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Resolving taxonomic ambiguities in extant Himalayan lazy toads: A new species of the genus *Scutiger* (Anura, Megophryidae) from eastern Nepal

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Abstract. The biodiversity of the Himalaya remains significantly understudied and, at the same time, is increasingly threatened by habitat loss due to rising anthropogenic pressures and climate change. Lazy Toads of the genus *Scutiger* are endemic to the Himalaya-Tibet orogen and form a diverse and characteristic component of the Himalayan montane zone. In our study, we re-assess material of *Scutiger sikimmensis* s. lat. using both molecular and morphological data. Our findings support the description of a new species, *Scutiger khumbu* sp. nov., with the nominotypical subspecies distributed in the Nepalese Khumbu Himal, and the subspecies *Scutiger khumbu makalu* subsp. nov. from the adjacent Makalu range.

Keywords. Amphibia, Himalaya, molecular systematics, morphology, *Scutiger*, taxonomy.

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Introduction

The Himalaya, one of the world's most biologically diverse regions (Mittermeier *et al.* 2011), remains significantly understudied despite its critical ecological importance. Its vast array of species, many still unknown to science, faces growing threats from habitat destruction due to rising anthropogenic pressures, including deforestation and climate change (Pandit *et al.* 2007, 2014; Chauhan *et al.* 2023). These accelerating changes not only impact fragile ecosystems but also risk the loss of countless species before they can be fully recorded or understood. Comprehensive research and documentation of Himalayan biodiversity is, therefore, not only urgent for conservation efforts but also crucial for advancing our knowledge of this unique region.

Lazy Toads of the genus *Scutiger* Theobald, 1868, family Megophryidae Bonaparte, 1850, are endemic to the Himalaya-Tibet orogenic system and adapted to high montane and alpine areas. They occur in northern Pakistan, through India, Nepal, Bhutan, northern Myanmar, in the valleys of the southern Tibet Plateau and along the eastern and southeastern plateau margins. About 30 species are currently recognized in this genus (Frost 2024), most of which are distributed along the eastern margins of the Tibetan Plateau in the Provinces Sichuan and Yunnan, China (Fig. 1). Only nine species are known from the Greater Himalaya: *S. occidentalis* Dubois, 1978 from the Western Himalaya; *S. ghunsa* Khatiwada, Shu, Subedi, Wang, Ohler, Cannatella, Xie & Jiang, 2019, *S. kanjiroba* Hofmann, Jablonski & Schmidt, 2024, *S. nepalensis* Dubois, 1974, and *S. sikimmensis* (Blyth, 1855) from the Central Himalaya; *S. bhutanensis* Delorme & Dubois, 2001, *S. nyingchiensis* Fei, 1977, *S. spinosus* Jiang, Wang, Li & Che, 2016, and *S. wuguanfui* Jiang, Rao, Yuan, Wang, Li, Hou, Che & Che, 2012 from the East Himalaya. Most of these species exhibit a disjunct distribution pattern, which is hypothesized to have arisen from the displacement of their habitats from ancestral Tibet during the surface uplift of the Himalaya-Tibet orogen (Hofmann *et al.* 2024a). This uplift, associated with the aridification of a warm temperate Miocene Tibet, combined with high extirpation rates of ancestral populations and shifts in species ranges along drainage systems and the transverse valleys of the rising Himalaya, provides the most parsimonious explanation for the evolution of the current Himalayan *Scutiger* fauna (Hofmann *et al.* 2024a).

Interestingly, the assumed wide geographic range of the long-known species *Scutiger sikimmensis* differs considerably from the disjunct distribution of other Himalayan species of that genus. The species was described as *Bombinator sikimmensis* by Blyth (1855), presumably from Sikkim (Theobald 1868). Based on databases and literature, this species is supposed to have a wide distribution in Central and East Nepal through Sikkim and Meghalaya (India), Bhutan, and adjacent borderlands of southern Tibet (China), occurring at elevations between 2800 and over 4000 m (Schleich & Kästle 2002; Jetz *et al.* 2012; Frost 2024; but see Hofmann *et al.* 2024b).

Such an extensive range appears implausible for a single species and stands in stark contrast to the aforementioned biogeographic scenario, from which one would expect deep genetic structure as between other spatially restricted Himalayan *Scutiger* taxa. Recent advancements in the phylogeography of *Scutiger* have unveiled deeply divergent lineages with limited distributions within the two Himalayan taxa *S. nepalensis* and *S. sikimmensis* (Hofmann *et al.* 2024a). These new insights necessitate a thorough morphological and molecular reassessment of specimens. In this regard, museum collections offer a unique source of specimens that may provide crucial new information. Notably, tadpoles are rarely subjected to detailed analysis, despite their potential to contribute significant biological and ecological information that can inform species taxonomy, life history traits, and conservation strategies. Here, we sequenced tadpoles of the genus *Scutiger* with precisely known origin from museum collections and used the resulting information to identify additional museum material of adult specimens of *Scutiger* aff. *sikimmensis* collected at the same respective localities. Most of these adult specimens could not be used for genetic analyses due to formalin treatment during preservation, but they allow for morphological analyses.

Our study also provides molecular and morphological evidence that a phylogenetic clade (previously confounded with *S. sikimmensis*) requires taxonomic revision.

Material and methods

Sampling

All voucher specimens and tissue samples for newly generated molecular data were obtained from the following museum holdings: Muséum national d'Histoire naturelle, Paris (MNHN), Museum Koenig, Bonn (ZFMK), and Natural History Museum, Erfurt (NHME). In total, 21 specimens of *Scutiger* aff. *sikimmensis* from eastern Nepal were investigated morphologically, and we could obtain molecular data for four of these specimens. Additional DNA sequencing data were generated from ethanol-preserved tadpoles, imagos or tissue, available at the MNHN and NHME. The list of samples and their associated metadata are presented in Supp. file 1A–C.

Comparative specimens

Scutiger aff. *sikimmensis*: 21 specimens of *S. sikimmensis* s. lat. stored at the MNHN (1977.1246–1262, 2003.3041–3042) and the ZFMK (104174–104175). Notably, Dubois (1987: 20) listed over 100 specimens

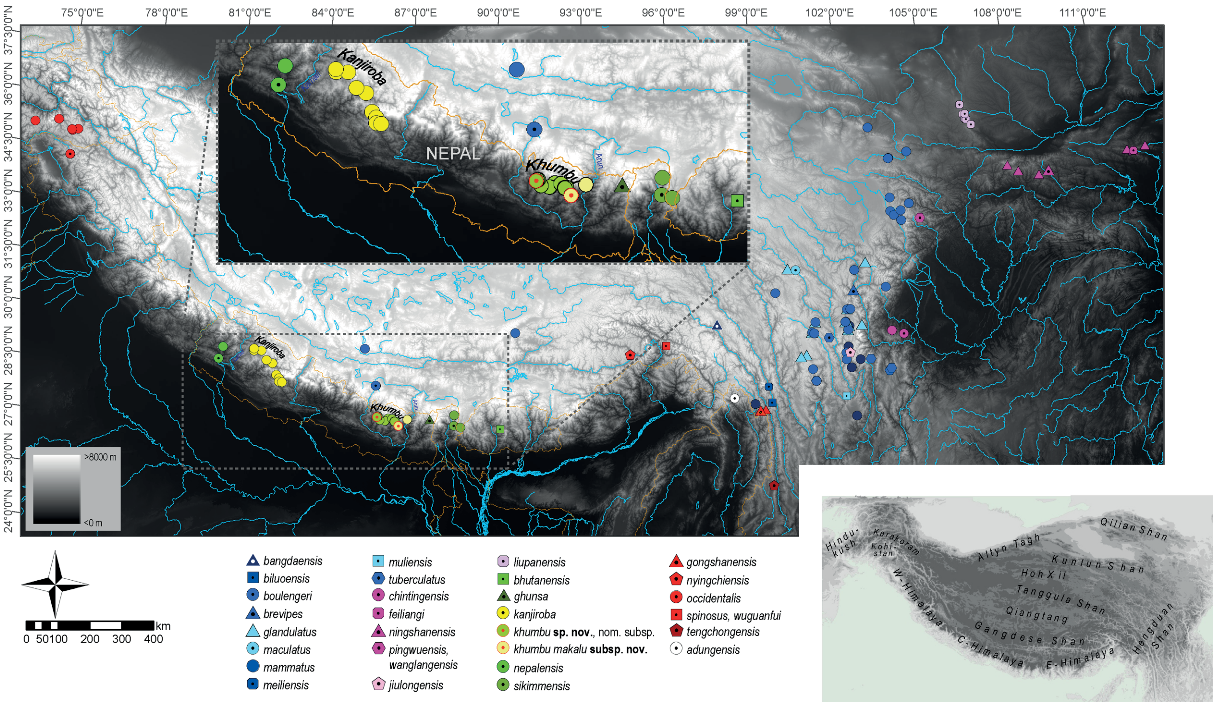

Fig. 1. Overview of the Himalaya-Tibet orogenic area and occurrences of species of *Scutiger* Theobald, 1868. Holotype localities are indicated by symbols with a dot. The species *S. glandulatus* (Liu, 1950) and *S. mammatus* (Günther, 1896) lack the georeferenced type locality, some type localities could only be roughly approximated due to imprecise information in the original description (e.g., *S. adungensis* Dubois, 1979, *S. bhutanensis* Delorme & Dubois, 2001, and *S. brevipes* (Liu, 1950)).

referred to *Scutiger sikimmensis*, several of which originated from the Everest region. From these, we selected only those specimens where the collection site matched the location for which molecular data were available (obtained from tadpoles or tissue), but for which no specimens suitable for morphological analyses had previously been examined. Since it is highly unlikely that distinct lineages would occur at the same locality—we are not aware of any case of sympatry or syntopy among Himalayan species of *Scutiger*—the available molecular data can be confidently linked to museum specimens lacking genetic data, provided that all data come from the same locality.

Morphological data of other *Scutiger* species were mined from the original species descriptions and/or recompiled treatises, particularly Fei *et al.* (2009, 2012) and Hofmann *et al.* (2024b).

Specimens were assigned to the genus *Scutiger* based on the following combination of features: general Megophryidae morphology, tympanum and tympanic ring entirely absent, pupil vertically elliptic, vomerine teeth absent, maxillary teeth absent or indistinct, femoral glands indistinct, tongue rounded or slightly indented behind, fingers free, toes free or with some webbing, dorsum warty, and pectoral (and axillary) glands and fingers with nuptial spines (in males) (Myers & Leviton 1962; Fei *et al.* 2009; Fei & Ye 2016).

Laboratory work and molecular analysis

Total genomic DNA was isolated from tissues preserved in ethanol using the Qiagen DNeasy kit (Qiagen Inc.) following the manufacturer's protocol. We amplified partial sequences of the following three mitochondrial (mt) and three nuclear (nu) loci via the polymerase chain reaction (PCR): 16S rRNA, cytochrome oxidase subunit 1 (COI), and cytochrome b (cytb), as well as beta-fibrinogen intron 7 (bfib7), cyclin B2 gene intron 3 (ccnb2), and recombination activating protein 1 gene (rag1); for primers and PCR conditions see Hofmann *et al.* (2017). Heterozygotes in electropherograms of the nuclear loci were identified based on secondary peak calling. All protein-coding gene fragments were translated into amino acids; no frameshift mutations or premature stop codons were observed. Nuclear alleles were not phased because most populations were represented by only a few or single individuals, which did not allow a robust statistical inference of haplotypes. Therefore, polymorphic sites were encoded with the appropriate IUPAC ambiguity code. All newly generated sequences were deposited in GenBank (accession numbers: Supp. file 1B–C). Additional *Scutiger* and appropriate outgroup sequences corresponding to the molecular target loci were retrieved from GenBank, combined with our new sequences, and subsequently aligned for each marker using Mega11 software (Tamura *et al.* 2021).

DNA sequences from the three mitochondrial loci of each species were concatenated and used for the Bayesian inference (BI) analysis (2203 bp: 550 bp 16S, 668 bp COI, 985 bp cytb), while the alignments of the three nuclear gene fragments were used separately for network analysis (bfib7: 508 bp; ccnb2: 777 bp; rag1: 957 bp). Phylogenetic trees were inferred with MrBayes ver. 3.2.7a using five million generations, sampling every 500th generation. We used four parallel Markov chain Monte Carlo simulations with four chains and discarded the first 25% of the samples of each run as burn-in. Chain convergence was monitored with Tracer ver. 1.7.1 (Rambaut *et al.* 2018). Phylogenetic networks were generated based on uncorrected p-distances using the Neighbor-Net algorithm (Bryant & Moulton 2004) implemented in SplitsTree ver. 4.19.2 (Huson & Bryant 2006).

To identify molecular characters which can discriminate between taxa we used the DeSignate web server (Hütter *et al.* 2020). This tool detects two types of signature characters (diagnostic molecular characters): (i) Binary signatures, comprising only two different character states, i.e., one in the query group (e.g., nucleotide base C) and a different one in the reference group (e.g., nucleotide base G); (ii) Asymmetric signatures, comprising at least two character states in the reference group (e.g., nucleotide bases C, G, or T) that are different from the uniform character state in the query group (e.g., nucleotide base A). We concentrated our analysis on the protein-coding mitochondrial barcoding gene COI, as sequence data are available for this marker in most *Scutiger* species (24 out of 30). The size of the search parameter 'k-window' was set to 1 for the individual signature. We used the annotated mitochondrial genome of *Scutiger ningshanensis* Fang, 1985 (NCBI Reference Sequence: NC_031426.1) as a reference to determine base pair positions.

Morphological analysis

The following measurements were taken with a dial caliper and recorded to the nearest 0.1 mm:
ED = horizontal diameter of eye
END = eyelid-naris distance (from naris to anterior edge of the eye)
FAL = forearm length (from flexed elbow to base of inner metacarpal tubercle)
FEL = femur (thigh) length (from vent to outer edge of flexed knee)
FOL = foot length (distance from proximal edge of inner metatarsal tubercle to tip of 4th toe)
HAL = hand length (from base of inner metacarpal tubercle to tip of 3rd finger)
HL = head length (distance from angle of jaws to snout-tip)
HW = head width (measured at posterior angle of jaws)
IND = internarial distance
NSD = distance of naris to tip of snout
SVL = snout-vent length (distance from tip of snout to posterior edge of vent)
SL = snout length (from tip of snout to anterior corner of eye)
TaL = length of tarsus (distance from heel to proximal edge of inner metatarsal tubercle)
TIBL = tibia (shank) length (distance from outer edge of flexed knee to tip of heel)

We further recorded the relative length of fingers and toes, presence/absence of subarticular tubercles, presence/absence of vocal sac, presence/absence of vomerine (v)/maxillary (m) dentition, presence/absence of tympanum, webbing of toes (developed, weak, rudimentary, absent), finger(s) with nuptial spines, presence/absence of pectoral (p)/axillary (ax) glands, gland size relation (p much larger (>>) than ax; p only slightly larger (>) than ax; p of the same size (=) as ax), presence/absence of spines on p/ax, presence/absence of spines on inner forearms, presence/absence of spines on belly, presence/absence of tubercles/warts on dorsal (and lateral) surfaces of body and/or limbs, presence/absence of black spines on dorsal tubercles. Sex was determined by the presence of nuptial spines on fingers and chest in males in breeding condition.

All statistical analyses were conducted using R ver. 4.3.3 (RCoreTeam 2024). Each metric character, except SVL and ratios, with a minimum sample size per group of three was allometrically adjusted using the package GroupStruct (Chan & Grismer 2021) and the function 'allom' with the correction modus 'species'. This method returns log-transformed and body-size-adjusted measurements using a separate regression slope for each species and trait.

A Levene's test for the normalized characters and ratios was conducted to test for equal variances across all groups. Characters with equal variances ($F \geq 0.05$) were analyzed by an analysis of variance (ANOVA) and TukeyHSD post hoc test. Those with unequal variances ($F < 0.05$) were subjected to Welsh's ANOVA and Games-Howell post hoc test. We then used the normalized characters for a Principal Components Analysis (PCA) with the packages FactoMineR (Le *et al.* 2008), ggfortify (Tang *et al.* 2016; Horikoshi & Tang 2018), and ggplot2 ver. 3.5.0 (Wickham 2016). We included specimens from the candidate species together with the geographically closest species described, namely *Scutiger ghunsa*, *S. kanjiroba*, and *S. nepalensis* (data of the latter three species are from Hofmann *et al.* 2024b). For *S. sikimmensis*, comparable morphometric data for individual features were not available to us (see also Hofmann *et al.* 2024b) – noting that despite previous confusions, this species is not phylogenetically closer to the new species than the three species mentioned above. Analyses were conducted for a combined dataset of both sexes, because of the small sample size per group.

The labial tooth row formula (LTRF) of each tadpole was recorded according to Dubois (1995), and the developmental stage was determined following Gosner (1960).

Results

mtDNA analysis and phylogenetic networks of nuDNA

Phylogenetic trees of the mtDNA genes (Fig. 2, concatenated 16S, COI and cytb, 2203 bp) and networks of the nuclear genes bfib7, ccnb2, and rag1 (Fig. 3) recover specimens from the Khumbu Himal and Makalu regions as a distinct clade. This clade consists of two clearly divergent lineages (one from the Khumbu and the other from the Makalu region), which are fully supported in the mitochondrial tree. The placement of this clade among other *Scutiger* species varies depending on the amount and type of molecular data, as is the case for the majority of known *Scutiger* taxa, given that the phylogeny of this genus remains unresolved (Hofmann *et al.* 2024a). However, their distinctness is robust and supported by genetic distances to congeners which range between 11.1% and 15.4% for COI, between 9.8% and 16.5% for cytb, and between 2.5% and 5.4% for 16S, which falls well within the overall range of genetic distances reported between other *Scutiger* species (4.0%–16.0% in COI, 2.8%–17.7% in cytb, and 1.1%–6.6% in 16S; Supp. file 1D–F). The genetic distances between the lineages from the Khumbu and Makalu regions were calculated at 8.8% for COI, 6.3% for cytb, and 2.5% for 16S (Supp. file 1D–I).

Due to low quality and concentration of the DNA and resulting difficulties in amplification, the following specimens were only barcoded through 16S: the sequence of MNHN2003.3039 (GenBank accession no PQ576545) was identical to sequences with accession numbers KY310802–KY310808 (Khumbu lineage) (95% of sequence coverage); MNHN2003.3042 (GenBank accession no PQ576548) was identical to sequences KY310797–KY310800 (Makalu lineage) (94% of sequence coverage).

We identified several molecular signatures in the COI alignment that distinguish the candidate species from other *Scutiger* species (Table 1). The lineage from the Khumbu Himal and the lineage from the Makalu region were clearly differentiated from each other and from known *Scutiger* species. The Khumbu lineage was separated by eight diagnostic characters of the asymmetric type, while the Makalu lineage was distinguished by two binary diagnostic characters and four asymmetric diagnostic characters.

Morphological comparison

Given their geographic distribution (Fig. 1), our previous phylogenomic findings (Hofmann *et al.* 2024a), as well as the molecular results presented here, the distinction between specimens that belong to the newly discovered phylogenetic clade and specimens from the clades comprising *S. kanjiroba*, *S. nepalensis*, as well as *S. ghunsa* is particularly relevant: PCA performed on the trait matrix of these specimens yielded two significant principal components (eigenvalues > 1), which captured 82.8% of the morphological variation. Ordination is plotted for the first two components in Fig. 4, showing a clear separation of the species *S. ghunsa*, *S. kanjiroba*, *S. nepalensis*, and specimens of the newly discovered clade. PC1 described the highest variance of the model (64.4%), with the most important explanatory variables being the head length (-0.31), foot length (-0.30), and head width (-0.30); PC2 accounted for 16.5% variability, mainly linked to the hand length (-0.58) and the HW/HL ratio (-0.53) (Table 2). Significant differences were found between the species for almost all metric characters (Fig. 5). Results remained largely unchanged after excluding the two representatives from the Makalu lineage (MNHN2003.3041, MNHN2003.3042; Supp. file 1J). Accordingly, specimens of the newly discovered clade can be readily distinguished from *S. kanjiroba* and *S. nepalensis* by their significantly smaller body size, relatively smaller head and smaller eyes, a relatively shorter snout, relatively shorter eyelid-naris and internarial distance, relatively shorter

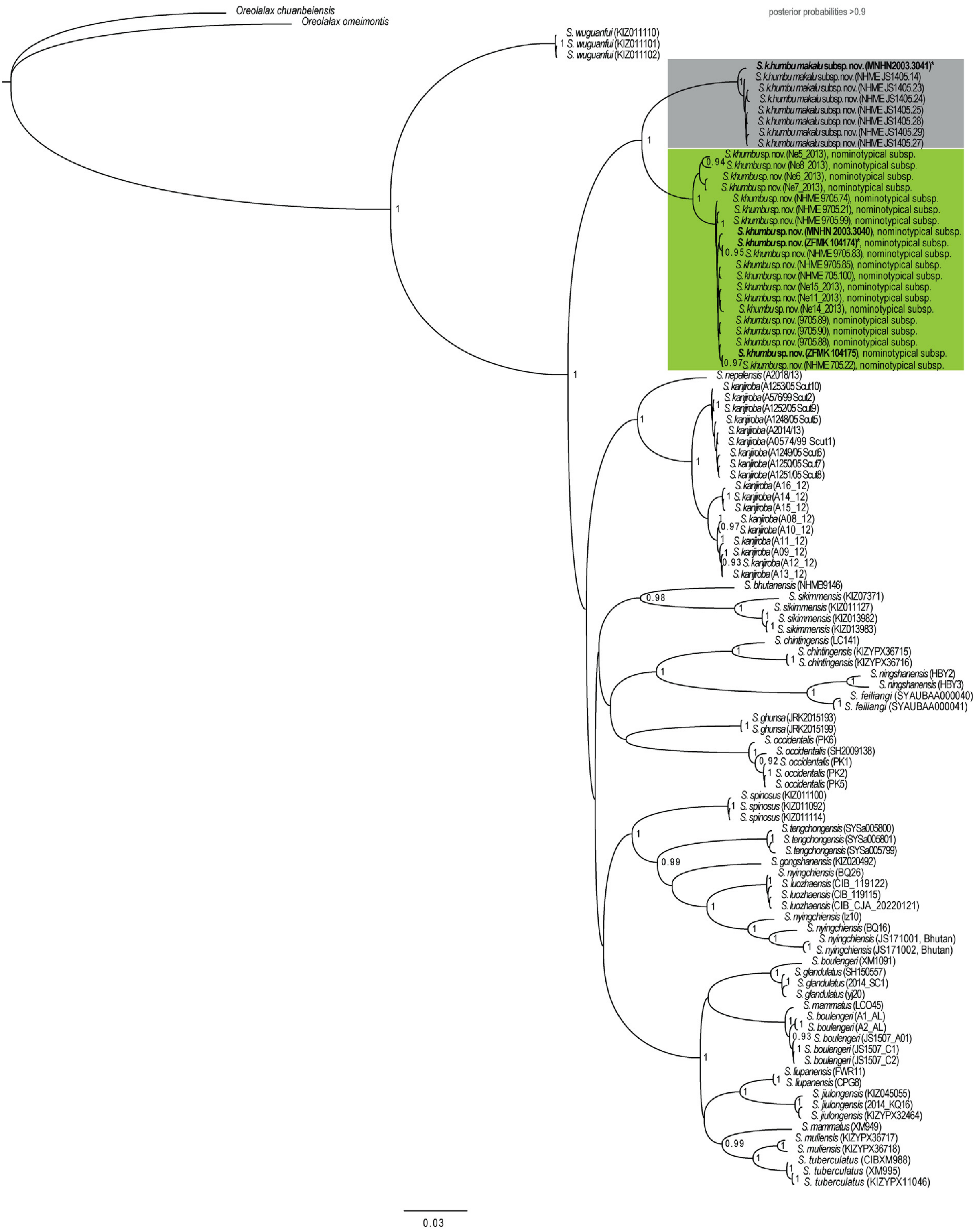

Fig. 2. Majority rule consensus tree from 10 000 trees from a Bayesian Inference analysis (5 million generations) of *Scutiger* Theobald, 1868 based on the concatenated mtDNA sequences of 16S, COI, and cytb. Node values are Bayesian posterior probabilities ≥0.9. Holotype (*) and adult paratype specimens are indicated in bold. Only samples with data for more than one locus were included.

Fig. 3. Neighbor-Net networks (Bryant & Moulton 2004) of the nuclear genes retrieved in *Scutiger* Theobald, 1868. **A**. Beta-fibrinogen gene, intron 7. **B**. Cyclin B2 gene, intron 3. **C**. Rag1 gene.

Table 1. Detailed list of signature characters detected in the COI alignment (668 bp; for accession numbers see Supp. file 1B) using **(A)** nominotypical subspecies (nom. subsp.) of *Scutiger khumbu* sp. nov. **(B)** *Scutiger khumbu makalu* subsp. nov. as query and sequences of 24 currently recognized species as reference group (n_ref_spec); character state in query group (q_rank) and most frequent character state in reference group (r_rank), discrete (disc_entropy) and average (avg_entropy) entropy values as well as the type of signature character are given. Position refers to the annotated mitochondrial genome of *Scutiger ningshanensis* Fang, 1985 (NCBI Reference Sequence: NC_031426.1), followed by the relative position in the local alignment in brackets. For the following currently recognized *Scutiger* species sequence data of COI are not available in GenBank: *S. adungensis* Dubois, 1979, *S. bangdaensis* Rao, Hui, Ma & Zhu, 2022, *S. biluoensis* Rao, Hui, Zhu & Ma, 2022, *S. brevipes* (Liu, 1950), *S. maculatus* (Liu, 1950), and *S. meiliensis* Rao, Hui, Zhu & Ma, 2022.

(A) query (n = 19)	**n_ref_ spec**	**n_ref**	**position**	**q_rank**	**r_rank**	**disc_ entropy**	**avg_ entropy**	**type**	**comment**
S. khumbu sp. nov., nom. subsp.	24	73	5963 (282)	(1 ,a‘)	(2 ,c‘)	1.564	0.4845	asymmetric	‘a’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	6065 (384)	(1 ,c‘)	(2 ,a‘)	1.022	0.2202	asymmetric	‘c’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	6104 (423)	(1 ,a‘)	(2 ,t‘)	0.789	0.3154	asymmetric	‘a’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	6245 (564)	(1 ,c‘)	(2 ,t‘)	0.847	0.4054	asymmetric	‘c’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	6008 (327)	(1 ,g‘)	(3 ,c‘)	1.516	0.3667	asymmetric	‘g’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	6227 (546)	(1 ,c‘)	(3 ,a‘)	1.570	0.4307	asymmetric	‘c’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	5771 (90)	(1 ,t‘)	(4 ,a‘)	1.600	0.4211	asymmetric	‘t’ signature character for nominotypical subsp.
S. khumbu sp. nov., nom. subsp.	24	73	5774 (93)	(1 ,c‘)	(4 ,a‘)	1.278	0.453	asymmetric	‘c’ signature character for nominotypical subsp.

(B) query (n = 6)	**n_ref_ spec**	**n_ref**	**position**	**q_rank**	**r_rank**	**disc_ entropy**	**avg_ entropy**	**type**	**comment**
S. khumbu makalu subsp.nov.	24	73	5930 (249)	(1 ,c‘)	(1 ,t‘)	0.332	0.2016	binary	same when including nominotypical subsp. in n_ref
S. khumbu makalu subsp.nov.	24	73	5964 (283)	(1 ,t‘)	(1 ,c‘)	0.332	0.5049	binary	same when including nominotypical subsp. in n_ref
S. khumbu makalu subsp.nov.	24	73	5867 (186)	(1 ,t‘)	(2 ,c‘)	0.668	0.1974	asymmetric	same when including nominotypical subsp. in n_ref
S. khumbu makalu subsp.nov.	24	73	5963 (282)	(1 ,a‘)	(2 ,c‘)	1.564	0.4845	asymmetric	same when including nominotypical subsp. in n_ref
S. khumbu makalu subsp.nov.	24	73	6059 (378)	(1 ,t‘)	(2 ,c‘)	0.732	0.2552	asymmetric	same when including nominotypical subsp. in n_ref
S. khumbu makalu subsp.nov.	24	73	6266 (585)	(1 ,t‘)	(2 ,a‘)	0.732	0.3456	asymmetric	same when including nominotypical subsp. in n_ref

forearm, femur, shank, foot, tarsus and hand length, and from *S. ghunsa* by a relatively longer head and snout, relatively longer forearm and tibia, and relatively shorter hand length (Fig. 5).

Full data of the morphological comparisons between the *Scutiger* specimens of the newly discovered clade and their congeners are available in Table 3 and Supp. file 1K.

Species delimitation and systematic revisions

To delimit species in the genus *Scutiger*, we considered sets of populations that belong to deeply diverged lineages supported by mitochondrial and nuclear evidence, eventually accompanied by external differences (Wiley 1978; Dufresnes *et al.* 2023; Vences *et al.* 2024), and with levels of differentiation similar or above the differentiation reported between currently recognized species of the genus. We designated robustly supported phylogeographic lineages as subspecies when their genetic divergence was typically lower than that observed among other *Scutiger* species. The subspecies rank serves as an appropriate compromise, recognizing their distinct diversity while avoiding taxonomic inflation at the species level in the absence of more definitive evidence for speciation (Dufresnes *et al.* 2023).

Accordingly, and based on our phylogenetic and morphological findings, we consider the *Scutiger* populations inhabiting the central-eastern Nepal Himalaya between the Tama Koshi and Arun transverse valleys as the new species composed of two allopatric subspecies, for which we provide taxonomic descriptions.

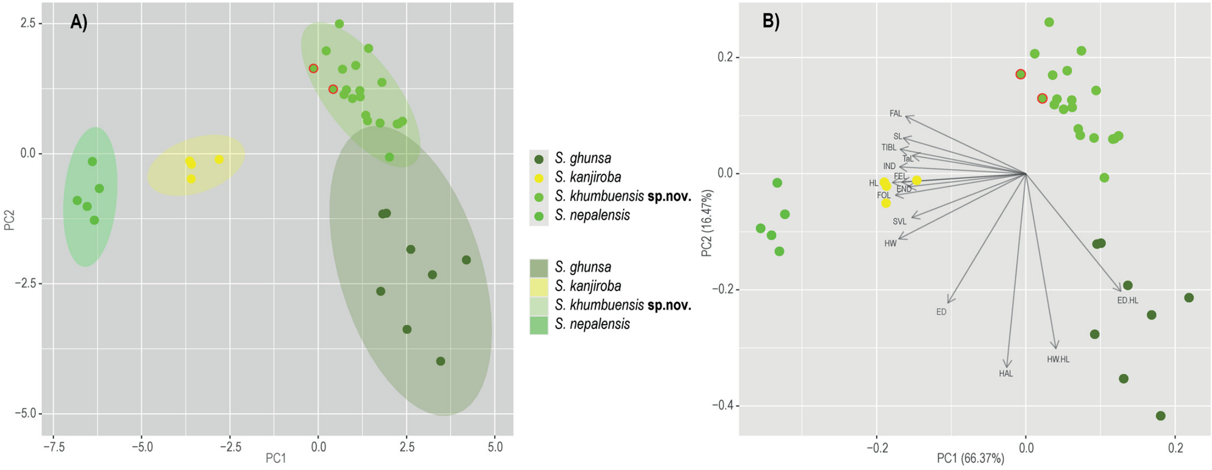

Fig. 4. PCA of metric variables in 37 adult specimens of closely related Himalayan species of *Scutiger* Theobald, 1868. Notably, *Scutiger khumbu* sp. nov. includes all members of the nominotypical subspecies and the subspecies *S. k. makalu* subsp. nov. (placements of the voucher specimens of *Scutiger khumbu makalu* subsp. nov. are indicated by red-outlined circles). **A**. With 95% confidence ellipses. **B**. With loadings. ED = horizontal diameter of eye; ED.HL = ratio ED/HL; END = eyelid-naris distance; FAL = forearm length; FEL = femur (thigh) length; FOL = foot length; HAL = hand length; HL = head length; HW = head width; HW.HL = ratio HW/HL; IND = internarial distance; SL = snout length; SVL = snout-vent length (raw data); TaL = length of tarsus; TIBL = tibia (shank) length.

Table 2. (A) Eigenvalues of the first six principal components. **(B)** Loadings of body size-adjusted measures (except SVL and ratios). **(C)** Values of each PC's eigenvector with the proportion of variation explained by each eigenvalue, and the cumulative proportions of variation explained. For raw measurements see Table 3.

(A)	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Eigenvalue	3.1553	1.5718	0.8842	0.6438	0.5884	0.5222
% variance explained	0.6637	0.1647	0.0521	0.0276	0.0231	0.0182
Cumulative variance	0.6637	0.8284	0.8805	0.9082	0.9313	0.9494

(B)	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
SVL (raw data)	-0.2661	-0.1317	-0.0604	-0.2020	0.3077	-0.0800
HL	-0.3114	-0.0265	-0.0643	-0.1434	0.0100	0.0955
HW	-0.2965	-0.1957	0.0614	-0.0430	0.1347	0.0561
SL	-0.2859	0.1071	-0.2243	0.0041	0.3541	-0.3841
ED	-0.1821	-0.3877	-0.6004	-0.0704	-0.0113	0.0762
END	-0.2742	-0.0391	0.2500	-0.2574	-0.4185	-0.4597
IND	-0.2948	0.0205	-0.0212	-0.1557	0.1910	-0.3042
FAL	-0.2808	0.1724	0.0107	-0.1402	-0.0185	0.5365
HAL	-0.0449	-0.5810	0.2423	-0.2792	-0.3508	0.0945
FEL	-0.2893	-0.0255	0.1483	0.2968	0.0684	0.2824
TIBL	-0.2933	0.0733	0.0996	0.3590	0.0768	0.0918
TaL	-0.2647	0.0543	-0.1521	0.5919	-0.4965	-0.2349
FOL	-0.3043	-0.0646	0.0233	0.0248	-0.1358	0.2654
Ratio HW/HL	0.0699	-0.5245	0.4170	0.3838	0.3845	-0.1152
Ratio ED/HL	0.2216	-0.3526	-0.4758	0.1687	-0.0567	0.0161

(C)	**Eigenvalue**	**Variance %**	**Cumulative variance %**
Dim.1	9.956	66.372	66.372
Dim.2	2.470	16.470	82.842
Dim.3	0.782	5.212	88.054
Dim.4	0.415	2.763	90.817
Dim.5	0.346	2.308	93.125
Dim.6	0.273	1.818	94.943
Dim.7	0.260	1.736	96.679
Dim.8	0.198	1.321	98.000
Dim.9	0.095	0.634	98.634
Dim.10	0.079	0.524	99.159
Dim.11	0.055	0.367	99.525
Dim.12	0.039	0.257	99.783
Dim.13	0.028	0.186	99.968
Dim.14	0.004	0.025	99.993
Dim.15	0.001	0.007	100.000

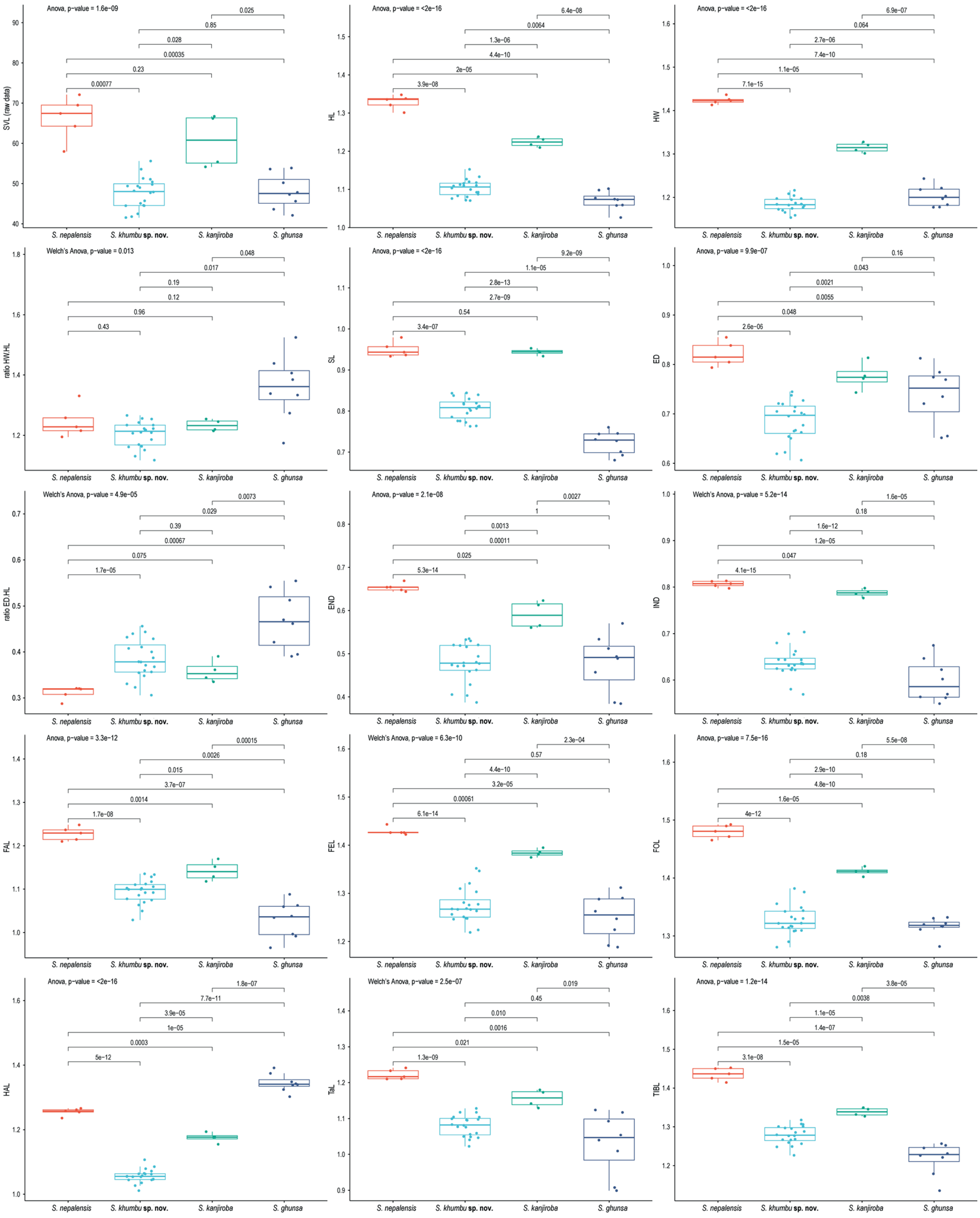

Fig. 5. Graphic representation of results of the one-way ANOVA and PCA for *Scutiger khumbu* sp. nov. (including specimens of both taxa, the nominotypical subspecies and *S. khumbu makalu* subsp. nov.; n = 20) for SVL, body ratios, and the normalized morphometric characters and pairwise comparison between groups. SVL = snout-vent length (raw data); HL = head length; HW = head width; ratio HW/HL; SL = snout length; ED = horizontal diameter of eye; ratio ED/HL; END = eyelid-naris distance; IND = internarial distance; FAL = forearm length; FEL = femur (thigh) length; FOL = foot length; HAL = hand length; TaL = length of tarsus; TIBL = tibia (shank) length.

Table 3 (continued on next page). Morphological evaluation of *S. nepalensis* Dubois, 1974, *S. kanjiroba* Hofmann, Jablonski & Schmidt, 2024, *S. khumbu* sp. nov. with its nominotypical subspecies *S. khumbu* sp. nov. and *S. k. makalu* subsp. nov., and *S. ghunsa* Khatiwada, Shu, Subedi, Wang, Ohler, Cannatella, Xie & Jiang, 2019. SVL = Snout–vent length; HL = head length; HW = head width; SL = snout length; NSD = distance of naris (center) to tip of snout; ED = horizontal diameter of eye; END = eyelid-naris distance; IND = internarial distance; FAL = forearm length; HAL = hand length; FEL = femur (thigh) length; TIBL = tibia (shank) length; TaL = length of tarsus; FOL = foot length; 1 = relative length of fingers; 2 = relative length of toes; 3 = subarticular tubercles present (1) / absent (0); 4 = vocal sac present (1) / absent (0); 5 = vomerine/maxillary dentation present (1) or absent (0); 6 = tympanum present (1) / absent (0); 7 = webbing toes (rud.=rudimentary; 0=absent); 8 = finger(s) with nuptial spines (males); 9 = pectoral/axillar glands (males); 10 = gland size (p, ax); 11 = spines on p/ax present (1) or absent (0); 12 = spines on (inner) (fore)arms of males present (1)/absent (0); 13 = belly with (1) or without (0) spines; 14 = tubercles/warts on dorsal (and lateral) surfaces of body and/or limbs present (1) or absent (0); 15 = dorsal tubercles with (1) or without (0) black spines in breeding condition (males). Age: a = adult, sa = subadult; sex: f = female, m = male. MNHN = Muséum national d'Histoire naturelle, Paris, France; NHME = Natural History Museum Erfurt, Germany; ZFMK = Museum Koenig, Bonn, Germany.

Source	ID	Species	Type	N	E	Age	Sex	SVL	HL	HW	HW/HL	SL	NSD	ED	ED/HL	END	IND	FAL	HAL	FEL	TIBL	TaL	FOL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
MNHN	1974.1096	*nepalensis*	para	29.30	80.99	a	m	67.5	21.9	26.1	1.2	9.3	4.6	6.3	0.3	4.6	6.6	16.6	17.6	28.2	27.3	16.7	29.7	3>4>2=1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1	0	0	1	1
MNHN	1974.1097	*nepalensis*	para	29.30	80.99	a	f	64.3	21.9	26.9	1.2	9.2	4.1	7.0	0.3	4.3	6.4	15.7	17.7	26.0	24.9	15.5	30.0	3>4>2>1	4>3>2>5>1	0	0	0/0	0	rud.	0	0	—	—	0	0	1	—
MNHN	1974.1098	*nepalensis*	para	29.30	80.99	a	f	58.0	19.5	24.5	1.3	7.2	3.4	6.0	0.3	4.1	5.8	14.2	15.7	23.9	23.4	14.1	26.6	3>4>2>1	4>3>2>5>1	0	0	0/0	0	rud.	0	0	—	—	0	0	1	—
MNHN	1989.3361	*nepalensis*	para	29.30	80.99	a	m	69.5	20.5	27.3	1.3	9.4	3.8	6.6	0.3	4.8	6.5	19.0	19.0	27.8	29.2	17.6	31.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1	0	0	1	(1; a few)
MNHN	1989.3362	*nepalensis*	para	29.30	80.99	a	m	72.1	22.8	27.7	1.2	9.7	5.1	7.3	0.3	4.7	6.8	19.1	20.2	28.3	31.8	19.7	33.7	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1	0	0	1	1
NHME	A0570/99	*kanjiroba*	para	29.30	82.34	a	f	66.2	19.1	23.2	1.2	9.6	5.7	6.4	0.3	4.3	6.4	14.6	16.4	25.9	23.4	15.0	27.6	3>4>2>1	4>3>5>2>1	0	0	0/0	0	0	—	0	—	—	0	0	1	0
NHME	A0574/99	*kanjiroba*	para	29.10	82.58	a	f	66.7	18.1	22.0	1.2	9.6	5.5	6.5	0.4	3.9	6.8	15.5	16.5	26.4	22.3	17.0	29.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	0	—	0	—	—	0	0	1	1
NHME	A0576/99	*kanjiroba*	holo	29.02	82.79	a	m	55.4	15.4	19.1	1.3	7.9	3.4	6.0	0.4	4.0	5.8	13.6	13.0	23.0	21.2	13.3	23.5	3>4>2>1	4>3>5>2>1	0	0	0/0	0	0	I,II,III	2/2	p>/=ax	1/1	0	0	1	0-1
NHME	A1248/05	*kanjiroba*	para	29.36	82.40	a	f	54.2	14.5	18.2	1.3	8.1	5.3	5.0	0.3	3.4	5.6	11.8	14.0	21.5	20.3	12.1	23.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	0	—	0	—	—	0	0	1	0
Khatiwada *et al.* 2019	2015-118	*ghunsa*	holo	27.66	87.93	a	m	43.6	11.4	16.4	1.4	4.9	na	4.8	0.4	3.1	4.1	10.0	23.4	17.5	17.1	11.1	19.3	3>4>2>1	4>3>5>2>1													
Khatiwada *et al.* 2019	2015-119	*ghunsa*	para	27.66	87.93	a	m	47.8	11.4	15.2	1.3	4.9	na	4.5	0.4	3.7	3.7	11.5	21.8	19.4	17.0	13.1	21.4	3>4>1>2	4>5>3>2>1													
Khatiwada *et al.* 2019	2015-120	*ghunsa*	para	27.66	87.93	a	m	45.6	10.1	15.4	1.5	4.7	na	5.6	0.6	2.3	3.5	9.4	21.4	19.4	17.6	11.4	20.1	3>2>1>4	4>3>5>2>1													
Khatiwada *et al.* 2019	2015-121	*ghunsa*	para	27.66	87.93	a	m	47.3	11.7	14.9	1.3	4.7	na	6.0	0.5	2.4	3.5	12.1	19.9	16.5	13.6	8.1	18.9	3>4>2>1	4>3>5>2>1													
Khatiwada *et al.* 2019	2015-122	*ghunsa*	para	27.66	87.93	a	m	42.1	10.4	14.4	1.4	4.7	na	4.8	0.5	2.7	3.6	8.9	20.3	13.4	16.0	10.4	18.6	3>4>2>1	4>5>3>2>1													
Khatiwada *et al.* 2019	2015-123	*ghunsa*	para	27.66	87.93	a	f	53.6	13.3	17.8	1.3	6.2	na	7.2	0.5	3.2	4.0	10.1	25.1	20.6	17.4	13.1	22.4	3>4>2>1	4>3>5>2>1													
Khatiwada *et al.* 2019	2015-124	*ghunsa*	para	27.66	87.93	a	f	50.2	13.2	15.5	1.2	6.1	na	6.2	0.5	3.4	4.9	11.9	21.6	16.3	15.3	12.3	22.2	3>4>2=1	4>3>5=2>1													
Khatiwada *et al.* 2019	2015-125	*ghunsa*	para	27.66	87.93	a	f	53.9	12.8	18.0	1.4	6.2	na	5.0	0.4	3.5	4.6	12.0	23.7	20.0	18.7	7.8	22.8	3>4>2>1	4>5>3>2>1													
ZFMK	104174	*khumbu* sp. nov.	holo			a	m	41.7	11.4	14.4	1.3	6.5	2.8	4.9	0.4	2.6	4.2	11.9	10.5	18.6	18.0	12.2	18.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1/?	0	0	1	1
ZFMK	104175	*khumbu* sp. nov.	para			sa		34.1	9.7	11.8	1.2	5.4	3.0	3.7	0.4	2.6	3.5	9.7	9.0	16.1	14.4	9.4	14.7	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	—	0	—	—	0	0	1	0

Table 3 (continued).

Source	ID	Species	Type	N	E	Age	Sex	SVL	HL	HW	HW/ HL	SL	NSD	ED	ED/ HL	END	IND	FAL	HAL	FEL	TIBL	TaL	FOL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
MNHN	1977.1246	*khumbu* sp. nov.	para			a	m	49.0	11.9	14.4	1.2	6.0	2.4	4.5	0.4	3.4	3.8	12.6	11.5	17.7	18.4	11.9	21.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1247	*khumbu* sp. nov.	para			a	m	47.7	12.9	15.3	1.2	6.6	2.7	4.6	0.4	2.9	4.4	13.1	11.8	20.1	20.3	13.1	21.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1248	*khumbu* sp. nov.	para			a	m	45.1	13.2	15.3	1.2	6.8	2.7	5.4	0.4	3.3	4.2	12.6	10.5	18.6	19.9	12.5	21.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1/1	0	0	1	1
MNHN	1977.1249	*khumbu* sp. nov.	para			a	m	42.5	12.4	14.5	1.2	6.2	2.9	4.4	0.4	3.0	4.3	12.1	9.6	19.2	19.2	12.1	19.6	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1250	*khumbu* sp. nov.	para			a	m	50.4	12.6	15.4	1.2	7.1	2.3	5.4	0.4	3.1	3.7	12.8	11.5	16.7	20.1	11.1	22.6	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1251	*khumbu* sp. nov.	para			a	f	49.4	13.2	16.4	1.2	6.7	3.1	5.0	0.4	3.0	5.0	11.6	11.8	17.8	18.1	11.2	19.8	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	—	—	—	—	0	0	1 (dorso-lateral)	1 (dorso-lateral)
MNHN	1977.1252	*khumbu* sp. nov.	para			a	m	44.5	11.5	14.0	1.2	5.6	2.3	5.1	0.4	2.7	4.2	12.3	11.1	16.6	18.7	11.4	20.7	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1253	*khumbu* sp. nov.	para			a	f	53.6	12.5	15.7	1.3	6.6	2.8	5.7	0.5	2.5	4.2	11.3	12.2	17.6	17.5	12.4	21.8	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	—	—	—	—	0	0	1 (dorso-lateral)	(1; dorso-lateral)
MNHN	1977.1254	*khumbu* sp. nov.	para			a	m	49.4	13.0	15.1	1.2	7.0	3.2	5.3	0.4	3.3	4.4	12.6	11.3	17.6	19.9	12.7	21.3	3>4>2>1	4>3>5=2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1255	*khumbu* sp. nov.	para			a	f	55.6	13.0	16.3	1.3	6.9	3.2	5.2	0.4	2.4	4.3	12.0	12.1	18.2	17.7	11.4	21.8	3>4>2=1	4>3>5>2>1	0	0	0/0	0	rud.	—	—	—	—	0	0	1 (dorso-lateral)	1
MNHN	1977.1256	*khumbu* sp. nov.	para			a	m	41.8	11.6	14.0	1.2	5.6	2.7	5.1	0.4	3.0	4.2	10.6	10.5	18.6	18.8	12.0	19.5	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1257	*khumbu* sp. nov.	para			a	m	44.5	12.4	15.3	1.2	5.9	2.9	4.1	0.3	3.0	4.8	12.6	10.9	18.1	19.2	12.6	22.0	3>4>2=1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1258	*khumbu* sp. nov.	para			a	m	48.2	13.0	14.7	1.1	6.0	2.6	4.2	0.3	3.3	4.4	12.9	10.7	20.4	19.8	13.1	22.1	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1/1	0	0	1	1
MNHN	1977.1259	*khumbu* sp. nov.	para			a	m	49.8	12.4	15.3	1.2	6.6	3.3	4.8	0.4	3.3	4.3	12.4	11.4	18.9	19.9	12.5	21.8	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1260	*khumbu* sp. nov.	para			a	m	51.2	13.4	16.2	1.2	6.0	2.9	4.1	0.3	3.0	4.3	13.5	12.0	22.4	20.6	13.4	23.0	3>4>2=1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1261	*khumbu* sp. nov.	para			a	m	45.7	12.4	15.1	1.2	6.2	2.8	4.6	0.4	3.4	4.6	12.9	11.7	18.5	19.4	11.2	20.0	3>4>2>1	4>3>5=2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1	1
MNHN	1977.1262	*khumbu* sp. nov.	para			a	f	51.3	13.5	16.5	1.2	7.0	2.8	4.7	0.4	3.4	4.5	11.8	12.1	18.8	16.7	10.5	21.0	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	—	—	—	—	0	0	1 (dorso-lateral)	(1; dorso-lateral)
MNHN	2003.3041	*k. makalu* subsp. nov.	holo			a	m	47.9	13.6	15.2	1.1	6.5	3.1	5.0	0.4	3.0	5.1	13.6	12.2	22.2	19.4	12.7	23.8	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>>ax	1/1	0	0	1 (dorso-lateral)	1
MNHN	2003.3042	*k. makalu* subsp. nov.	para			a	m	44.6	13.9	16.0	1.2	6.2	2.9	5.0	0.4	2.9	4.3	13.6	12.3	21.0	19.1	11.0	23.4	3>4>2>1	4>3>5>2>1	0	0	0/0	0	rud.	I,II,III	2/2	p>ax	1/1	0	0	1 (dorso-lateral)	1

Taxonomy

Class Amphibia, Linne, 1758
Order Anura Fischer von Waldheim, 1813
Family Megophryidae Bonaparte, 1850
Genus *Scutiger* Theobald, 1868

Scutiger khumbu sp. nov.

urn:lsid:zoobank.org:act:3F5B9602-4B6E-467E-9AF3-77D66724ACB7
Figs 6–10; Table 3; Supp. file 1J, L–O

Diagnosis

Scutiger khumbu sp. nov. is assigned to the genus *Scutiger* based on morphological characteristics and its phylogenetic position (Fig. 2). It can be distinguished based on multiple nucleotide substitutions in mitochondrial COI, cytb, and 16S sequences, as well as private alleles at the nuclear genes bfib7, ccnb2 and rag1. It can be distinguished from all other congeners by the following combination of morphological features: medium body size (male 41.6–51.1 mm SVL, female 49.4–55.6 mm; Table 3, Supp. file 1J); head wider than long; vomerine and maxillary teeth absent; vocal sac absent; relative length of fingers $3 > 4 > 2 > 1$; small black nuptial spines on dorsal surface of first and second fingers, and inner side of third finger in males in breeding condition; inner forearm without spines; relative length of toes $4 > 3 > 5 \geq 2 \geq 1$; subarticular tubercles absent; toes unwebbed or rudimentary webbed; a pair of pectoral glands and a pair of axillary glands with small black spines on both glands; abdomen/belly without spines; tubercles on dorsal and lateral surfaces of body (often arranged in lines) and upper limbs; tubercles conical, each tubercle with keratinized tips or 1–2 black spines in breeding condition, entire cone with horned, black coating, studded with small black tips, shimmering like black mica schist when moistened in the preserved state, in particular in specimens from the Khumbu region (Fig. 6). A triangular or Y-shaped dark brownish pattern can be present on dorsal side of the head (Supp. file 1L–M).

Etymology

The specific epithet '*khumbu*' is a noun in apposition referring to the Khumbu Himal (also called the Everest region) in Nepal and thus remains unchanged regardless of the gender of the genus.

Type material

Holotype

NEPAL • ♂; Bagmati Province, Dolakha District, Jiri; 27°41′48″ N, 86°16′30″ E (WGS 84); 3396 m a.s.l.; Jun. 1997; local resident leg.; ZFMK 104174.

Paratypes

NEPAL • 1 subadult; Bagmati Province, Ramechhap District, Gokulganga; 27°35′43″ N, 86°20′24″ E (WGS 84); Jun. 1997; local resident leg.; ZFMK 104175 • 13 ♂♂; Solu Khumbu District, Najing Dingma; 27°34′33″ N, 86°48′08″ E (WGS 84); 1 Jul. 1973; Alain Dubois and Dominique Payen leg.; MNHN 1977.1246 to MNHN 1977.1250, MNHN 1977.1252, MNHN 1977.1254, MNHN 1977.1256 to MNHN 1977.1261 • 4 ♀♀; same data as for preceding; MNHN 1977.1251, MNHN 1977.1253, MNHN 1977.1255, MNHN 1977.1262 • 3 imago; Solu Khumbu District, Paiya [= Puiyan]; 27°38′41″ N, 86°43′40″ E (WGS 84); 8 Jun. 2003; Annemarie Ohler and Nicolas Pruvost leg.; MNHN 2003.3038 to MNHN 2003.3040.

Other material examined

NEPAL • 4 tadpoles; Ramechhap District; 27°35′ N, 86°20′ E (WGS 84); 3084 m a.s.l.; Jun. 1997; local resident leg.; NHME (uncatalogued, field numbers 9705.10, 9705.15, 9705.21, 9705.22) • 4 tadpoles; same locality as for holotype; Jun. 1997; local resident leg.; NHME (uncatalogued, field numbers 9705.73–76) • 3 tadpoles; Dolakha District; 27°40′ N, 86°14′ E (WGS 84); 2790 m a.s.l.; Jun. 1997; local resident leg.; NHME (uncatalogued, field numbers 9705.99, 9705.100, 9705.102).

Description (holotype)

Adult male, well preserved (Fig. 7). Measurements are provided in Table 3. SVL 41.6 mm.

Head. Large and flat, wider than long (HW/HL = 1.27); snout short and rounded; canthus rostralis distinct; nostril dorsolateral, just below canthal, midway between tip of snout and eye (NSD/END = 1.10); loreal region slightly concave; eye large (ED/HL = 0.43); internarial surface flat (IND = 4.20); pupil vertical; interorbital space flat; tympanum and tympanic ring absent; tongue oval; choanae small, visible when viewed from below; vomerine and maxillary teeth absent; vocal sac absent; supratympanic fold distinct, extending from posterior corner of eye to supra-axillary region, associated with parotoid glands.

Forelimbs. Robust; forearm of median length (FAL/SVL = 0.29) and longer than hand (HAL/SVL = 0.25), without spines; fingers slender, free of dermal fringes or web; all fingertips rounded, not dilated; relative finger lengths: 3 > 4 > 2 > 1; subarticular tubercles absent; inner metacarpal tubercle flat and large; outer metacarpal tubercle indistinct; small black nuptial spines on dorsal and lateral surface of first and second fingers, and on inner side of third finger.

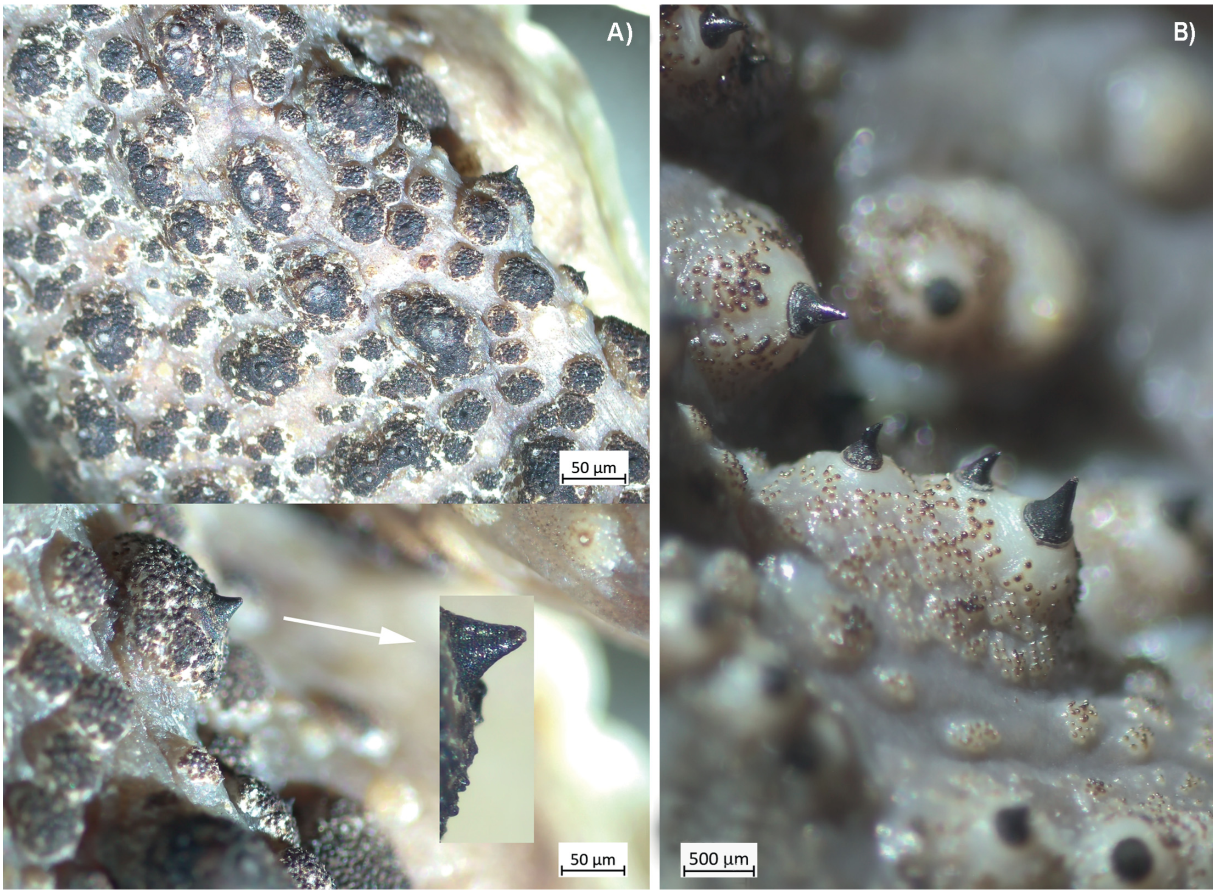

Fig. 6. Close-up of dorsal skin. **A**. Nominotypical subspecies of *Scutiger khumbu* sp. nov. in preservation (paratype, ♂, MNHN 1977.1252). **B**. *Scutiger khumbu makalu* subsp. nov. in preservation (holotype, ♂, MNHN 2003.3041). Photo credits: S. Hofmann.

Hindlimbs. Robust, moderately long (TIBL/SVL = 0.43; FEL/TIBL = 1.00), heels are not in contact when folded at right angles to the body (see Fig. 8 and Supp. file 1L); foot same length as shank; tips of toes round; toes not webbed, relative lengths 4 > 3 > 5 > 2 > 1; subarticular tubercles absent; moderately large inner metatarsal tubercle, outer metatarsal tubercle absent.

Fig. 7. Holotype, ♂ (ZFMK 104174) of *Scutiger khumbu* sp. nov. nominotypical subspecies, in preservative. **A**. Dorsal view of body. **B**. Ventral view. **C**. Dorsolateral view of body. **D**. Ventral view of left foot. Scale bar: A–C = 1 cm; D not in scale. Photo credits: M. Flecks.

Skin. Body dorsally and laterally with distinct tubercles in life and in preservative, each tubercle with one or two keratinized tips, only a few tubercles with spines; few scattered tubercles on upper and lower mandibles; forehead and surfaces of lower arm and tarsus relatively smooth; tubercles present below and on supratympanic fold; upper arms and legs with spineless tubercles; throat and belly surface smooth; a pair of pectoral glands and a pair of axillary glands present on chest, pectoral glands slightly larger than axillary, pectoral glands covered by small black spines.

Coloration

In life, dorsal surface of head, body, and extremities brownish; a small dark brown band extending from anterior edge of eye to nostril and further to tip of snout, and from posterior edge of eye along supratympanic fold; irregular dark brown spots or transverse stripes on all limbs including fingers and toes; ventral and dorsal surface of lower forelimbs and dorsal surface of hands with small irregular creamy white warts; flanks light brown; throat, belly, and partly ventral surfaces of extremities light melon-yellow; belly covered by irregular gray-brown network.

In preservative, color of dorsal surfaces has changed from brown to gray and that of ventral surfaces from yellowish to grayish white.

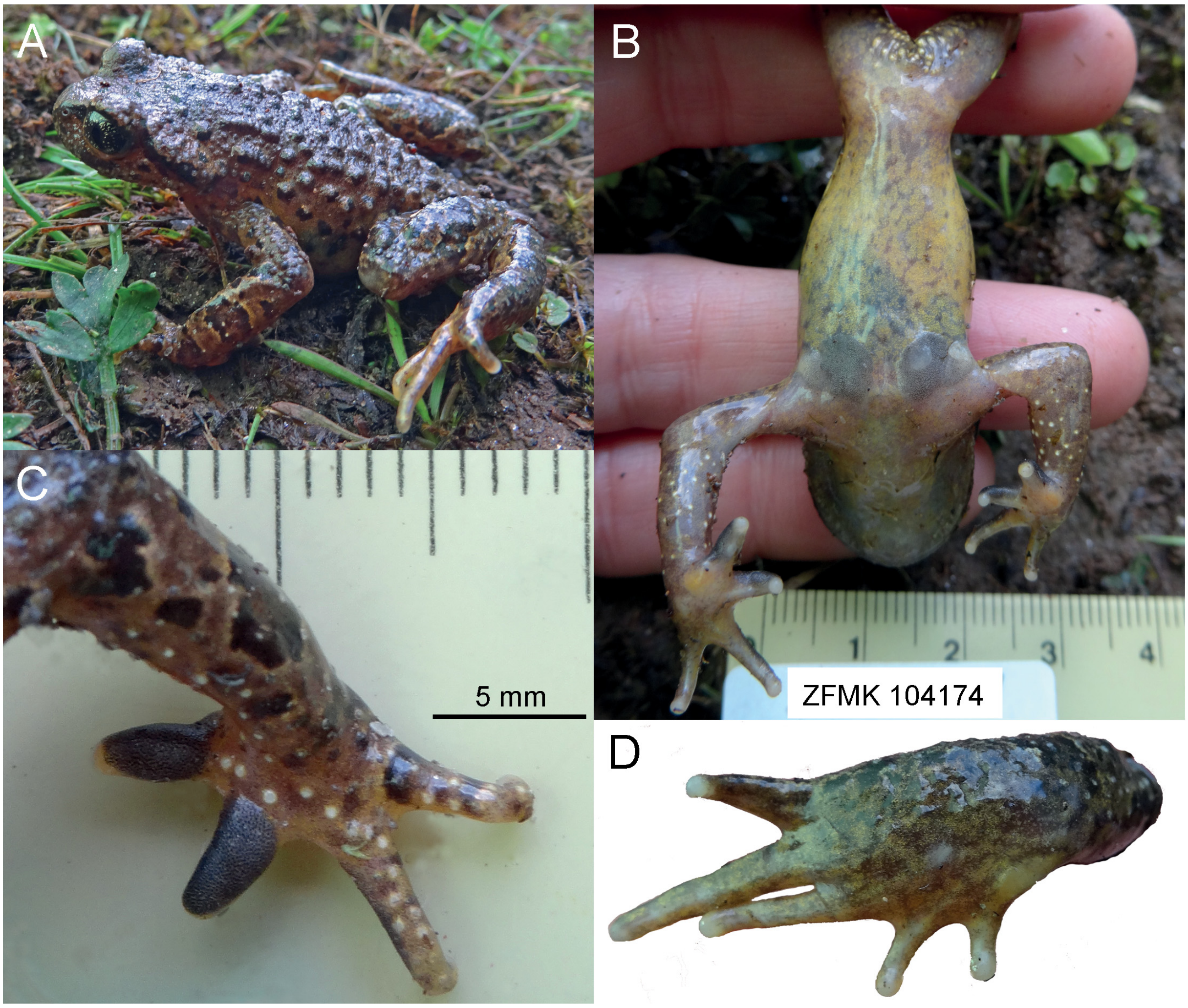

Fig. 8. Holotype, ♂ (ZFMK 104174) of *Scutiger khumbu* sp. nov., nominotypical subspecies, adult male in life. **A**. Dorsolateral view. **B**. Ventral view. **C**. Dorsal view of hand. **D**. Dorsal view of foot.

Variation

Measurements of the type series are provided in Table 3. Color can vary substantially from light to dark brown and even to olive (Supp. file 1L–M).

Distribution

Occurs in mountain forests in high-montane areas of the drainage area of the Koshi basin, Northeastern Nepal, more specifically, along the Khumbu Himal and adjacent Makalu region between ca 2800 and 3900 m a.s.l. (Fig. 1; Supp. file 1P). This species is known from the Sagarmatha and Koshi Zone, specifically the Dolakha District (Jiri), Ramechhap District, Solu Khumbu District (Lamjura La, Paiya, Surkie La, Taksindu), Bhojpur District (Salpa Pokhari), and in the Sankhuwasabha District. Eastern populations of this species that occur in the Bhojpur District (Salpa Pokhari), and in the Sankhuwasabha District are genetically distinct. This genetic differentiation supports the recognition of the eastern populations as a separate subspecies (see below).

Taxonomic remarks

In phylogenetic analyses, the new species belongs to a clade that branches with the clades previously identified in the genus *Scutiger*. The species distinction is supported by substantial molecular divergence from other *Scutiger* species, namely ≥11.1% uncorrected distance in the COI, ≥9.8% in the cytb, and ≥2.5% in the 16S gene (Supp. file 1D–F), by the resulting phylogenetic divergence (Fig. 2), as well as by morphological differences (Figs 4–5). *Scutiger khumbu* sp. nov. features two clearly divergent, fully allopatric mitochondrial lineages: one from the Khumbu Himal and the other from the Makalu region. These lineages show high mitochondrial sequence divergence, with uncorrected distance in COI, cytb,

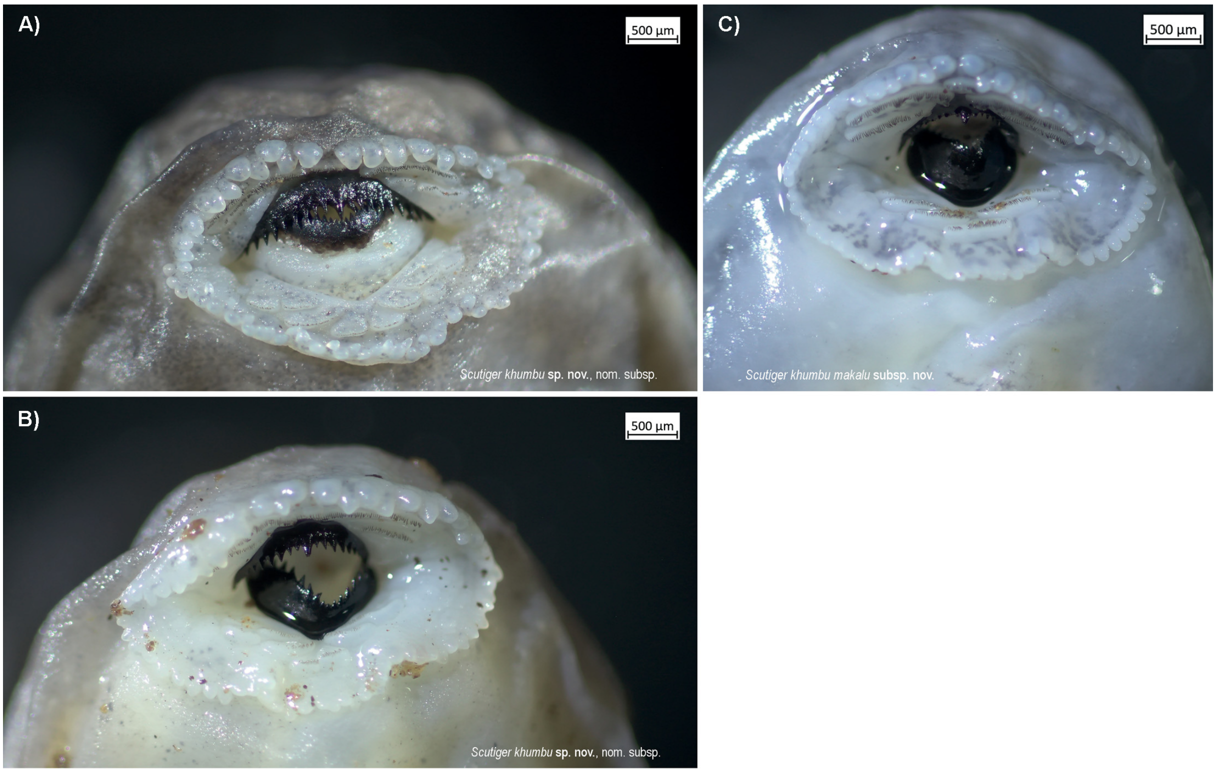

Fig. 9. Tadpole mouthparts. **A–B**. Nominotypical subspecies of *Scutiger khumbu* sp. nov. **A**. NHME 9705.73. **B**. NHME 9705.100. **C**. *Scutiger khumbu makalu* subsp. nov. in preservation (specimen NHME JS 1405.25). Photo credits: S. Hofmann.

Fig. 10. *Scutiger khumbu makalu* subsp. nov. in preservative; dorsal view of body; ventral view; dorsolateral view of body. **A**. holotype, ♂ (MNHN 2003.3041). **B**. Paratype, ♂ (MNHN 2003.3042). Scale bar = 1 cm. Photo credits: M. Flecks.

and 16S ranging 8.5–9.3%, 5.0–7.4%, and 2.4–2.6% (Supp. file 1G–I), respectively, private alleles at the nuclear genes bfib7 and ccnb2, allele sharing at rag1, and lack notable morphological differences. Bioacoustic variation in the new species remains to be investigated. Given their deep phylogeographic structure, but younger divergence (including some nuclear allele sharing) and the absence of clear phenotypic differences, we consider the lineage from the Makalu region as distinct subspecies of *Scutiger khumbu* sp. nov., namely *Scutiger khumbu makalu* subsp. nov.

Remarks on larvae

Eleven tadpoles of western populations of *Scutiger khumbu* sp. nov. at different stages ranging from 26 to 39 (Gosner 1960) (Fig. 9); LTRF: 3(2–3)/3(1–2), 3(2–3)/3(1–3), 3(2–3)/4(1–3), or 4(2–4)/4(1–3).

Scutiger khumbu makalu subsp. nov.

urn:lsid:zoobank.org:act:A5A7AE1C-43D3-4489-ACDA-AE0DEB942DB3

Figs 6, 9–10; Tables 1, 3; Supp. file 1J

Diagnosis

Scutiger khumbu makalu subsp. nov. can be distinguished from the nominotypical subspecies and other *Scutiger* taxa based on multiple nucleotide substitutions in mitochondrial COI, cytb, and 16S sequences, as well as private alleles at the nuclear genes bfib7 and ccnb2 (Supp. file 1D–I), but not at the nuclear gene rag1. Specifically in the barcoding gene COI, *Scutiger khumbu makalu* subsp. nov. is separated from the nominotypical subspecies and other currently recognized *Scutiger* species by two binary and four asymmetric molecular signature characters (Table 1). Morphologically, this taxon closely resembles the nominotypical subspecies of *Scutiger khumbu* sp. nov. but it exhibits a relatively larger foot length and tubercles that are less densely covered with small, keratinized tips, which also do not appear as dark as in the nominotypical subspecies (Fig. 6).

Etymology

The subspecific epithet '*makalu*' refers to the Makalu region in Nepal.

Type material

Holotype

NEPAL • ♂; Bhojpur District, Salpa Pokhari; 27°26′47″ N, 86°56′01″ E (WGS 84); 22 Jun. 2003; Thierry Deuve leg.; donated by Thierry Deuve; MNHN 2003.3041.

Paratype

NEPAL • 1 ♂; same locality as for holotype; 22 Jun. 2003; Thierry Deuve leg.; donated by Thierry Deuve; MNHN 2003.3042.

Other specimens examined

NEPAL • 5 tadpoles; Sankhuwasabha District; 27°38′ N, 87°13′ E (WGS 84); 3600 m a.s.l.; Jun. 1997; local residents leg.; NHME (uncatalogued, field numbers JS1405.23–27).

Description (holotype)

Adult male, well preserved (Fig. 10). Measurements are provided in Table 3. SVL = 47.9 mm.

HEAD. Large and flat, wider than long (HW/HL = 1.22); snout short and rounded; canthus rostralis distinct; nostril dorsolateral, just below canthal, midway between the tip of snout and eye (NSD/END = 1.00); loreal region slightly concave; eye relatively large (ED/HL = 0.37); internarial surface flat (IND = 5.10); pupil vertical; interorbital space flat; tympanum and tympanic ring absent; tongue oval; choanae small, visible when viewed from below; vomerine and maxillary teeth absent; vocal sac absent; supratympanic fold distinct, extending from posterior corner of eye to supra-axillary region, associated with parotoid glands.

FORELIMBS. Robust; forearm of median length (FAL/SVL = 0.28) and longer than hand (HAL/SVL = 0.26), without spines; fingers slender, free of dermal fringes or web; all fingertips rounded, not dilated; relative finger lengths: 3 > 4 > 2 > 1; subarticular tubercles absent; inner metacarpal tubercle flat and large; outer metacarpal tubercle large, nearly round, and flat; black nuptial spines on dorsal and lateral surface of first and second fingers, and on inner side of third finger.

HINDLIMBS. Robust, moderately long (TIBL/SVL = 0.41; FEL/TIBL = 1.10), heels are not in contact when folded at right angles to the body (see also Fig. 10); foot longer than shank; tips of toes round; toes not webbed, relative lengths 4 > 3 > 5 > 2 > 1; subarticular tubercles absent; moderately large inner metatarsal tubercle, outer metatarsal tubercle absent.

SKIN. Body dorsally and laterally with distinct tubercles in preservative, each tubercle with one large keratinized spine in the center (Fig. 6B), surrounded by small, keratinized dark brown or blackish tips; small scattered spines on upper and lower mandibles; dorsal surface of forehead and surfaces of lower arm relatively smooth; tubercles with spines present below and on supratympanic fold; upper arms and legs with tubercles, most of them with spines; throat and belly surface smooth; a pair of pectoral glands and a pair of axillary glands present on chest, connected, pectoral glands larger than axillary, all covered by small black spines.

Coloration

In preservative, dorsal surfaces gray, ventral surfaces grayish white.

Distribution

This subspecies is known from cloud forests in high-montane areas in the Makalu region in Nepal at altitudes between ca 3000 and 3600 m a.s.l., specifically in the Bhojpur District (Salpa Pokhari), and in the Sankhuwasabha district.

Taxonomic remarks

Scutiger khumbu makalu subsp. nov. was previously identified as a distinct phylogeographic lineage by Hofmann *et al.* (2017) based on molecular data of a few samples. It is characterized by high genetic divergence in the COI (8.8%), cytb (6.3%), and 16S (2.5%) genes, distinct alleles at the nuclear bfib7 and ccnb2 genes, and shared alleles at the rag-1 gene, with the nominotypical subspecies of *Scutiger khumbu* sp. nov., to which it is allopatric and lacks a clear morphological differentiation. The divergence being lower than in most *Scutiger* species, it is therefore described as a new subspecies of *Scutiger khumbu* sp. nov.

Remarks on larvae

Five tadpoles of *Scutiger khumbu makalu* subsp. nov. at different stages ranging from 26 to 29 (Gosner 1960) (Fig. 9); LTRF: 3(2–3)/3(1–2) or 3(2–3)/4(1–3).

Discussion

Using morphological and molecular analyses, our study highlights unrecognized diversity within the Himalayan amphibian genus *Scutiger* and substantiates a new species composed of two subspecies for which we provided taxonomic descriptions.

Scutiger represents a diverse genus of toads that are characteristic faunal elements of the Himalaya-Tibet orogen. These toads, adapted to high-montane environments, have limited dispersal abilities and are typically found across the Himalaya Mountain range. The distributions of *Scutiger* species are predominantly allopatric and geographically restricted, being likely associated with separate drainage systems and/or geological formations, resulting in a notable degree of local endemism. The newly described species *Scutiger khumbu* sp. nov. illustrates well this pattern. It belongs to a phylogenetic clade distinct from any other known lineage in the genus, which is characterized by both high molecular and morphological differences from the species we could compared it to, namely the geographically distant Himalayan species *S. nepalensis* and *S. kanjiroba* (West Nepal), as well as the neighboring *S. ghunsa* (East Nepal). Specifically, the range of the new species is completely disconnected from the range of *S. ghunsa* by the Arun River valley, which likely serves as a strong physical barrier to dispersal for non-flying terrestrial organisms (Nanhoe & Ouboter 1987). The new species is itself a hallmark of local Himalayan endemism and diversity, as it is diversified into two distinct evolutionary units that we recognized as subspecies, restricted to the Khumbu Himal and adjacent Makalu regions, respectively. The distribution of the nominotypical subspecies follows the Dudh Koshi drainage system, while *Scutiger khumbu makalu* subsp. nov. is found across the catchment area toward the Arun River, east of the Surkie La. This pattern suggests that the watershed between the two river basins serves as a natural boundary. Future studies should focus on investigating the role of this separation in the genetic diversity and integrity of these two lineages and test whether they occasionally experienced gene flow, notably using genomic approaches.

The discovery of *Scutiger khumbu* sp. nov. in the drainage area of the Koshi basin, Everest region, East Nepal, adds to the recent identification of *S. kanjiroba* in West Nepal (Hofmann *et al.* 2024b) and *S. ghunsa* (Khatiwada *et al.* 2019) east of the Arun River, underscoring the remarkable amphibian diversity within Himalayan cloud forests, suggesting that they may harbor even more undiscovered taxa, and emphasizing the conservation importance of these habitats.

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Conflict of interest

The authors have declared that no competing interests exist.

Author contributions

Conceptualization: SH. Data curation: SH, AO, CD, DJ. Formal analysis: SH. Funding acquisition: SH. Investigation: SH. Methodology: SH, JS. Project administration: SH. Resources: all authors. Visualization: SH, MF. Writing – original draft: SH. Writing – review and editing: all authors.

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Supplementary file

Supp. file 1. Supplementary data and information associated with the description of *Scutiger khumbu* sp. nov. and *S. khumbu makalu* subsp. nov.
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