



Unnecessary splitting of genus-level clades reduces taxonomic stability in amphibians

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Abstract

Although the differentiation of clades at the species level is usually based on a justifiable and testable conceptual framework, the demarcation of supraspecific boundaries is less objective and often subject to differences of opinion. The increased availability of large-scale phylogenies has in part promulgated a practice of what we consider excessively splitting clades at the “genus” level. Many of these new genus-level splits are predicated on untenable supporting evidence (e.g., weakly supported phylogenies and purportedly “diagnostic” but actually variable, non-exclusive, or otherwise problematic opposing character state differences) without careful consideration of the effects on downstream applications. As case studies, we critically evaluate several recent examples of splitting established monophyletic genera in four amphibian families that resulted in the creation/elevation of 20 genus-level names (Dicoglossidae: *Phrynoglossus*, *Oreobatrachus*, *Frethia* split from *Occidozyga*; Microhylidae: *Nanohyla* split from *Microhyla*; Ranidae: *Abavorana*, *Amnirana*, *Chalcorana*, *Humerana*, *Hydrophylax*, *Indosylvirana*, *Papurana*, *Pulchrana*, *Sylvirana* split from *Hylarana*; Rhacophoridae: *Tamixalus*, *Vampyrus*, *Leptomantis*, *Zhangixalus* split from *Rhacophorus*, *Rohanixalus* split from *Feihyla*, *Orixalus* split from *Gracixalus*, and *Taruga* split from *Polypedates*), and also address the taxonomic status of the monotypic genus *Pterorana* relative to *Hylarana*. We reassess the original claims of diagnosability and justifications for splitting and argue that in many cases, the generic splitting of clades is not only unnecessary but also destabilizes amphibian taxonomy, leading to a host of downstream issues that affect categories of the user community (stakeholders such as taxonomists, conservationists, evolutionary biologists, biogeographers, museum curators, educators, and the lay public). As an alternative, we advocate for the use of the subgenus rank in some cases, which can be implemented to establish informative partitions for future research without compromising on information content, while avoiding gratuitous (and often transient) large-scale binomial (genus-species couplet) rearrangements. We encourage taxonomists to consider the actual needs and interests of the larger non-taxonomic end-user community who fund the majority of taxonomic research, and who require a system that remains reasonably stable and is relatively intuitive, without the need for inaccessible laboratory equipment or advanced technical scientific knowledge to identify amphibian species to the genus level.

Keywords

Dicoglossidae, Microhylidae, Ranidae, Rhacophoridae, subgenus, synonym, taxonomic inflation

Introduction

Taxonomic classifications are increasingly being informed by molecular phylogenies, both at the specific and supraspecific levels (e.g., Brown et al. 2015; Chan and Grismer 2019; Wood et al. 2020). Ideally, the Linnaean classification system should reflect the hierarchical structure of phylogenetic relationships, where nested, monophyletic units, inferred in robust phylogenetic analyses receive an assignment of Linnaean rank (genus, family, order, etc.). Because the species is the basic unit of classification and biodiversity, and the fundamental unit of evolution, delimiting clades at the species level can be based on a testable, biological, and conceptual framework (de Queiroz 2007; Sukumaran et al. 2021). In contrast, the demarcation of supraspecific boundaries is less objective and can be subject to interpretation and differences of opinion. Species-rich genera inherently contain higher levels of genetic structure, making them more amenable (and susceptible) to splitting (Malhotra and Thorpe 2004; Frost et al. 2006; Nicholson et al. 2012; Poe 2013; Poe et al. 2017). Consequently, the increasing availability of large-scale phylogenies encompassing deeper and broader taxonomic scales has facilitated the splitting of medium to large (and occasionally small) clades at the genus level into smaller subclades, each representing a separate genus (Mausfeld and Schmitz 2003; Malhotra and Thorpe 2004; Arnold et al. 2007; Hedges and Conn 2012; Nicholson et al. 2012). This clade-splitting exercise is becoming more prevalent in amphibian systematics (e.g., Frost et al. 2006; Biju et al. 2010, 2020; Oliver et al. 2015; Jiang et al. 2019; Dubois et al. 2021; Gorin et al. 2021), ostensibly to enhance taxonomic stability, usefulness, ease of management, and occasionally to create more regionally-circumscribed genus groups in the hope of improving conservation measures by developing local pride in biodiversity preservation. However, this practice is often predicated on untenable supporting evidence (e.g., weakly supported phylogenies, phylogenetic uncertainty, or ineffective and inaccurate “diagnostic” characters state comparisons; Oliver et al. 2015; Chandramouli et al. 2020; Dubois et al. 2021) without weighing the effects on downstream applications. When splits are supported solely on the basis of molecular data, they are more akin to a clade-naming exercise, rather than a practical and intelligible progression of taxonomic knowledge for the majority of end-users that require a genus name to apply to a phenotypic group that can be relatively easily distinguished from others, and thus aid in species identification. In fact, this practice of taxonomic inflation often confers little to no taxonomic value but instead, adds more confusion for the majority of end-users. As case studies, we investigate the supporting evidence used in several recent genus-level splitting examples from four families of amphibians [Dicroglossidae Anderson, 1871, Microhylidae Günther, 1858, Ranidae Batsch, 1796, and Rhacophoridae Hoffman, 1932] to highlight the undesirable confusion and instability created by the widespread

genus-species binomial rearrangements resulting from this clade-splitting exercise.

Rhacophoridae is a large family containing more than 450 species that are mostly distributed across Asia with a disjunct occurrence in Africa (Frost 2024). The largest genus in this family is *Rhacophorus* Kuhl & van Hasselt, 1822 *sensu lato*, which comprises at least 99 species (Chan et al. 2018; Kropachev et al. 2022; Li et al. 2022; Brakels et al. 2023). Naturally, several large-scale phylogenetic studies revealed high levels of phylogenetic structure within this large genus (Li et al. 2008, 2009, 2013; Hertwig et al. 2013; Chan et al. 2018, 2020c). *Rhacophorus sensu lato* was subsequently split into several additional genera: *Leptomantis* Peters, 1867 (13 spp.) and *Zhangixalus* Li, Jiang, Ren & Jiang, 2019 (40 spp.) were recognized based on arguments reliant on phylogenetic structure and several putatively diagnostic morphological characters, distribution range, and reproductive mode (Jiang et al. 2019), while *Tamixalus* Dubois, Ohler & Pyron, 2021 and *Vampyrus* Dubois, Ohler & Pyron, 2021, were erected solely based on phylogenetic position—generic diagnoses were recapitulated from the published descriptions of type species without any reported examination of specimens (Dubois et al. 2021). Dubois et al. (2021) also split the relatively small genus *Gracixalus* Delorme et al., 2005 (19 species; Tran et al. 2023) creating *Orixalus* Dubois, Ohler & Pyron, 2021 based on the same criteria. Two other rhacophorid genera, *Rohanixalus* Biju et al., 2020 and *Taruga* Meegaskumbura et al., 2010, represent subclades of taxa previously assigned to the genus *Feihyla* Frost et al., 2006 and *Polypedates* Tschudi, 1838, respectively (Meegaskumbura et al. 2011; Biju et al. 2020). The genus *Nanohyla* Poyarkov, Gorin & Scherz, 2021 from the family Microhylidae is reciprocally monophyletic with the genus *Microhyla* Tschudi, 1838 and was split from it largely based on osteological characters, geographic distribution, and clade age (Gorin et al. 2021). In the family Dicroglossidae, the genus *Phrynoglossus* Peters, 1867 was recognized as distinct based on reciprocal monophyly with its sister genus *Occidozyga* Kuhl & van Hasselt, 1822 and other putative characters pertaining to morphology, ecology, and amplexus mode (Köhler et al. 2021). The genera *Oreobatrachus* Boulenger, 1896 and *Frethia* Dubois, Ohler & Pyron, 2021 were further split from *Occidozyga* solely based on inconclusive phylogenetic placements, without further supporting evidence (Dubois et al. 2021).

One of the most radical examples of wholesale supraspecific changes in amphibian taxonomy occurred in true frogs (family Ranidae) of the genus *Hylarana* Tschudi, 1838 *sensu lato*, which included the en bloc elevation of eight subgenera to the genus rank (*Amnirana* Dubois, 1992, *Chalcorana* Dubois, 1992, *Humerana* Dubois, 1992, *Hydrophylax* Fitzinger, 1843, *Hylarana*, *Papurana* Dubois, 1992, *Pulchrana* Dubois, 1992, *Sylvirana* Dubois, 1992) and the creation of two new genera (*Abavorana* Oliver, Prendini, Kraus & Raxworthy, 2015 and *Indosylvirana* Oliver, Prendini, Kraus & Raxworthy, 2015). This taxonomic upheaval was based on a weakly supported phylogeny, distribution ranges, and non-diag-

nostic (i.e., non-opposing, or non-discrete) morphological character comparisons (Oliver et al. 2015).

In this study, we review updated phylogenies from the latest studies or perform additional phylogenetic analysis using more comprehensive datasets, and evaluate the putatively diagnostic characters of the aforementioned newly-proposed genera (*Rohanixalus*, *Taruga*, *Leptomantis*, *Zhangixalus*, *Tamixalus*, *Vampyrius*, *Orixalus* [Rhacophoridae]; *Nanohyla* [Microhylidae]; *Phrynoglossus*, *Frethia*, *Oreobatrachus* [Dicroglossidae]; and *Hylarana* sensu lato [Ranidae]) to determine whether their recognition at the genus level is warranted. We also evaluate the status of *Pterorana* Kiyasetuo & Khare, 1986, which has repeatedly been demonstrated to be a member of *Hylarana* sensu lato in recent literature, but its status has not been resolved. We echo the recommendations of Vences et al. (2013) for a sensible, robust, and critical nomenclatural framework to guide practitioners, reviewers, and journal editors to consider before proposing, refuting, or supporting proposals, for splitting clades at the supraspecific level. We follow numerous other systematists, and advocate for the use of the subgenus rank (e.g., McCranie and Townsend 2008; Van et al. 2009; Brown et al. 2015; Mahony et al. 2017; Cox et al. 2018; Wood et al. 2020; Vogel et al. 2022) and/or informally-recognized taxonomic “groups” or “complexes” as convenient (e.g., Mahony et al. 2017; Flury et al. 2021; Grismer et al. 2021) for cases where subclades are phylogenetically supported but lack strong, unambiguously discrete, and opposing diagnostic characters based on comprehensive comparative studies of all (or at least most) known species. The subgenus rank can establish informative taxonomic partitions to facilitate research and conservation without compromising on information content, while simultaneously avoiding unnecessary and large-scale taxonomic disruptions to numerous formally named/long-established genus-species couplets (Smith and Chiszar 2006; Pauly et al. 2009; Vences et al. 2013; Cox et al. 2018), so, we embrace the practice of recognizing subgenera.

Our disagreement with the creation of the aforementioned new genera in no way undermines the research that was presented in the respective papers, as all have undeniably contributed to our knowledge of these (and/or other) taxonomic groups. The genera included in the case studies here were selected based on our own (admittedly subjective) familiarity with the taxa involved, and are in no way exhaustive or representative of the quality of the research presented therein. We are fully aware that there are many conflicting concepts and opinions held amongst members of the taxonomic community, on what should constitute a genus, how much support is needed, the type of characters and criteria that are sufficient to recognize a new genus-level split, whether the recognition of subgenera is an advisable or generally preferred practice, and whether taxonomists should even consider downstream effects for end users of binomials. We are also aware that there are differing opinions on what constitutes as “taxonomic progress.” The evolutionary relationships between species are not changing, but rather only our understanding of these relationships—as we gain more data

and improved methods of analyzing them. We are of the opinion that the primary goal of taxonomy is to reflect, and eventually help us understand the true evolutionary tree, at which point we must achieve a stable taxonomy, at least at the genus level, where species will no longer be needlessly moved between genera. At this point, intra-generic taxonomic progress will continue with minimal impact to the binomial system, which is what everyone (not just taxonomists) uses as a system to communicate about biodiversity in general, and the species themselves. We have the utmost respect for our peers regardless of whether they share our opinions, and the expression of our opinions are in no way intended to create controversy or offense. We do not claim to offer any new approaches or concepts in this paper, but merely highlight what we consider to be a growing problem in Asian amphibian taxonomy and suggest options for how to reduce the impact of the problem.

In summary, in this paper, we offer our opinions on the negative impact of prematurely splitting genera based on inconclusive evidence such as incomplete taxon sampling (for morphological, molecular, biogeographical, and behavioral data), omission of relevant published data, and/or weakly supported phylogenies, which are often overturned with the availability of larger datasets consisting of more extensive taxon and gene sampling (Chan et al. 2020a, 2020b; Chandramouli et al. 2020), or just a more comprehensive review of the available literature.

Materials and methods

To facilitate consistent and objective assessments, we agree with and thus follow the Taxon Naming Criteria (TNC) framework proposed by Vences et al. (2013) to evaluate the criteria upon which the new genera were established. Of particular importance are the priority TNCs of Clade Stability and Phenotypic Diagnosability. The Clade Stability TNC refers to the stability of the monophyletic clade that is predicated on the strength of evidence for monophyly. Following Vences et al. (2013), strong evidence for monophyly should be based on (i) explicit phylogenetic analysis and independent analytical methods such as Maximum Likelihood and Bayesian Inference. Preferably, phylogenies should be consensual across a wider array of different analytical methods; phenetic methods such as Neighbor-joining are considered insufficient; (ii) robust clade support based on a relevant method that is explicitly justified (e.g., Hillis and Bull 1993; Goldman et al. 2000; Pauly et al. 2009; Hoang et al. 2017); (iii) dense taxon sampling to increase topological accuracy and taxonomic coverage to ensure that species can be reliably allocated to genera; and (iv) support by high-quality and independent datasets (e.g., from different genetic markers, such as both mitochondrial and nuclear genes that contain sufficient informative sites).

Because this study addresses supraspecific ranks, we employ the absolute diagnosability criterion for the Phe-

notypic Diagnosability TNC. This is the strictest form of the criterion that requires diagnostic characters to be shared by all species included in the genus and not found in any other species from closely related genera. We further add that characters detected in a small subset of representative taxa and assumed to be present in all other constituent species without evidence to support that assumption are deemed insufficient. Furthermore, the identification of proposed diagnostic characters must be based on a demonstrated thorough review of the pertinent literature (preferably supplemented with the examination of vouchered specimens). If authors disagree with the previous descriptions of published morphological characters, they must be discussed and corrected based on evidence, since overlooked published morphological variation is demonstrated herein to be a regular source of erroneous phenotypic definitions. We acknowledge that exceptions for certain characters and species can exist (defined as relative diagnosability by Vences et al. 2013) but this should necessarily be restricted to a small number of characters and minor representation of included species. In such cases, relative diagnosability should be clearly justified and accompanied by other sources of evidence (e.g., biogeography). The choice of characters included in the diagnosis should also be appropriate at the genus level. Following recommendations by Vences et al. (2013), diagnostic characters should be discrete, conspicuous, readily observable in live and preserved species of different sexes and life-history stages, and should not require overly specialized conditions, methods, skills, or equipment to observe (e.g., CT Scans). See Vences et al. (2013) for more detailed discussions on TNCs.

For the previously proposed genera *Rohanixalus*, *Phrynoglossus*, *Frethia*, and *Oreobatrachus*, we performed new phylogenetic analyses using more comprehensive datasets to determine whether the proposed genera are phylogenetically stable. We incorporated sequences of *Rohanixalus* from Biju et al. (2020) into the multilocus Sanger dataset by Chan et al. (2018) to determine whether the inclusion of additional *Rohanixalus* taxa could affect phylogenetic inference. We used Chan et al.'s (2018) dataset because it is larger (3483 bps [base pairs] vs. 1937 bps in length) compared to Biju et al.'s (2020) dataset and hence, should provide improved resolution. For *Occidozyga*, *Phrynoglossus*, *Frethia*, and *Oreobatrachus*, we collated 12S and 16S mitochondrial sequences from most recent studies (Chan et al. 2021, 2022b; Flury et al. 2021; Köhler et al. 2021; Trageser et al. 2021) resulting in a comprehensively sampled *Occidozyga* dataset (13 out of 18 described species). We used IQ-TREE 2 (Minh et al. 2020) to perform a maximum likelihood (ML) analysis (partitioned by gene) with model selection and 1000 bootstrap replicates. Sequences used in this study are listed in Table S1.

To determine the reliability of published morphological diagnoses purported to justify the division of *Hylarana* sensu lato and *Microhyla* sensu lato, we examined specimens (including type specimens whenever possible) or photographs of type specimens from the following museums: **BMNH** (British Museum of Natural History;

now the **NHMUK**—Natural History Museum, London, UK); **FMNH** (Field Museum of Natural History, Chicago, Illinois, USA); **JUHG** (Jahangirnagar University Herpetological Group, Savar, Dhaka, Bangladesh); **MCZ** (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA); **MNHN** (Museum National d'Histoire Naturelle, Paris, France); **ZSI/ERS** (Zoological Survey of India, Eastern Regional Station, Shillong, Meghalaya, India); **ZSI/K** (Zoological Survey of India, Kolkata, West Bengal, India); **LSUHC** (La Sierra University Herpetological Collection, Riverside, California, USA); and **ZRC** (Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore). The list of examined materials is provided in the Appendix. All measurements were made using digital calipers in millimeters rounded to the nearest 0.1 mm.

Results

Family Rhacophoridae: *Leptomantis*, *Zhangixalus*, *Tamixalus*, *Vampyrus*, and *Orixalus*

Jiang et al. (2019) used a mitochondrial phylogeny, “distinct morphological differences,” geographic distribution patterns, and reproductive modes to diagnose the three subclades of *Rhacophorus* sensu lato as the genera *Rhacophorus* sensu stricto, *Leptomantis*, and *Zhangixalus*. However, our evaluation of the six morphological characters presented by Jiang et al. (2019) demonstrate that the diagnostic characters were objectively inaccurate and not operationally diagnostic. Body size and dorsal coloration are highly variable and overlap across genera; longitudinal dermal folds on limbs are purportedly absent in both *Leptomantis* and *Zhangixalus* (Jiang et al. 2019) but are actually present, for example, in *Z. achantharrhena* (Harvey, Pemberton & Smith, 2002), *Z. pachyproctus* Yu et al., 2019, *Z. dulitensis* (Boulenger, 1892), *Z. prominanus* (Smith, 1924), and *Z. franki* Ninh et al., 2020 (Harvey et al. 2002; Inger et al. 2017; Yu et al. 2019; Ninh et al. 2020; Haas et al. 2021); a supraocular fold is purportedly absent in *Zhangixalus* (Jiang et al. 2019) but is actually present, for example, in *Z. dorsovirens* (Bourret, 1937), *Z. pachyproctus*, *Z. dulitensis*, and *Z. prominanus* (Zhang et al. 2011; Inger et al. 2017; Yu et al. 2019; Haas et al. 2021); upper eyelid projections are absent in all three genera, or present (only) in *Leptomantis* (Jiang et al. 2019). Thus, the non-exclusiveness of these characters provides no diagnostic utility, and none of the characters that putatively distinguish the three genera comply with the Phenotypic Diagnosability TNC.

The distribution of *Leptomantis* was described as Maritime Southeast Asia, whereas *Rhacophorus* sensu stricto was reported from across Southeast Asia (Jiang et al. 2019). However, the former is almost a complete subset of the latter (Jiang et al. 2019: fig. 2) and hence, has no differentiating power in terms of biogeography. The dis-

tribution of *Zhangixalus* was stated as eastern Asia and northern Indochina, which is erroneous as *Z. achantharrhena* occurs in Indonesia (Harvey et al. 2002), while *Z. dulitensis* and *Z. prominans* occur in Malaysia (Chan et al. 2010; Inger et al. 2017). Although genomic data showed that clade support for the monophyly of *Leptomantis* and *Zhangixalus* is strong (Chan et al. 2020c; Chen et al. 2020), there are no clear differences in morphology, ecology, or distribution (secondary and accessory TNCs; Vences et al. 2013) that can reliably diagnose *Leptomantis*, *Zhangixalus*, and *Rhacophorus* sensu stricto. Thus, we formally propose to assign *Leptomantis* Peters, 1867 and *Zhangixalus* Li, Jiang, Ren & Jiang, 2019 (in Jiang et al. 2019) to the subgenus rank within the genus *Rhacophorus* Kuhl & van Hasselt, 1822.

Tamixalus and *Vampyrus* were proposed as monotypic genera that were previously congeneric with *Rhacophorus*. Their recognition as distinct genera was solely based on their phylogenetic positions that were inferred to be paraphyletic with regard to *Rhacophorus* (Dubois et al. 2021). However, these relationships were not strongly supported. According to Dubois et al. (2021), the genus *Vampyrus* is sister to the genus *Gracixalus* with weak support, which is not surprising because the sequence data available to them for *Vampyrus* on GenBank (Benson et al. 2017) was demonstrably insufficient (fewer than 600 bps of a partial 16S mtDNA fragment; see Chan et al. 2022a). In contrast, the genomic study by Chan et al. (2020c), which included genomic sequences of *Vampyrus* and several species of *Gracixalus*, and was based on a dataset comprising more than 2.5 million bps in length, inferred *Vampyrus* within the genus *Rhacophorus* with strong support. Similarly, Dubois et al. (2021) established the genus *Tamixalus* based on its weakly supported relationship as the sister lineage to the clade comprising *Feihyla* + *Ghatixalus* + *Taruga* + *Polypedates* (also derived from < 600 bps of a partial 16S mitochondrial fragment). Other studies have shown *Tamixalus* to be nested within *Rhacophorus* (Biju et al. 2016; Pan et al. 2017). The genus *Orixalus* is a subclade within *Gracixalus* (Dubois et al. 2021) and thus, has no precedent to be recognized as a distinct genus. Furthermore, the “diagnoses” for *Tamixalus*, *Vampyrus*, and *Orixalus* were merely recapitulations of morphological diagnoses from previously published descriptions (see Dubois et al. 2021) without any context to their relevance when compared to related taxa; hence, such non-diagnostic “diagnoses” do not demonstrate diagnosability in the context of the Phenotypic Diagnosability TNC. We, therefore, consider *Tamixalus* Dubois, Ohler & Pyron, 2021 **syn. nov.** and *Vampyrus* Dubois, Ohler & Pyron, 2021 **syn. nov.** to be junior subjective synonyms of *Rhacophorus* Kuhl & van Hasselt, 1822, and *Orixalus* Dubois, Ohler & Pyron, 2021 **syn. nov.** a junior subjective synonym of *Gracixalus* Delorme, Dubois, Grosjean & Ohler, 2005.

Our proposed treatment of *Zhangixalus* at the rank of subgenus requires the return of 37 (most) species back to the genus *Rhacophorus* in which they all have either been originally named or had been placed almost continuously for several decades before the most recent episode

of taxonomic rearrangements. Four species have been recently named in *Zhangixalus* (Yu et al. 2019; Nguyen et al. 2020; Ninh et al. 2020; Brakels et al. 2023), so their reallocation to *Rhacophorus* requires the creation of the following new combinations: *Rhacophorus* (*Zhangixalus*) *franki* (Ninh et al., 2020) **comb. nov.**, *Rhacophorus* (*Zhangixalus*) *jodiae* (Nguyen et al., 2020) **comb. nov.**, *Rhacophorus* (*Zhangixalus*) *melanoleucus* (Brakels et al. 2023) **comb. nov.**, *Rhacophorus* (*Zhangixalus*) *pachyproctus* (Yu et al., 2019) **comb. nov.** The proposed treatment of *Leptomantis* as a subgenus-level taxon and the synonymy of *Tamixalus* and *Vampyrus* requires only that all those species be returned to the genus *Rhacophorus*, without the need for the creation of any new binomial combinations. The same applies to the synonymy of *Orixalus* into *Gracixalus*.

Family Rhacophoridae: *Rohanixalus*

Justification for the formation of the genus *Rohanixalus* was partly based on its phylogenetic position as the sister lineage to *Chiromantis* Peters, 1854 as opposed to *Feihyla*, despite weak node support (Biju et al. 2020). This relationship was also recovered in previous studies (Pyron and Wiens 2011; Meegaskumbura et al. 2015). Alternatively, other studies have recovered *Rohanixalus* within the *Feihyla* clade, implying that *Rohanixalus* could be congeneric with *Feihyla* (Hertwig et al. 2013; Li et al. 2013; Chan et al. 2018). Although the aforementioned studies were based on a limited number of Sanger-derived markers, had weak branch support, and thus, could not reject either hypothesis, two recent independent studies that employed different sets of genomic markers and analytical methods conclusively demonstrated that *Rohanixalus* forms a clade with *Feihyla* with strong support (Chan et al. 2020c; Chen et al. 2020). Chan et al. (2020c) further demonstrated that high levels of gene tree discordance and incomplete lineage sorting were the deterministic processes underlying the conflicting phylogenetic relationships of numerous rhacophorid clades. In our ML analysis, the inclusion of new *Rohanixalus* sequences did not alter the initial topology inferred by Chan et al. (2018). *Rohanixalus* was not reciprocally monophyletic with *Feihyla* and was inferred as the sister lineage to the *F. kajau* + *F. inexpectata* clade with moderate support (bootstrap = 77; Fig. S1). These results demonstrate that Sanger markers are insufficient to resolve the phylogenetic placement of *Rohanixalus*.

In their “Comparison” section, Biju et al. (2020) stated that *Rohanixalus* can be distinguished from *Feihyla* by the following characters: (i) “the presence of a pair of contrasting light-colored dorsolateral stripes (with variable degree of prominence, prominent to faint, continuous or discontinuous) starting from the snout tip, extending over the upper eyelid margins, and ending close to the vent on either side (vs. absent...);” (ii) “presence of prominent and dense minute speckles throughout the dorsal and lateral surfaces of the body (including dorsum, lateral surfaces, and dorsal surface of limbs) (vs. absent);”

(iii) “freshly laid eggs light green and unpigmented (vs. creamy-white with pigmentation on poles, except in some members of *Feihyla vittiger* group);” (iv) “eggs laid in bubble nests (vs. jelly nests);” and (v) “absence of a prominent white streak along the upper lip margins from below the eye up to shoulder (vs. present).” We found all these characters to have been improperly characterized, four were not mutually exclusive and the fifth character is only questionably diagnostic for adults of these two groups. The presence of dorsolateral stripes is not only known to be variable within several rhacophorid genera [e.g., not just in *Rhacophorus* which was implied in Biju et al. (2020), but also in *Polypedates*, *Raorchestes* Biju et al., 2010, and *Pseudophilautus* Laurent, 1943; Manamendra-Arachchi and Pethiyagoda (2005); Biju and Bossuyt (2009)], but also even within species [e.g., *Raorchestes akroparallagi* (Biju & Bossuyt, 2009), *Pseudophilautus pleurotaenia* (Boulenger, 1904); Manamendra-Arachchi and Pethiyagoda (2005); Biju and Bossuyt (2009)], and was even shown to be occasionally indiscernible in *Rohanixalus* (see Biju et al. 2020: fig. 7D). The presence of speckling is not exclusive to *Rohanixalus* as some individuals of *F. vittiger* (Boulenger, 1897) also have distinct speckling on their dorsal and lateral surfaces (e.g., Biju et al. 2020: fig. 6H). The light green and unpigmented eggs in *Rohanixalus* are not unique to this genus, as the authors themselves noted for the *F. vittiger* group [further corroborated by Kusriani et al. (2017)].

Biju et al. (2020) stated in their “Comparison” section for *Rohanixalus* (point iv, above) that *Feihyla* and *Rohanixalus* differed regarding their nest structures but gave conflicting information elsewhere in their paper. The “Diagnosis” section for *Feihyla* stated “...; eggs laid in terrestrial jelly nests (Fig. 3)”, and in the “Discussion” section, they stated, “*Feihyla* have jelly-nests with a complete absence of bubbles even in freshly laid egg clutches”. However, Biju et al. (2020: fig. 3F) gave a “schematic illustration of egg clutch morphology in the *Feihyla vittiger* group” directly referring to it as a “bubble nest” in the figure, thus demonstrating that *Feihyla* can have either a “jelly” or “bubble” nest. Confusingly, Biju et al. (2020) also referred to the nests of *Rohanixalus* as a “jelly-nest” in several places (e.g., in their fig. 10 caption). The distinction between bubble and jelly nesting requires further investigation. Numerous “bubble” nests of *Rohanixalus* depicted in Biju et al. (2020: figs 10A, C, 18H) appear to be essentially bubble-free, including a relatively fresh one-day-old egg clutch depicted in their fig. 11B.

Finally, the fifth stated diagnostic character for *Feihyla* is neither consistent, given as “prominent white streak along the upper lip margins from below the eye up to shoulder” in the comparison for *Rohanixalus*, or stated in the “Diagnosis” section for *Feihyla* as “a white streak extends along the upper lip margins, either from below the eye up to the shoulder (in *Feihyla palpebralis* group) or from snout tip to the groin (in *Feihyla vittiger* group)”, nor is it properly characterized in either description since in some cases details given in the original descriptions of the species have been apparently overlooked for the species diagnoses sections in Biju et al. (2020). For ex-

ample, in some individuals of *F. kajau* (Dring, 1983), *F. vittiger*, and *F. inexpectata* (Matsui, Shimada & Sudin, 2014), this stripe is thin (not “prominent”), irregular, can begin below the nostril or at the anterior border of the orbit, extending around the ventral border of orbits, across or above the tympanum (but not bordering the upper lip margin in these species), and ends on the mid-flanks in some individuals or continues to the inguinal region in others (e.g., Pratihari et al. 2014: fig. 104; Haas et al. 2018: fig. 5, 2021; Biju et al. 2020: fig. 6). In the holotype description of *F. kajau*, Dring (1983) wrote “Upper lip, temporal area below supratympanic ridge, lower flanks, entire inguinal area, ... all unpigmented, except for white spots on lips, tympanum, flanks, ...”, and in the variation section (for eight paratypes) Dring (1983) wrote “There is little pattern variation, but sometimes the lateral white pigment forms a broken band from below the eye to the mid-flank.” In contrast, and despite citing Dring (1983), Biju et al. (2020) wrote in the species “Diagnosis” for *F. kajau* “presence of a narrow white streak starting from the snout tip and extending along the lateral surfaces up to the groin, that separates the dorsal and lateral body colouration”. Similarly, in the original description of *F. inexpectata*, Matsui et al. (2014) stated that the white stripe extended to half the body length in the holotype and adult paratype, but for the juvenile paratype, “ventral white stripe is not recognizable”. In contrast, Biju et al. (2020) wrote in the species diagnosis for *F. inexpectata*, “a narrow white streak starting from the snout tip and extending along the lateral surfaces up to the groin...”. In this case, no citation was provided for the characters listed in their species “Diagnosis”, and besides mentioning the examination of “Chinese *Feihyla* specimens, including the type series of *F. fuhua*”, no voucher specimen numbers of any examined *Feihyla* species were explicitly listed in Biju et al. (2020). Besides the photographed animals shown in the figures, it is not clear from where the information provided in this section originated. In the *Feihyla palpebralis* group, the streak extends beyond the shoulder, and nearly to the groin on some individuals (e.g., Biju et al. 2020: fig. 5A, B). No white streak or “spots” are present laterally on the head in *Rohanixalus* that we are aware of making this perhaps the only character to potentially diagnose adult individuals of these two groups, however this character is apparently highly variable, and reported as “not recognizable” on at least one juvenile (Matsui et al. 2014). Morphological variation in all *Feihyla* species is still very poorly documented in the literature and considering many rhacophorid genera exhibit high levels of variation in markings that exceeds those seen in *Feihyla* sensu lato, we consider that this character alone is insufficient to justify splitting the genus.

Dubois et al. (2021) synonymized *Rohanixalus* with *Feihyla*, though without providing any discussion or justifications besides the position of taxa in their phylogeny. The community is currently divided on the correct genus name for this clade, e.g., Portik et al. (2023b) followed the synonymy of *Rohanixalus*, whereas Ellepola et al. (2022) and Liu et al. (2023) treated *Rohanixalus* as valid. Our study substantiates the synonymization of *Rohanix-*

alus with *Feihyla* by demonstrating that only one of the stated diagnostic characters proposed for *Rohanixalus* in Biju et al. (2020) might be diagnostic pending further study. Furthermore, genomic analyses indicate that *Rohanixalus* forms a clade with *Feihyla* (Chan et al. 2020c; Chen et al. 2020). Although there is evidence to support the monophyly of the *Rohanixalus* clade, its uncertain phylogenetic placement and the lack of proper diagnostic characters do not comply with the Clade Stability and Phenotypic Diagnosability priority TNCs and as such do not warrant generic recognition. Thus, we confirm the proposed synonymization of Dubois et al. (2021) and consider *Rohanixalus* Biju et al., 2020, to be a junior subjective synonym of *Feihyla* Frost et al., 2006. Our proposed synonymy requires *F. hansenae* (Cochran, 1927) and *F. vittata* (Boulenger, 1887) to be returned to the genus *Feihyla*, and the formal genus reallocation resulting in new binomial combinations for the following five species that prior to Biju et al. (2020), four were placed in the genera *Chirixalus* Boulenger, 1893 or *Chiromantis* (Wilkinson et al. 2003; Chan et al. 2011; Riyanto and Kurniati 2014), or one has subsequently been described as new (Liu et al. 2023): *Feihyla baladika* (Riyanto & Kurniati, 2014) **comb. nov.**, *Feihyla marginis* (Chan et al., 2011) **comb. nov.**, *Feihyla nauli* (Riyanto & Kurniati, 2014) **comb. nov.**, and *Feihyla punctata* (Wilkinson et al., 2003) **comb. nov.**, and *Feihyla wuguanfui* (Liu et al., 2023) **comb. nov.** Biju et al. (2020), presumably unintentionally, also created the new binomial combinations of “*Feihyla senapatiensis*” (Mathew & Sen, 2009) and “*Feihyla shyamrupus*” (Chanda & Ghosh, 1989) in the captions for their figures 17, and 18 and 19, respectively. The species epithet for *F. punctata* is here changed from “*punctatus*” to accommodate the feminine genus name *Feihyla*. How to treat the species epithet “*shyamrupus*” is not so obvious. According to Chanda and Ghosh (1989), “The species is named after Dr. Shyamrup Biswas, ...”, who was a man. Rather than adopting the typical naming convention for a species epithet formed as a patronym, i.e., as a noun in the genitive case, “*shyamrupi*” (ICZN 1999; Art. 31.1.2), the authors instead chose to Latinize the personal name by adding the suffix -us and thus treating it as a noun in apposition. This treatment is acceptable according to the Code (ICZN 1999; Art. 31.1), so the gender of the specific epithet does not change, i.e., *Feihyla shyamrupus* (Chanda & Ghosh, 1989).

Family Rhacophoridae: *Taruga*

Meegaskumbura et al. (2010) erected a new genus, *Taruga*, to represent the clade of *Polypedates* that is sister to a second clade that contains all other *Polypedates* species, and diagnosed the two clades from each other based on a comparison of morphological data obtained from a very limited sample of species. Adult specimens of all three *Taruga* species [*T. eques* (Günther, 1858), *T. fastigo* (Manamendra-Arachchi & Pethiyagoda, 2001), and *T. longinasus* (Ahl, 1927)] were compared only against specimens of three other *Polypedates* species [*P. macu-*

latus (Gray, 1830), *P. cruciger* Blyth, 1852, and *P. leucomystax* (Gravenhorst, 1829)—out of 20 valid species recognized at that time]. Here, we provide the stated diagnostic characters and evidence that demonstrates that those characters are not unique to the clade described as *Taruga*: (i) “*Taruga* possess a dorsolateral glandular fold that extends from the posterior margin of the upper eyelid to the mid-flank (vs. a supratympanic fold that curves over the dorsal margin of the tympanic membrane in *Polypedates*);”, we do not consider this character as diagnostic because many published photographs of *Taruga* clearly show that the “dorsolateral glandular fold” does not extend to the mid-flank, but terminates above the forelimb insertion or slightly beyond (e.g., *T. eques*: Dawundasekara and De Silva 2011: fig. on pg. 30; *T. fastigo*: Manamendra-Arachchi and Pethiyagoda 2001: fig. 1; Meegaskumbura et al. 2010: fig. 2; *T. longinasus*: Bopage et al. 2011: fig. 1C; Peabotuwage et al. 2012: fig. 14), no different to the supratympanic folds in other *Polypedates* species. Also, the supratympanic folds in most *Polypedates* are straight (not curved); (ii) “a prominent calcar at the distal end of the tibia (absent in most *Polypedates*)”, as indicated, this is not an exclusive or robust character as a prominent calcar is present in *P. ottilophus* (Boulenger, 1893) and *P. pseudotilophus* Matsui, Hamidy & Kuraishi, 2014 (Boulenger 1893; Matsui et al. 2014a), a blunt calcar in *P. ranwellai* Wickramasinghe, Munindradasa & Fernando, 2012 (Wickramasinghe et al. 2012), or a calcar that is reduced to a tubercle on some other taxa [e.g., *P. colletti* (Boulenger, 1890) and *P. discantus* Rujirawan, Stuart & Aowphol, 2013 (Rujirawan et al. 2013)]; (iii) “a more acutely pointed snout;”, the three *Taruga* species were only compared with *P. cruciger* and *P. maculatus*, and not with species that have distinctly more pointed snouts such as *P. colletti* (Inger et al. 2017), *P. ottilophus*, and *P. pseudotilophus* (Matsui et al. 2014a). Furthermore, the degree of “pointedness” within *Taruga* also varies between species and the sexes. For example, *T. eques* has a markedly less “pointy” snout compared to *T. fastigo* and *T. longinasus* and no intraspecific variation was provided (Meegaskumbura et al. 2011). This qualitative character provides no objective distinguishing properties and hence, does not qualify as a diagnostic character; (iv) “6–10 prominent conical tubercles surrounding the cloaca (absent in *Polypedates*)”; some *Polypedates* species also possess tubercles on the cloacal region (e.g., *P. discantus*: Rujirawan et al. 2013). In addition to comparing adult specimens, tadpole specimens were compared between *T. eques* and *P. cruciger*. However, no attempt was made to expand the comparison to include tadpole descriptions of other *Polypedates* species and the authors even suggested that further work is required to determine if the differences observed were diagnostic for the genera. Senevirathne et al. (2017) made a detailed comparison of osteological characters between *Taruga eques*, *T. longinasus*, *P. cruciger*, and *P. maculatus* and identified some additional characters that diagnosed these two pairs of species. But such limited sampling of *Polypedates* (two of 24 valid species ca. 2017, which excluded the type species, *P. leucomystax*), pre-

vents any meaningful assessment of the diagnostic utility of these characters at the genus level. In terms of priority TNCs, *Taruga* satisfies the monophyly and clade stability criteria but not the phenotypic diagnosability criterion. Therefore, we recommend that *Taruga* Meegaskumbura et al., 2010 be considered a subgenus of *Polypedates* Tschudi, 1838, and recognize its sister clade as the nominal subgenus, *Polypedates* (*Polypedates*), which contains all remaining species in the genus. The proposed relegation of *Taruga* to the subgenus rank returns the three currently valid taxa back to their previously widely accepted species-genus combinations.

Family Microhylidae: *Nanohyla*

The genus *Nanohyla* was split from the genus *Microhyla* based on monophyly, morphological diagnosability, biogeography, and clade age, which the authors claimed to satisfy all three priority TNCs of Monophyly, Clade Stability, and Diagnosability, as well as the secondary TNCs of Time Banding and Biogeography (Gorin et al. 2021). We demonstrate that of all those criteria, only monophyly and clade stability were adequately satisfied, albeit less important because *Nanohyla* is reciprocally monophyletic with *Microhyla*. Below, we provide justifications in support of our argument:

Diagnosability

Gorin et al. (2021) were inconsistent in different parts of the paper regarding the presence/absence of a distinct external tympanum in *Nanohyla*. Numerous statements were ambiguous including: “externally visible tympanum in most of species of the genus” or “tympanum externally visible or barely visible” or “tympanum externally distinct at least in males (*N. annamensis*, *N. annectens*, *N. arboricola*, *N. marmorata*, *N. nanapollexa*, *N. pulchella*) or barely distinct (*N. hongiaoensis*, *N. perparva*, *N. petrigena*),” but concluded, “In some species ..., we were not able to detect an externally visible tympanum (*N. hongiaoensis*, *N. perparva*, *N. petrigena*). It is not clear whether this reflects an actual character state in these species, or if this apparent state relates to the small sample size of specimens and photographs available to us. Further studies are needed to clarify the variation of the external tympanum in *Nanohyla* gen. nov.” The ambiguity of Gorin et al.’s concluding statement is exemplified in their figure 11, which demonstrates that three species of *Nanohyla* do not appear to have a discernible external tympanum (similar to *Microhyla* spp.).

The outer metatarsal tubercle in *Nanohyla* was claimed to be absent on all species except maybe *N. marmorata* (Bain & Nguyen, 2004), which they stated, “usually is not discernible or is indistinct,” a contradiction of Bain and Nguyen (2004) who described the outer metatarsal tubercle of *N. marmorata* as “varies from short, conical to long and projecting.” Gorin et al. (2021) questioned Hoang et al. (2020) regarding the presence of an outer metatarsal tubercle in *N. hongiaoensis* (Hoang et al.,

2020) erroneously stating that it was described as “indistinct” in the holotype description (“weak”: Hoang et al. 2020) and that it is not visible in Hoang et al. (2020: fig. 3F). Though the resolution on Hoang et al. (2020: fig. 3) is not optimal on the pdf version, we consider the outer metatarsal tubercle to be visible in both figure 3B and 3F. Gorin et al. (2021) concluded by saying, “In all the remaining species of *Nanohyla* gen. nov. it is absent, and we, therefore, consider this state to be diagnostic for the genus (in comparison to *Microhyla* s. str., which has two metatarsal tubercles in all species but *M. maculifera*, see comment below).” However, Gorin et al.’s (2021) statement also conflicted with Poyarkov et al. (2014) who stated for *N. annamensis* (Smith, 1923), that the outer metatarsal tubercle “may be present in various conditions: usually it is present and prominent (60% of specimens examined, as in their Fig. 4B), in some specimens it is small and flat (15%), or totally absent (35%),” and for *N. pulchella* (Poyarkov et al., 2014) wrote, “outer metatarsal tubercle rounded and indistinct.” Poyarkov et al. (2014: table 1) provided measurements of outer metatarsal tubercles for these two species based on 81 specimens in total. The absence of an outer metatarsal tubercle in *Nanohyla* is therefore not diagnostic with respect to *Microhyla*. The state of the digits being dorsoventrally flattened, and Finger I often reduced to a nub or shortened in *Nanohyla* (vs. variably longer in *Microhyla*) is also subjective and not exclusive to all members of either genus (Fig. 1). Other putatively diagnostic characters involve osteological characters that cannot be readily observed, require special equipment and techniques to observe, and were examined on a subset of species from all but one clade (representing 40% of *Microhyla* sensu stricto and 44% of *Nanohyla*). The clade missing from their osteological analyses, comprising *M. palmipes* Boulenger, 1897, was resolved in their phylogenetic analyses as sister to all other species in the *Microhyla* sensu stricto clade in their mtDNA analysis (its position unresolved in their combined mtDNA and nuDNA analysis). Thus, this taxon may be considered an important species (/clade) for morphological comparison as its most recent common ancestor may be closest to the most recent common ancestor of the *Nanohyla* clade.

Biogeography

The restricted distribution of *Nanohyla* was stated as, “montane forest areas in the Annamite (Truong Son) Mountains in East Indochina (Vietnam, eastern Laos, northeastern Cambodia), Malayan Peninsula (Titiwangsa Mountain Range), mountains of Borneo (Sarawak, Sabah of Malaysia, Brunei and northern Kalimantan, Indonesia), and the southwestern-most islands of the Sulu Archipelago of the Philippines” (Gorin et al. 2021), which is only partly true, as *N. perparva* (Inger & Frogner, 1979) and *N. petrigena* (Inger & Frogner, 1979) are widely distributed across the lowlands of Borneo (Inger & Frogner 1979; Inger et al. 2017). Thus, we do not consider biogeography as a valid TNC to support the recognition of *Nanohyla* because the distribution of *Nanohyla* overlaps

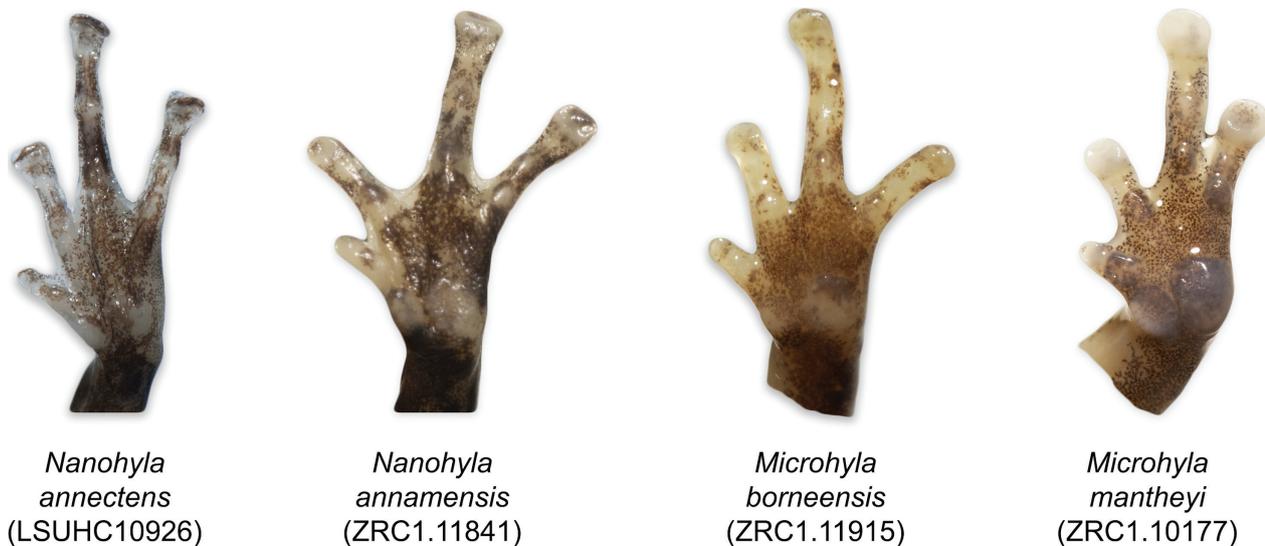


Figure 1. Ventral view of the left hand of various *Nanohyla* and *Microhyla* spp. demonstrating the subjective and variable character states pertaining to the digits being dorsoventrally flattened and the first finger often reduced to a nub or shortened (in *Nanohyla*). Voucher specimen numbers are in parentheses. See Material and Methods for institutional abbreviations.

with *Microhyla* in Borneo—the distribution of the former being a subset of the latter.

Time banding

Divergence-time estimations were based on a small molecular dataset consisting of two fragments of mitochondrial DNA (12S, 16S rRNA) and one relatively uninformative nuclear gene (BDNF), which is likely to produce inaccurate estimates even under the best of circumstances (Zheng et al. 2011; Filipowski et al. 2014). We obtained from GenBank the BDNF sequences of the ingroup taxa published by Gorin et al. (2021) and found that those sequences contained only 59 parsimony-informative sites (proportion of parsimony-informative sites = 0.08). Gorin et al. (2021) reported that their estimated age for the most recent common ancestor (MRCA) of *Microhyla* and *Glyphoglossus* Günther, 1869 (50.9 mya; HPD = 44.2–58.7) was similar to estimates obtained by Feng et al. (2017) (48.8 mya; HPD = 45.9–53.2). However, these estimates are considerably older than those subsequently inferred by Hime et al. (2021) (38.0 mya; HPD = 33.6–42.4) and Portik et al. (2023b) (31.7 mya; HPD reported to be in their associated supplementary file S5 which was not available online at the time of writing), which were based on the most in-depth and comprehensive genomic datasets to date. These discrepancies demonstrate the difficulty in obtaining accurate and consistent divergence time estimates between studies, making time banding a generally unreliable TNC.

Gorin et al. (2021) noted that the origin of *Microhyla*, *Nanohyla*, and *Glyphoglossus* was similar and notably older (~44 mya) than the ages of other currently recognized microhylinae genera such as *Kaloula* Gray, 1831 and *Uperodon* Duméril & Bibron, 1841 estimated at 27.4 mya (19.4–34.9), and the split between *Phrynellia* Boulenger, 1887 and *Metaphrynellia* Parker, 1934 estimated at 23.0 mya (16.2–29.1). However, their phylogeny also showed

at least 16 intrageneric splits within *Microhyla*, *Nanohyla*, and *Glyphoglossus* that are as old or older than their aforementioned intergeneric threshold examples (see nodes 19 and 21–35 in Gorin et al. 2021: fig. S3, table S4). Vences et al. (2013) cautioned against such use of time banding to justify taxonomic classification by stating that: “In a classification, in our opinion, reflecting this variation [in clade ages] is more informative than absolute age. Hence, attempting to standardize rank by age might feed some biological information into the Linnaean system, but at expense of other kinds of information and of the main purpose of this system: to facilitate communication.” Vences et al. (2013) further stated that “We support Zachos’ (2011) opinion that time banding and time clipping as an obligatory procedure would be deleterious in taxonomic practice ...” Though Gorin et al. (2021) did not imply that the most recent divergence times between closely related genera could or should be used as a relative time banding threshold in Microhylinae, they did consider relative time banding as a primary justification to divide *Microhyla* sensu lato into two difficult to diagnose genera that require specialized knowledge and equipment to assign species to, thus losing the communication value of the genus for the non-expert user.

The non-exclusive distribution ranges, questionable time estimates that are based on relatively small amounts of molecular data, non-diagnostic external characters, and difficult to characterize internal osteological characters do not fulfill the Diagnosability, Time Banding, and Biogeography TNCs. Based on the low support Gorin et al. (2021) obtained for the monophyly of *Microhyla* sensu lato in their mtDNA only trees and mtDNA + nuDNA ML tree, they stated that “... recognizing the two clades [*Nanohyla* and *Microhyla*] as separate genera would ... fully stabilize the taxonomy of the *Microhyla*–*Glyphoglossus* assemblage (if coalescent phylogenomic reconstructions were to reveal the clades to be paraphyletic with respect to *Glyphoglossus*, no taxonomic changes

would be necessary)". However, monophyly of *Microhyla* sensu lato received high support on their mtDNA + nuDNA Bayesian tree. Since their analyses estimate higher overall support for a monophyletic *Microhyla*–*Nanohyla* clade (as observed in other phylogenetic studies they cited, and more recently, Portik et al. 2023b), splitting *Microhyla* sensu lato based on phylogenetic uncertainty is not in our opinion a strong justification. As such, we disagree with Gorin et al. (2021) who stipulated that recognizing *Nanohyla* and *Microhyla* would “enhance the diagnosability of the respective genera.” On the contrary, recognizing *Nanohyla* as a separate genus creates more confusion and ambiguity because the vast majority of end-users, including many researchers, will not be able to reliably assign frogs or tadpoles of many *Microhyla* sensu lato taxa into the proposed *Nanohyla* versus *Microhyla* sensu stricto clades due to the lack of evidently differentiating characters. We agree with Vences et al. (2013) that ranked taxa (especially at the supraspecific level) serve as communication tools among biologists and between biologists and society. Therefore, the information content of a taxon should be reasonably easily grasped by non-taxonomists and if differences can only be observed at the molecular or osteological level, using less prominent ranks such as subgenera is desirable (Vences et al. 2013). Gorin et al. (2021) considered the subgenus recognition scenario but rejected it based on a secondary TNC stating, “We also contend that this solution [*Nanohyla* at genus level] is superior to the obvious alternatives, which are... (ii) recognizing the two clades within *Microhyla* s. lat. as subgenera... would continue to satisfy the three priority TNCs [Monophyly, Clade Stability, Diagnosability] but would not optimize under the Time Banding TNC.” However, we have shown that their time banding argument is not reliable due to notable differences among absolute divergence time estimates across different studies and that the recognition of genera using relative time banding across the microhylid tree if arbitrarily set at the more recent splits between currently recognized genera would require further atomization of *Microhyla*, *Nanohyla*, and *Glyphoglossus* in an attempt to homogenize divergence times within a subfamily for genus rank. We fully acknowledge that the *Nanohyla* clade is evolutionarily distinct from the *Microhyla* sensu stricto clade to a certain degree. However, both clades are reciprocally monophyletic and more importantly, lack distinct or operationally diagnostic characters for adults, juveniles and tadpoles. As such, we consider the recognition of *Nanohyla* at the genus rank to be unwarranted because it creates unnecessary confusion and problems for non-specialist microhylid taxonomist end-users. As a solution, we recommend treating *Nanohyla* Poyarkov, Gorin & Scherz, 2021 (in Gorin et al. 2021) as a subgenus of *Microhyla* Tschudi, 1838, which satisfies all three priority TNCs (as acknowledged by Gorin et al. 2021) and simultaneously preserves the long-term taxonomic stability of the genus *Microhyla*, while maintaining the information content of the lineages for those end users that wish to discuss intrageneric relationships (Smith and Chiszar 2006). Our recommendation requires the creation

of one new species-genus name combination, *Microhyla* (*Nanohyla*) *albopunctata* (Poyarkov, Gorin & Trofimets, 2023, in Gorin et al. 2023) **comb. nov.**, and restores the original and stable binomial combinations for all other species in the subgenus *Nanohyla*.

Family Dicroglossidae: *Phrynoglossus*, *Frethia*, and *Oreobatrachus*

Phrynoglossus was removed from the synonymy of *Occidozyga* and elevated to the genus level by Köhler et al. (2021) based on reciprocal monophyly with *Occidozyga* and various aspects of morphology, ecology, and amplexus mode. However, their inferred reciprocal monophyly was based on a phylogeny that only included taxa from Indochina, neglecting the majority of other species of *Occidozyga* that occur throughout the countries of Malaysia, Indonesia, and the Philippines (Frost 2024), many of which had representative sequences on GenBank. Dubois et al. (2021) established the genus-level name *Frethia* for the species previously known as *Occidozyga celebensis* Smith, 1927, *O. diminutiva* (Taylor, 1922), *O. floresiana* Mertens, 1927, *O. laevis* (Günther, 1858), *O. semipalmata* Smith, 1927, and *O. tompotika* Iskandar, Arifin & Rachmanasah, 2011, and further resurrected the genus-level name *Oreobatrachus* for the species previously known as *Occidozyga baluensis* (Boulenger, 1896). However, this decision was solely based on a weakly supported and highly incomplete phylogeny of *Occidozyga* sensu lato represented by only five out of the then 15 described taxa. The expanded phylogeny presented here, which includes 13 out of 18 described species shows that *Frethia* and *Phrynoglossus* are not monophyletic and that the recognition of *Oreobatrachus* induces paraphyly within the *baluensis* + *diminutiva* clade (Fig. 2; also see Chan et al. 2022a). Both the phylogenies presented here and in Dubois et al. (2021) have numerous poorly supported relationships, but the latter’s phylogeny is vastly under-represented. Despite this impediment, Dubois et al. (2021) proceeded to establish the new genera without presenting any supporting information, accompanying data, new analyses, or provision of diagnostic characters. The negative ramifications of this untenable practice are exemplified by the phylogenetically incoherent allocations of numerous species such as the assignment of *Occidozyga sumatrana* (Peters, 1877) to *Phrynoglossus*; and *O. diminutiva*, *O. semipalmata*, and *O. celebensis* to *Frethia*, all of which rendered their respective genera paraphyletic. Finally, Dubois et al. (2021) further assigned *O. floresiana* and *O. tompotika* to the genus *Frethia* without any supporting evidence. Specimens of those two species were not reported to have been examined, nor have they ever been sequenced, and hence, their generic allocation appears to be conjecture. The classification proposed by Dubois et al. (2021) also leaves numerous distinct lineages without a genus including lineages previously assignable to *O. cf. rhacoda*, *O. cf. baluensis* (Flury et al. 2021) and *O. berbeza* Matsui et al., 2021 (Fig. 2). We do not claim our phylogeny to be more accurate because several

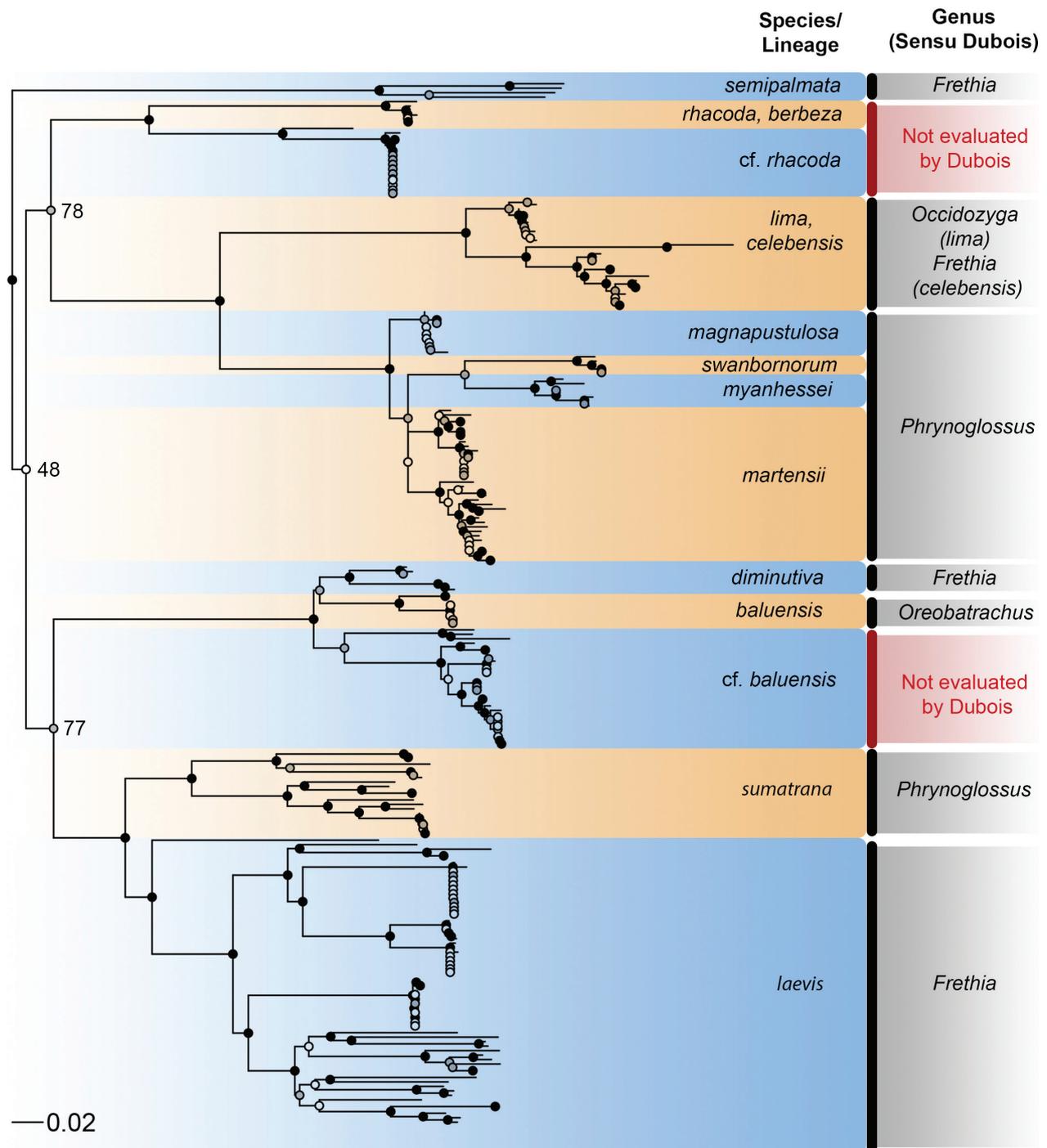


Figure 2. Maximum likelihood phylogeny based on expanded taxon sampling of 242 sequences (13 out of 18 described species; 2117 bps) of the 16S rRNA mitochondrial gene. Black circles = high bootstrap support ($BS \geq 95$), gray circles = moderate bootstrap support ($70 \leq BS < 95$), open circles = low bootstrap support ($BS < 70$). Low bootstrap values along the backbone of the phylogeny are shown. Lineages highlighted in red were not evaluated by Dubois et al. (2021) and are not reciprocally monophyletic with any currently named genera and hence, had no assignable genus.

major clades remain poorly supported (Fig. 2). Moreover, the first and only genomic study of this group to-date that analyzed ~2.7 million base pairs comprising more than 1.2 million parsimony-informative-sites also failed to resolve fully the relationships among all *Occidozyga* species and further demonstrated that extensive gene flow produced misleading patterns of phylogenetic topology and clade divergence (Chan et al. 2022b). Because the generic classification proposed by Köhler et al. (2021) and

Dubois et al. (2021) not only fails to satisfy any TNCs but also creates additional taxonomic chaos, we agree with Lyu et al. (2022) for the return of the genera *Phrynoglossus* Peters, 1867 and *Oreobatrachus* Boulenger, 1896 to the synonymy of *Occidozyga* and the synonymization of the genus *Frethia* Dubois, Ohler & Pyron, 2021 with *Occidozyga* Kuhl & van Hasselt, 1822 to preserve taxonomic stability until more robust data suggests otherwise. This taxonomic action restores most species to their long

accepted binomial combinations except for the following two recently described species: *Occidozyga myanhessei* (Köhler, Vargas, Than & Thammachoti, 2021, in Köhler et al. 2021), and *Occidozyga swanbornorum* (Trageser et al., 2021), which were recently published in this combination by Chen et al. (2022) and Lyu et al. (2022), who also provisionally rejected the splitting of *Occidozyga* on the grounds of inadequate species sampling and lack of nuDNA sequence data used in Dubois et al. (2021) and Köhler et al. (2021).

Family Ranidae: *Abavorana*, *Amnirana*, *Chalcorana*, *Humerana*, *Hydrophylax*, *Indosylvirana*, *Papurana*, *Pterorana*, *Pulchrana*, and *Sylvirana*

Oliver et al. (2015) split the long recognized monophyletic genus *Hylarana*, elevating eight subgenera to the genus rank (*Amnirana*, *Chalcorana*, *Humerana*, *Hydrophylax*, *Hylarana*, *Papurana*, *Pulchrana*, *Sylvirana*) and creating two new genus-level names (*Abavorana*, *Indosylvirana*) based on phylogenetic relationships, biogeography, and purported diagnostic characters. Their phylogeny, that comprised 69 of the 97 taxa recognized at that time, was overall weakly supported and numerous proposed genera were not strongly supported as monophyletic (Oliver et al. 2015: fig 2). Oliver et al. (2015) used their phylogeny for the biogeographical analyses (ancestral area reconstructions) which ideally requires a well-supported phylogeny with complete (or near complete) extant taxon sampling to provide reasonably reliable estimates, hence, their dataset was inadequate for this kind of analysis. Although a subsequent genomic study by Chan et al. (2020b) was able to infer a more robust phylogeny, the taxonomic coverage was still relatively low. In their genomic tree (Chan et al. (2020b: fig. 1) comprising taxa from eight out of ten of the then recognized genera, only *Chalcorana* and *Pulchrana* formed a stable clade, while the relationships among other genera exhibited varying levels of gene tree discordance [*Amnirana*, *Hylarana*, *Humerana*, *Hydrophylax*, *Sylvirana*, *Papurana* and “*Indosylvirana*” *nicobariensis* (Stoliczka, 1870)]. Chan et al. (2020b: fig. 8) also analyzed a combined genomic and 16S dataset (adding 55 additional taxa from all genera), totalling 77 out of 103 currently recognized species, but still, the phylogenetic relationships among several of the currently recognized genera remained uncertain (i.e., within the clade comprising *Indosylvirana*, *Hydrophylax*, *Sylvirana* and *Papurana* and “*Indosylvirana*” *nicobariensis*). The topology of the genomic+16S tree differed from the tree derived from genomic data only (i.e., “*Indosylvirana*” *nicobariensis* was inferred as the sister lineage to *Indosylvirana*, albeit with weak branch support), further demonstrating that the evolutionary history of *Hylarana* sensu lato is far from being fully understood. Dubois et al. (2021) proposed to continue treating *Abavorana* as valid but synonymized all remaining genera into *Hylarana* due to low support obtained between the taxa in their phylogeny (comprising Sanger data), an

opinion that was inconsistent with their proposals to split other genera that contained poorly supported subclades (e.g., *Occidozyga*). This synonymy has not been universally adopted (e.g., Conradie et al. 2023; Griesbaum et al. 2023). The estimated topology by Dubois et al. (2021) differed considerably from those obtained by Oliver et al. (2015) and Chan et al. (2020). For example, *Chalcorana macrops* (Boulenger, 1897) formed a unique clade with “*Indosylvirana*” *nicobariensis* and this clade was indicated as distantly related to both *Chalcorana* and *Indosylvirana*, whereas these two taxa were individually placed within these genera in Oliver et al. (2015) and Chan et al. (2020), respectively, though with low support in both studies. The topological incongruences between analyses using different datasets demonstrates continued instability in the *Hylarana* sensu lato. In all three studies (Oliver et al. 2015; Chan et al. 2020; Dubois et al. 2021), and others (e.g., Reilly et al. 2022; Portik et al. 2023b; Liu et al. 2024) the inclusion of taxa not previously sampled molecularly, but assigned to “genera” based on perceived morphological similarities, continue to demonstrate polyphyly in these *Hylarana* sensu lato genera indicating a lack of reliable morphological diagnosability for some of these clades. The combination of all these factors account as clade instability (Vences et al. 2013), and is in itself a strong argument against the ten-genus division of *Hylarana* sensu lato.

Oliver et al. (2015) presented 18 morphological characters that putatively diagnosed their proposed genera within *Hylarana* sensu lato. However, most of these characters were either qualitative and subject to interpretation and/or circumstances of preservation (e.g., skin texture) or represent variable characters pertaining to color pattern (e.g., dorsal coloration) and overlapping continuous traits (e.g., ratios of finger disc widths). The low diagnostic power of these characters was openly acknowledged by Oliver et al. (2015), who stated that their “diagnostic” characters were only potentially informative, primarily based on “states” reported in the literature or the examination of limited voucher specimens and may be subject to change following additional specimen-based research. Here, we provide additional data taken from our own examination of specimens and a wider review of the literature, to demonstrate that none of the morphological characters proposed by Oliver et al. (2015) can unambiguously diagnose any of their proposed genera (Table 1). Because their splitting of *Hylarana* does not fulfill either Clade Stability or Phenotypic Diagnosability TNCs, we formally relegate the following genus-level nomina to the subgenus rank within *Hylarana* Tschudi, 1838: *Abavorana* Oliver, Prendini, Kraus & Raxworthy, 2015, *Amnirana* Dubois, 1992, *Chalcorana* Dubois, 1992, *Humerana* Dubois, 1992, *Hydrophylax* Fitzinger, 1843, *Indosylvirana* Oliver, Prendini, Kraus & Raxworthy, 2015, *Papurana* Dubois, 1992, *Pulchrana* Dubois, 1992, *Sylvirana* Dubois, 1992.

Pterorana, is a poorly known monotypic genus created for a *Hylarana*-like species, *P. khare* Kiyasetuo & Khare, 1986, with the sole diagnostic character of having extensive loose skin folds on the flanks and legs of

Table 1 – Part A: Summary of re-examined morphological diagnoses for each “genus” of *Hylarana* based on Oliver et al. (2015). See Appendix for details on materials examined. BA, BB = subclades of the Clade B based on purported morphological differences identified in Oliver et al. (2015); expanded morphological characters from this study are provided in square brackets; texts not within square brackets are directly reproduced from Table 3 of Oliver et al. (2015); all observations on nuptial pads are from this study (not provided in Oliver et al. 2015); “ES” refers to specimens examined in this study; non taxonomic citations are substituted by bold font numbers in order of appearance as follows: **1** Quah et al. (2017); **2** Inger (1966); **3** Oliver et al. (2015); **4** Boulenger (1920); **5** Dubois (1992); **6** Brown and Guttman (2002); **7** Inger et al. (2009); **8** Haas et al. (2018); **9** Poynton and Broadley (1985); **10** Dewynter and Fretey (2019); **11** Jongtsma et al. (2018); **12** Rödel and Bangoura (2004); **13** Stuart et al. (2008); **14** Parker (1936); **15** Channing (2001); **16** Boulenger (1892); **17** Smith (1922); **18** Bourret (1942); **19** Liu (1936); **20** Taylor (1962); **21** Biju et al. (2014); **22** Ohler et al. (2002); **23** Chuaynkern et al. (2004); **24** Sheridan and Stuart (2018); **25** Smith (1917); **26** Padhye et al. (2015); **27** Ao et al. (2006); **28** Griesbaum et al. (2023); **29** Conradie et al. (2023); **30** Matsui et al. (2012); **31** Hasan et al. (2019).

| | Clade A | Clade B | Clade C | Clade D |
|---|---|--|--|--|
| | <i>Abavorana</i> | <i>Pulchrana</i> | <i>Chalcorana</i> | <i>Amnirana</i> |
| Posterior part of abdominal skin | Granular. [“finely shagreened” on <i>A. nazgul</i>]. | BA is smooth and BB is granular. | Granular. | Smooth or granular. |
| Length of 1 st versus 2 nd finger | 1 > 2 | 1 ≥ 2 | 1 ≤ 2 | 1 ≥ 2 |
| Width of disc on Finger 3 / Width of Finger 3 | 1–1.5 | 1.2–1.7 | 2–3.5 | 1–1.8 [1.3–2.0 on <i>A. parva</i> (28)] |
| Width of disc on Toe 4 / Width of Toe 4 | 1–1.5 | 1–1.7 | 1.5–2 | 1–1.8 [discs may be absent (30)] |
| Dorsolateral folds: texture | Indistinct. [absent on <i>A. nazgul</i> and <i>A. luctuosa</i> (Peters, 1871) (1 ; 2)]. | Fine or warty and poorly developed. [or absent (30)] | Thin or made up of a line of warts. | Absent to extremely well-developed (<i>A. galamensis</i>). [9–14 ; 28 ; 29] |
| Dorsolateral folds: color | May be white or yellow. [“orange to yellow in colour” on <i>A. nazgul</i> (1)]. | Pale or bright coloration, or as dorsum. | Generally colored as dorsum. | Variable. |
| Humeral gland (1) raised or flat, (2) size, and (3) position on upper arm | (1) Prominent and raised, (2) 2/3 length of upper arm, and (3) centrally positioned on the ventral surface. [relatively shorter on <i>A. nazgul</i> (1)]. | (1) Prominent and raised, (2) 2/3 length of upper arm, and (3) centrally positioned on the anteroventral surface. [can be 1/2 or entire length of upper arm (30)] | (1) Raised, (2) 1/3 to 1/2 length of upper arm, and (3) centrally positioned on the anteroventral surface. [present, large and protruding to indistinct externally though only visible through dissection (7); positioned on proximal anteroventral surface on <i>C. eschatia</i> (Fig. 3), as observed in other groups, e.g., <i>Sylvirana</i> , <i>Indosylvirana</i> , <i>Hydrophylax</i> (ES)]. | (1) Prominent and raised, (2) 2/3 to 3/4 length of upper arm, and (3) positioned on the anteroventral surface. May be variable in size and position. [can be relatively less prominent on some species (e.g., 28 ; 29)] |
| Rictal ridge | Weak or absent. | Medium to well-developed. | Medium to well-developed. | Very large and well-developed. [can be relatively small (e.g., 28)] |
| Upper lip coloration | Gray or as rest of face. [“distinct cream spots on ... upper lip” on <i>A. nazgul</i> (1)]. | May be mottled, spotted, or uniform. [or white (6)] | Usually white. | Usually white; dark in <i>A. lepus</i> . |
| Outer metatarsal tubercle | Absent. [present or absent on <i>A. nazgul</i> and <i>A. luctuosa</i> (1)]. | Present and large. | Present or absent. [present on all (7)]. | Present or absent. |
| Dorsum texture and coloration | Shagreened and may have a vivid red or reddish–brown coloration. [“smooth or finely shagreened” and “mid-dorsal region of dorsum black” on <i>A. nazgul</i> (1); smooth on <i>A. luctuosa</i> (2)]. | Mottled to spotted. [or plain with no distinct markings, smooth, finely granular, or rugose, with or without scattered tubercles (6 ; 30)] | Shagreened, fine mottles, and may have small, round glands which may be tipped with spicules. [described as “granular” rather than shagreened (7)]. | Smooth to shagreened and uniform to mottled. [also “tubercular” with/without spinules (12 ; 28)]. |
| Pattern on dorsal surface of hind limbs | Fine pale speckles or mottled. [or spotted or with transverse stripes on <i>A. nazgul</i> and <i>A. luctuosa</i> (1)]. | Bars with wavy edges, spotted, or vermiculated. | General lack of bars, but may be faint. | Mottled or blotched, occasionally striped. |
| Pattern on posterior surface of thigh | Faintly stippled or mottled. | Generally mottled, spotted, or reticulated. | Same as dorsum. | Speckled to strongly vermiculated. [or marbled (28)] |
| Body size and shape | Medium and robust. | Small and gracile in BA. Large and robust in BB. | Small to medium-sized with a long head and bullet-shaped body, limbs and body gracile. | Robust and medium to large [adult males may be slender (e.g., 28)] |

| | Clade A | Clade B | Clade C | Clade D |
|--|---|---|---|---|
| | <i>Abavorana</i> | <i>Pulchrana</i> | <i>Chalcorana</i> | <i>Amnirana</i> |
| Flank coloration | Dark brown or black below dorsal fold grading to pale on ventrum. [with or without speckling or spots (1)]. | Mottled or spotted, if pattern present, or as dorsum (ground color may be paler). | Coloration as dorsum. [dorsum can be brown but flanks green on some individuals (8)]. | Variable, but usually mottled. |
| Flank texture and glands | Smooth. [“finely shagreened” on <i>A. nazgul</i> (1)]. | Clade BB is strongly warty. Clade BA is weakly warty. | Accessory glandular ridges often present and often arranged linearly. | Glandular or warty. |
| Tympanum | No faint pale coloration on margins. | No faint pale coloration on margins. | No faint pale coloration on margins. | May have faint pale coloration anteriorly and posteriorly. [or not (28; 29)] |
| Nuptial pads | [Not mentioned in 3; absent (1; 2)]. | [Not mentioned in 3; present or absent (4; 6)]. | [Not mentioned in 3; present (7)]. | [Not mentioned in 3; present, small to large (12; 29)]. |
| Vocal sacs | Males without vocal sacs (2). [presence/absence of internal vocal slits is unclear (1; 2)]. | Males with or without paired internal vocal sacs (5). | Males with or without paired vocal sacs, which do not protrude externally (5). [internal vocal slits present on <i>C. eschatia</i> , <i>C. rufipes</i> (Inger et al., 2009), <i>C. parvaccola</i> (Inger et al., 2009), character not mentioned for other species (7)]. | Males with paired vocal sacs, which may be internal, or protrude externally, as reported by 15. |
| Notes and additional putative characters | Brown or black throat and sometimes with small, pale spots (4). Was grouped with <i>Pulchrana</i> in 5. | See 6 for species-level characters. | May have many, species-specific accessory body glands. | Morphologically a highly variable clade. May be highly glandular on ventrum and have other accessory body glands. |

Table 1 – Part B: Summary of re-examined morphological diagnoses for each “genus” of *Hylarana* based on Oliver et al. (2015).

| | Clade E | Clade F | Clade G |
|---|--|--|---|
| | <i>Humerana</i> | <i>Hylarana</i> | <i>Indosylvirana</i> |
| Posterior part of abdominal skin | Smooth or slightly wrinkled. | Smooth or slightly wrinkled. | Granular or wrinkled. [or smooth (ES)]. |
| Length of 1 st versus 2 nd finger | 1 > 2 | 1 = 2 [1 < 2 or 1 > 2 (31)] | 1 > 2 |
| Width of disc on Finger 3 / Width of Finger 3 | 1–1.2 [to 1.4 in some <i>H. humeralis</i> (ES)]. | 1.2–1.7 | 1.4–2 |
| Width of disc on Toe 4 / Width of Toe 4 | 1–1.2 | 1–1.7 | 1.5–2 |
| Dorsolateral folds: texture | Complete and thin to well-developed. | Well-developed. | Thin and well-defined. [weakly to well defined (ES; 21)]. |
| Dorsolateral folds: color | Pale coloration. [same as body color on <i>H. humeralis</i> and <i>H. miopus</i> (Boulenger, 1918) (ES)]. | Pale. | Differential coloration to dorsum. [or the same as dorsal coloration (ES; 21)]. |
| Humeral gland (1) raised or flat, (2) size, and (3) position on upper arm | 5 states suprabrachial glands are present and large (not seen during this study). [relative size and position typical of other groups, e.g., <i>Sylvirana</i> (ES; 16)]. | Variable. [absent on <i>H. erythraea</i> (Schlegel, 1837) and <i>H. macrodactyla</i> Günther, 1858 (4)]. | (1) Prominent and raised, (2) 3/4 length of upper arm and (3) on anteroventral surface. [indistinct, weakly developed, or “distinct” (ES; 21)]. |
| Rictal ridge | Relatively large and broken. [varies from medium to large, broken or unbroken (ES)]. | Large and well-developed and white or cream. | Medium and white. [no less developed than on <i>Hydrophylax</i> or <i>Sylvirana</i> (ES; 21)]. |
| Upper lip coloration | White. | White and relatively thicker than in other clades. | White. [usually pale, white, cream, or pale brown (ES; 21)]. |
| Outer metatarsal tubercle | Absent or small. | Present and medium. [present or absent (5)]. | Present and large. |
| Dorsum texture and coloration | Shagreened to slightly warty and with a pale or dark mid-dorsal line. [or granular; mid-dorsal line only present on <i>H. oatesii</i> (Boulenger, 1892), absent on <i>H. humeralis</i> and <i>H. miopus</i> (ES)]. | Striped, mottled or uniform, and shagreened, smooth, white spicules. | Shagreened, with spicules and uniform with speckles or faint spots. [“shagreened, granular or horny spinular skin” (ES; 21)]. |
| Pattern on dorsal surface of hind limbs | Faint bars to mottled and shanks may have faint lines. | Generally not barred, except for the gracile ‘grass’ adapted species. Calves may have faint lines. | Barred on the calf and shanks. Calves may have ridges or lines of spicules. |

| | Clade E | Clade F | Clade G |
|--|--|---|---|
| | <i>Humerana</i> | <i>Hylarana</i> | <i>Indosylvirana</i> |
| Pattern on posterior surface of thigh | Vermiculated to mottled. | Mottled to striped. | Lightly stippled to vermiculated. |
| Body size and shape | Variable in size and gracile to robust. | Gracile to medium and robust. | Medium and robust. |
| Flank coloration | As dorsum or dark and mottled. | Uniform to bicolor to mottled. | As dorsum. [darker than dorsum in some species, e.g., <i>I. caesari</i> (Biju et al., 2014) and the <i>I. aurantiaca</i> group (ES; 21)]. |
| Flank texture and glands | Smooth. [or weakly granular with/without small tubercles on <i>H. humeralis</i> and <i>H. miopus</i> (ES)]. | Smooth. [to granular, with or without small tubercles] | Shagreened or few, scattered warts. [or smooth, or distinctly granular (ES; 21)]. |
| Tympanum | Faint pale coloration on margins. | Faint pale coloration on margins. | No faint pale coloration on margins. |
| Nuptial pads | [Not mentioned in 3; present on <i>H. humeralis</i> and <i>H. miopus</i> (ES; 17); presence/absence not mentioned for <i>H. oatesii</i> (4; 5; 16; 18)]. | [Not mentioned in 3; present on <i>H. erythraea</i> and <i>H. macrodactyla</i> , or absent on <i>H. taipehensis</i> (Van Denburgh, 1909) (19; 20)]. | [Not mentioned in 3; present on all species (ES; 21)]. |
| Vocal sacs | Males reported to have paired vocal sacs, which protrude externally (5). | 5 stated ... males lack vocal sacs. | [Not mentioned in 3; internal slits present, external sacs present or absent (ES; 21)]. |
| Notes and additional putative characters | Pointed snout. [no more pointed than many other species, e.g., <i>Amnirana fonensis</i> Rödel and Bangoura, 2004 or several <i>Indosylvirana</i> spp. (12; ES)]. | 5 stated outer metatarsal tubercle present or absent. | See 21 for species-level characters ... Included in <i>Sylvirana</i> by 5. |

Table 1 – Part C: Summary of re-examined morphological diagnoses for each “genus” of *Hylarana* based on Oliver et al. (2015).

| | Clade H | Clade I | Clade J | Clade K |
|---|---|--|---|--|
| | <i>Sylvirana</i> | <i>Hydrophylax</i> | <i>Papurana</i> | <i>Pterorana</i> |
| Posterior part of abdominal skin | Smooth or granular. | Smooth or granular. | Smooth. | [Smooth or granular (ES; 27)] |
| Length of 1 st versus 2 nd finger | 1 ≥ 2 | 1 > 2 | 1 > 2 | [1 > 2 (ES; 27)] |
| Width of disc on Finger 3 / Width of Finger 3 | 1.2–1.9 [to 2.0 in some <i>S. lacrima</i> (ES)]. | 1–1.5 | 1.5–2 | [Measurements not taken, distinctly expanded, ratio estimated from photographs of specimens as ~1.1–1.5 (ES); 1.7 (27)] |
| Width of disc on Toe 4 / Width of Toe 4 | 1–1.9 | 1–1.5 | 1.3–2 | [Measurements not taken, distinctly expanded, ratio estimated from photographs of specimens as ~1.5–2.0 (ES); 2.2 (27)] |
| Dorsolateral folds: texture | Medium and well-developed. | Thick and well-developed. [relatively weak on some individuals of <i>H. bahuvistara</i> (26)]. | Fine and granular with asperities to absent. | [Distinct, moderately well developed, granular (ES; 27)] |
| Dorsolateral folds: color | Pale or same coloration as dorsum. | Differential coloration to dorsum and often with dark stripe underneath. [sometimes without differential coloration, e.g., <i>H. bahuvistara</i> , some <i>H. leptoglossa</i> (26; ES)]. | Variable. | [Same colour as dorsum (ES); “latero-dorsal folds dark brown” on holotype of <i>P. khare</i> (27)] |
| Humeral gland (1) raised or flat, (2) size, and (3) position on upper arm | (1) Prominent and raised with dark pigment, (2) 2/3 length of the upper arm, and (3) on anteroventral surface. [or on <i>S. faber</i> (Ohler et al., 2002) referred to as “little prominent” or “flat, not convex” (22; 23)]. | (1) Less prominent than <i>Sylvirana</i> and with dark pigment, (2) 2/3 length of upper arm, and (3) on anteroventral surface. [referred to as prominent in lectotype description, but as “weakly developed” in “Secondary sexual characters” section for <i>H. malabaricus</i> (Tschudi, 1838) in 21; entire length of upper arm, large and prominent on <i>H. leptoglossa</i> and <i>H. bahuvistara</i> (ES, Fig. 3; 26)]. | (1) Less prominent than <i>Sylvirana</i> and with dark pigment (2) 2/3 length of upper arm, and (3) on anteroventral surface. | [Only adult male of <i>P. khare</i> examined: (1) flat, (2) ~1/3 length of upper arm, and (3) on anteroventral surface (ES)] |

| | Clade H | Clade I | Clade J | Clade K |
|--|--|---|--|---|
| | <i>Sylvirana</i> | <i>Hydrophylax</i> | <i>Papurana</i> | <i>Pterorana</i> |
| Rictal ridge | Medium to well developed and white or cream. | Very large and well-developed and white or cream. [no more developed than on <i>Indosylvirana</i> or <i>Sylvirana</i> (ES; 21)]. | Thin and distinct or linear series of warts and variable color. | [Medium to well developed and white or cream (ES)] |
| Upper lip coloration | Gray, off-white, or occasionally mottled. | White glandular ridge on upper part and dark mottles on lower part of jaw. [or yellow, within variation of species in other groups, e.g., <i>Indosylvirana</i> (ES)]. | May be gray, white, vermiculated or dark. | [White on <i>H. garoensis/danieli</i> , brown with mottling on <i>P. khare</i> (ES); “grey” on referred specimens, “dark brown with small white spots” on holotype of <i>P. khare</i> (27)] |
| Outer metatarsal tubercle | Present and large. [relatively small to large (ES)]. | Present and large. | Present and medium to large. | [Present, distinct on all specimens (ES; 27)] |
| Dorsum texture and coloration | Shagreened with spicules or may be warty. [or granular (ES)]. | Finely to coarsely shagreened, sometimes with white spicules, and usually mottled or spotted, but may have stripes. | Evenly shagreened to warty, with or without spicules. | [Granular, brown (ES; 27), or “shagreened” (27)] |
| Pattern on dorsal surface of hind limbs | Finely or coarsely barred to mottled. Calves may have linearly arranged spicules. | Thin, irregular bars on dorsal surface of shanks only. White spicules on dorsal surface of legs in breeding males. | Strong glandular bars to no bars. May be uniformly warty | [With narrow transverse bars (ES; 27)] |
| Pattern on posterior surface of thigh | Mottled or vermiculated. | Strongly vermiculated. | Vermiculated to finely mottled, but variable among species. | [With weak narrow transverse bars or mottled (ES; 27)] |
| Body size and shape | Generally medium and robust. | Robust, small to medium-sized. | Robust, medium to extremely large. | [Medium, slender to robust (ES)] |
| Flank coloration | Dark coloration underneath lateral ridges fading to pale with well-defined dark spots. [can be same as dorsum (24)]. | Strongly mottled and usually with darker background. [variable as in other groups (ES; 21)]. | Mostly as dorsum, but may have dark patches or be mottled. | [Dark coloration underneath lateral ridges fading to pale with well-defined dark spots (ES; 27)] |
| Flank texture and glands | Smooth or with small warts. [or shagreened (ES)]. | Flanks may be strongly warty and glandular, but not arrayed in lines. [shagreened to sparsely granular (ES; 21)]. | May have warts. | [Smooth on <i>H. garoensis/danieli</i> , densely granular on <i>P. khare</i> (ES)] |
| Tympanum | Sometimes with faint pale coloration on margins. | Large; no faint pale coloration on margins. | Very small in <i>P. jimienensis</i> (Tyler, 1963) to large; no faint pale coloration on margins. | [Relatively small to medium, margins without contrasting colouration (ES)] |
| Nuptial pads | [Not mentioned in 3; present, weakly developed to well developed on all species (ES; 24)]. | [Not mentioned in 3; present on all species (21; 26; ES)]. | [Not mentioned in 3; present (4)]. | [Only one adult males of <i>P. khare</i> examined: present, well developed, covered in small spines (ES; 27)] |
| Vocal sacs | Paired vocal sacs may be internal or external (5). [confirmed, however presence/absence of internal vocal slits is variable in <i>S. nigrovittata</i> (ES; 24; 25)]. | Paired external vocal sacs (5). [paired on <i>H. malabaricus</i> and <i>H. leptoglossa</i> (21; ES); stated as “single internal vocal sac visible as loose skin on the throat in live specimens” on <i>H. bahuvistara</i> , but a photo of a paratype clearly shows paired external vocal sacs (26: fig. 2)]. | Paired external vocal sacs (5). [or internal vocal sacs present but absent externally, e.g., on <i>H. daemeli</i> (Steindachner, 1868) (4)]. | [Only one adult male of <i>P. khare</i> examined: external vocal sac absent, internal vocal sac not determined (ES); absent (27)] |
| Notes and additional putative characters | Similar postocular masks as in <i>Papurana</i> . Disc with circum-marginal groove is sometimes absent on finger 1 (5). | Femoral granules are 3/4 the length of the thigh or more. [not clear what this character is referring to (ES)]. | Postocular mask present in many species. | [Male <i>P. khare</i> have loose skin on flanks and thighs during breeding season and enlarged oval gland above forelimb insertion (ES; 27)] |

breeding males (Kiyasetuo and Khare 1986). This species has recently been included in several phylogenetic studies that resolved it as nested within *Hylarana* sensu lato (Hime et al. 2021; Muansanga et al. 2021; Portik et al. 2023a, 2023b). Hime et al. (2021) included a specimen (CAS 234711) collected from Chin State, Myanmar identified as *P. khare* (CAS Herpetology Collection Database, <https://researcharchive.calacademy.org/>

research/herpetology/catalog/index.asp?xAction=get-rec&close=true&CatalogNo=CAS+234711), represented by 194 out of total 220 loci of genomic data in their amphibian phylogeny. They resolved (100% bs in ML; 99.5 ASTRAL) this sample as sister to “*Sylvirana*” *nigrovittata* (Blyth, 1856), within a well-supported (100% bs in ML; 85.5 ASTRAL) clade that also included *Papurana* and *Pulchrana*. Portik et al. (2023a) included the

194 loci of Hime et al. (2021) in their anuran phylogeny that sampled representatives of all major *Hylarana* sensu lato subclades resolving *P. khare* as sister to *Sylvirana* (thus deeply nested within *Hylarana* sensu lato) in all trees. Portik et al. (2023b) expanded this dataset to include 5242 anurans species, including most (84 species) of *Hylarana* sensu lato and the aforementioned *P. khare* data, and resolved the sample as nested within a subclade of *Sylvirana* that received 100% support and included *S. nigrovittata*, the type species of *Sylvirana*. Muansanga et al. (2021) sequenced a partial 16S gene fragment from a *P. khare* specimen collected from Mizoram State, India, which they included in a partial 16S gene tree along with a selection of ranids that included at least one representative of most *Hylarana* sensu lato genera. Their tree was largely unresolved (e.g., *Polypedates* shown as nested within Ranidae) and generally uninformative. However, their *P. khare* sequence was fully resolved as a member of a clade also comprising a sequence (KU589215.1) identified as “*Hydrophylax leptoglossa*” (Cope, 1868) and five sequences of *Sylvirana lacrima* Sheridan & Stuart, 2018. The GenBank record for the aforementioned “*H. leptoglossa*” sequence, KU589215, cited both Ao et al. (2003) and Bortamuli et al. (2010) as the source and gave the voucher number IASST AR79, however, neither study mentioned examining this specimen nor did they mention generating any sequences. Further, Ao et al. (2003) did not mention collecting *H. leptoglossa* but did include three specimens (MA 115–117) they identified as “*Rana khare*”. *Hydrophylax* was also paraphyletic on their tree (Muansanga et al. 2021), forming three clades, one of which included three additional sequences from three different studies that were all identified as *H. “leptoglossa.”* A BLAST search of GenBank for one of these sequences (KR264065.1) shows that it is >98% identical to 23 other sequences identified as *H. leptoglossa*. We conclude that the “*H. leptoglossa*” sequence, KU589215.1, found to be sister to *P. khare* in Muansanga et al. (2021) is misidentified on GenBank and represents *P. khare* (>98% identical), or a very closely related species.

Biju et al. (2014) included sequences from a specimen (SDBDU 2009.293) collected from the type locality of *H. danieli* (Pillai & Chanda, 1977), but identified as “*H. cf. danieli*” in their ML analysis. This analysis comprised 2208 bp of concatenated mtDNA and nuDNA, and placed this specimen within a clade comprising *Sylvirana* species with relatively high support (bs 87%). *Hylarana leptoglossa* is the only other *Hylarana* species reported from the vicinity of the type locality, but only based on unverified anecdotal evidence (Mahony 2008). Therefore, we do not doubt the identity of the specimen reported in Biju et al. (2014) as “*H. cf. danieli*”. We did a BLAST of the partial 16S sequence (KM069009.1) of this *H. danieli* specimen and found it to be 98.6% identical to *P. khare* from Muansanga et al. (2021). *Hylarana danieli* is currently considered a junior subjective synonym of *H. garoensis* (Boulenger, 1920) (Ao et al. 2003) which together are herein considered to be very closely related to *Pterorana khare* based on genetic and morphological similarity

(Boulenger 1920; Pillai and Chanda 1977; Ao et al. 2006; examined specimens).

The systematic position of *Pterorana* is not at all surprising. Dubois (1992) placed both *Rana garoensis* and *Rana danieli* in the genus *Rana* Linnaeus, 1758 (sensu Dubois 1992) subgenus *Sylvirana*, and considered *Pterorana* a subgenus closely related to *Sylvirana* based on general morphology. Ao et al. (2006) had a similar opinion but specifically excluded *Pterorana* from *Sylvirana* stating that it “lacks the beard-like papillae on lower lip of larvae, which are an apomorphic character for *Sylvirana* + *Hylarana*”. Chanda et al. (2001) rejected the synonymy of *Pterorana* into *Rana* by Dubois (1992) for the reason that Dubois had not examined the type specimens, and that they considered the “patagium” as a distinctive character. The loose skin on the flanks and hindlimbs originally considered unique is relatively common across the anuran tree on species that are largely aquatic in the breeding season (Ao et al. 2006; Zheng 2019), so this character alone is not considered taxonomically informative. Despite this, most subsequent authors treated *Pterorana* as valid (e.g., Frost et al. 2006). One of us (SM) has examined type material for *P. khare*, *H. danieli* and *H. garoensis* and found no diagnostic morphological characters that exclude these species from *Hylarana* sensu lato (Table 1). We herein formally synonymize *Pterorana* Kiyasetuo & Khare, 1986 with the subgenus *Sylvirana* Dubois, 1992 based on the combined morphological and strong molecular evidence that confirm this placement (Biju et al. 2014; Hime et al. 2021; Muansanga et al. 2021; Portik et al. 2023a, 2023b; Table 1).

The taxonomic hierarchical restructuring we propose here require the creation of new binomial combinations for a relatively small proportion of the included species, whereas all remaining taxa had either previously been placed within the genus *Hylarana* prior to the recent nomenclatural destabilization (Oliver et al. 2015; Dubois et al. 2021), or have most recently been published in combination with *Hylarana* by implication of proposals in Dubois et al. (2021). Unfortunately, the major systematic papers dealing with *Hylarana* suggested blanket rearrangements without explicitly listing all the included taxa with their updated binomials (i.e., Che et al. 2007; Oliver et al. 2015; Dubois et al. 2021). Following these proposals, Frost (2024, and earlier versions) implemented the changes on the Amphibian Species of the World online database citing those papers for the new genus-species combinations “by implication.” Subsequently, following the taxonomy in Frost (2024, and earlier versions) or the original papers that suggested rearrangements, some authors unknowingly/unintentionally published the new combinations for many *Hylarana* species for the first time in unexpected places (e.g., in species checklists, in phylogenetic trees, papers on parasitology, etc.), making it difficult, if not impossible, to determine who first used these new combinations, or whether some species have yet been published in combination with the genus *Hylarana* at all (e.g., in “gray literature”/obscure publications). For the following comb. nov. list, we provide the



Figure 3. *Hylarana* species showing examples of humeral gland variation on live adult males, photographed in-situ, specimens not collected. **Left:** *Hylarana (Chalcorana) cf. eschatia* (Inger, Stuart & Iskandar, 2009) from Khlong Sok, Phanom District, Surat Thani Province, Thailand. **Right:** *Hylarana (Hydrophylax) leptoglossa* from Laityra Village, East Khasi Hills District, Meghalaya State, India.

binomials that we think might not have been published previously based on a search of each species in Google Scholar as “*Hylarana* xxxx” and/or “*H. xxxx*.” We recognize the obvious limitations of this method and encourage more exhaustive literature searches for those interested in creating accurate chresonymies: *Hylarana (Abavorana) decorata* (Mocquard, 1890) **comb. nov.**; *Hylarana (Abavorana) nazgul* (Quah et al., 2017) **comb. nov.**; *Hylarana (Amnirana) adiscifera* (Schmidt & Inger, 1959) **comb. nov.**; *Hylarana (Amnirana) parva* (Griesbaum et al., 2023) **comb. nov.**; *Hylarana (Pulchrana) fantastica* (Arifin et al., 2018) **comb. nov.**; *Hylarana (Sylvirana) khare* (Kiyasetuo & Khare, 1986) **comb. nov.**

Discussion

The taxonomic recommendations outlined in this study are based on the guiding principles that promote name stability and economy of change (Smith and Chiszar 2006; Vences et al. 2013; Cox et al. 2018). Because taxonomic nomenclature serves the primary function of name recognition—and because primary users are non-taxonomists—nomenclatural changes, especially at the supra-specific level should not only be predicated on robust, transparent, and reproducible evidence but should also serve a practical purpose. Therefore, the splitting of stable, long-established, and monophyletic genera should be based on clear and diagnosable traits that enhance taxonomic stability and the understanding of evolutionary history. We believe that splitting a stable and established genus should minimally be supported by (i) robust phylogenetic evidence, and be accompanied by (ii) evident diagnostic characters that enhance diagnosability for most end-users, carefully determined through both a comprehensive review of literature and preferably the direct examination of explicitly identified specimens, thus ensuring transparency and repeatability. Here we have shown

that the establishment of the genera *Rohanixalus*, *Vampyrus*, *Orixalus*, *Tamixalus* (Rhacophoridae), *Phrynoglossus*, *Frethia*, and *Oreobatrachus* (Dicroglossidae) do not even meet the first minimal criterion and, hence, these genus-level names are herein considered synonyms. Other previously proposed genera such as *Leptomantis*, *Zhangixalus*, *Taruga* (Rhacophoridae), *Nanohyla* (Microhylidae), and some genera within *Hylarana* sensu lato meet the minimal criterion, but not the additional criterion of diagnosability, which causes more taxonomic uncertainty (Fig. 2) as opposed to enhancing stability (Chan et al. 2020a). However, we recognize that the partitioning and recognition of these clades could potentially facilitate future research and, hence, we consider the use of the subgenus rank to be an ideal compromise because it provides a formal rank with which to discuss intrageneric clades for the portion of scientists who would use them without requiring large-scale genus level rearrangements of species (Brown et al. 2015; Mahony et al. 2017; Wood et al. 2020).

Although molecular phylogenetics can be leveraged to enhance taxonomic clarity, the misuse and misinterpretation of phylogenetic trees has repeatedly instigated the reverse engineering of characters to match the arbitrary partitioning of clades. This can lead to undiagnostic or lengthy combinations of characters that are coerced to fit the pre-conceived conception of a phylogenetically-derived taxonomic rank (Oliver et al. 2015; Dubois et al. 2021). In this study, we argue that carving up clades at the genus level and finding discriminating patterns where none exist (taxonomic pareidolia) destabilizes instead of enhances taxonomy. Inaccurate diagnoses of genera can lead to incorrect interpretations of morphological evolution, or can have cascading ramifications in other fields such as biogeography and comparative phylogenetic studies. For example, improper characterization of distribution ranges, e.g., in *Nanohyla* (Gorin et al. 2021) and *Zhangixalus* (Jiang et al. 2019), can potentially lead to erroneous inferences of ancestral ranges, distribution/niche modelling, and biogeographic interpretations.

We accept that taxonomy in amphibians has relied heavily on internal morphology to diagnose amphibian genera (e.g., Parker [1934] for microhylids; Boulenger [1920] for ranids). Historically (in the 1800 to mid 1900s), taxonomists catered primarily to the very small community of academics and naturalists. Systematic rearrangements had little effect on the non-taxonomic community due to a lack of access to taxonomic publications and a limited use for the binomial system when subjects such as conservation, ecology, biogeography, phylogenetics, herpetoculture (pet trade), etc., were non-existent or barely in their infancy. Furthermore, classical taxonomists had only a negligibly small sample size of the currently known diversity to study, and even today, few if any taxonomic groups (at least in Asian amphibians) have been comprehensively reviewed with the goal of determining whether the historically purported diagnostic internal morphological characters have withstood the test of time. Although we applaud the extensive efforts of taxonomists who have made large strides in the field on some groups (e.g., Meegaskumbura et al. 2010; Gorin et al. 2021) and we fully agree that the study of internal morphology is incredibly valuable for our understanding of amphibian evolution, the end user community of binomials is now far larger than the taxonomic community. It has not escaped our attention that splitting established monophyletic genera entirely or primarily based on internal morphology is not a justifiable disruption to that much larger community who may view such actions as unnecessary or even scientific elitism.

Recently, several studies have invoked phylogenetic uncertainty as justification to form new genera as a means to stabilize taxonomy (Biju et al. 2020; Chandramouli et al. 2020; Gorin et al. 2021), while others carve up large, weakly supported phylogenies without providing diagnostic characters (Dubois et al. 2021). We oppose both practices and argue that creating new genera in the light of insufficient data, uninformative data, or weakly supported phylogenetic relationships destabilizes taxonomy by creating cascading and compounding taxonomic problems. Uncritical splitting can create paraphyly, which requires the creation of more genera to resolve (taxonomic inflation), resulting in increasingly small or monotypic genera. This was exemplified by the elevation of eight subgenera in *Hylarana* to the genus rank, resulting in several paraphyletic clades that necessitated the creation of more genera to obtain monophyly—*Abavorana* (two spp.) and *Indosylvirana* (uncertain membership; Oliver et al. 2015). Similarly, in the family Rhacophoridae, the recognition of *Leptomantis* at the genus-level resulting in the paraphyly of *Rhacophorus* *sensu lato*, and thereby necessitating the creation of *Zhangixalus* to obtain monophyly. Unresolved phylogenies that are based on poor taxonomic coverage at the species level can create genera with uncertain membership, leading to frequent changes in generic names of species. For example, genomic data (Chan et al. 2020b) revealed that *Indosylvirana nicobariensis* was incorrectly placed in the African genus *Amnirana* by Oliver et al. (2015). Subsequently, the monotypic genus *Bijurana* Chandramouli, Hamidy & Amarasinghe, 2020

was proposed to accommodate this taxon based on the illogical justification of uncertain phylogenetic relationships (Chandramouli et al. 2020), and then, subsequently, was synonymized with *Indosylvirana* due to the lack of supporting evidence (Chan et al. 2020a). Injudicious splitting has caused this taxon to switch genus no less than five times in the last 17 years (Frost et al. 2006; Frost 2024), which we consider to be an outcome typifying extreme taxonomic instability. Similarly, numerous poorly defined and unresolved clades within *Hylarana* *sensu lato* have caused more than 20 taxa to be repeatedly transferred among the genera *Amnirana*, *Sylvirana*, *Indosylvirana*, *Hydrophylax*, *Papurana*, and *Chalcorana* (Frost 2024). Several other species were regarded as incertae sedis because they were not included in the study by Oliver et al. (2015) (Frost 2024). This confusion is compounded by the lack of diagnostic characters of the proposed genera, making it impossible to reliably assign species to genera for which no corresponding molecular data are available. Ironically, Dubois et al. (2021) opposed the splitting of *Hylarana* by Oliver et al. (2015) on the basis of poor branch support in their phylogeny, only to commit the same transgression by proposing numerous new genera based on their own poorly supported phylogeny (e.g., *Frethia*, *Tamixalus*, and *Vampyrurus*). Instead of facilitating a better systematic understanding of their respective groups, these unwarranted nomenclatural acts have created more confusion and misunderstanding, all of which could have been avoided by applying a more robust, sensible, and critical framework for taxonomic partitioning—or, simply, by not proposing taxonomic rearrangements at all (Wiens 2007; Spinks et al. 2009, 2014; Poe 2013; Langer et al. 2017; Parker 2018). Therefore, we outline a simple, sensible, and effective framework based on the TNCs of Vences et al. (2013) to guide nomenclatural practice and the splitting of clades at the genus level (Fig. 4).

The downstream effects of widespread genus-level rearrangements for the end-user have rarely been a strong consideration for the proposed splitting of monophyletic genera. Proposed end-user benefits of splitting large genera, if mentioned at all, have included reasons like large genera being difficult to manage, which we find to be an illogical argument (see Manageability Accessory TNC in Vences et al. 2013; Hedges and Conn 2012; Nicholson et al. 2012). Due to a lack of expertise (Smith and Chiszar 2006) or data to refute proposed splits, the vast majority of the end-user community typically offers little or no resistance and blindly follows taxonomic changes, resulting in rapid, unquestioned normalization and perceived “acceptance” due to the volume of usage of the newly proposed combinations (Pauly et al. 2009; but also see counter argument by Frost et al. 2009; Wüster and Bérnills 2011). Splitting genera and creating large-scale rearrangements of species create an illusion of importance, quality of work, or progression in the field. The immortalization and sense of prestige from creating new taxonomic names for some are strong incentives for proposing large scale rearrangements (Borrell 2007; Kaiser et al. 2013; Wüster et al. 2021). The perception that papers proposing larges-

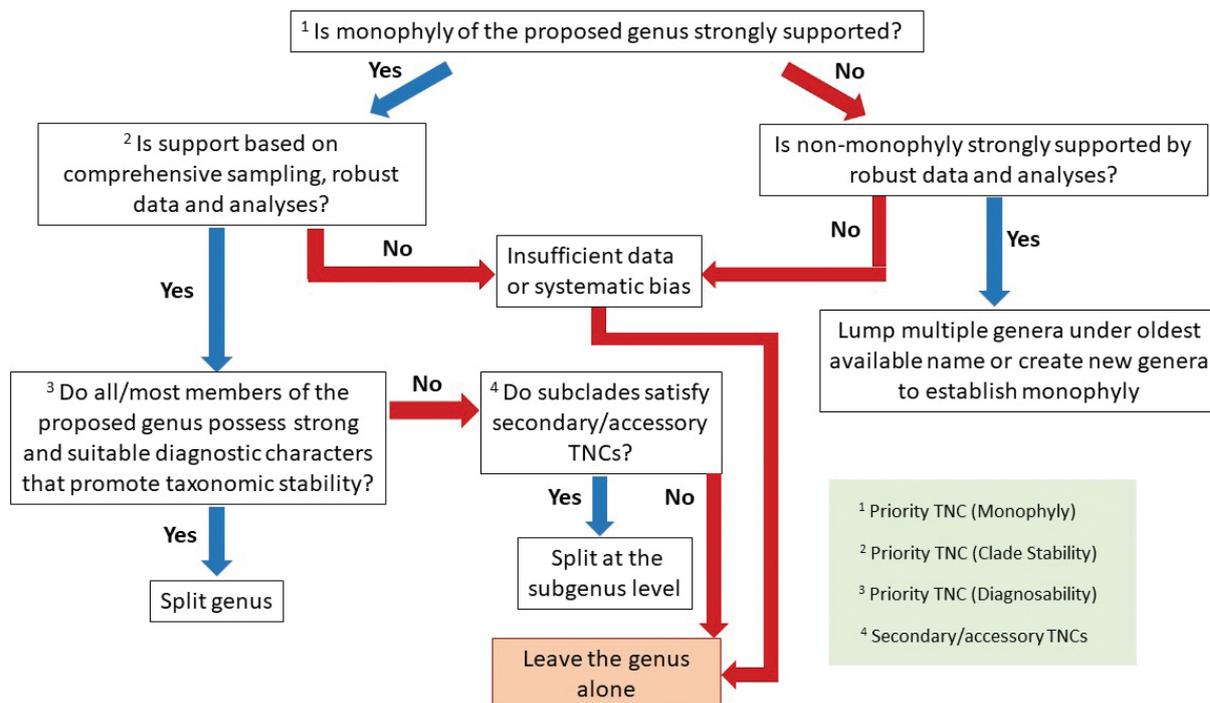


Figure 4. A suggested guide for sensible nomenclatural practice at the genus level based on Taxon Naming Criteria (TNC) sensu Vences et al. (2013).

cale rearrangements rapidly accumulate citations could also incentivize such actions by improving researchers' nomenclatural acts, bibliometrics, potential employment opportunities, promotions, access to funding, higher impact journals, and general appearance of scientific merit. Most large museum collections worldwide no longer attempt to keep up with the systematic fluctuations, resorting to outdated taxonomic arrangements while awaiting stability that will not be obtained without a widespread change in current attitudes towards genus-level splitting. Museum collections arranged using outdated taxonomies directly hinder scientific progress in all fields that rely on such collections, including and especially taxonomy. The practice of unnecessary splitting at the genus level, therefore, is usually (almost always) far more beneficial for the authors of the papers that propose the splits than for the vast majority of the scientific and non-scientific community of end-users who feel obliged to follow such proposals and are forced to tolerate the ensuing instability, confusion, and chaos.

It may be argued that online taxonomic databases can somehow negate the need for a stabilized taxonomy as frequent changes can be logged and curated as they are proposed. However, databases on large taxonomic groups (e.g., Amphibian Species of the World [Frost 2024]; AmphibiaWeb [AmphibiaWeb 2024]), though invaluable, are subject to their own unique issues, e.g., errors in synonymies, intentional/unintentional omissions of taxonomic changes due to simply missing a paper, misinterpretation of published data, or subjective decisions by database curators to reject published proposals for taxonomic rearrangements (Frost et al. 2009; Liedtke 2019; Dubois et al. 2021; Dubois 2022; Dufresnes et al. 2022; Mahony and Kamei 2022; Frost 09 July 2020, [\[ansofttheworld.amnh.org/Curator-s-blog\]\(https://amphibi-ansofttheworld.amnh.org/Curator-s-blog\)\). Despite this, non-taxonomists and even taxonomists without extensive expertise on the literature of a particular group can easily misinterpret information on such databases \(e.g., unintentional publication of many new genus-species combinations in *Hylarana* as mentioned above\). Users often also wrongly assume recently proposed systematic rearrangements that are reflected on major databases are stable and widely accepted \(Wüster and Bérnills 2011\). For example, *Phrynodesma* Fitzinger, 1843, split from *Euphlyctis* Fitzinger, 1843 by Dubois et al. \(2021\), was subsequently updated on Frost \(2024, in 2021\), and is now reflected on the official revised Indian Wild Life \(Protection\) Amendment Bill 2022 where four species are listed as *Phrynodesma* under the Schedule II category, the second highest national protection level \(Anonymous 2022\). Dufresnes et al. \(2022\) subsequently rejected the genus level recognition of *Phrynodesma*, due to a lack of diagnosability and necessity, and instability due to the absence of a taxonomic revision of the type series of the type species for both *Phrynodesma* and *Euphlyctis*. Three additional species are listed in Schedule II in the genera *Zhangixalus*, *Sylvirana* and *Hydrophylax* \(Anonymous 2022\), herein proposed to be treated as subgenera. Besides an immediately outdated taxonomy in an infrequently revised government legislation for the protection of species considered vulnerable to national level extinction, the segregation of species into undiagnosable genera and appearance of these same species in literature and on databases with different genus-species combinations to those on the legislation will lead to unnecessary confusion for those responsible for the enforcement of laws related to the protection of these species. This will have a direct negative impact on conservation efforts. Online](https://amphibi-</p>
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taxonomic databases can certainly not be held responsible for how users interpret (or misinterpret) the reliability of presented binomial arrangements when the aim of such databases is usually to try to objectively reflect changes proposed in the cited taxonomic literature. In cases where multiple taxonomies are simultaneously reflected in the literature, expecting databases to be able to select the most popular/prevalent taxonomy at any single point in time is unreasonable, especially when preferences for one taxonomy over another can be regional, or even political. Therefore, blindly following the taxonomy displayed in databases, without demonstrably referring directly to the relevant cited literature, should be avoided at least in scientific writing or when preparing important legislation.

Although we have focused on a few recent examples where we demonstrate that the splitting of genera was arguably unnecessary, many other similar examples certainly require further investigation using the same or similar criteria and justifications outlined herein. However, we emphasize that nomenclatural stability and end-user consideration should be prioritized since the unnecessary synonymization of genera is as destabilizing as unnecessarily splitting them. For this reason alone, some originally poorly justified generic splits are probably now best maintained. As an example, phylogenetic analyses in Biju et al. (2010) demonstrated that the mainly South Asian genus *Pseudophilautus* comprised two clades. Biju et al. (2010) created the genus *Raorchestes* to apply to one of the clades, diagnosing the “genus” simply as the clade that did not include the type species of *Pseudophilautus* (they called their taxa inclusion/exclusion through phylogenetic framework an “Entexognosis”). The authors defined the group through “brief characterization of characters” (they called an “Idiognosis”) listing non-diagnostic morphological characters, the general distribution, and reproductive mode, without comparison to related taxa. Although this action fitted no obvious practical purpose beyond splitting a monophyletic *Pseudophilautus* into two biologically and morphologically indistinguishable genera, its recognition was widely and blindly followed by biologists. At that time, the genus *Pseudophilautus* had only recently been elevated from synonymy (Li et al. 2009), so most of the historically named *Raorchestes* taxa spent little time in the genus *Pseudophilautus* *sensu lato*. Since its inception, at least 35 new species have been described in the genus *Raorchestes* comprising almost half the currently recognized taxa. As a result, despite not fulfilling most of the criteria for recognition discussed herein, we would not suggest now synonymizing the genus *Raorchestes* with *Pseudophilautus* as it would require the creation of a large number of new genus-species name combinations that would lead to largescale instability.

We duly acknowledge the existence of distinct subclades within the genera *Rhacophorus*, *Feihyla*, *Polypedates*, *Gracixalus*, *Microhyla*, *Occidozyga*, and *Hylarana*. However, we reject the need for those clades to be recognized as separate genera because they are not predicated on strong evidence of clade stability and/or phenotypic diagnosability. We demonstrate that the premature

recognition of poorly supported and undiagnosable subclades as distinct genera promotes taxonomic instability and compounding downstream issues, especially given that genus, in Linnaean rank, is arguably the most prominent supraspecific rank (and of high public profile) for communication amongst biologists, and between biologists and the general public (Smith and Chiszar 2006; Vences et al. 2013). We request that authors refrain from suggesting any changes without clearly providing strongly supported phylogenetic justification, operationally functional diagnoses, explicitly addressing TNCs, and, finally, clearly demonstrating how the vast majority of end-users (i.e., non-taxonomic community) will benefit from the subdivision of a well-established genus and subsequent taxonomic rearrangements that result from its recognition. We emphasize that the latter must be predicated on information content. Editors and reviewers are also asked to consider the mostly unavailable resources and huge expense that museums and databases globally must bear to update the taxonomy of their collections, occasionally simply to gratify the whims of authors intent on splitting monophyletic genera, when assessing the merits and making recommendations to publish such papers (Kaiser et al. 2013). Finally, the scientific community is asked to question the quality of work/data, the need, and the value of all proposed taxonomic changes. We believe that justified pushback from both amateur and professional taxonomists is the best safeguard against disruptive taxonomy, which create large-scale taxonomic upheavals, often for the sake of change itself. Most research in our field is essentially publicly funded, so modern taxonomists have a responsibility to the public to ensure that their actions serve the needs of the broader end-user community.

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Appendix

Specimens examined.

- Hylarana (Humerana) humeralis* (Boulenger, 1887): MYANMAR • 2 females, adult, paralectotypes of *Rana humeralis*; “Teinzo, Upper Burma”; BMNH 1947.2.2.33 (ex. BMNH [18]89.3.25.45), FMNH 9795 • 1 male, adult; “Upper portion of Pegu River, east of Pegu Yomas, Burma”; ZSI/K 17240.
- H. (Hum.) lateralis* (Boulenger, 1887): MYANMAR • 1 female, adult; “Moulmien, lower Burma”; ZSI/K 2758.
- Hylarana (Hydrophylax) cf. bahuvistara* (Padhye et al., 2015): INDIA • 1 male, adult; “Orissa, Badrama, Sambalur Dist”; ZSI/K NOA5 • 2, adults unsexed, paralectotypes of *Rana malabarica*; “Bengale”; *MNHN-RA-0.4439, 1989.3348.
- H. (Hyd.) gracilis* (Gravenhorst, 1829): SRI LANKA • 1 male, adult, holotype of *Lymnodytes macularius* Blyth, 1855; “Ceylon”; ZSI/K 10037.
- H. (Hyd.) leptoglossa*: MYANMAR • 3, unsexed, syntypes of *Hylarana leptoglossa*; “near Rangoon, Burmah”; *MCZ A1588, 125024, 125025 • 1 female, adult, syntype of *Hylarana granulosa* Anderson, 1871; “Pegu”; ZSI/K 4009. – INDIA • 1 female, adult, syntype of *Hylarana granulosa*; “Sebsaugar, Assam”; ZSI/K 2790 • 3, subadults unsexed; “stn. 14, Patichhani, S. Tripura”; ZSI/K A8123 (3 specimens) • 1, subadult unsexed; “stn. 5, Sepahijala Bio Complex, e. of Agartala, Tripura”; ZSI/K A8116. – BANGLADESH • 1 male, 1 female, adult; “Kaptai”; JUHG 0109, 0107.
- H. (Hyd.) malabarica*: INDIA • 1 female, adult, lectotype; “Malabar”; *MNHN-RA-0.4440 • 2 adult unsexed, paralectotypes of *Rana malabarica*; “Cote de Malabar”; *MNHN-RA-1989.3351, 1989.3352.
- H. (Indosylvirana) aurantiaca* Boulenger, 1904: INDIA • 1 female, adult, holotype of *Rana aurantiaca*; “Trivandrum, Travancore”; BMNH 1947.2.2.92 (ex. BMNH 1903.9.26.1).
- H. (I.) flavescens* (Jerdon, 1853): INDIA • 1 male, adult, “syntype” fide Chanda et al. 2001 (type status indirectly rejected by Biju et al. 2014); “S. India” [Coonor, Nilgiris]; ZSI/K 4301.

- H. (I.) montana* (Rao, 1922): INDIA • 1 female adult, lectotype of *Rana gracilis* var. *montanus*; “Mysore”; BMNH 1947.2.2.66 (ex. BMNH 1921.1.20.6) • 1 female adult, paralectotype of *Rana gracilis* var. *montanus*; “Mysore”; BMNH 1947.2.29.43 (ex. BMNH 1921.1.20.7) • 1 female, juvenile, holotype of *Rana bhagmandlensis* Rao, 1922; “Bhagmandola R., Coorg”; BMNH 1947.2.2.12 (ex. BMNH 1921.1.20.1).
- H. (I.) temporalis*: SRI LANKA • 1 female, adult, lectotype of *Hylorana temporalis*; “Ceylon”; BMNH 1947.2.3.5 (ex. BMNH [18]53.7.9.11) • 1 female, adult, paralectotype of *Hylorana temporalis*; “Ceylon”; BMNH 1947.2.29.46 (ex. BMNH [18]58.10.15.5) • 2 males, adult, paralectotype of *Hylorana temporalis*; “Ceylon”; BMNH 1947.2.2.6 (ex. BMNH [18]58.10.15), 1947.2.29.47 (ex. BMNH [18]58.10.15.6) • 3 juveniles, unsexed, paralectotype of *Hylorana temporalis*; “Ceylon”; BMNH 1947.2.2.7 (ex. BMNH [18]58.10.18), 1947.2.29.44 (ex. BMNH [18]52.2.19.43), 1947.2.29.45 (ex. BMNH [18]52.2.19.44).
- H. (“Indosylvirana”) nicobariensis*: INDIA • 1 male, adult, syntype of *Hylorana nicobariensis*; “Nicobar” [Nicobar Is.]; ZSI/K 3362 • 1 male, adult; “Kopen Heat, Galathea, Great Nicobars”; ZSI/K A9137.
- H. (Sylvirana) cf. annamitica* (Sheridan & Stuart, 2018): VIETNAM • 1 male, 1 female, adults; “Mau-Son Mts, 3000–4000ft., Tonkin, Kwango Frontier”; BMNH 1903.4.29.50, 1903.4.29.47.
- H. (S.) danieli*: INDIA • 1 female, adult, holotype of *Rana danieli*; “Mawphlang forest (Alt. 1535 m), Khasi Hills” [Meghalaya State]; ZSI/K A6966 (ex. ZSI/V/ERS 804) • 1 unsexed, paratype of *Rana danieli*; “Mawphlang forest (Alt. 1535 m), Khasi Hills” [Meghalaya State]; ZSI 6967 (ex. ZSI/V/ERS 818) • 1 female, adult, paratype of *Rana danieli*; “Nongkrem (Alt. 1520 m), Shillong, Khasi Hills” [Meghalaya State]; ZSI 6968 (ex. ZSI/V/ERS 805).
- H. (S.) faber*: CAMBODIA • 1 male, adult, holotype of *Rana (Sylvirana) faber*; “Phnom Aural Wildlife Sanctuary, Kampong Speu Province Southwest Cambodia (UTM 1328200N 0307700E)”; *MNHN RA 2001.0261.
- H. (S.) garoensis*: INDIA • 1 juvenile unsexed, syntype of *Rana garoensis*; “Garo hills, Assam, above Tura, at an altitude of 3500 to 3900 feet.” [Meghalaya State]; ZSI/K 18557.
- H. (S.) guentheri* (Boulenger, 1882): CHINA • 2 females, adults, syntypes of *Rana guentheri*; “Amoy” [Fujian]; BMNH (18)76.3.14.1, (18)76.3.14.2.
- H. (S.) khare comb. nov.*: INDIA • 1 male, adult, holotype of *Pterorana khare*; “Sanuoru river, Kohima, Nagaland (alt. 1440 m a. s. l.)”; ZSI/K A9095 (ex. ZSI/V/ERS 8214) • 1 male, adult, paratype of *Pterorana khare*; “Rukhroma river, Kohima, Nagaland (alt. 1400 m a. s. l.)”; ZSI/K A9097 (ex. ZSI/V/ERS 8215).
- H. (S.) lacrima*: BANGLADESH • 2 females, adults; “Kaptai village, Kaptai, Rangamati, Chittagong Div., Bangladesh”; JUHG 0006, JUHG 0104 • 1 male, adult; “Kaptai village, Kaptai, Rangamati, Chittagong Div., Bangladesh”; JUHG 0071 • 2 females, adults; “Bandarban, Chittagong Div., Bangladesh”; JUHG 0191, 0192 • 3 males, adults; “Bandarban, Chittagong Div., Bangladesh”; JUHG 0174 to 0176.
- H. (S.) latouchii* (Boulenger, 1899): CHINA • 1 male, 1 female, adults, syntypes of *Rana latouchii*; “Kuatun, N.W. Fokien”; BMNH 1947.2.1.81 (ex. BMNH [18]98.9.15.4), 1947.2.1.83 (ex. BMNH [18]99.4.24.71).
- H. (S.) maosonensis* Bourret, 1937: VIETNAM • 1 male, adult, lectotype of *Hylarana maosonensis*; “Mau Son, Lang Son Province, Vietnam”; *MNHN RA 1938.50.
- H. (S.) mortenseni* (Boulenger, 1903): THAILAND • 1 female, adult, topotype; “Koh Chang Is., Siam” [Thailand] BMNH 1921.2.12.1.
- H. (S.) nigrovittata*: MYANMAR • 1 male, 1 female, adult, paralectotypes of *Lymnodytes nigrovittatus*; “Mergui”; ZSI/K 2685, 2773 • 1 female, adult, lectotype of *Lymnodytes nigrovittatus*; “Mergui”; BMNH 1947.2.2.99 (ex. [18]93.2.14.4) • 1 female, adult; “Nyaungbin, a village at the north end of Indawgyi Lake, Myitkyina Dist., Upper Burma”; BMNH 1929.12.1.2.
- H. (S.) cf. nigrovittata*: THAILAND • 1 male, adult; “Pran River, P. Siam”; BMNH 1931.1.14.1.
- H. (S.) spinulosa* (Smith, 1923): CHINA • 1 female, adult, paratype of *Rana (Hylarana) spinulosa*; “Tun Fao, Kachek R., Hainan, 400ft.”; *MCZ A9427 (ex. field number 6886).
- Microhyla (N.) annectens* Boulenger, 1900: MALAYSIA • 1 female, adult; “Parit Falls, Cameron Highlands, Pahang”; LSUHC 10926, • 1 female, adult; “Brinchang Swamp, Cameron Highlands, Pahang”; LSUHC 7219.
- M. (N.) annamensis*: VIETNAM • 1 female, adult; “Suoi Mo, Sung Thuy Loan Basin, Danang Province”; ZRC 1.11841.
- M. (M.) borneensis* Parker, 1928: MALAYSIA • 1 female, adult; “Kubah National Park, Sarawak”; ZRC 1.11915.
- M. (M.) mantheyi* Das, Yaakob & Sukumaran, 2007: MALAYSIA • 1 female, adult; “Engkabang Trail, FRIM, Kepong, Selangor”; ZRC 1.10177.

Notes:

^Biju et al. (2014: 320) designated “NHM 1947.2.2.5” as the lectotype. They then identified that there was confusion regarding the current and original number in the “Comments” section and treated “1947.2.3.5” as the correct number. In the caption for figures 17d–f and 18d–f they stated the specimen number as “lectotype of *Hylorana temporalis* (NHM 1947.2.3.5 [ex BMNH 53.7.19.11]):...”, using one of the dubious original numbers. We here resolve the conflicting information found between different sources regarding the specimen numbers of the lectotype. On the specimen jar, the current and original specimen numbers are given as “1947.2.2.5” and “53.7.9.11”, respectively; in the BMNH Accession Register they are given as “1947.2.3.5” and “53.7.9.11”, respectively, the BMNH Specimen Catalogue gives only the original number as BMNH “53.7.19.11” and the specimen tag gives the number “1947.2.3.5”. We only regard the combination of numbers (both current and original) given in the BMNH Accession Register as the correct numbers for the lectotype of *Hylorana temporalis* Günther, 1864.

^^These specimens have previously been reported as “*Hylarana cf. nigrovittata*” by Mahony et al. (2009). The specimens correspond morphologically with the original description of *H. (S.) lacrima* and populations from nearby Mizoram State, India have subsequently been confirmed molecularly to represent this species (e.g., Lalronunga et al. 2021). This represents the first confirmed country record of *Hylarana (S.) lacrima* from Bangladesh.

*photos of museum specimens only.

Supplementary Material 1

Figure S1

Authors: Mahony S, Kamei RG, Brown RM, Chan KO (2024)

Data type: .pdf

Explanation notes: Maximum likelihood phylogenetic tree estimating the systematic placement of *Rohanixalus* within Rhacophoridae.

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Link: <https://doi.org/vz.74.e114285.suppl1>

Supplementary Material 2

Table S1

Authors: Mahony S, Kamei RG, Brown RM, Chan KO (2024)

Data type: .pdf

Explanation notes: GenBank accession numbers of the sequences and genes used in this study.

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