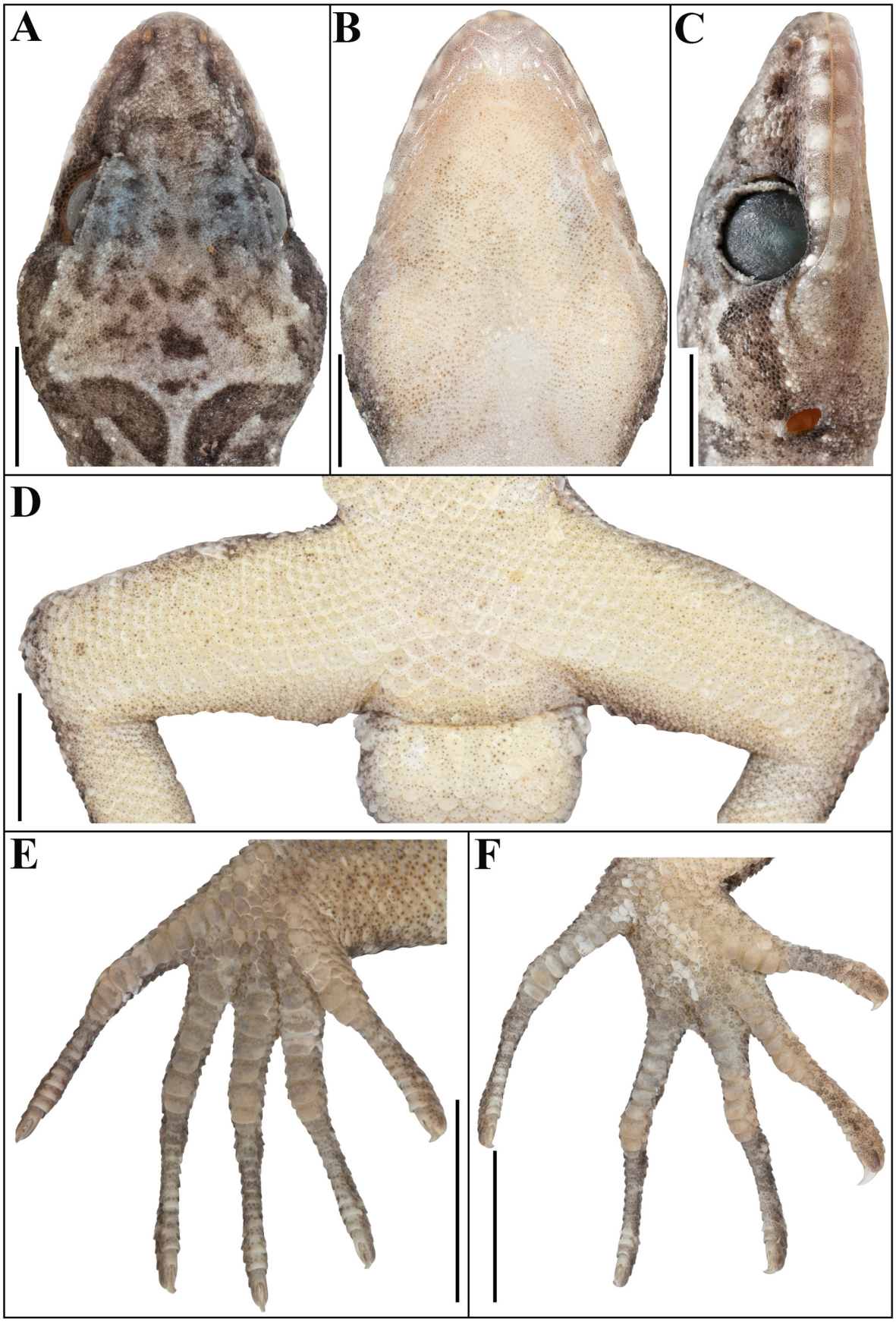

FIGURE 8. Holotype of *Cyrtodactylus chitwanensis* **sp. nov.** (male, NHM 2023/376): (A) dorsal view of head, (B) ventral view of head, (C) lateral view of head on right, (D) view of femoral region showing continuous series of precloacal-femoral pores, (E) ventral view of left manus, and (F) ventral view of left pes. Scale bars 5 mm; photos by Akshay Khandekar.

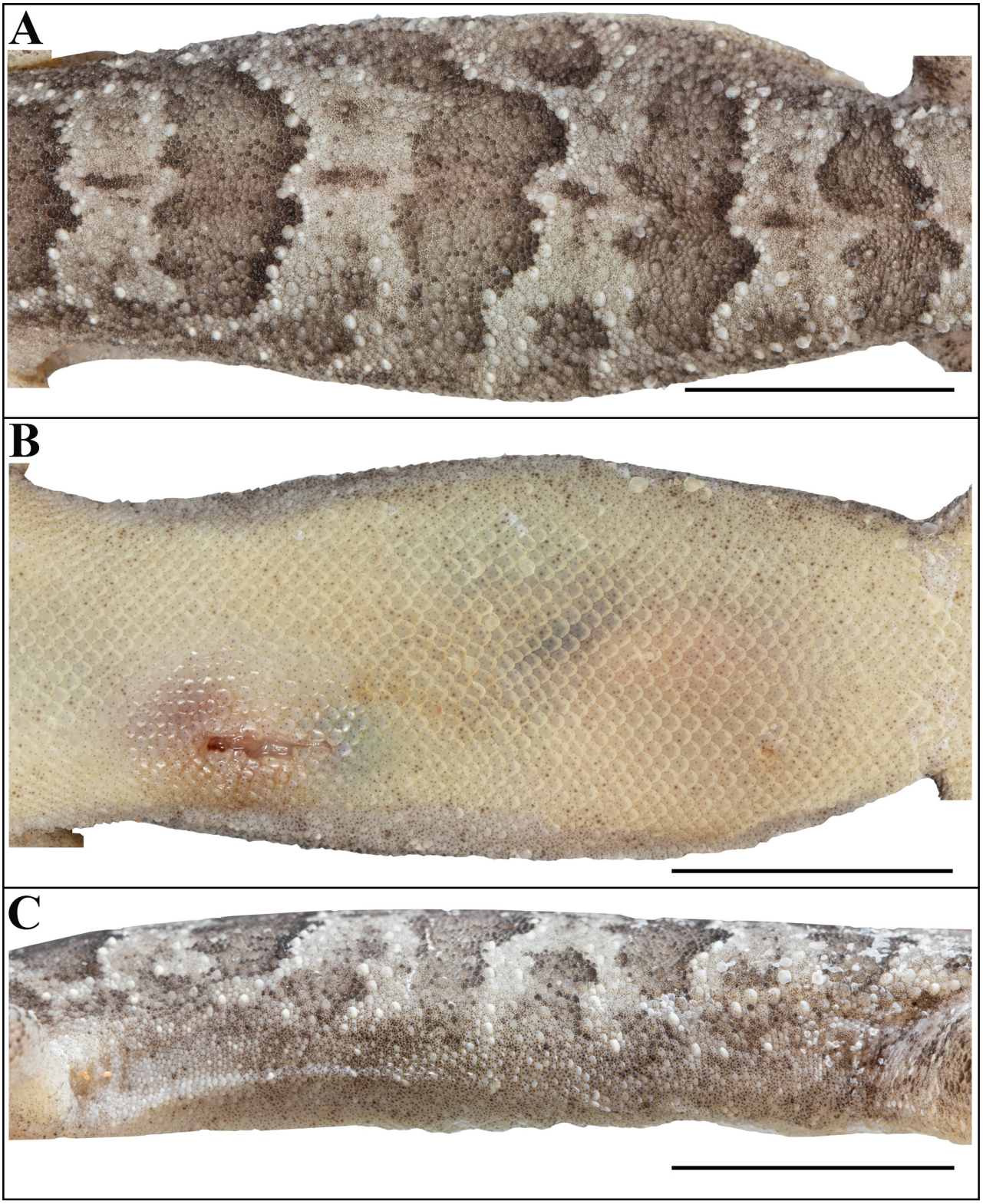

FIGURE 9. Holotype of *Cyrtodactylus chitwanensis* **sp. nov.** (male, NHM 2023/376): (A) dorsal view of midbody, (B) ventral view of midbody, and (C) lateral view of midbody on right. Scale bars 10 mm; photos by Akshay Khandekar.

subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base (Fig. 7C). Scales on tail venter much larger than those on dorsal aspect, smooth, flattened, subimbricate; median series smooth, slightly enlarged scales, of

which a few are divided on anterior half of the tail (Fig. 7D). Scales on tail base much smaller, smooth, subimbricate; distinct hemipenial bulge present; three subequal and smooth postcloacal tubercles on either side (Fig. 8D).

Colouration in life (Fig. 10A). Dorsal ground colour of head, body, limbs and tail yellow-brown; head dorsum with small dark brown spots, a pair of brown C-shaped markings on the occiput, a brown pre-orbital streak and a more prominent post-orbital streak that extends to the ear opening and just meets occipital markings on either side; labials with some yellow streaks; eight irregular dark brown bands edged by a fine black border posteriorly between neck and tail base, first and seventh formed by paired blotches; a row of small spots on the mid-vertebral line alternating with dark bands; dorsal bands broken on flanks interspersed with other dark mottling; limbs with dark brown and grey reticulations; 10 dark and light caudal bands on complete original tail; underside of tail with mottling/ indistinct dark and light bands, rest of ventral surfaces immaculate; iris green-grey with dark reticulations, pupil black.

Variation and additional information from the paratype series (Figs 10B, C; 11). Mensural, meristic and additional character state data for the type series is given in Tables 4 & 5 respectively. There are five adult females, and a single adult and subadult male ranging in size from 52.4–86.6 mm (Fig. 11A, B). All paratypes resemble the holotype except as follows: three paratypes—NHM 2023/362, NHM 2023/364 and NHM 2023/366 with three internasals, and NHM 2023/365 and NHM 2023/378 with single internasal. Inner postmentals bordered by mental, infralabial I, and outer postmental in all paratypes; additionally, bordered by six smaller chin shields in NHM 2023/362, NHM 2023/364 and NHM 2023/377. Outer postmentals bordered by inner pair and infralabial I & II in all paratypes; additionally, bordered by four smaller chin shields on left and five on right side in NHM 2023/362. Five paratypes—NHM 2023/362, NHM 2023/363, NHM 2023/364, NHM 2023/365, and NHM 2023/378 with original and complete tail, slightly longer than SVL (TL/SVL 1.23, 1.14, 1.26, 1.26 and 1.13 respectively); remaining two paratypes, NHM 2023/366 and NHM 2023/377 with complete but almost fully regenerated tail, marginally shorter than body (TL/SVL 0.93 and 0.90 respectively) (Fig. 11A). Original tail distinctly banded with 9–11 alternating dark and lighter bands; regenerated tail light brown with darker brown spots in NHM 2023/366 and NHM 2023/377 (Figs 10C, D; 11A, B).

TABLE 4. Mensural (mm) data for *Cyrtodactylus chitwanensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: M = male, F = female, and SA = subadult male.

Type	Holotype	Paratypes						
Specimen Number	NHM 2023/376	NHM 2023/362	NHM 2023/363	NHM 2023/364	NHM 2023/365	NHM 2023/366	NHM 2023/377	NHM 2023/378
Sex	M	F	F	F	F	F	M	SA M
SVL	72.8	65.4	80.2	60.7	81.2	86.3	73.3	52.4
TL	82.3	80.6	91.6	76.4	102.3	80.1	66.3	59.3
TW	8.1	5.5	6.8	5.8	7.1	8.0	7.8	4.3
LAL	10.3	9.6	11.9	9.0	11.9	13.0	10.8	7.4
CL	13.1	11.6	14.3	10.8	14.3	15.1	12.6	8.6
AGL	32.9	29.3	37.1	26.9	35.6	37.9	33.8	24.0
BH	7.8	6.1	8.1	5.3	7.8	7.7	7.0	4.9
BW	13.7	11.7	15.8	10.6	15.9	15.9	12.6	9.6
HL	18.2	16.7	19.6	16.1	21.5	21.9	18.3	12.9
HW	13.2	12.7	15.1	11.8	15.3	15.8	13.7	10.0
HD	8.0	6.9	8.7	6.9	8.4	9.5	7.9	5.9
ED	3.9	4.4	4.4	3.9	4.5	4.9	4.2	3.2
EE	5.6	5.4	6.6	5.1	6.8	7.0	5.5	4.3
ES	7.9	7.5	9.0	7.2	9.4	9.5	8.7	5.7
EN	5.9	5.7	6.3	5.3	7.0	7.1	6.6	4.2
IN	2.2	1.9	2.5	2.0	2.4	2.6	2.4	1.6
IO	3.5	3.8	4.3	3.5	4.5	5.2	3.6	2.3
EL	1.9	1.6	2.0	0.9	1.5	1.7	1.5	1.1

TABLE 5. Meristic data for *Cyrtodactylus chitwanensis* **sp. nov.**. The values in parentheses are the number of pitted scales in females. Abbreviations are listed in Materials and Methods except for: M = male, F = female, SA = subadult, L&R = left & right, P/A = present/absent, * = incomplete count, / = data unavailable; numbers in parentheses for FS indicates number of pitted scales in females.

Type	Holotype	Paratypes						
Specimen Number	NHM 2023/376	NHM 2023/362	NHM 2023/363	NHM 2023/364	NHM 2023/365	NHM 2023/366	NHM 2023/377	NHM 2023/378
Sex	M	F	F	F	F	F	M	SA M
INS	2	3	0	3	1	3	2	1
SL L&R	13&13	11&10	12&12	11&12	12&12	12&11	12&12	11&11
IL L&R	10&10	9&9	11&11	10&10	10&10	10&11	10&10	9&10
SL M L&R	10&10	8&8	8&8	8&9	8&9	8&8	9&9	9&9
IL M L&R	6&6	6&7	7&6	6&6	7&8	6&7	7&7	7&7
PVT L&R	34&33	31&33	36&36	35&33	32&32	32&34	33&35	34&32
DTR	20	17	19	18	18	19	19	20
MVSR	42	40	43	41	41	40	40	40
VS1	65	75	74	73	70	75	64	63
VS2	161	182	183	168	177	172	158	156
DLAMF1 L&R	11&11	10&10	11&11	10&10	11&11	11&11	11&11	11&11
BLAMF1 L&R	5&5	7&7	6&6	5&5	7&7	5&5	5&5	5&5
DLAMF4 L&R	13&13	13&13	13&14	12&13	14&13	14&13	14&14	14&14
BLAMF4 L&R	5&6	7&7	7&6	6&6	5&5	6&6	6&6	6&6
DLAMT1 L&R	10&10	11&11	10&11	10&10	11&11	11&11	11&10	10&10
BLAMT1 L&R	5&5	5&5	5&5	5&5	5&5	6&5	5&5	5&5
DLAMT4 L&R	14&14	15&14	15&15	13&14	14&14	15&15	14&14	15&15
BLAMT4 L&R	10&10	9&9	9&11	9&8	9&10	9&9	10&10	9&9
DLAMT5 L&R	14&14	15&14	15&15	15&14	15&15	14&14	15&14	14&15
BLAMT5 L&R	6&6	6&6	8&8	7&7	7&7	7&7	6&6	7&6
TLAMF1 L&R	16&16	17&17	17&17	15&15	18&18	16&16	16&16	16&16
TLAMF4 L&R	18&19	20&20	20&20	18&19	19&18	20&19	20&20	20&20
TLAMT1 L&R	15&15	16&16	15&15	15&15	16&16	17&16	16&15	15&15
TLAMT4 L&R	24&24	24&23	24&26	22&22	23&24	24&24	24&24	24&24
TLAMT5 L&R	20&20	21&20	23&23	22&21	22&22	21&21	21&20	21&21
FS	33	30	33 (17)	30	32 (27)	31 (29)	33	32
P-F	32	A	A	A	A	A	31	28*
PCS	A	A	A	A	A	A	A	A
PP	A	A	A	A	A	A	A	A
PCT L&R	3&3	2&2	2&4	2&2	3&3	2&3	3&3	3&3
Caudal tubercles P/A	A	A	A	A	A	/	/	A
Subcaudals enlarged or not	Slightly enlarged with a few divided scales	Slightly enlarged with a few divided scales	Slightly enlarged with a few divided scales	Slightly enlarged with a few divided scales	Slightly enlarged with a few divided scales	/	/	Slightly enlarged with a few divided scales

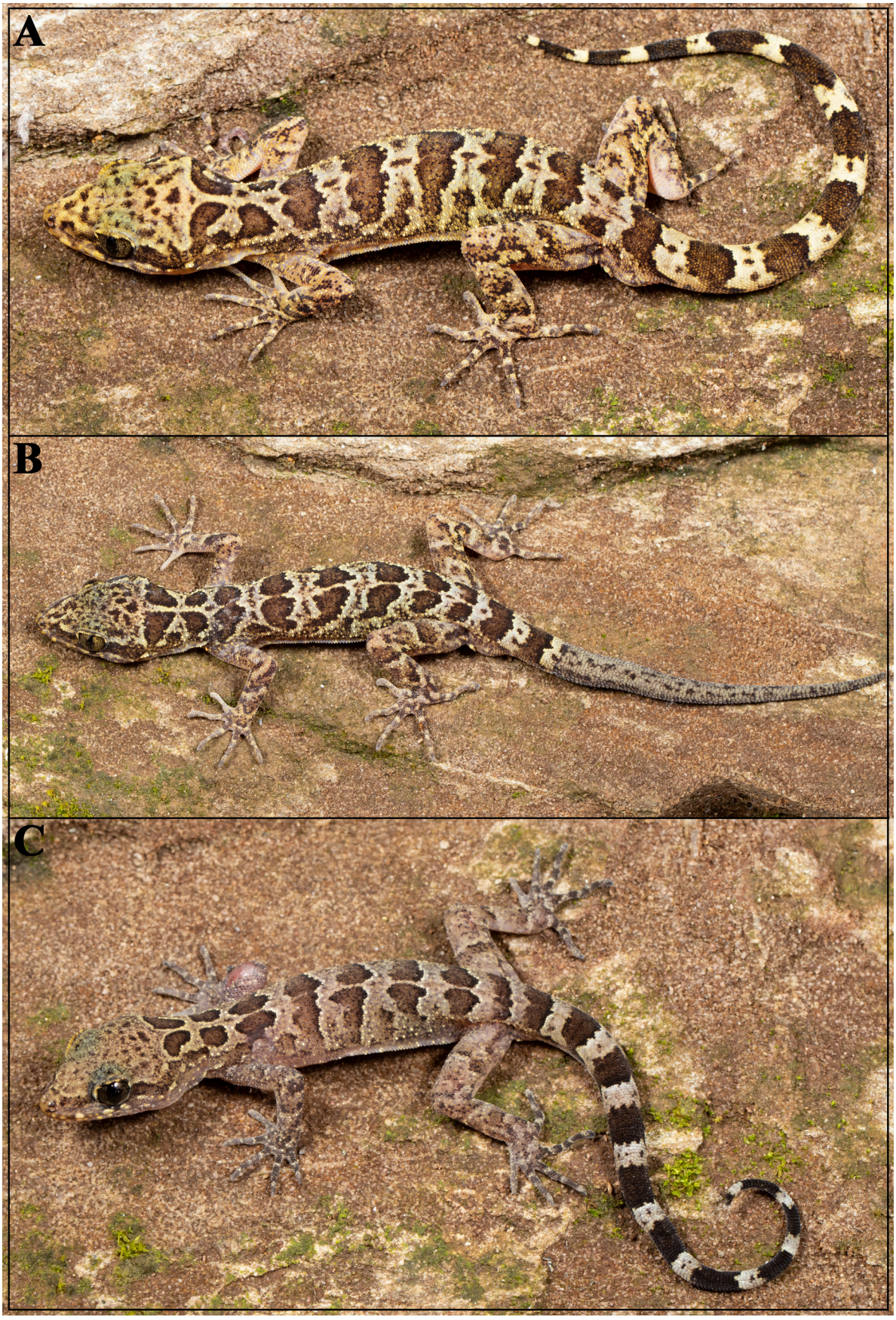

FIGURE 10. *Cyrtodactylus chitwanensis* **sp. nov.**, in life: (A) holotype (adult male, NHM 2023/376), (B) paratype (adult male, NHM 2023/377), and (C) paratype (subadult male, NHM 2023/378). Photos by Akshay Khandekar.

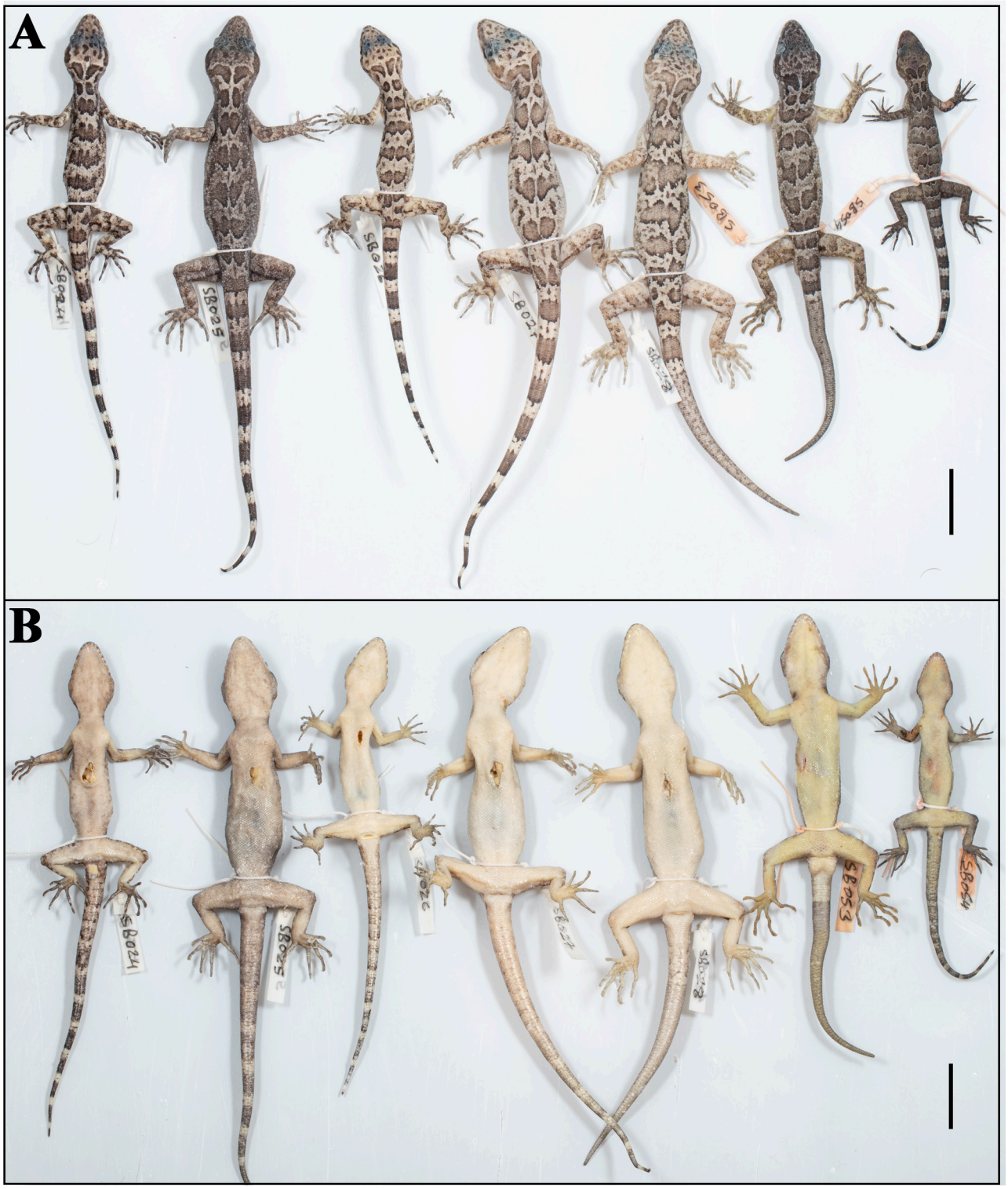

FIGURE 11. The paratype series of *Cyrtodactylus chitwanensis* **sp. nov.**, from left to right, NHM 2023/362–366, NHM 2023/377, and NHM 2023/378: (A) dorsal view, and (B) ventral view. Scale bars 20 mm; photos by Akshay Khandekar.

Distribution and natural history (Fig. 12A, B). Individuals were found on rocks and in caves after dark, about 1–3 m above ground. The habitat in Chitwan used to be a regular-use trail from Kabilas to Jugedi. The construction of motorable roads to Kabilas from northern side of the hill has made this trail less disturbed. We observed more than 10 individuals in a cave and on a rock during the survey between 19:30 and 22:30 in Chitwan. We also observed *Eutropis carinata*, *Calotes versicolor* and *Laudakia tuberculata* (Gray) in the same habitat during daytime. The

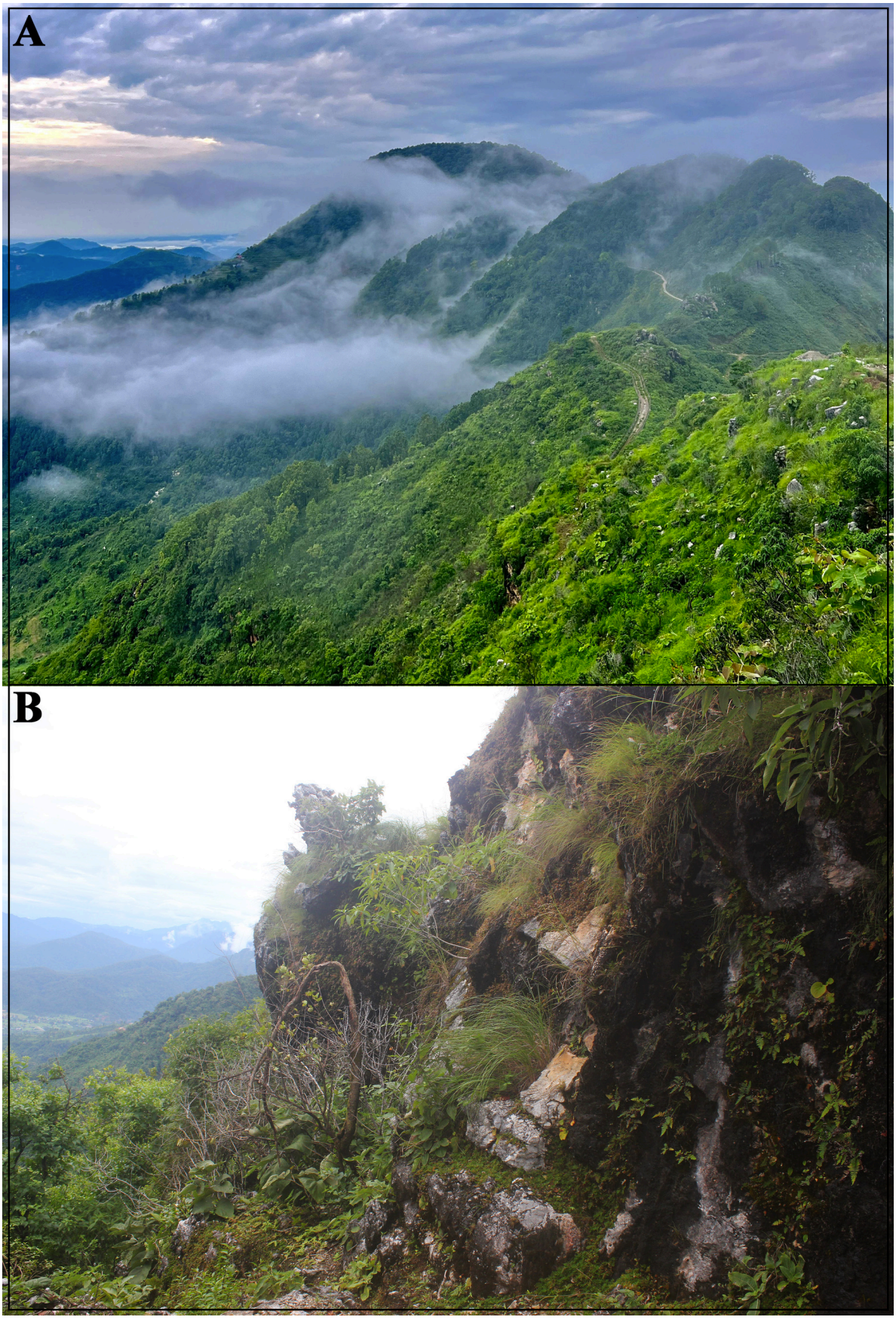

FIGURE 12. Habitat of *Cyrtodactylus chitwanensis* **sp. nov.**: (A) general view of the hilly forest at the type locality, Bandipur, Tanahun District, Gandaki Province; and (B) microhabitat at the paratype locality Kabilas, Chitwan District, Bagmati Province, from where individuals of the new species were collected. Photos by (A) Akshay Khandekar and (B) Santosh Bhattarai.

habitat at Bandipur is rocks and boulders and stone walls at the base along the trail from Bandipur towards to the hilltop at Thanimai temple. Individuals were observed on the rocks of the trails *ca.* 1.5–3 m high. The trail is used by local people and visitors during the daytime; therefore, some sheds have been constructed rest stops for those hiking to the hilltop. We observed *Hemidactylus frenatus* Duméril & Bibron on the sheds and walls of the temple.

Cyrtodactylus annapurnaensis sp. nov.

http://www.zoobank.org/urn:lsid:zoobank.org:act:AB1250AC-B9A1-4929-902D-AD4153FA0074
(Figs 13–18; Tables 6 & 7)

Cyrtopodion martinstollii [non *Gonydactylus martinstollii* Darevsky, Helfenberger, Orlov & Shah, 1998]—Schleich & Kästle 2002, p. 416, fig. 195 [depicts ZMB 57898, paratype of *C. annapurnaensis* sp. nov. from Birethanti].
Cyrtodactylus sp.—Tillack & Grossmann 2001, p. 4, (refer to Naudanda population of *C. annapurnaensis* sp. nov.).
Cyrtodactylus (*Cyrtopodion*?) spec.—Schleich & Kästle 2002, p. 1058 (refer to Naudanda population of *C. annapurnaensis* sp. nov.).

Holotype. NHM 2023/367 (SB029), adult male, from Lwang (28.3295°N, 83.8728°E; *ca.* 1450 m asl.), Kaski District, Gandaki Province, Nepal; collected by Santosh Bhattarai on 15th September 2023.

Paratypes. NHM 2023/368 (SB030) and NHM 2023/369 (SB031), adult females, NHM 2023/370 (SB032) adult male, same collection data as the holotype. ZMB 57898, adult male, from Birethanti (28.310833°N, 83.773056°E; *ca.* 1050 m asl.), Kaski District, Gandaki Province, Nepal, collected by F. Tillack, M. Lorenz, and W. Eckert on 10th July 1997; ZMB 61691 (field no. 6670), adult male, from 1 km east of Naudanda (28.135833°N, 83.8625°E; *ca.* 1450 m asl.), Kaski District, Gandaki Province, Nepal, collected by F. Tillack and W. Eckert on 12th July 1998; ZMB 61692–61694 (field nos. 6671–6673) adult females, from the eastern outskirts of Naudanda (28.283333°N, 83.870277°E, *ca.* 1430 m asl.), Kaski District, Gandaki Province, Nepal, collected by F. Tillack and W. Eckert from 13–19th July 1998.

Referred material. ZMB 61695 (field no. 6674), juvenile, from the eastern outskirts of Naudanda (28.283333°N, 83.870277°E, *ca.* 1430 m asl.), Kaski District, Gandaki Province, Nepal, collected by F. Tillack, W. Großmann, and P. Tillack on 13th July 1999.

Etymology. The specific epithet is a toponym for the Annapurna Range and the Annapurna Conservation Area Project (ACAP), within which the type locality falls. The Annapurna Conservation Area is the largest undertaking of the National Trust for Nature Conservation (NTNC) and the largest Protected Area in Nepal; initiated community conservation since 1986; prior to establishment as a Conservation Area in 1992. Since 1986, NTNC is managing the ACAP with a modality to allow people live inside the Conservation Area and own their private property; and promote sustained natural resources conservation.

Suggested common name. ACAP bent-toed gecko.

Diagnosis. A moderately small-sized *Cyrtodactylus*, snout to vent length up to 63.9 mm (*n*=9). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled to smooth, weakly pointed tubercles; a ventrolateral fold of skin present on lower flank; 18–20 (rarely 21, *n*=1/9) rows of dorsal tubercles at midbody, 28–35 tubercles in paravertebral rows; ventral scales subequal from chest to vent, smooth, subcircular, and subimbricate with rounded end; 32–35 scales across belly at midbody, 84–91 longitudinal scales between axilla to groin, 179–195 longitudinal scales from mental to cloaca; subdigital scansors smooth, unnotched, and mostly entire; 11–13 lamellae under digit I of manus and 11–14 under digit I of pes, 16–18 lamellae under digit IV of manus and 17–23 lamellae under digit IV of pes; males with continuous series of three or four precloacal pores and 8–10 enlarged precloacal scales on pore bearing scale row (*n*=4); female without pores but having three pitted scales, and nine or 10 enlarged precloacal scales on pit bearing scale row (*n*=5); scales on non-regenerated tail dorsum homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base; subcaudal scales in median series smooth, variable in size and shape, and not enlarged; variegated dorsal pattern, original tail with 9–11 alternating dark and lighter bands.

Genetic divergence. *C. annapurnaensis* **sp. nov.** is 11.7–27.8 % divergent from described members of the Indo-Burma clade, with 1.0 % intraspecific divergence (Table S1). The species falls in the mountain subclade of the *khasiensis* group within the Indo-Burma clade (Fig. 2).

Comparisons with regional congeners. *Cyrtodactylus annapurnaensis* **sp. nov.** can be differentiated from all regional congeners based on the following differing or non-overlapping characters: no femoral pores and three or four precloacal pores in males (*versus* femoral pores present in *C. chitwanensis* **sp. nov.**, *C. fasciolatus*, *C. gubernatoris*, and *C. nepalensis*; 6–9 pores in *C. cayuensis*, five pores in *C. chamba*, 10 in *C. himalayicus,* 7–11 in *C. kamengensis*, 4–9 in *C. lawderanus*, eight in *C. martinstolli*); length of original tail > SVL (*versus* length of original tail < SVL in *C. lawderanus*); median row of subcaudals not enlarged (*versus* median row of subcaudals enlarged in *C. chitwanensis* **sp. nov.**, *C. fasciolatus*, and *C. nepalensis*); 18–20 (rarely 21, *n*=1/9) rows of dorsal tubercles at midbody and 32–35 scales across belly at midbody (*versus* 24 or 25 DTR and 37 or 38 MVSR in *C. bhupathyi*, 13–15 DTR in *C. chamba*, 17 DTR in *C. nepalensis*, 15 or 16 DTR and 40–45 MVSR in *C. siangensis*); and moderate body size with maximum SVL up to 63.9 mm (*versus* maximum SVL > 70 mm in *C. cayuensis, C. chitwanensis* **sp. nov.***, C. fasciolatus, C. gubernatoris, C. kamengensis, C. siangensis, C. martinstolli,* and *C. nepalensis*).

Description of the holotype. Adult male in good state of preservation except tail detached from the body, a 7.6 mm long incision in sternal region for tissue collection, a small skin injury (0.9 mm) near precloacal pores and on ventral side of shank (3.1 mm) on right side (Fig. 13A–D). SVL 63.7 mm, head short (HL/SVL 0.25), wide (HW/HL 0.69), not strongly depressed (HD/HL 0.46), distinct from neck. Loreal region inflated, canthus rostralis indistinct. Snout half of head length (ES/HL 0.43), almost two times eye diameter (ES/ED 1.84); scales on snout and canthus rostralis smooth, oval, subequal, flattened, much larger than those on forehead and interorbital region; scales on forehead similar to those on snout and canthus rostralis except slightly smaller; scales on interorbital region even smaller, granular and smooth; scales on occiput and temporal region heterogeneous, composed of granular scales intermixed with enlarged, feebly keeled to smooth, rounded tubercles (Fig. 14A). Eye small (ED/HL 0.23), with vertical pupil having crenulated margins; supraciliaries short, larger anteriorly; 17 interorbital scale rows across narrowest point of frontal; 43 scale rows between left and right supraciliaries at mid-orbit (Fig. 14A, C). Ear-opening deep, oval, small (EL/ HL 0.06); eye to ear distance much greater than diameter of eye (EE/ED 1.24) (Fig. 14C). Rostral almost two times wider (2.8 mm) than high (1.7 mm), incompletely divided dorsally by a strongly developed rostral groove for almost than half of its height; a single enlarged, roughly rectangular supranasal on each side, more than five or six times than upper postnasal, separated by each other behind rostral by three much smaller internasal scales; rostral in contact with supralabial I, nostril and supranasal, and single internasal on either side; nostrils oval, surrounded by five postnasals, supranasal, rostral, and supralabial I on either side; five postnasals on either side, upper postnasal roughly circular, much larger than others; other postnasals roughly circular, similar size to each other; two rows of scales separate orbit from supralabials (Fig. 14C). Mental enlarged, subtriangular, wider (2.3 mm) than high (1.7 mm); two pairs of postmentals, inner pair rectangular, similar in length (1.7 mm) to mental, in strong contact with each other below mental (1.0 mm); inner pair bordered by mental, infralabial I, outer postmental on either side and additionally by four slightly enlarged chin shields on left and five on right side; outer postmentals roughly rectangular, much smaller (0.6 mm) than inner pair, bordered by inner postmentals, infralabial I & II, and three chin shields on either side, eight enlarged gular scales between left and right outer postmentals; all chin shields bordering postmentals somewhat protrudent, subequal, subcircular, smooth, and much smaller than outermost postmentals; scales on rest of throat, granular, much smaller, smooth, and subcircular (Fig. 14B). Infralabials bordered below by a row or two of slightly enlarged, much elongated scales, decreasing in size posteriorly. Eleven supralabials up to angle of jaw and eight at midorbital position on left and seven on right side; supralabial I largest, gradually decreasing in size posteriorly; 10 infralabials up to angle of jaw on either side, and seven at midorbital position on either side; infralabial I largest, gradually decreasing in size posteriorly (Fig. 14C).

Body relatively slender (BW/AGL 0.40), trunk marginally less than half of SVL (AGL/SVL 0.44) with ventrolateral fold of skin on lower flank (Fig. 15A–C). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled to smooth, weakly pointed tubercles; granular scales gradually increasing in size towards each flank, largest on mid-flank; granular scales on occiput slightly smaller than paravertebral granules; enlarged tubercles in approximately 20 longitudinal rows at midbody; 28 tubercles in paravertebral row on left side and 30 on right side (Fig. 15A). Ventral scales much larger than granular scales on dorsum, subequal from chest to vent, smooth, subcircular and subimbricate with rounded end; scales on precloacal region distinctly enlarged; midbody scale rows across belly 35; 186 scales from mental to anterior border of cloaca and 86 scales between limb insertions (Fig. 15B). A continuous series of four precloacal pores, femoral pores absent (Fig. 14D).

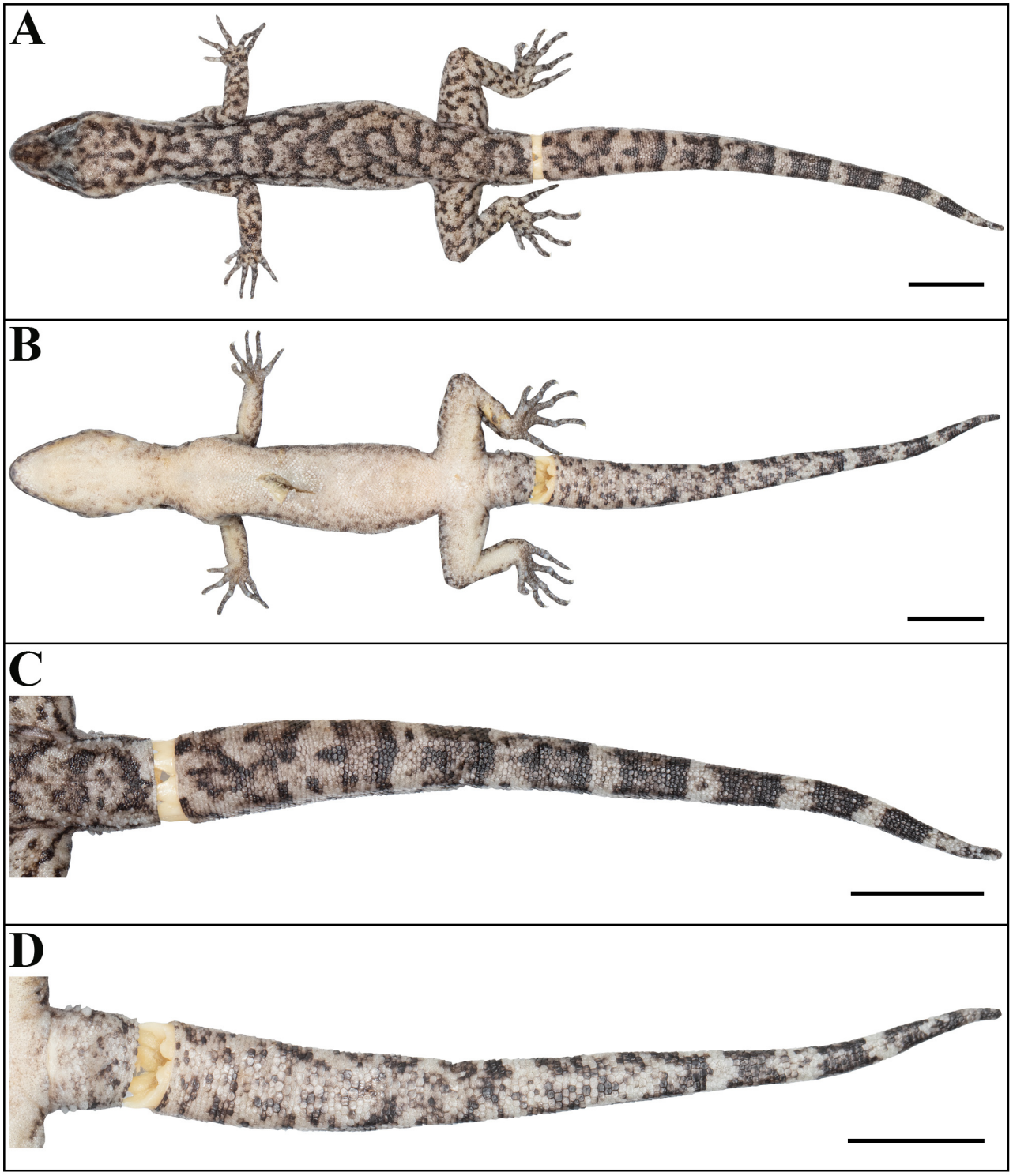

FIGURE 13. Holotype of *Cyrtodactylus annapurnaensis* **sp. nov.** (male, NHM 2023/367): (A) dorsal view of body, (B) ventral view of body, (C) dorsal view of tail, and (D) ventral view of tail. Scale bars 10 mm; photos by Akshay Khandekar.

Scales on palm and soles, smooth, oval or rounded, and flattened on palm and weakly protrudent on the soles; scales on dorsal aspects of limbs heterogenous; composed of slightly smaller, smooth granular scales intermixed with enlarged, feebly keeled to smooth, and blunt tubercles which are slightly larger on thigh and shank than upper and lower arm; scales on ventral aspect of upper arm smooth, granular, slightly smaller than granular scales on body dorsum, scales on ventral aspect of lower arm with much larger scales than those on upper arm, smooth, subcircular, weakly protrudent to flattened, and non-imbricate; ventral aspect of thigh and shank with enlarged, smooth, roughly

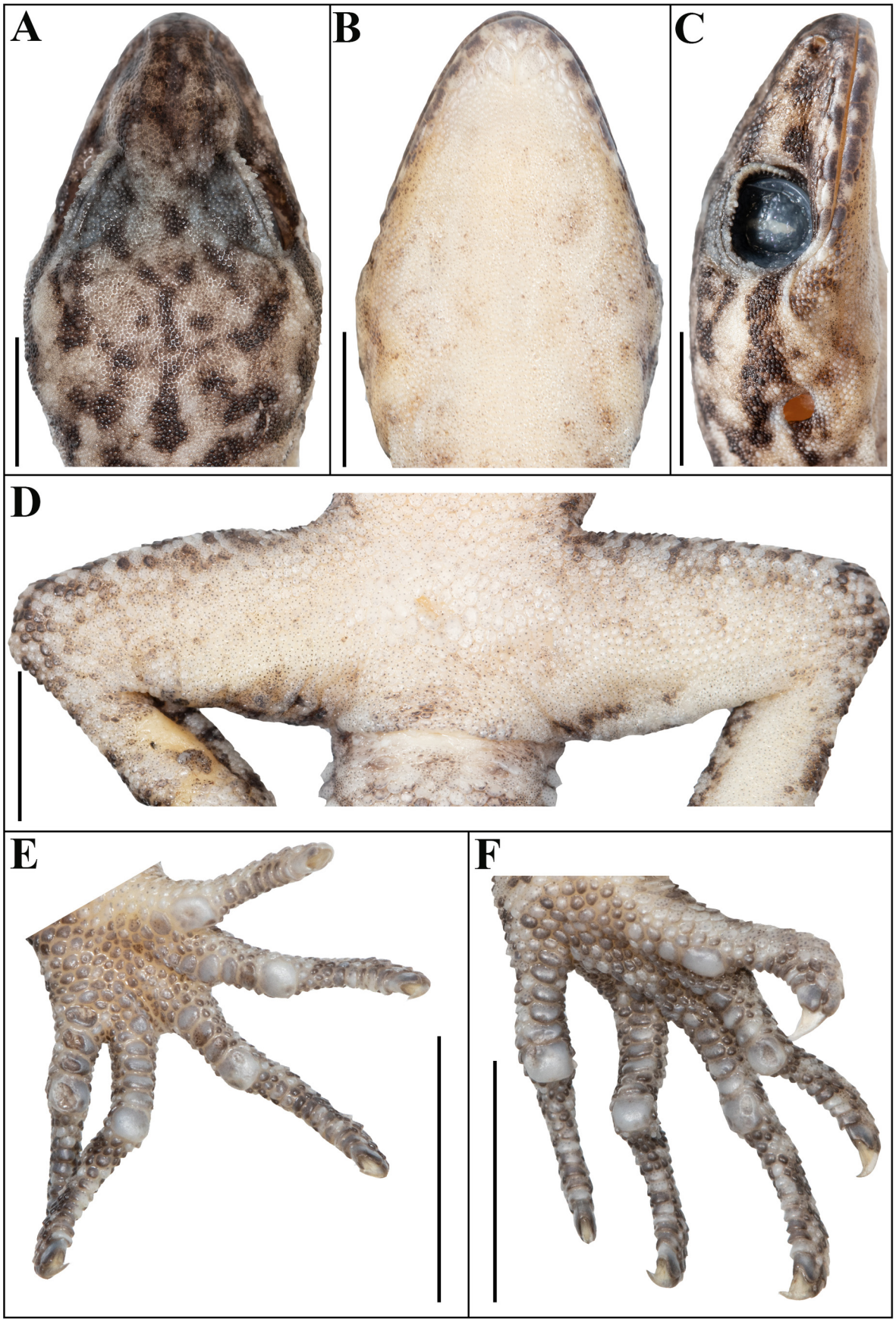

FIGURE 14. Holotype of *Cyrtodactylus annapurnaensis* **sp. nov.** (male, NHM 2023/367): (A) dorsal view of head, (B) ventral view of head, (C) lateral view of head on right, (D) view of femoral region showing continuous series of precloacal pores, (E) ventral view of right manus, and (F) ventral view of right pes. Scale bars 5 mm; photos by Akshay Khandekar.

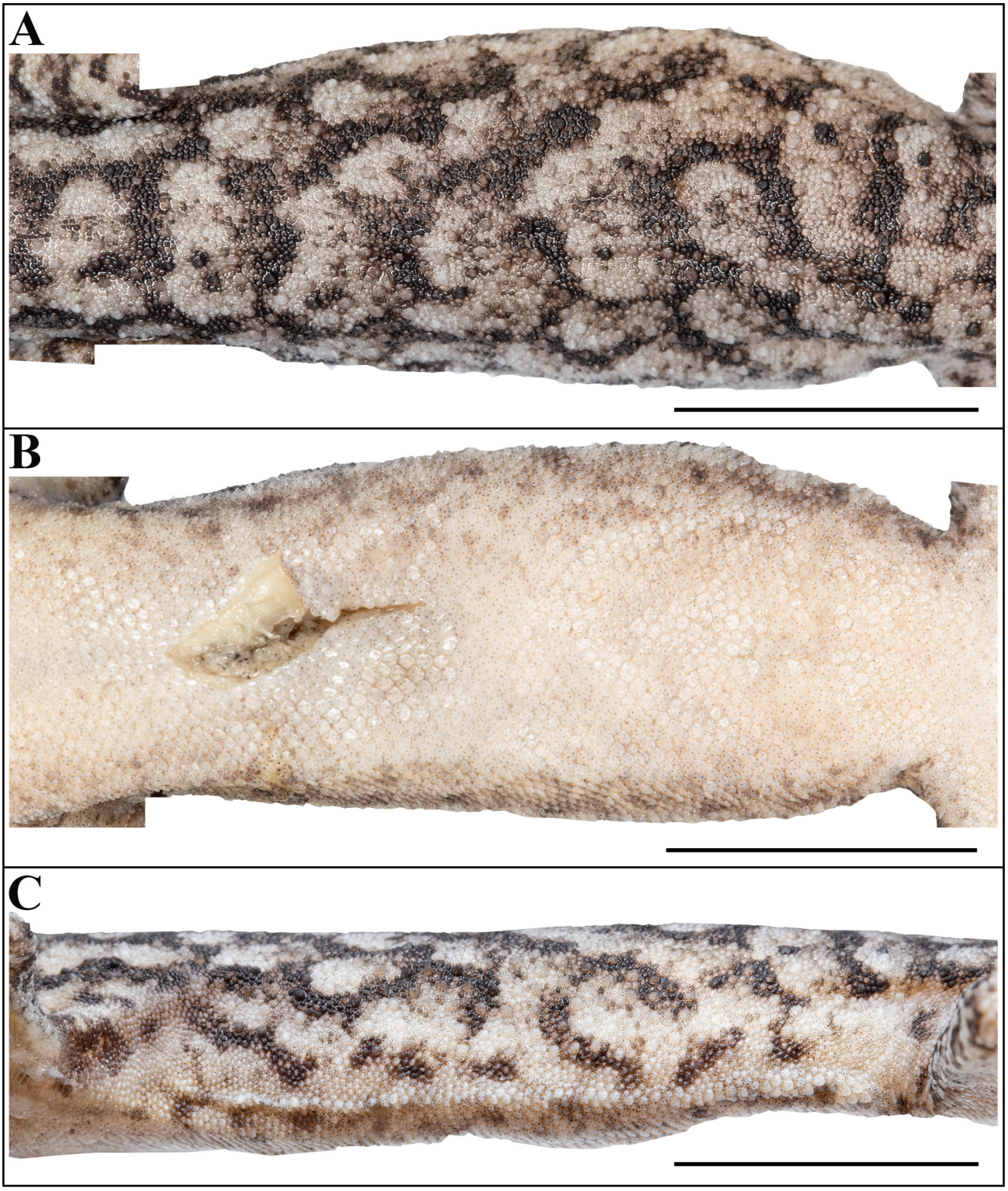

FIGURE 15. Holotype of *Cyrtodactylus annapurnaensis* **sp. nov.** (male, NHM 2023/367): (A) dorsal view of midbody, (B) ventral view of midbody, and (C) lateral view of midbody on right. Scale bars 10 mm; photos by Akshay Khandekar.

rounded, flattened, subimbricate scales, slightly larger and oval on the shank but otherwise similar in size to those on body ventrals (Fig. 13A, B). Forelimbs and hindlimbs slightly long, slender (LAL/ SVL 0.14; CL/SVL 0.17); digits long, with a strong, recurved claw, distinctly inflected, distal portions laterally compressed conspicuously. Digits with mostly unpaired lamellae, separated into a basal and narrower distal series by single enlarged lamella at inflection; basal lamellae series: (3-4-4-6-4 right manus, Fig. 14E; 2-5-7-9-6 right pes, Fig. 14F), (3-4-5-6-4 left

manus, 2-5-7 9-6 left pes); distal lamellae series: (8-9-11-11-10 right manus, Fig. 14E; 10-10-12-12-12 right pes, Fig. 14F), (8-9-12-11-10 left manus, 10-10-12-13-12 left pes). Relative length of digits (measurements in mm in parentheses): IV (4.9) = III (4.9) > V (4.2) = II (4.2) > I (3.0) (left manus); IV (6.3) > III (6.1) > V (5.8) > II (5.0) > I (3.3) (left pes).

FIGURE 16. *Cyrtodactylus annapurnaensis* **sp. nov.**, in life: (A) paratype (adult female, NHM 2023/368), and (B) paratype (adult male, NHM 2023/370). Photos by Santosh Bhattarai.

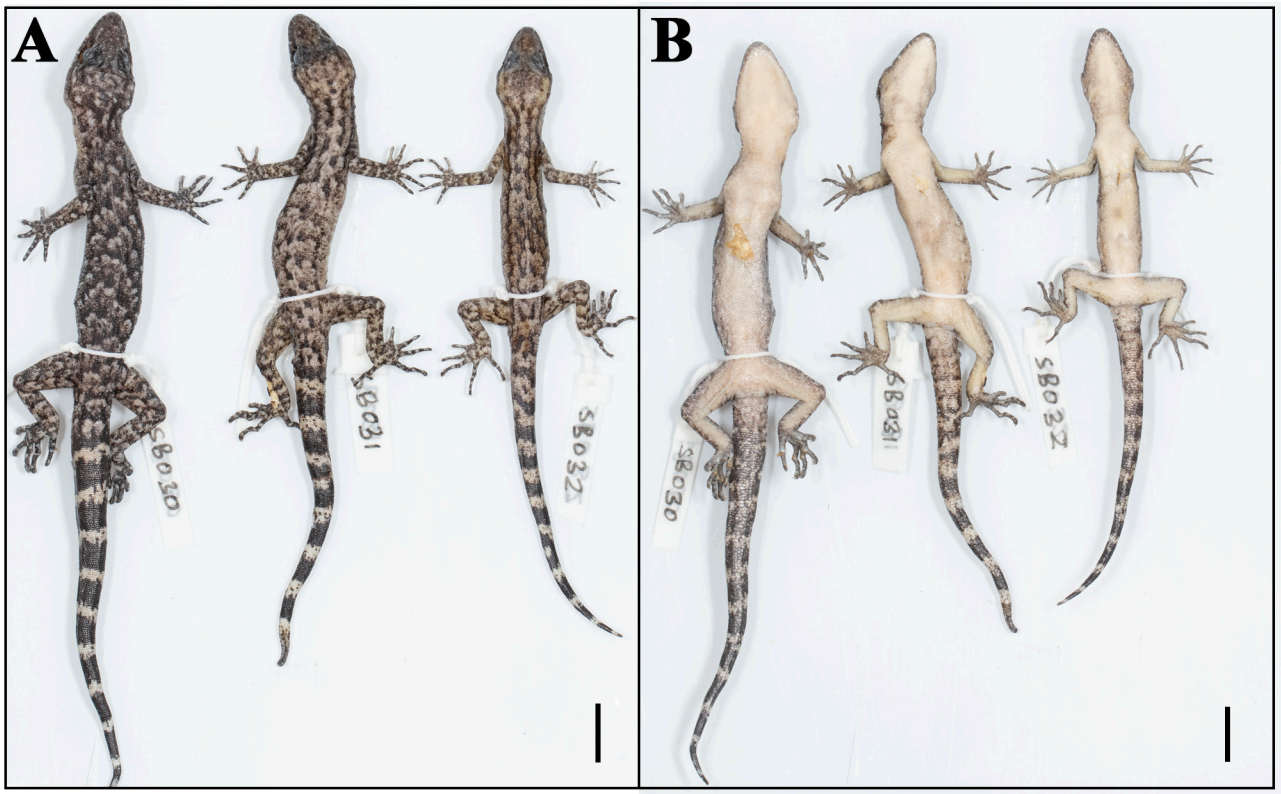

FIGURE 17. Partial paratype series of *Cyrtodactylus annapurnaensis* **sp. nov.**, from left to right, NHM 2023/368–370: (A) dorsal view, and (B) ventral view. Scale bars 10 mm; photos by Akshay Khandekar.

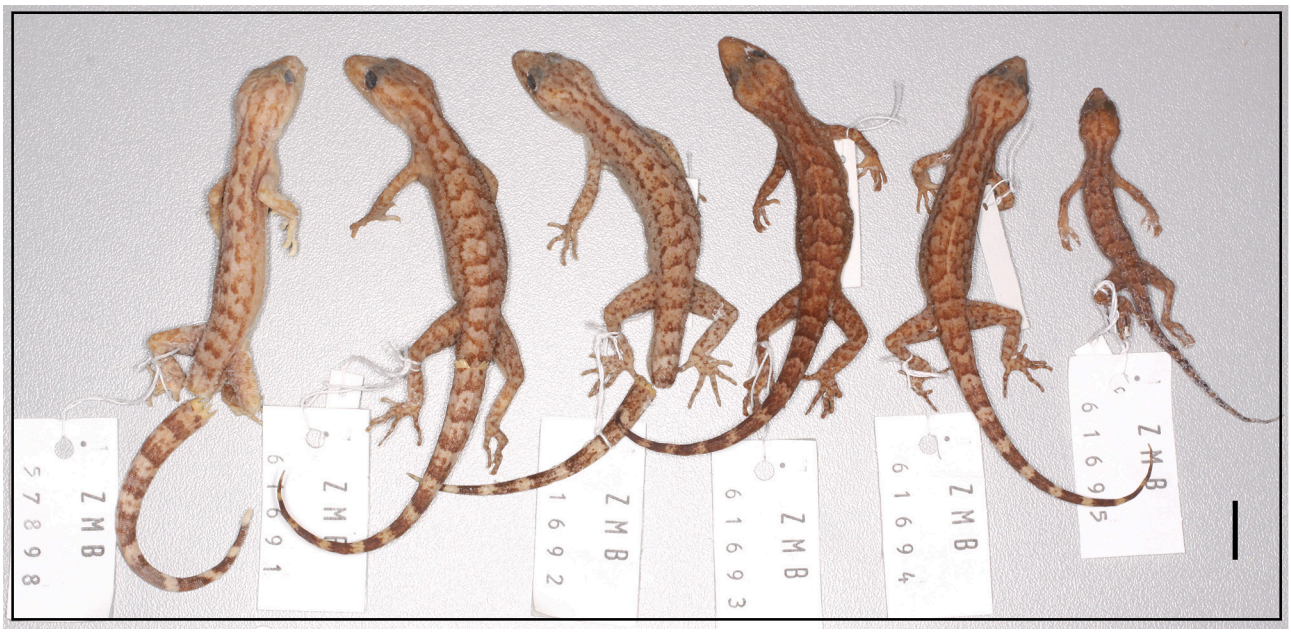

FIGURE 18. Additional paratype series of *Cyrtodactylus annapurnaensis* **sp. nov.**. Scale bar 10 mm; photo by Frank Tillack.

Tail original, subcylindrical, slender, entire, marginally longer than body (TL/SVL 1.06) (Fig. 13C, D); detached from the body completely from the base. Dorsal pholidosis on tail homogeneous; composed of fairly regularly arranged, smooth, subcircular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the

tail base (Fig. 13C). Scales on tail venter much larger than those on dorsal aspect, smooth, flattened, subimbricate; median series smooth, variable in size and shape, and not enlarged (Fig. 13D). Scales on tail base much smaller, smooth, subimbricate; three subequal and smooth postcloacal tubercles on either side (Fig. 14D).

Colouration in life (Fig. 16A). Dorsal ground colour of head, body, limbs and tail light grey-brown, strongly variegated with dark brown reticulations and light grey blotches; labials slightly darker than top of head and with a few yellow streaks; pre and postorbital streaks not distinct; a fine, light mid-vertebral stripe between forelimb insertions and tail base; 11 dark and 12 light caudal bands on original tail; rest of ventral surfaces immaculate; iris green-grey with dark reticulations, pupil bordered by light orange.

Variation and additional information from the paratype series (Figs 16B, 17A, B; 18). Mensural, meristic and additional character state data for the type series is given in Tables 6 & 7 respectively. There are five adult females and three adult males ranging in size from 50.7–63.9 mm (Figs 17A, B; 18). All paratypes resemble the holotype except as follows: paratypes NHM 2023/369 and NHM 2023/370 with smaller internasals. Inner postmentals bordered by mental, infralabial I, and outer postmental in all paratypes (except NHM 2023/370); additionally, bordered by eight smaller chin shields in NHM 2023/368 and four in NHM 2023/369; inner postmentals bordered by mental, infralabial I on right and I & II on left, outer postmental, and six enlarged chin shields in NHM 2023/370. Outer postmentals bordered by inner pair and infralabial I & II in all paratypes; additionally, bordered by four smaller chin shields on left and three on right side in NHM 2023/368 and by four smaller chin shields on either side in NHM 2023/369; outer postmentals bordered by inner pair and infralabial I & II on right and infralabial I on right side, and by four smaller chin shields on either side in NHM 2023/370. All eight paratypes are with original and complete tail, marginally longer or equal to body; ZMB 57898, ZMB 61691, and ZMB 61692 with tail detached from the body; and original tail distinctly banded with 9–11 alternating dark and lighter bands in all paratypes (Figs 16B, 17A, B; 18).

TABLE 6. Mensural (mm) data for *Cyrtodactylus annapurnaensis* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: M = male, F = female.

Type	Holotype	Paratypes							
Specimen Number	NHM 2023/367	NHM 2023/368	NHM 2023/369	NHM 2023/370	ZMB 57898	ZMB 61691	ZMB 61692	ZMB 61693	ZMB 61694
Sex	M	F	F	M	M	M	F	F	F
SVL	63.7	63.9	54.6	50.7	63.4	62.0	59.0	56.4	56.1
TL	67.3	71.3	57.2	58.1	71.5	69.5	69.0	57.0	63.0
TW	6.4	5.9	4.8	4.8	6.6	6.2	6.1	5.4	5.4
LAL	8.9	9.3	7.7	7.2	10.7	9.1	7.5	8.0	8.0
CL	10.6	11.2	9.2	8.5	11.6	11.3	10.9	10.3	10.1
AGL	28.0	29.3	23.9	22.7	28.1	25.8	24.5	24.2	23.5
BH	6.7	6.2	5.4	5.1	7.7	8.4	8.2	7.8	7.4
BW	11.1	10.7	9.1	7.5	9.8	11.4	10.2	10.5	9.3
HL	16.0	16.2	13.3	12.2	17.4	17.7	15.8	15.8	14.4
HW	11.1	11.4	9.5	8.7	10.8	10.9	10.5	9.9	9.5
HD	7.3	7.0	6.1	5.6	8.2	7.0	7.0	6.9	6.8
ED	3.7	3.6	2.7	2.5	3.8	3.6	3.2	3.0	3.1
EE	4.6	5.1	4.0	3.8	4.7	4.9	4.9	4.9	4.5
ES	6.8	7.2	6.2	5.7	7.6	7.3	6.9	7.1	6.3
EN	4.9	5.0	4.6	3.8	5.8	5.3	5.0	5.1	4.5
IN	2.2	2.5	1.8	1.6	2.2	2.2	2.2	2.3	2.1
IO	3.9	3.8	2.9	2.7	4.5	4.6	4.4	4.4	4.1
EL	0.9	1.4	0.9	1.9	0.9	1.5	1.0	1.3	0.7

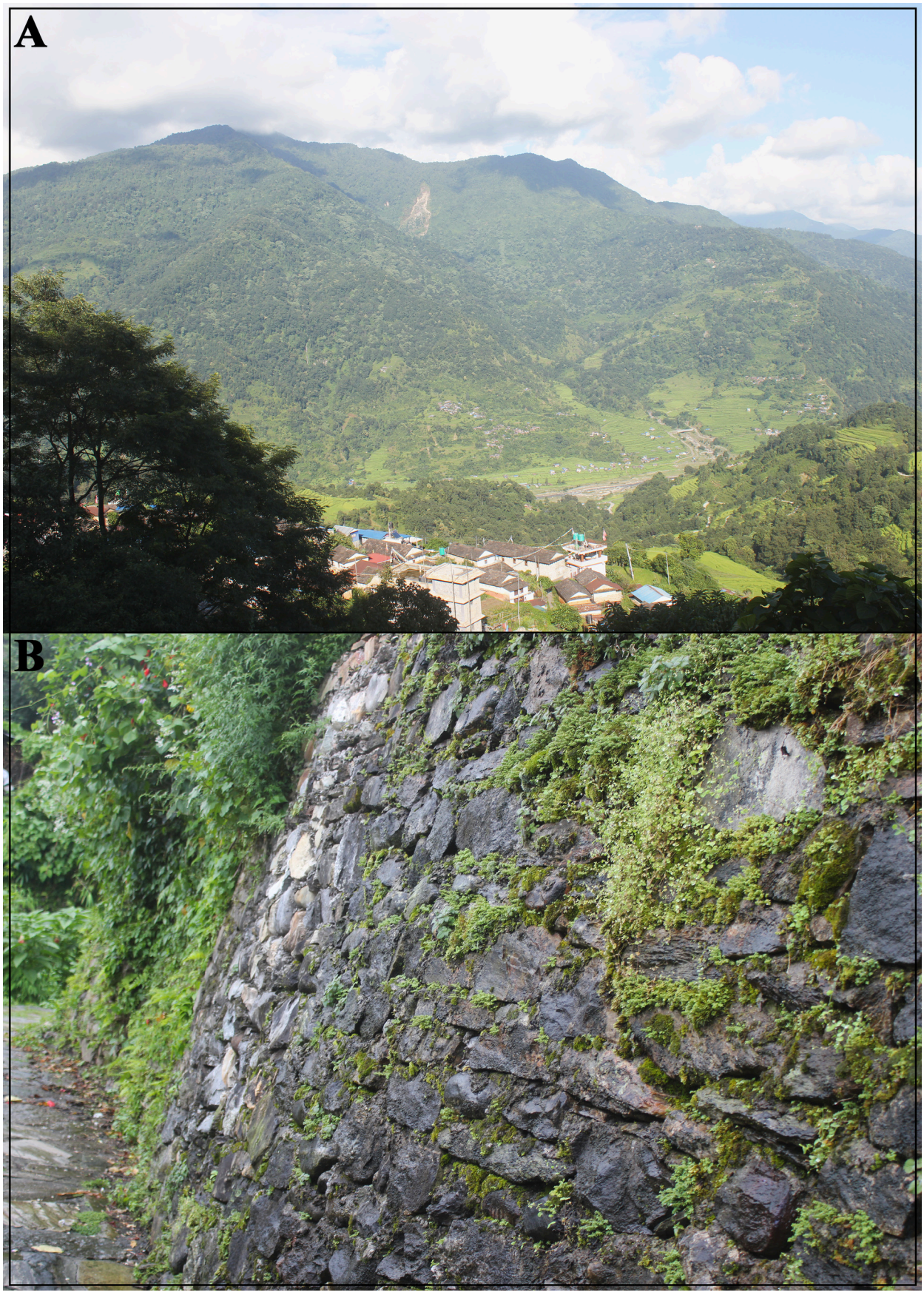

FIGURE 19. Habitat of *Cyrtodactylus annapurnaensis* **sp. nov.** at the type locality: (A) general view of the hilly forest at Lwang, Kaski District, Gandaki Province; and (B) microhabitat from where individuals of the new species were collected. Photos by Santosh Bhattarai.

TABLE 7. Meristic data for *Cyrtodactylus annapurnaensis* **sp. nov.**. The value in parentheses is the number of pitted scales in female. Abbreviations are listed in Materials and Methods except for: M = male, F = female, L&R = left & right, P/A = present/absent, * = incomplete paravertebral counts, / = data unavailable, and NOT EN = not enlarged; numbers in parentheses for PCS indicates number of pitted scales in females.

Type	Holotype	Paratypes							
Specimen Number	NHM 2023/367	NHM 2023/368	NHM 2023/369	NHM 2023/370	ZMB 57898	ZMB 61691	ZMB 61692	ZMB 61693	ZMB 61694
Sex	M	F	F	M	M	M	F	F	F
INS	3	3	2	2	2	3	3	4	4
SL L&R	11&11	11&11	10&11	10&10	11&11	11&11	11&11	11&11	11&10
IL L&R	10&10	10&10	10&10	11&10	9&10	10&10	11&10	10&10	10&9
SL M L&R	8&7	8&7	8&8	7&7	8&9	9&9	8&9	9&8	8&7
IL M L&R	7&7	7&7	7&7	7&7	7&7	7&7	8&8	7&7	7&7
PVT L&R	28&30	31&32	31&30	29&28	30&29	30&31	30&30	35&31	30&34
DTR	20	20	19	18	20	21	19	20	19
MVSR	35	33	35	33	33	34	32	35	34
VS1	86	87	86	84	87	88	89	90	91
VS2	186	190	191	179	188	189	195	191	183
DLAMF1 L&R	8&8	8&8	8&8	8&8	8&8	9&9	8&8	8&8	8&9
BLAMF1 L&R	3&3	5&5	5&5	5&5	4&4	3&3	3&3	3&3	3&3
DLAMF4 L&R	11&11	11&10	12&11	11&12	11&10	13&13	11&12	12&11	12&12
BLAMF4 L&R	6&6	6&6	5&6	6&6	5&6	5&5	5&5	5&5	6&5
DLAMT1 L&R	10&10	10&10	10&10	9&10	10&9	9&10	10&10	9&9	10&10
BLAMT1 L&R	2&3	3&3	3&3	3&4	2&2	2&2	2&2	3&3	2&2
DLAMT4 L&R	13&12	12&11	13&12	12&12	14&14	15&15	12&12	12&14	15&14
BLAMT4 L&R	9&9	7&6	7&7	7&7	7&7	7&8	6&7	6&8	6&6
DLAMT5 L&R	12&12	12&12	13&13	13&13	13&13	14&14	14&14	13&13	14&13
BLAMT5 L&R	6&6	5&5	7&6	6&5	6&6	5&6	6&6	6&6	5&6
TLAMF1 L&R	11&11	13&13	13&13	13&13	12&12	12&12	11&11	11&11	11&12
TLAMF4 L&R	17&17	17&16	17&16	17&18	16&16	18&18	16&17	17&16	18&17
TLAMT1 L&R	12&13	13&13	13&13	12&14	12&11	11&12	12&12	12&12	12&12
TLAMT4 L&R	22&21	19&17	20&19	19&19	21&21	22&23	18&19	18&22	21&20
TLAMT5 L&R	18&18	17&17	20&19	19&18	19&19	19&20	20&20	19&19	19&19
FS	A	A	A	A	A	A	A	A	A
P-F	A	A	A	A	A	A	A	A	A
PCS	8	9 (3)	/	10	10	9	10	10	10
PP	4	A	A	4	3	/	A	A	A
PCT L&R	3&3	3&3	2&3	3&3	4&3	3&3	3&4	3&4	4&3
Caudal tubercles P/A	A	A	A	A	A	A	A	A	A
Subcaudals enlarged or not	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN	NOT EN

Distribution and natural history (Fig. 19A, B). Individuals were found after dark (~1930–2330 hrs) on 15th September 2023 on roadside walls and along stone wall fences at the type locality, Lwang Village which is a part of Annapurna Conservation Area. The species was patchily distributed, and 5–7 individuals were observed in one spot at one to two meter above the ground. The walls were partially shaded with bushes and stone fences

had crevices to hide the animals. There is no traffic movement in the night on the roads in Lwang village; this could be the reason that the animals were very sensitive to flashlights. Other lizards observed were *Hemidactylus flaviviridis* and sleeping *Calotes* sp. The specimen from Birethanti was collected at the south-western bridgehead of the suspension bridge over the Bhurungdi Khola at 29°C during a drizzle at 2300 hr. Sympatric lizards observed were *Ablepharus sikimmensis* (Blyth), *Hemidactylus garnotii* Duméril & Bibron. Specimens from Naudanda were found both on the sides of low, ~ 60 cm high rock walls, and on herbaceous vegetation at a height of about one meter above the lateral drainage channel next to the road of the eastern outskirts of the village. All Naudanda specimens were collected at night (2145–2300 hrs) during the Monsoon, in rainy or foggy weather and temperatures between 21–23°C. Sympatric lizards observed were *Calotes versicolor* (see Tillack & Grossmann 2001, p. 4).

***Cyrtodactylus karanshahi* sp. nov.**

http://www.zoobank.org/urn:lsid:zoobank.org:act:854865D4-9E62-497C-A2F0-48BE812C8F42

(Figs 20–24; Tables 8 & 9)

Holotype. NHM 2023/372 (SB034), adult male, collected on the way from Philim to Chisapani (28.4014°N, 84.8941°E; *ca.* 1590 m asl.), Gorkha District, Manaslu Conservation Area Gandaki Province, Nepal; collected by Santosh Bhattarai on 23rd June 2023

Paratypes. NHM 2023/371 (SB033), NHM 2023/373 (SB035), and NHM 2023/375 (SB037), adult males, NHM 2023/374 (SB036), adult female; same collection data as the holotype.

Etymology. The specific epithet is a patronym in honor of Prof Karan Bahadur Shah (b. 1954), for his remarkable contributions to the ecology, taxonomy and socioeconomics of the vertebrate fauna and in particular the herpetofauna of his home country, Nepal, in a career spanning over 40 years. He also led the feasibility study of the area for the formal establishment of the Manaslu Conservation Area Project (MCAP).

Suggested common name. Karan's bent-toed gecko.

Diagnosis. A medium-sized *Cyrtodactylus*, snout to vent length up to 74.5 mm (*n*=5). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled to smooth, weakly pointed tubercles; a ventrolateral fold of skin present on lower flank; 18 or 19 rows of dorsal tubercles at midbody, 34–36 (rarely 32, *n*=1/5) tubercles in paravertebral rows; ventral scales subequal from chest to vent, smooth, subcircular, and subimbricate with rounded end; 39–42 scales across belly at midbody, 86–89 longitudinal ventral scales between axilla to groin, 181–189 longitudinal ventral scales from mental to cloaca; subdigital scansors smooth, unnotched, and mostly entire; 12 (rarely 13, *n*=1/5) lamellae under digit I of manus and 11–13 under digit I of pes, 16 or 17 lamellae under digit IV of manus and 19–21 lamellae under digit IV of pes; males with continuous series of seven or eight precloacal pores (*n*=4), additionally, one or two pores below the precloacal row (*n*=3/4), and 8–10 enlarged precloacal scales on pore bearing scale row; female without pores but having nine enlarged precloacal scales on otherwise pore bearing scale row (*n*=1); scales on non-regenerated tail dorsum homogeneous; composed of fairly regularly arranged, smooth, elongated or rectangular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base; subcaudal scales in median series smooth, variable in size and shape, and not enlarged; dorsal pattern of scattered, irregular, fine, black markings and numerous fine light spots on brown dorsum, original tail with 10 alternating dark and lighter bands.

Genetic divergence. *Cyrtodactylus karanshahi* is 11.7–30.0 divergent from other members of the Indo-Burma clade and closest to its sister taxon *C. karanshahi* **sp. nov.**, with 1.5 % intraspecific divergence (Table S1). The species falls in the mountain subclade of the *khasiensis* group within the Indo-Burma clade (Fig. 2)

Comparisons with regional congeners. *Cyrtodactylus karanshahi* **sp. nov.** can be differentiated from all regional congeners based on the following differing or non-overlapping characters: no femoral pores and seven or eight precloacal pores in males with one or two pores below the main series (*versus* femoral pores present in *C. chitwanensis* **sp. nov.**, *C. fasciolatus*, *C. gubernatoris*, and *C. nepalensis*; precloacal pores in a single row of three or four in *C. annapurnaensis* **sp. nov.**, 6–9 in *C. cayuensis*, five in *C. chamba*, 10 in *C. himalayicus,* 7–11 in *C. kamengensis*, 4–9 in *C. lawderanus,* eight in *C. martinstolli*); length of original tail > SVL (*versus* length of original tail < SVL in *C. lawderanus*); median row of subcaudals not enlarged (*versus* median row of subcaudals enlarged in *C. chitwanensis* **sp. nov.**, *C. fasciolatus*, and *C. nepalensis*); 18 or 19 rows of dorsal tubercles at midbody and 39–42 scales across belly at midbody (*versus* 24 or 25 DTR and 37 or 38 MVSR in *C. bhupathyi*, 13–15 DTR in

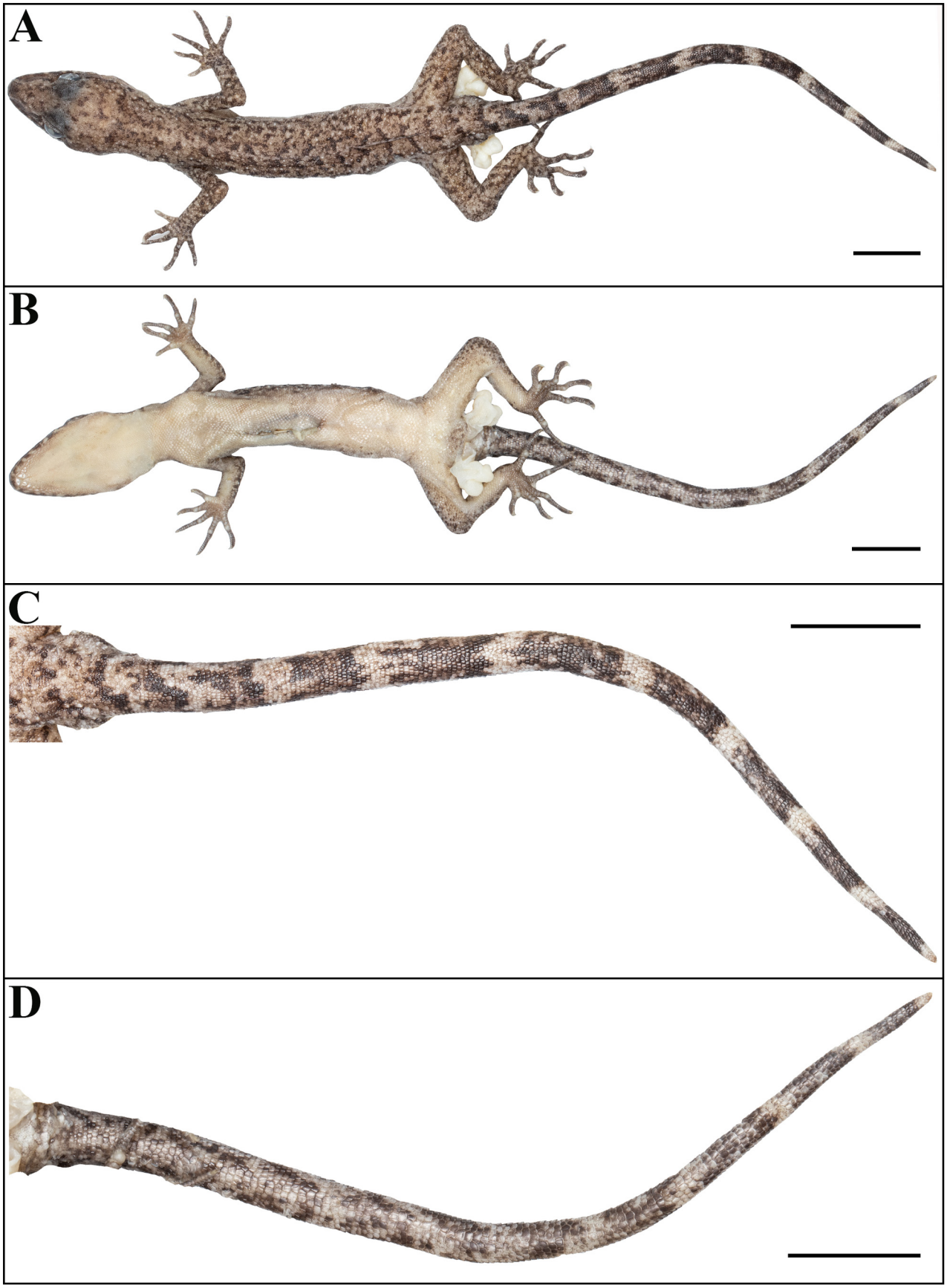

FIGURE 20. Holotype of *Cyrtodactylus karanshahi* **sp. nov.** (male, NHM 2023/372):(A) dorsal view of body, (B) ventral view of body, (C) dorsal view of tail, and (D) ventral view of tail. Scale bars 10 mm; photos by Akshay Khandekar.

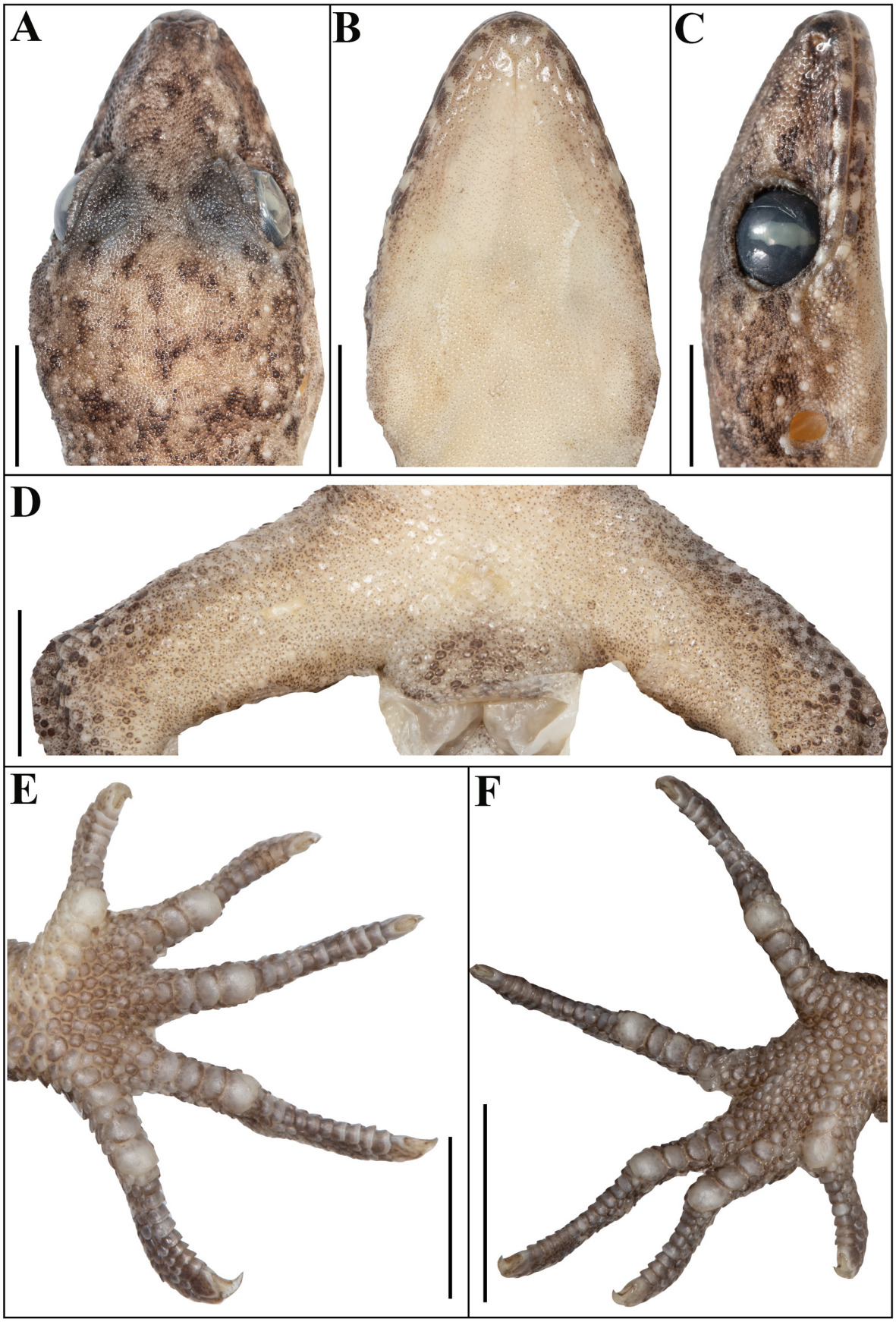

FIGURE 21. Holotype of *Cyrtodactylus karanshahi* **sp. nov.** (male, NHM 2023/372):(A) dorsal view of head, (B) ventral view of head, (C) lateral view of head on right, (D) view of femoral region showing continuous series of precloacal pores, (E) ventral view of right manus, and (F) ventral view of right pes. Scale bars 5 mm; photos by Akshay Khandekar.

C. chamba, 17 DTR in *C. nepalensis*, 15 or 16 DTR and 40–45 MVSR in *C. siangensis*); and moderate body size with maximum SVL up to 74.5 mm (*versus* maximum SVL < 65 mm in *C. annapurnaensis* **sp. nov.**, *C. bhupathyi, C. chamba, C. himalayicus* and maximum SVL > 80 mm in *C. cayuensis, C. chitwanensis* **sp. nov.**, *C. fasciolatus,* and *C. martinstolli*).

Description of the holotype. Adult male in good state of preservation except tail bent towards right, a 11.3 mm long incision in sternal region for tissue collection, and hemipenis everted on both the sides (Fig. 20A–D). SVL 63.4 mm, head short (HL/SVL 0.26), wide (HW/HL 0.66), not strongly depressed (HD/HL 0.38), distinct from neck. Loreal region inflated, canthus rostralis indistinct. Snout half of head length (ES/HL 0.44), almost two times eye diameter (ES/ED 1.92); scales on snout and canthus rostralis oval, subequal, weakly keeled to smooth, much larger than those on forehead and interorbital region; scales on forehead similar to those on snout and canthus rostralis except slightly smaller; scales on interorbital region even smaller, granular and weakly keeled to smooth; scales on occipital, and temporal region heterogeneous, composed of granular scales intermixed with enlarged, weakly keeled, rounded tubercles (Fig. 21A). Eye small (ED/HL 0.23), with vertical pupil having crenulated margins; supraciliaries short, larger anteriorly; 16 interorbital scale rows across narrowest point of frontal; 39 scale rows between left and right supraciliaries at mid-orbit (Fig. 21A, C). Ear-opening small, oval, deep (EL/ HL 0.08); eye to ear distance much greater than diameter of eye (EE/ED 1.34) (Fig. 21C). Rostral almost two times wider (2.9 mm) than high (1.5 mm), incompletely divided dorsally by a strongly developed rostral groove for almost than half of its height; a single enlarged, roughly circular supranasal on each side, more than three times the size of upper postnasal, separated from each other behind rostral by two much smaller internasal scales; rostral in contact with supralabial I, nostril and supranasal, and internasals on either side; nostrils oval, surrounded by four postnasals, supranasal, rostral, and supralabial I on either side; four postnasals on either side, upper postnasal roughly rectangular, much larger than others; other postnasals roughly circular and subequal; two to three rows of scales separate orbit from supralabials (Fig. 21C). Mental enlarged, subtriangular, wider (2.5 mm) than high (1.5 mm); two pairs of postmentals, inner pair rectangular, marginally longer (1.7 mm) than mental, in strong contact with each other below mental (1.0 mm); inner pair bordered by mental, infralabial I, outer postmental, and two slightly enlarged chin shields on either side; outer postmentals roughly rectangular, much smaller (0.9 mm) than inner pair, bordered by inner postmentals, infralabial I & II, and four chin shields on left and five on right side, four enlarged gular scales between left and right outer postmentals; all chin shields bordering postmentals somewhat protrudent, subequal, subcircular, smooth, and much smaller than outermost postmentals; scales on rest of throat, granular, much smaller, smooth, and subcircular (Fig. 21B). Infralabials bordered below by a row or two of slightly enlarged, much elongated scales, decreasing in size posteriorly. Eleven supralabials to angle of jaw and eight at midorbital position on either side; supralabial I largest, gradually decreasing in size posteriorly; 10 infralabials to angle of jaw on either side and seven at midorbital position on left and six on right side; infralabial I largest, gradually decreasing in size posteriorly (Fig. 21C).

Body relatively slender (BW/AGL 0.30), trunk just less than half of SVL (AGL/SVL 0.48) with ventrolateral fold of skin on lower flank (Fig. 22A–C). Dorsal pholidosis heterogeneous; smooth granular scales intermixed with fairly regularly arranged rows of enlarged, feebly keeled to smooth, weakly pointed tubercles; granular scales gradually increasing in size towards each flank, largest on mid-flank; granular scales on occiput slightly smaller than paravertebral granular scales; enlarged tubercles in approximately 18 longitudinal rows at midbody; 35 tubercles in paravertebral rows (Fig. 22A). Ventral scales much larger than granular scales on dorsum, subequal from chest to vent, and smooth, subcircular and subimbricate with rounded end; scales on precloacal region distinctly enlarged; midbody ventral scale rows across belly 39; 188 ventral scales from mental to anterior border of cloaca and 88 ventral scales between limb insertions (Fig. 22B). A continuous series of seven precloacal pores, and an additional central, tiny precloacal pore below the precloacal pore series; femoral pores absent (Fig. 21D).

Scales on palm and soles, smooth, oval or rounded, and flattened; scales on dorsal aspects of limbs heterogenous; composed of slightly smaller, smooth granular scales intermixed with enlarged, weakly keeled, weakly pointed tubercles which are slightly larger on thigh and shank than upper and lower arm; scales on ventral aspect of upper arm smooth, granular, slightly smaller than granular scales on body dorsum, scales on ventral aspect of lower arm much larger than those on upper arm, smooth, subcircular, weakly conical to flattened, and subimbricate; ventral aspect of thigh and shank with enlarged, smooth, roughly rounded, flattened, subimbricate scales, slightly larger and oval on the shank but otherwise similar in size to those on body ventrals (Fig. 20 A, B). Forelimbs and hindlimbs slightly long, slender (LAL/ SVL 0.14; CL/SVL 0.19); digits long, with a strong, recurved claw, distinctly inflected, distal portions laterally compressed conspicuously. Digits with mostly unpaired lamellae, separated into a basal and narrower distal series by a single, much enlarged lamella at inflection; basal lamellae series: (4-4-4-6-5 right manus,

Fig. 21E; 3-5-5-7-7 right pes, Fig. 21F), (4-4-5-5-5 left manus, 3-5-5-7-7 left pes); distal lamellae series: (8-9-12-11-10 right manus, Fig. 21E; 9-9-12-13-13 right pes, Fig. 21F), (8-9-11-12-10 left manus, 9-9-13-13-12 left pes). Relative length of digits (measurements in mm in parentheses): IV (6.3) > III (5.7) > V (4.9) > II (4.5) > I (3.1) (left manus); IV (7.4) > V (6.6) = III (6.6) > II (5.5) > I (3.5) (left pes).

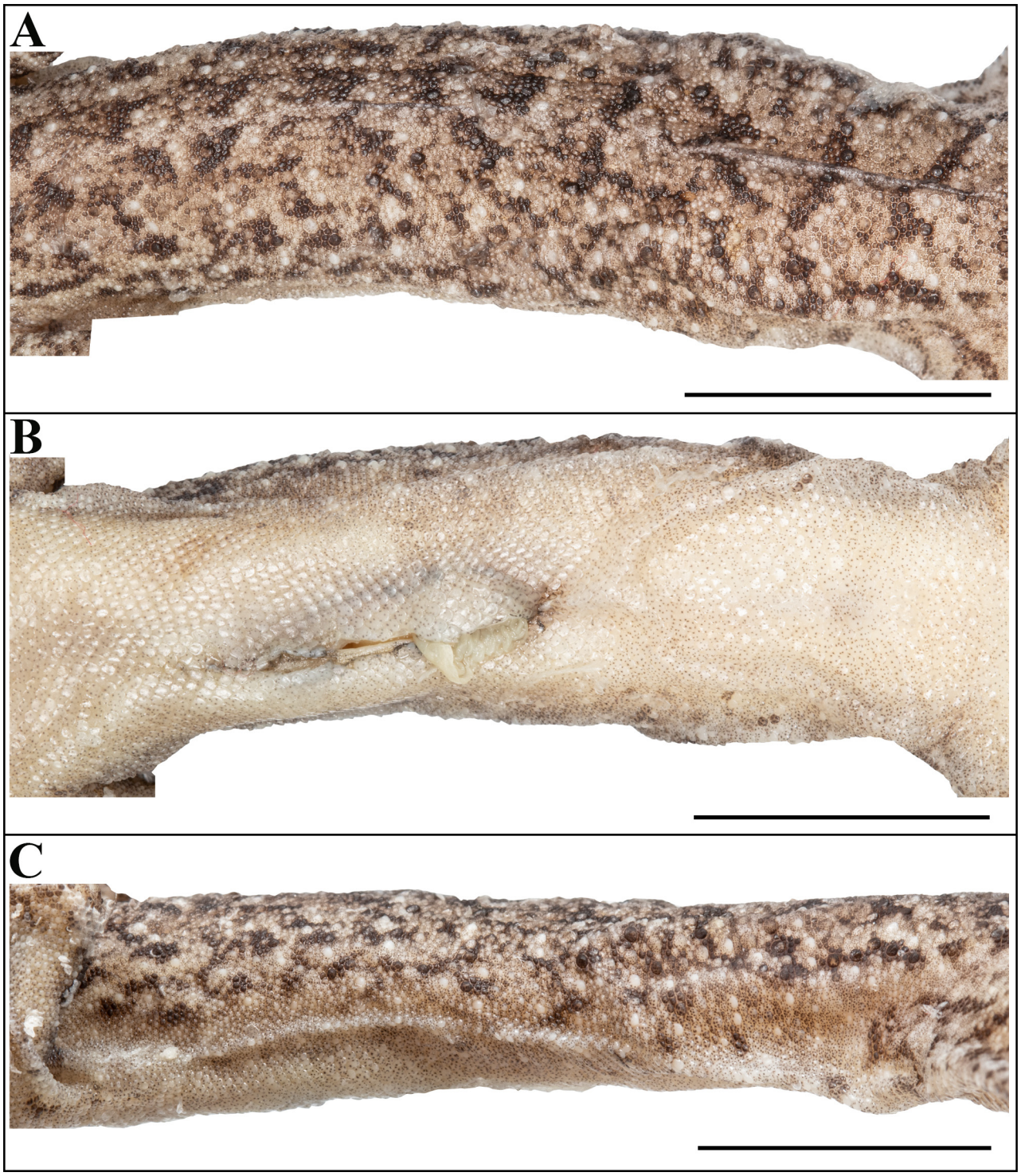

FIGURE 22. Holotype of *Cyrtodactylus karanshahi* **sp. nov.** (male, NHM 2023/372):(A) dorsal view of midbody, (B) ventral view of midbody, and (C) lateral view of midbody on right. Scale bars 10 mm; photos by Akshay Khandekar.

Tail original, subcylindrical, slender, entire, slightly longer than body (TL/SVL 1.21) (Fig. 20C, D). Dorsal pholidosis on tail homogeneous; composed of fairly regularly arranged, smooth, elongated or rectangular, flattened, and subimbricate scales that are larger than granular scales on midbody dorsum, gradually becoming larger

posteriorly and dorsolaterally; a few scattered enlarged tubercles present on the tail base (Fig. 20C). Scales on tail venter much larger than those on dorsal aspect, smooth, flattened, subimbricate; median series smooth, variable in size and shape, and not enlarged (Fig. 20D). Scales on tail base much smaller, smooth, subimbricate; three subequal and smooth postcloacal tubercles on left and four on right side (Fig. 21D).

Colouration in life (Fig. 23A). Dorsal ground colour of head, body, limbs and tail brown; top of head with scattered fine black and light spots; labials slightly darker than head dorsum with some pale yellow streaks; pre and postorbital streaks not distinct; neck and limbs with numerous fine, black and light grey spots; dorsum with scattered, irregular, fine, black markings with a fine off-white posterior border and numerous off-white tubercles and fine spots; ten dark and ten light caudal bands on complete original tail, bands broken up on anterior 1/3 of tail; rest of ventral surfaces immaculate; iris green-grey with dark reticulations, pupil bordered by orange-red.

Variation and additional information from the paratype series (Figs 23B, 24A, B). Mensural, meristic and additional character state data for the type series is given in Tables 8 & 9 respectively. There are three adult males and an adult female ranging in size from 53.2–74.5 mm (Fig. 24A, B). All paratypes resemble the holotype except as follows: inner postmentals bordered by mental, infralabial I, and outer postmental in all paratypes; additionally, bordered by six smaller chin shields in NHM 2023/373 and NHM 2023/375, eight in NHM 2023/374. Outer postmentals bordered by inner pair and infralabial I & II in all paratypes; additionally, bordered by four smaller chin shields on either side in NHM 2023/371, by three on either side in NHM 2023/374 and NHM 2023/375, by three on left and four on right side in NHM 2023/373. Two paratypes—NHM 2023/373 and NHM 2023/375 with original and complete tail, marginally longer than SVL (TL/SVL 1.07 and 1.05 respectively), original tail in NHM 2023/375 is detached from the body; remaining two paratypes, NHM 2023/371 and NHM 2023/374 with complete but partially regenerated tail, slightly longer and marginally shorter than body (TL/SVL 1.21 and 0.87 respectively) (Fig. XA). NHM 2023/371 and NHM 2023/373 with fully everted hemipenis on both sides and hemipenis partially everted only on left side in NHM 2023/375 (Fig. 24A, B). Original tail distinctly banded with 10 or 11 dark and light bands; regenerated tail light brown in NHM 2023/371 and NHM 2023/374 (Figs 23B; 24A, B).

TABLE 8. Mensural (mm) data for *Cyrtodactylus karanshahi* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: M = male, F = female.

Type	Holotype	Paratypes			
Specimen Number	NHM 2023/372	NHM 2023/371	NHM 2023/373	NHM 2023/374	NHM 2023/375
Sex	M	M	M	F	M
SVL	63.4	72.1	53.2	74.5	54.4
TL	76.4	58.4	57.1	64.8	57.0
TW	5.6	6.8	4.5	5.3	4.1
LAL	9.1	9.7	7.1	10.5	7.8
CL	11.9	12.0	9.3	12.2	9.1
AGL	30.2	32.2	24.8	35.5	24.5
BH	5.4	5.1	3.5	11.2	3.7
BW	9.1	11.1	7.8	13.7	8.2
HL	16.6	17.9	13.7	17.5	13.7
HW	11.0	12.2	9.1	13.1	9.5
HD	6.3	6.6	5.5	7.3	5.5
ED	3.8	3.9	3.1	3.9	3.1
EE	5.1	5.5	4.4	5.9	3.8
ES	7.3	7.6	5.8	7.9	5.9
EN	5.3	5.5	4.4	5.9	4.2
IN	2.1	2.1	1.6	2.3	1.9
IO	3.6	4.1	3.1	4.1	3.1
EL	1.3	1.7	1.2	1.3	1.2

TABLE 9. Meristic data for *Cyrtodactylus karanshahi* **sp. nov.**. Abbreviations are listed in Materials and Methods except for: M = male, F = female, L&R = left & right, P/A= present/absent, * = incomplete paravertebral counts, / = data unavailable, and NOT EN = not enlarged.

Type	Holotype	Paratypes			
Specimen Number	NHM 2023/372	NHM 2023/371	NHM 2023/373	NHM 2023/374	NHM 2023/375
Sex	M	M	M	F	M
INS	2	2	2	2	2
SL L&R	11&11	11&11	12&11	10&10	10&10
IL L&R	10&10	10&11	11&11	10&10	10&10
SL M L&R	8&8	8&8	8&8	7&7	7&8
IL M L&R	7&6	6&8	6&7	6&6	6&7
PVT L&R	35&35	35&36	33*&33*	36&36	32&34
DTR	18	19	19	19	18
MVSR	39	42	/	39	41
VS1	88	89	/	87	86
VS2	188	189	/	185	181
DLAMF1 L&R	8&8	8&8	8&8	8&8	8&8
BLAMF1 L&R	4&4	4&4	4&4	4&4	5&4
DLAMF4 L&R	12&11	11&11	12&12	11&11	11&11
BLAMF4 L&R	5&5	5&6	5&5	5&5	6&5
DLAMT1 L&R	9&9	9&8	9&9	8&9	8&8
BLAMT1 L&R	3&3	4&4	3&3	4&4	3&3
DLAMT4 L&R	13&12	13&13	14&14	13&13	12&13
BLAMT4 L&R	7&7	7&7	7&6	8&8	7&7
DLAMT5 L&R	12&13	14&13	12&13	13&13	12&12
BLAMT5 L&R	7&7	7&7	7&7	7&7	6&6
TLAMF1 L&R	12&12	12&12	12&12	12&12	13&12
TLAMF4 L&R	17&16	16&17	17&17	16&16	17&16
TLAMT1 L&R	12&12	13&12	12&12	12&13	11&11
TLAMT4 L&R	20&19	20&20	21&20	21&21	19&20
TLAMT5 L&R	19&20	21&20	19&20	20&20	18&18
FS	A	A	A	A	A
P-F	A	A	A	A	A
PCS	10	10	9	9	8
PP	7 + 1 below main series	8 + 2 below main series	7 + 1 below main series	A	7
PCT L&R	4&4	4&4	4&4	4&3	4&4
Caudal tubercles P/A	A	/	A	A	A
Subcaudals enlarged or not	NOT EN	/	NOT EN	NOT EN	NOT EN

Distribution and natural history (Fig. 25A, B). Individuals were found after dark (~2300–0000hrs) during dry weather and around 21°C along the trail from Phillim village towards Chisapani village inside Manaslu Conservation Area. The geckos were observed among solitary rocks and boulders partly covered by small trees and bushes along the trail. The species appears abundant, with two or more geckos in most rocks. The only sympatric lizard observed in the area was *Laudakia tuberculata*.

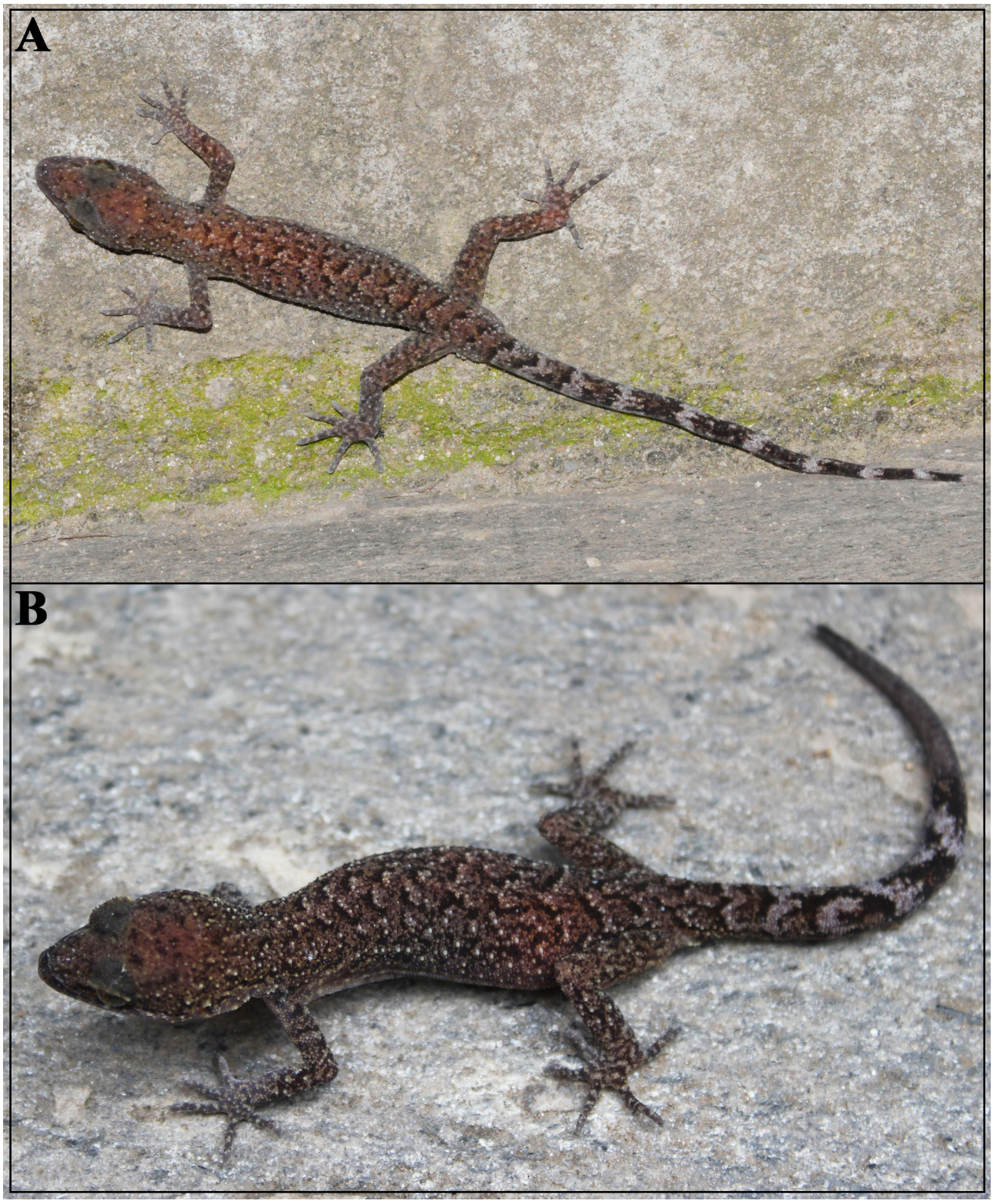

FIGURE 23. *Cyrtodactylus karanshahi* **sp. nov.**, in life: (A) holotype (adult male, NHM 2023/372), and (B) paratype (adult female, NHM 2023/374). Photos by Frank Tillack (A) and Santosh Bhattarai (B).

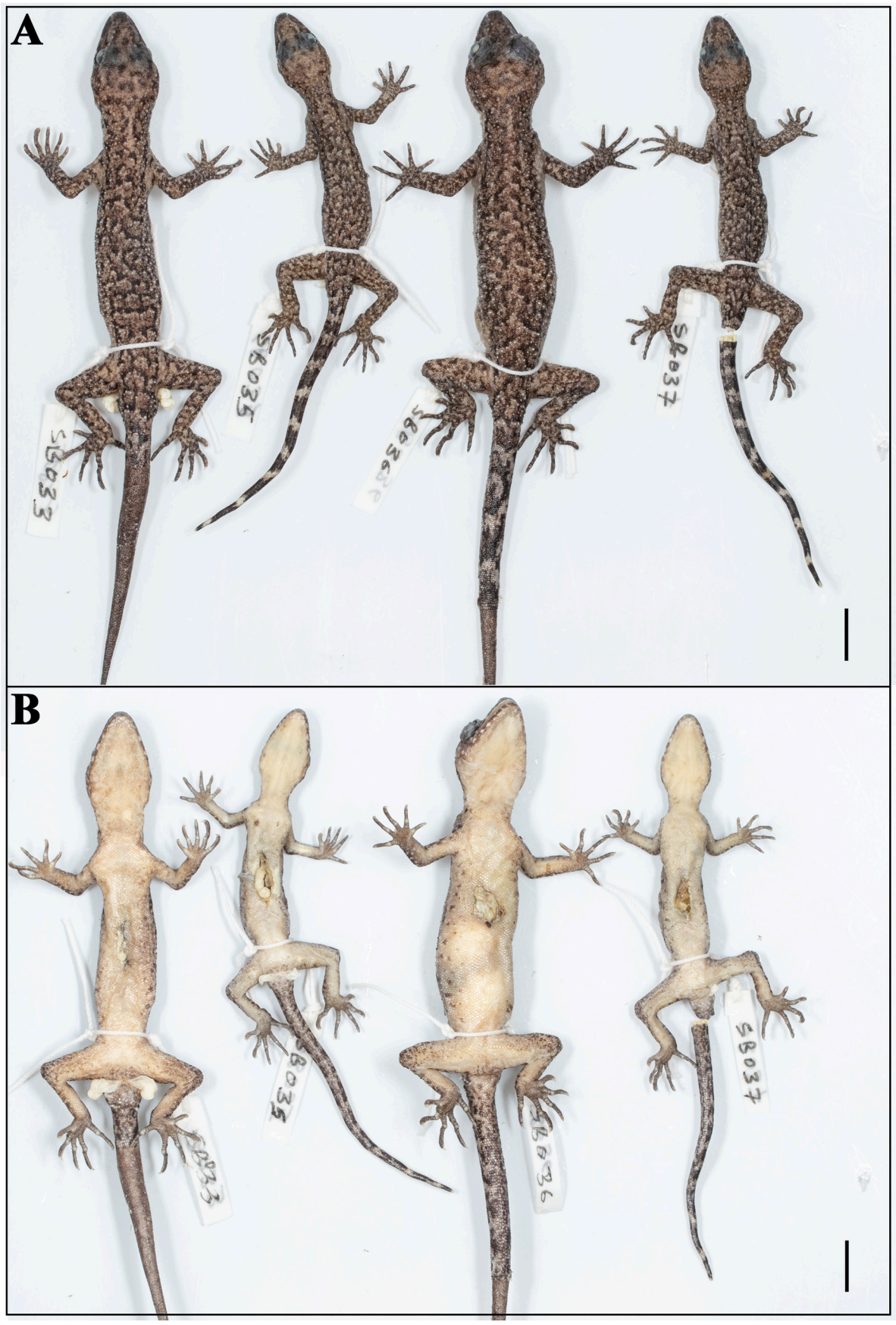

FIGURE 24. Paratype series of *Cyrtodactylus karanshahi* **sp. nov.**, from left to right, NHM 2023/371, NHM 2023/373–375: (A) dorsal view, and (B) ventral view. Scale bars 10 mm; photos by Akshay Khandekar.

FIGURE 25. Habitat of *Cyrtodactylus karanshahi* **sp. nov.** at the type locality: (A) general view of the habitat at Philim, Gorkha District, Manaslu Conservation Area, Gandaki Province; and (B) microhabitat from where individuals of the new species were collected. Photos by Frank Tillack (A) and Santosh Bhattarai (B).

Discussion

The discovery of three new species from a small region of Central Nepal is significant given that just ten species of lizards have been described from the country, the agamids *Japalura dasi* (Shah & Kästle), *Sitana fusca* Schleich & Kästle, *S. schleichi* Anders & Kästle, *S. sivalensis* Schleich, Kästle & Shah; the geckos *Cyrtodactylus markuscombaii, C. martinstolli* and *C. nepalensis*; and the skinks *Ablepharus mahabharatus* (Eremchenko, Shah & Panfilov), *A. nepalensis* and *Scincella capitanea* Ouboter (Ouboter 1986; Darevsky *et al.* 1998; Eremchenko *et al.* 1998; Schleich & Kästle 1998a, b; Schleich *et al.* 1998). Of these, *C. markuscombaii* is no longer considered a distinct species and *Sitana sivalensis* also occurs in India (Deepak *et al.* 2018), leaving eight species endemic to Nepal in addition to the three new species described in this study. The discovery of the three new species from Central Nepal indicates the low number of known endemic species in Nepal is a sampling artefact.

Species diversity of *Cyrtodactylus* varies across the Himalaya—the Western Himalaya include four species of the *lawderanus* group (*C. battalensis* Khan*, C. chamba, C. himalayanus* Duda & Sahi*, C. lawderanus*) and just two of the Indo-Burma clade, *C. fasciolatus* and *C. nepalensis*; the Central Himalaya seven species of the Indo-Burma clade, *C. annapurnaensis, C. bhupathyi, C. chitwanensis, C. gubernatoris, C. himalayicus, C. karanshahi, C. martinstolli*; and the Eastern Himalaya just *C. siangensis* and the widely distributed *C. cayuensis*. The majority of species within the Indo-Burma clade are found in northeast India and adjacent Myanmar, and there are several independent lineages in the Himalaya that have diversified into 2–4 known lineages each: the *fasciolatus* group in Western and Central Himalaya with three species, the Eastern Himalayan subclade (sensu Agarwal *et al.* 2014) in Central and Eastern Himalaya with three phylogenetically sampled species, the *cayuensis* clade in Eastern Himalaya with two species, and an exclusively Nepali radiation of the mountain subclade of the *khasiensis* group in Central Himalaya with four species (Fig. 2). Grismer *et al (*2020) categorized nine major habitat types for *Cyrtodactylus* species; and all species of *Cyrtodactylus* from Nepal including the three newly described species, use the general habitat types which include microhabitats such as rocks, tree trunks, vegetation, and their immediate microhabitats. There are still many such habitats to be surveyed in Nepal. Given the vast areas of suitable habitat and significant topographic and climatic heterogeneity, it is very likely that more *Cyrtodactylus* species are yet to be discovered in Nepal.

In an attempt to break *Cyrtodactylus* up into more manageable groups, Grismer *et al.* (2021) partitioned the genus into 31 well-supported species groups based on mitochondrial and nuclear phylogenies. The Indo-Burma clade includes the *fasciolatus, khasiensis* and *peguensis* species groups based on ND2 data with the *khasiensis* group paraphyletic and the *peguensis* group polyphyletic in the nuclear phylogeny (Grismer *et al.* 2021). In our ND2 phylogeny, *C. russelli* + *C. slowinskii* fall outside the *peguensis* group, while the composition of the *khasiensis* group remains the same apart from added species. Within the *khasiensis* group are two well-supported subclades containing most species diversity, a lowland and a mountain clade (after Agarwal *et al.* 2014). The *fasciolatus* species group includes *C. fasciolatus* and its sister lineage *C.* cf. *fasciolatus*, *C. nepalensis* and its sister lineage *Cyrtodactylus* sp. 1, along with the morphologically closely allied but phylogenetically poorly supported sister taxon to these two, *C. chitwanensis*. Further sampling of taxa and genes may help stabilize the species groups within the Indo-Burma clade.

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References

Agarwal, I., Bauer, A.M., Jackman, T.R. & Karanth, K.P. (2014) Insights into Himalayan biogeography from geckos: A molecular phylogeny of *Cyrtodactylus* (Squamata: Gekkonidae). *Molecular Phylogenetics and Evolution*, 80, 145–155. https://doi.org/10.1016/j.ympev.2014.07.018

Agarwal, I., Mahony, S., Giri, V.B., Chaitanya, R. & Bauer, A.M. (2018a) Two new species of *Cyrtodactylus* Gray, 1827 (Squamata: Gekkonidae) with comments on name-bearing types from northeast India. *Zootaxa*, 4420 (3), 334–356. https://doi.org/10.11646/zootaxa.4420.3

Agarwal, I., Mahony, S., Giri, V.B., Chaitanya, R. & Bauer, A.M. (2018b) Six new *Cyrtodactylus* (Squamata: Gekkonidae) from northeast India. *Zootaxa*, 4524 (5), 501–535. https://doi.org/10.11646/zootaxa.4524.5.1

Amano, T. & Sutherland, W. J. (2013) Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. *Proceedings of the Royal Society B*, 280 (1756), 20122649. https://doi.org/10.1098/rspb.2012.2649

Anonymous [International Commission of Zoological Nomenclature] (1999) International code of zoological nomenclature. Fourth edition. International Trust for zoological Nomenclature, London, xxix + 306 pp.

Bauer, A.M., Masroor, R., Titus-McQuillan, J., Heinicke, M.P., Daza, J.D. & Jackman, T.R. (2013) A preliminary phylogeny of the Palaearctic naked-toed geckos (Reptilia: Squamata: Gekkonidae) with taxonomic implications. *Zootaxa*, 3599 (4), 301–324. https://doi.org/10.11646/zootaxa.3599.4.1

Bhattarai, S., Gurung, A., Lamichhane, B.R., Regmi, R., Dhungana, M., Kumpakha, B. & Subedi, N. (2020) *Amphibians and Reptiles of Chure Range, Nepal*. President Chure Terai-Madhesh Conservation Development Board and National Trust for Nature Conservation, Khumaltar, Lalitpur, 60 pp.

Boruah, B., Narayanan, S., Aravind, N.A., Lalronunga, S., Deepak, V. & Das, A. (2024) Description of six new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae) from northeastern India. *Vertebrate Zoology*, 74, 453–486. https://doi.org/10.3897/vz.74.e124752

Darevsky, I.S., Helfeberger, N. [sic], Orlov, N. & Shah, K. ("1997" 1998) Two new species of the genus *Gonydactylus* (Sauria: Gekkonidae) from eastern Nepal. *Russian Journal of Herpetology*, 4 (2), 89–93. https://doi.org/10.30906/1026-2296-1997-4-2-89-93

Deepak, V., Khandekar, A., Chaitanya, R. & Karanth, P. (2018) Descriptions of two new endemic and cryptic species of *Sitana* Cuvier, 1829 from peninsular India. *Zootaxa*, 4434 (2), 327–365. https://doi.org/10.11646/zootaxa.4434.2.5

Eremchenko, V., Helfenberger, N., Shah, K.B. & Panfilov, A.M. (1998) Two new species of skinks (Scincidae: Ligosominae [sic]) from Nepal. *News National Academy of Science of Republik, Bishkek*, 4, 41–45. [in Russian]

Grismer, L.L., Wood, P.L. Jr., Le, M.D., Quah, E.S.H. & Grismer, J.L. (2020) Evolution of habitat preference in 243 species of Bent-toed geckos (Genus *Cyrtodactylus* Gray, 1827) with a discussion of karst habitat conservation. *Ecology and Evolution*, 10 (24), 13717–13730. https://doi.org/10.1002/ece3.6961

Grismer, L.L., Wood Jr., P.L., Poyarkov, N.A., Le, M.D., Kraus, F., Agarwal, I., Oliver, P.M., Nguyen, S.N., Nguyen, T.Q., Karunarathna, S., Welton, L.J., Stuart, B.L., Luu, V.Q., Bauer, A.M., O'Connell, K.A., Quah, E.S.H., Chan, K.O., Ziegler, T., Ngo, H., Nazarov, R.A., Aowphol, A., Chomdej, S., Suwannapoom, C., Siler, C.D., Anuar, S., Tri, N.V. & Grismer, J.L. (2021) Phylogenetic partitioning of the third-largest vertebrate genus in the world, *Cyrtodactylus* Gray, 1827 (Reptilia; Squamata; Gekkonidae) and its relevance to taxonomy and conservation. *Vertebrate Zoology*, 71, 101–154. https://doi.org/10.3897/vz.71.e59307

Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P., Yang, Q., Zhu, C. & Qiao, H. (2021) Sampling biases shape our view of the natural world. *Ecography*, 44 (9), 1259–1269. https://doi.org/10.1111/ecog.05926

Kästle, W., Rai, K. & Schleich, H. (2013) *Field Guide to Amphibians and Reptiles of Nepal.* ARCO-Nepal e. V., Munich, 625

pp., 52 pls., 156 color photographs, 180 maps.
Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589.
https://doi.org/10.1038/nmeth.4285
Khan, M.S. (2003) Questions of generic designation of angular-toed geckos of Pakistan with descriptions of three new genera (Reptilia: Gekkonidae). *Journal of Natural History and Wildlife*, 2 (2), 1–9.
Kluge, A.G. (1985) Notes on gekko nomenclature (Sauria: Gekkonidae). *Zoologische Mededelingen*, 59 (10), 95–100.
Lalremsanga, H.T., Colney, Z., Vabeiryureilai, M., Malsawmdawngliana, F., Bohra, S.C., Biakzuala, L., Muansanga, L., Das, M. & Purkayastha, J. (2023) It's all in the name: Another new *Cyrtodactylus* Gray (Squamata: Gekkonidae) from northern Mizoram, North-east India. *Zootaxa*, 5369 (4), 553–575.
https://doi.org/10.11646/zootaxa.5369.4.5
Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2016) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34 (3), 772–773.
https://doi.org/10.1093/molbev/msw260
Macey, J.R., Larson, A., Ananjeva, N.B., Fang, Z. & Papenfuss, T.J. (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14 (1), 91–104.
https://doi.org/10.1093/oxfordjournals.molbev.a025706
Mahony, S., Ahmed, M., Hossain, M.K., Kabir, M.M. & Hasan, M.K. (2009) *Cyrtodactylus ayeyarwadyensis* Bauer, 2003 (Reptilia: Gekkonidae) in Bangladesh with habitat details of new collection localities and a discussion of morphological variation. *Salamandra*, 45 (4), 245–260.
Mahony, S. & Kamei, R.G. (2021) A new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae) from Manipur State, northeast India, with a critical review highlighting extensive errors in literature covering bent-toed geckos of the Indo-Burma region. *Journal of Natural History*, 55, 2445–2480.
https://doi.org/10.1080/00222933.2021.19946 67
Mani, M.S. (1974) Physical features. *In*: Mani, M.S. (Ed.), *Ecology and Biogeography in India*. Dr. W. Junk b.v. Publishers, The Hague, pp. 11–59.
https://doi.org/10.1007/978-94-010-2331-3_2
Mirza, Z.A., Bhosale, H., Ansari, F., Phansalkar, P., Sawant, M., Gowande, G. & Patel, H. (2021) A new species of geckos of the genus *Cyrtodactylus* Gray, 1827 from Arunachal Pradesh, India. *Evolutionary Systematics*, 5, 13–23.
https://doi.org/10.3897/evolsyst.5.61667
Mirza, Z.A., Bhosale, H.S., Thackeray, T., Phansalkar, P., Sawant, M., Gowande, G.G. & Patel, H. (2022) A new species of bent-toed geckos of the genus *Cyrtodactylus* Gray, 1827 from western Arunachal Pradesh, India. *Herpetozoa*, 35, 65–76.
https://doi.org/10.3897/herpetozoa.35.e80610
Nguyen, L.T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274.
https://doi.org/10.1093/molbev/msu300
Ouboter, P.E. (1986) A revision of the genus *Scincella* (Reptilia: Sauria: Scincidae) of Asia, with some notes on its evolution. *Zoologische Verhandelingen*, 229, 1–66.
Rai, T.P., Adhikari, S. & Antón, P.G. (2022) An updated checklist of amphibians and reptiles of Nepal. *Arco-Nepal Newsletter*, 23, 3–23.
Rösler, H. (2000) Kommentierte Liste der rezent, subrezent und fossil bekannten Geckotaxa (Reptilia: Gekkonomorpha). *Gekkota*, 2, 28–153.
Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19 (12), 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180
Ronquist, F., Teslenko, M., Mark, V.D.P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029
Schleich, H.H. & Kästle, W. (2002) *Amphibians and reptiles of Nepal*. *Biology, Systematics, Field Guide*. Koeltz Scientific Books, Koenigstein, 1211 pp.
Schleich, H.H. & Kästle, W. (1998a) Description of *Gonydactylus nepalensis* spec. nov. from the Inner Terai of far west Nepal (Reptilia: Sauria: Gekkonidae). *In*: Schleich, H.H. & Kästle, W. (Eds.), *Contributions to the Herpetology of South-Asia* (*Nepal, India*). Fuhlrott-Museum, Wuppertal, pp. 269–280.
Schleich, H.H. & Kästle, W. (1998b) *Sitana fusca* spec. nov., a further species from the *Sitana sivalensis*- complex. *In*: Schleich, H.H. & Kästle, W. (Eds.), *Contributions to the Herpetology of South-Asia* (*Nepal, India*). Fuhlrott-Museum, Wuppertal, pp. 207–226.
Schleich, H.H., Kästle, W. & Shah, K.B. (1998) Description of *Sitana sivalensis* spec. nov., (Sauria: Agamidae) from south Nepal. *In*: Schleich, H.H. & Kästle, W. (Eds.), *Contributions to the Herpetology of South-Asia* (*Nepal, India*). Fuhlrott-Museum, Wuppertal, pp. 87–100.

Shah, K.B. (1998) Checklist of the herpetofauna of Nepal with English and vernacular names. *NAHSON Bulletin*, 8 (1–4), 26–30.
Shah, K.B. & Tiwari, S. (2004) *Herpetofauna of Nepal. A Conservation Companion*. IUCN Nepal, The World Conservation Union, Kathmandu, viii + 237 pp.
Shrestha, T.K. (2001) *Herpetology of Nepal. A Field Guide to Amphibians and Reptiles of Trans-Himalayan Region of Nepal, India, Pakistan and Bhutan*. Variety Printers, Kathmandu, 280 pp.
Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28 (10), 2731–2739.
https://doi.org/10.1093/molbev/msr121
Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
https://doi.org/10.1093/nar/22.22.4673
Tillack, F. & Grossmann, W. (2001) Ein neuer Nachweis zur Schlangenfauna Nepals: *Bungarus niger* Wall, 1908 (Reptilia: Serpentes: Elapidae). *Sauria*, 23 (1), 3–9.
Trifinopoulos, J., Nguyen, L.T., Von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44 (W1), W232–W235.
https://doi.org/10.1093/nar/gkw256
Uetz, P., Rai, T.P., Thapa, R., Lester, B. & Freed, P. (2022) Herpetologische Reise nach Nepal [A herpetological trip to Nepal]. *Sauria*, 44 (4), 3–31. [bilingual German/English]
Uetz, P., Freed, P., Aguilar, R., Reyes, F., Kudera, J. & Hošek, J. (Eds.) (2024) The Reptile Database. Available from: http://www.reptile-database.org (accessed 30 August 2024)
Wood Jr., P.L., Heinicke, M.P., Jackman, T.R. & Bauer, A.M. (2012) Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetics and Evolution*, 65 (3), 992–1003.
https://doi.org/10.1016/j.ympev.2012.08.025

APPENDIX 1 Material examined.

Museum abbreviations are as follows: Centre for Ecological Sciences, Indian Institute of Science, Bangalore (CES); and Bombay Natural History Society, Mumbai (BNHS).

Cyrtodactylus bhupathyi: holotype, BNHS 2255, adult female; paratype BNHS 2256, adult female; from near Bagdogra, Darjeeling District, West Bengal, India.

Cyrtodactylus chamba: holotype, BNHS 2332, adult male; paratypes, BNHS 2330, adult male, BNHS 2333, juvenile male, BNHS 2331, BNHS 2334, and BNHS 2335, adult females, from near Chamba in Chamba District, Himachal Pradesh, India.

Cyrtodactylus fasciolatus: CES09/1269–1271 from near Tattapani; CES09/1337–1339, from near Subathu, both in Shimla District, Himachal Pradesh, India.

Cyrtodactylus gubernatoris: BNHS 2207, adult male, BNHS 2208–2210, adult females, from near Singtam, East Sikkim District, Sikkim, India. http://www.reptile-database.org

Cyrtodactylus himalayicus: holotype, ZSIK 15716, adult male, from Kurseong; ZSIK 19546, adult female from Gopaldhara; both from Darjeeling District, West Bengal, India.

Cyrtodactylus lawderanus: CES09/ 1253–1256, Nahan-Renuka road, Sirmaur District; CES09/ 1262 Sadhupul, Solan District; CES09/ 1264–1266, near Jutogh, Shimla District; CES09/ 1268 Shimla-Pujarli Road, Shimla District; CES09/ 1275–1281, Aut, Mandi District; CES09/ 1285–1288 Kangra-Jawala Mukhi Road, Kangra District; CES09/ 1288 Sujanpur-Tira, District; CES09/ 1335 Rewalsar, Mandi District; all from Himachal Pradesh. CES09/ 1330, near Mansar, Udhampur District, Jammu and Kashmir, India; CES09/ 1343–1344, Almora, Almora District, Uttarakhand, India.

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

TABLE S1. Pairwise uncorrected ND2 sequence divergence (%) within sampled members of the Indo-Burma clade. Nepal species names and maximum intraspecific divergence in bold.