

Over-splitting and inconsistently applied criteria: a response to recent changes on the taxonomy of mountain spiny frogs (Dicroglossidae, Nanorana)

Daniel JABLONSKI¹ & Sylvia HOFMANN^{2,3}

 ¹ Department of Zoology, Comenius University in Bratislava, Ilkovičova 6, Mlynská dolina, 842 15 Bratislava, Slovakia. <daniel.jablonski@uniba.sk>, https://orcid.org/0000-0002-5394-0114.
² Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig, Adenauerallee 160, D-53113 Bonn, North Rhine-Westphalia, Germany. <s.hofmann@leibniz-lib.de>.
³ Helmholtz-Centre for Environmental Research – UFZ, Department of Conservation Biology, Permoserstrasse 15, D-04318 Leipzig, Germany.

Amphibians face global threats, and their conservation necessitates accurate and coherent classification. Last year, Southeast Asian spiny frogs (Nanorana) were the focus of a surge of new species descriptions and taxonomic revisions, despite little new evidence. In this article, we re-evaluate available genetic data and discuss flaws in the interpretation of results reused to justify recent taxonomic changes. In conclusion, we call for caution regarding the status of newly proposed taxa. We highlight mostly that 1) two taxa described in 2023, N. huangi and N. laojunshanensis are genetically similar and probably represent the same species, 2) inconsistent phylogenetic lineage evaluation of several species (Allopaa hazarensis, Odorana arunachalensis, Nanorana minica) led to premature supraspecific reclassifications, and 3) the elevation of N. minica as a separate subgenus (Minipaa) lacks evidence and potentially contributes to supraspecific artificial taxonomic inflation. Moreover, our re-analysis of 16S sequences available on GenBank suggests that the recently described N. bangdaensis consists of phylogeographic variation of N. parkeri. These cases stress the need for informative data for accurate species delimitation in amphibian systematics, particularly in morphologically similar species like Nanorana frogs. Caution when proposing taxonomic changes, comprehensive literature crossreferencing, and integrative approaches are essential for precise taxonomic conclusions and informed conservation.

Keywords: China, nomenclature, south-east Asia, subgenus, taxonomic inflation.

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INTRODUCTION

Amphibians are a globally threatened group of vertebrates (Luedtke *et al.* 2023), and their accurate classification is crucial for their effective protection (Dufresnes *et al.* 2023). Therefore, hasty revisions that may cause taxonomical chaos and over-splitting might be detrimental. Here, we discuss recent taxonomic changes in mountain spiny frogs (*Nanorana* Günther, 1896) from Southeast Asia which might exemplify a broader trend of new species descriptions made from weak evidence in amphibians and reptiles (e.g., see Agarwal *et al.* 2017, Chan *et al.* 2020, Jablonski *et al.* 2021, Dufresnes & Jablonski 2022).

The observations described below stem from the recent paper by Tang *et al.* (2023) which contains several taxonomic revisions. First, they describe a new species from northwestern Yunnan, China, *Nanorana laojunshanensis* Tang, Liu & Yu, 2023. Second, they define a new subgenus *Minipaa* Tang, Liu & Yu, 2023, with *Nanorana minica* (Dubois, 1975) as its type species. Third, they re-classify *Odorrana arunachalensis* Saikia, Sinha & Kharkongor, 2017, with the genus *Nanorana*. Fourth, they suggest to re-classify *Allopaa* into subgenus *Chaparana* within *Nanorana*.

The study by Tang *et al.* (2023) was based on two genetic analyses: a 16S rRNA phylogeny, and a combined phylogeny of four concatenated mitochondrial (mt) and nuclear (nu) genes [mtDNA: 16S, cytochrome c oxidase subunit I (COI), cytochrome b (cyt b); nuDNA: recombination activating gene 1 (RAG1)]. The new species description was supplemented by morphological data (morphometry).

We recently published a series of studies related to the biogeography, genetic diversity based on both, mt and nu DNA data, and taxonomy of spiny frogs from the Hindu Kush-Himalaya region (Hofmann *et al.* 2021*a-b*, 2023*a-b*) and here present a response to the taxonomic revisions proposed by Tang *et al.* (2023). To this end, we reanalyze some of the genetic data associated with the newly described *N. laojunshanensis* and discuss several issues concerning the data interpretation and presentation by Tang *et al.* (2023), also in the light of our previous study on this group (Hofmann *et al.* 2023*a*). Noting that the study by Tang *et al.* (2023) is largely based on the re-analysis of our previously published sequences, we point out inconsistencies that undermine the taxonomic changes proposed by Tang *et al.* (2023) according to the available molecular evidence.

METHODS

Following the methodology and dataset described in Hofmann *et al.* (2023*a*), we re-evaluated and compared available 16S sequences through a Bayesian tree analysis including 286 sequences (571 bp) from 27 ingroup taxa and 10 outgroups. To assess specific cases, we further analyzed COI sequences using haplotype networks separately for *N. huangi* + *N. laojunshanensis* and *N. parkeri* + *N. bangdaensis* sequences (550 bp and 539 bp, respectively). We also computed between-group genetic distances (uncorrected p-distance, maximum composite likelihood) using MEGA-11 (Tamura *et al.* 2021), and nucleotide diversity (π) using DnaSP 6.00 (Rozas *et al.* 2017). For the case of *N. laojunshanensis*, we also considered RAG1 sequences (1165 bp) OR678581-82, KY172539, and MN032562, from which we measured pairwise divergence.

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RESULTS & DISCUSSION

The case of Nanorana laojunshanensis Tang, Liu & Yu, 2023 and another new taxon of the genus.

Tang et al. (2023) described *N. laojunshanensis* from the Hengduan Mountains in Yunnan province, China, as the sister lineage of the lineage leading to *Nanorana pleskei* Günther, 1896 and *Nanorana ventripunctata* Fei & Huang, 1985. Morphologically, *N. laojunshanensis* exhibits a distinct combination of characteristics from known congeners, such as the presences of a tympanum, equal lengths of fingers I and II, a small body size, a yellow ventral surface of limbs, distinct vomerine teeth, indistinct subarticular tubercles, a head width greater than head length, slender supratympanic fold, the absence of the dorsolateral fold, the presence of nuptial spines on fingers I and II in adult males, the absence of a vocal sac, and paired brown spines on the chest. Within the nominal subgenus *Nanorana*, this new taxon is distinguished by indistinct subarticular tubercles and by "*lacking dark blotches on ventral surface and ventral surface of limbs yolk yellow*" (Tang et al. 2023).

Coincidently, another species, Nanorana huangi Ji, Shi, Ma, Shen, Chang & Jiang, 2023, was described from the exact same area and published by a different team (Ji et al., 2023) during the same period (Autumn 2023). The type locality of N. huangi (26.874593° N, 99.544008° E; 3389 m a. s. l) is distanced by only about 30 km (by air line; Fig. 1C) from the type locality of N. laojunshanensis (Mt. Laojun, Lijiang, Yunnan, China; 26°37' N, 99°42' E, 3982 m a.s.l.) and both populations are morphologically similar. In this respect, the morphological assessment of N. huangi is based on a greater sample size than N. laojunshanensis, and accordingly captures higher intraspecific variability (particularly for quantitative traits), which challenges the characteristics previously reported as diagnostic for N. laojunshanensis (e.g., body size, shape of supratympanic fold, coloration). Our re-analysis of 16S and COI also reveals strong similarities, with both species sharing identical or closely related haplotypes (Fig. 1A, B) with low level of genetic diversity (π =0.2 %), and we therefore consider N. huangi and N. laojunshanensis as subjective synonyms (Fig. 1A, B). Since the description of N. huangi was published on September 28, 2023, [vs. November 7, 2023, for N. laojunshanensis], N. huangi is treated as the oldest available name. The genetic distances highlighted by Tang et al. (2023) to justify the split of the new taxon from its closest relatives N. ventripunctata and N. pleskei, are relatively low, namely 1.6 % for 16S and 7.4 % for COI, suggesting a young divergence (see also comment in Dufresnes and Litvinchuk 2022). These distances are typically lower than those presented for other species of the genus at the same loci (i.e., Liu et al. 2021). In addition, the study lacks a comparative analysis for a nuclear, biparentally inherited marker alone, although sequences of the nuclear gene RAG1 were included. Given the relatively low observed genetic distances for the mtDNA markers, we expect the RAG1 variability in the investigated sequences between taxa to be also low. Here, we found little differentiation in RAG1 (for comparison with other species pairs, see Hofmann et al. 2023a), namely 0.18 % between N. laojunshanensis and N. pleskei, 0.43 % between N. laojunshanensis and N. ventripunctata, and 0.18 % between N. pleskei and N. ventripunctata (all individual sequences were homozygous). Besides, the sequence KY172605 specified by the authors in their RAG1 dataset is a tyrosinase fragment. Drawing from these points, we advise caution towards the distinction of N. huangi as a separate species (see the



Figure. 1. (A) The 16S rRNA phylogeny of all available sequences of the genus *Nanorana* displays the positions of *N. huangi* and *N. parkeri* and their recently described synonyms/conspecific taxa. Numbers indicate branch support (posterior probability) for the main clades. (B) Haplotypes network of the COI gene fragment generated by the median-joining method for *N. huangi* and *N. laojunshanensis* (n = 25). (C) The geographic position and distance between type localities of two newly described species (Google Earth). (D) The median-joining COI network (n = 66) of major lineages (West and East) and their haplotypes related to taxa *N. bangdaensis* (green) and *N. parkeri* (orange) and its geographic position. (E). Alongside networks, GenBank accession numbers (with special highlighting of four subpopulations E1-4; Zhou *et al.* 2014, Wang *et al.* 2018) and genetic distances (uncorrected p-distance with the maximum composite likelihood, MCL, in parentheses) within and between sequences/taxa are presented. Dots in the network of *N. parkeri* and *N. bangdaensis* (pp baniel Jablonski).

topology in Fig. 1) without additional genetic (ideally genomic) evidence. This example is paradigmatic of hasty species descriptions and represents a certain trend observed in current taxonomic research that is not always beneficial for taxonomy/species conservation itself.

The case of Odorrana arunachalensis *Saikia, Sinha & Kharkongor, 2017 in* Nanorana

Reassigning this species to a different genus than *Nanorana* (where it was placed by Qi *et al.* 2019) was recently discussed by Hofmann *et al.* (2023*a*), based on its phylogenetic position in a 16S mitochondrial tree and its high sequence differentiation (>14 %) from any other *Nanorana* members. However, the type locality was not genetically assessed, and whether the analyzed vouchers correspond to this taxon deserves confirmation. Therefore, enforcing this species in *Nanorana* as Tang *et al.* (2023) suggested appears premature, and because its phylogenetic, and therefore taxonomic placement is unsettled, it would be correct and more parsimonious to classify this taxon as "*insertae sedis*", and continue to refer to it as *Odorrana arunachalensis* Saikia, Sinha & Kharkongor, 2017 (for more details see the discussion in Hofmann *et al.* 2023*a*).

The case of Allopaa hazarensis (Dubois & Khan, 1979) in subgenus Chaparana Bourret, 1939

In the 16S Bayesian phylogeny of Tang *et al.* (2023; Fig. 3), this taxon, endemic to northern Pakistan, branches (without support) as the sister lineage of *Nanorana unculuanus* (Liu, Hu, Yang, 1960) (subgenus *Chaparana*), noting that none of the known *Nanorana* subgenera form a monophyletic clade in this analysis. In their concatenated four genes phylogeny, *A. hazarensis* is robustly retrieved as the sister lineage of *Chaparana*. Based on these conflicting observations, Tang *et al.* (2023) present *Allopaa* as being lumped with *Chaparana*. However, the authors do not discuss this new arrangement, which otherwise appears superficial. According to Hofmann *et al.* (2021*a*, 2023*a*), the extremely disjunct distribution range (*Allopaa* is the westernmost Himalayan taxon among *Nanorana*, while *Chaparana* members occur at the opposite side of the Himalaya-Tibet orogen), as well as the morphological data of Ohler & Dubois (2006) on *Allopaa*, this taxon should continue to be treated as a separate subgenus of *Nanorana* (Hofmann *et al.* 2024).

The case of Nanorana minica (Dubois, 1975) as the new subgenus Minipaa Tang, Liu & Yu, 2023

The up ranking of *N. minica* as its own subgenus, *Minipaa*, is inconsistent with the phylogenetic evidence. Depending on analysis, this taxon is alternatively placed within an unsupported clade that includes some but not all representatives of *Chaparana*, *Paa* Dubois, 1975, and *Allopaa* (16S tree), or as the sister lineage of the clade regrouping *Paa* and *Nanorana* (the concatenated four genes phylogeny). For lumping *Allopaa* into *Chaparana* and erect *N. minica* as a separate subgenus, Tang *et al.* (2023) used published genetic data (see their Fig. 4) and mention two morphological

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information for *N. minica* taken from the Ohler & Dubois (2006), namely "transculent or creamy nuptial spines and entirely whitish or creamy eggs, without colored animal pole.". However, only 15 of the 34 known species of the genus Nanorana (and only 9 of 13 species of the subgenus Paa) have been evaluated at that time by Ohler & Dubois (2006). Moreover, neither of those two features are included in the original description of *N. minica*. Whether these two characteristics are unique to *N. minica* thus remain to be demonstrated by investigating other spiny frogs. In addition, the molecular background of the new subgenus still requires confirmation because it remains unclear if the sequences attributed to *N. minica* in Tang et al. (2023) belong to this species. Thus, for reasons of taxonomic stability, *N. minica* should continue to be treated as member of the subgenus Paa (Ohler & Dubois 2006).

The additional case of Nanorana bangdaensis Rao, Hui, Zhu & Ma, 2022

In addition to the above-mentioned four cases, our re-analysis of the 16S data available on GenBank also offer the opportunity to discuss the status of the recently described N. bangdaensis Rao, Hui, Zhu & Ma, 2022, which is nested within Nanorana parkeri (Stejneger, 1927) (Fig. 1A, D). Since the sequences of the latter originated from very different localities across the Tibetan Plateau (Fig. 1E), we suspect that N. bangdaensis might be conspecific with N. parkeri. This alpine species has been intensively studied by population genomics and standard single barcoding-gene approaches using sampling that covers its entire distribution range (Zhou et al. 2014, Wang et al. 2018). These studies revealed major populations [(E)ast and (W)est], defining them as evolutionarily significant units, and up to four subpopulations (E1-E4) with only low whole-genomic differentiation among them. A similar east-west population structure has been previously identified in the endemic Tibetan snake Thermophis baileyi (Wall, 1907) (Hofmann et al. 2014), consistent with a scenario of range expansion from different refugia during interglacial and post-glacial times. Since one of the eastern N. parkeri subpopulation (E4; KJ811207 and KJ811261) corresponds to the type locality of N. bangdaensis (Bangda, [Baxoi County], Qamdo Prefecture, Tibet Autonomous Region, China), we used the COI-sequence data of N. bangdaensis and of the N. parkeri (sub)populations W and E1-E4, comprehended by N. bangdaensis/N. parkeri sequence data of Ji et al. (2023) and Tang et al. (2023), to assess their respective sequence divergence (Fig. 1D, E). As suspected, the COI sequences of N. bangdaensis are identical to sequences representatives of the East lineage of N. parkeri suggesting that N. bangdaensis and N. parkeri are weakly differentiated and likely belong to the same species. The lack of clear morphological diagnostic features further supports this assessment (https://www.amphibiachina.org as cited from Rao et al. 2020; original in Chinese: "The length of the head is approximately equal to the width of the head; the tympanic membrane is not obvious; the skin on the back is smooth, with a few short warts or skin folds on the back; the back is gray-green in life, with no obvious dark spots; the sides of the body are light in color, mixed with irregular spots."). While examples of "super-cryptic species" (i.e., cryptic species that experienced a mitochondrial capture, thus necessitating nuclear data for their detection; Dufresnes et al. 2019) do exist, and notwithstanding the possibility for an unusually young speciation event, it appears more parsimonious to assume that N. bangdaensis is part of the high intraspecific variability of N. parkeri, and might either be synonymized or be distinguished as a subspecies (see genetic distances, Fig. 1D).

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CONCLUSIONS

Considering these examples, we advocate for more consistency when proposing taxonomic adjustments, may it be for generic, subgeneric and alpha taxonomy, notably by defining arguments that motivate the implemented changes. To this end, reliable phenotypic data to be compared across candidate taxa is essential. Here the supposedly diagnostic morphological criteria proposed by Tang *et al.* (2023) for *N. laojunshanensis* are fragilized by the low sample size on which they are based [6 specimens vs. 20 for the description of *N. huangi* in Ji *et al.* (2023)]. Likewise, the lack of comparative morphological data makes the new subgenus *Minipaa* unconvincing. More generally, the subgenus concept lacks a clear definition in amphibians, especially when assessed based only on genetic or morphology data (e.g., Mahony *et al.* 2024)

Unnecessary descriptions or divisions within intricate evolutionary lineages, particularly in phylogenetically complex groups, may destabilize the taxonomy and hinder our understanding of the global evolutionary history of threatened amphibians. Therefore, potential taxonomic changes should be exercised with great parsimony. Furthermore, authors should rigorously cross-check existing literature during the review process although it is fully understandable that recently published data may be overlooked. If authors encounter previously published research that aligns with their own work, we encourage them to acknowledge this alignment and consider revising or withdrawing their manuscript if necessary. This approach is essential to prevent data duplication and taxonomic redundancies, which can bias species trees and cause disorder within taxonomy.

Given the potential challenges in phylogeography and taxonomy in genera like *Nanorana*, which contains a high number of species with similar morphologies, we call for more meticulous evaluation of available data, ideally following integrative approaches and established workflow of species (e.g., Dufresnes *et al.* 2023), subgenus (e.g., Mahony *et al.*, 2024) and genus (e.g., Dubois *et al.*, 2021) delimitation. Applying universal criteria to rank biodiversity should enable better inventorying for research and protection.

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