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Phylogeny and classification of fejervaryan frogs (Anura: Dicroglossidae)

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Abstract. Systematics and classification of Asian frogs of the genus *Fejervarya* and related genera (family Dicroglossidae; hereafter referred to as fejervaryan frogs) have been the subject of intensive debates in the past few years. We complement previous phylogenetic studies with analyses of concatenated sequences from 14 nuclear loci and mitochondrial gene fragments, totaling 12,752 nucleotides for 46 species representing all major lineages and relevant outgroups. We find strong support for two major clades within *Fejervarya*: a South Asian clade and a Southeast Asian clade. Previously, South Asian species have been hypothesized to constitute a separate genus, *Zakerana* (currently considered a junior synonym of *Fejervarya*), and also include species previously described as members of the genus *Minervarya*. Although parsimony and species tree analyses found support for the monophyly of *Fejervarya* as currently understood, partitioned Bayesian inference and unpartitioned Maximum Likelihood analyses of concatenated sequences recovered Southeast Asian species as a clade sister to the genus *Sphaerotheca*, albeit with low nodal support. We discuss the advantages and disadvantages of alternative classification schemes in light of previously proposed criteria for naming supraspecific taxa. The current single-genus taxonomy would impart desirable economy of nomenclatural change, and morphological diagnosability. However, other taxon naming criteria such as support for monophyly, temporal framework for diversification, and biogeographic regionalism would support a contrasting two-genus alternative. Because new species of *Fejervarya* are increasingly being discovered and described, and because a single-genus classification (*Fejervarya*) will remain controversial, given ambiguous support for its inferred monophyly, we propose recognizing two genera: Southeast Asian *Fejervarya*, and South Asian *Minervarya*. This classification results in two genera whose monophyly is strongly supported, respectively, and unlikely to be challenged by future analyses. Accordingly, we transfer all species of the South Asian clade to the genus *Minervarya*.

Key words. Amphibia, *Fejervarya, Minervarya, Sphaerotheca, Zakerana*, systematics, Taxon Naming Criteria.

Introduction

The Asian frogs variably assigned to the genera *Fejervarya* Bolkay, 1915, *Minervarya* Dubois, Ohler & Biju, 2001, and *Zakerana* Howlader, 2011, popularly referred to as Rice Frogs (e.g., Sumida et al. 2007), Cricket Frogs (e.g., Suwannapoom et al. 2016), or fejervaryan frogs, represent a major unsolved phylogenetic and taxonomic conundrum. Currently, *Minervarya* and *Zakerana* are considered junior synonyms of *Fejervarya* (Dinesh et al. 2015, Frost 2017). Fejervaryan frogs, members of the family Dicroglossidae Anderson, 1871, are the closest relatives to the genus *Sphaerotheca* Günther, 1859. How exactly the different clades of fejervaryan frogs are related to each other, and to *Sphaerotheca,* is however disputed. Phenotypically, most taxa are inconspicuous, and many are difficult to distinguish by morphology, yet are genetically and ethologically diverse, as is evident from a recently marked increase of new species descriptions (e.g., Kuramoto et al. 2007, Howlader et al. 2016, Garg & Biju 2017). Molecular phylogenetic analyses have included a variable number of species, and recovered either the genera *Fejervarya* and *Sphaerotheca* as sister groups (Pyron & Wiens 2011, Dinesh et al. 2015), or recovered *Sphaerotheca* nested within *Fejervarya* (Frost et al. 2006, Kotaki et al. 2008, 2010, Hasan et al. 2014).

In general, previous studies all found support for two monophyletic groups within *Fejervarya* (Dinesh et al. 2015), one consisting of a clade primarily limited to South Asia, and another largely occurring in East and Southeast Asia (e.g., Kurabayashi et al. 2005, Kotaki et al. 2008, Dinesh et al. 2015). Of these, the Southeast Asian clade, which includes the type species of *Fejervarya* (*Rana limnocharis* Gravenhorst, 1829), has most often been found as sister to *Sphaerotheca* (Frost et al. 2006, Kotaki et al. 2008, 2010, Hasan et al. 2014). In contrast, the South Asian clade has been hypothesized to constitute a distinct genus *Zakerana,* based on peripheral molecular and morphological comparisons (Howlader 2011) which however were based on incomplete taxon sampling. Further complicating fejervaryan taxonomy, an additional genus has been previously proposed to accommodate a group of small-bodied South Asian species (*Minervarya* Dubois, Ohler & Biju 2001), which have later been found nested within the larger South Asian clade (Kuramoto et al. 2007, Dinesh et al. 2015).

In this work, we reconsider the systematics of fejervaryan frogs with the dual goals of (1) reconstructing phylogeny with an expanded dataset consisting of both nuclear and mitochondrial DNA sequences, and (2) evaluating implications of alternative generic taxonomy, following explicit taxon naming criteria (Vences et al. 2013).

Methods

Sequences of species from the genera *Fejervarya*, *Sphaerotheca*, *Euphlyctis*, *Nannophrys*, *Hoplobatrachus* and *Limnonectes* (family Dicroglossidae) were retrieved from GenBank for the nuclear and mitochondrial gene fragments: 12S ribosomal RNA (12S), 16S ribosomal RNA (16S), chemokine (C-X-C motif) receptor 4 (cxcr4), cytochrome b (cob), sodium/calcium exchanger 1 (ncx1), recombination activating gene 1 (rag-1; included as two different fragments named rag-1-3' and rag-1-5'), recombination activating gene 2 (rag-2), rhodopsin exon 1 (rho), tyrosinase (tyr), and brain-derived neurotrophic factor (bdnf). For some taxa, we further complemented the dataset for these genes with new sequences generated via standard polymerase chain reactions (PCR; Table SM1). Additionally, we used the same DNA extractions as Kotaki et al. (2010) to sequence fragments of leucine-rich repeat / WD repeat-containing protein (kiaa1239), sacsin (sacs), and titin (ttn) with primers and nested PCR as in Shen et al. (2012), and proopiomelanocortin (pomc) using standard PCR. Primers and PCR conditions are provided in Table SM1. Chromatograms were visually checked and edited using CodonCode Aligner v3.0.3 (CodonCode Corporation, Centerville, MA, USA). Newly generated sequences were submitted to GenBank (accession numbers MG719866-MG719921; Table SM2). Institutional abbreviations used herein are RBRL (Rondano Biodiversity Research Laboratory, St. Aloysius College, Mangalore, India) and ZSI (Zoological Survey of India); for additional institutional abbreviations, see Table SM2. Sequences were aligned using ClustalW (Thompson et al. 1994) as implemented in MEGA 5.2 (Tamura et al. 2011). Alignments of mitochondrial gene fragments (12S and 16S) were processed with Gblocks 0.91b (Castresana 2000) to remove ambiguously aligned sections, with 50% threshold and default settings. Flanking positions of the selected blocks are provided in Table SM3. Best-fitting models of molecular evolution and partition schemes were inferred by the Akaike Information Criterion (AIC) using PartitionFinder 2 (Lanfear et al. 2016) and are provided in Table SM4. Bayesian inference (BI) phylogenetic analyses of the concatenated DNA sequences were performed with MrBayes 3.2 (Ronquist et al. 2012). Our analysis was run for 20 million generations, with four Markov Chains (three heated and one cold), and trees were sampled every 1,000 generations. We confirmed stabilization and convergence of likelihood values using Tracer 1.4 (Rambaut & Drummond 2007). After discarding 25% of sampled trees as burn-in, a majority-rule consensus tree was used to summarize relationships, with posterior probabilities of nodes used to assess support. Several sequences from multiple species of *Limnonectes* were combined chimerically and designated as a distant outgroup; and sequences of *Euphlyctis*, *Nannophrys* and *Hoplobatrachus* were included as hierarchical outgroups. We also reconstructed topologies under the Maximum Parsimony (MP) optimality criterion in PAUP* v4.10 (Swofford 2002) using the tree-bisection-reconnection (TBR) branch-swapping algorithm and 100 random addition sequence replicates, and conducted bootstrap analyses of 2,000 pseudoreplicates with 10 random addition sequence replicates each. Furthermore, we estimated phylogeny under Maximum Likelihood (ML), implementing a GTR+G substitution model. From the ML analysis we obtained a best tree and a majority consensus rule tree of 1,000 full bootstrap replicates in RAxML V 7.2.7 (Stamatakis 2006). We also inferred a species tree using *BEAST v. 1.8.4 (Drummond et al. 2012), defining all nuclear genes as separate unlinked partitions, and merging all mitochondrial genes into a further partition, with a Yule prior and a relaxed clock model, and implementing GTR+G substitution models for each partition. The analysis was run for 500 million generations, and a consensus tree was generated after discarding 50% of sampled trees as burn-in using TreeAnnotator v. 1.8.4 (Drummond et al. 2012).

To explore individual gene histories, we estimated separate gene trees with BI and ML for each locus. A final BI analysis was performed on a smaller matrix of the concatenated dataset, in which all nucleotide positions with missing data were excluded, and at least two representative species from each main clades were included (resulting in the exclusion of the gene pomc from this analysis).

Results

Our preferred phylogenetic inference is based on DNA sequences from 14 genes, four of which were newly sequenced in this study (kiaa1239, pomc, sacs and ttn; Table SM2). Our final matrix contained 46 terminals, and 14.5% of the sequences were newly obtained for this study. After alignment and exclusion of hypervariable sites with Gblocks, the matrix consisted of 12,752 nucleotide sites for each terminal (having 52.5% missing data; i.e., total 278,631 nucleotides). Of all 12,752 sites, 2,860 were variable and 1,699 were parsimony-informative.

Bayesian Inference analysis of the concatenated dataset produced a largely resolved tree in which fejervaryan frogs (and, thus, the genus *Fejervarya* sensu lato; Frost 2017) are paraphyletic with respect to the genus *Sphaerotheca* (Fig. 1). The two primary clades are recovered with strong support (posterior probabilities PP=1.0). The South Asian clade contains species previously assigned to *Minervarya,* whereas the Southeast Asian clade was recovered sister

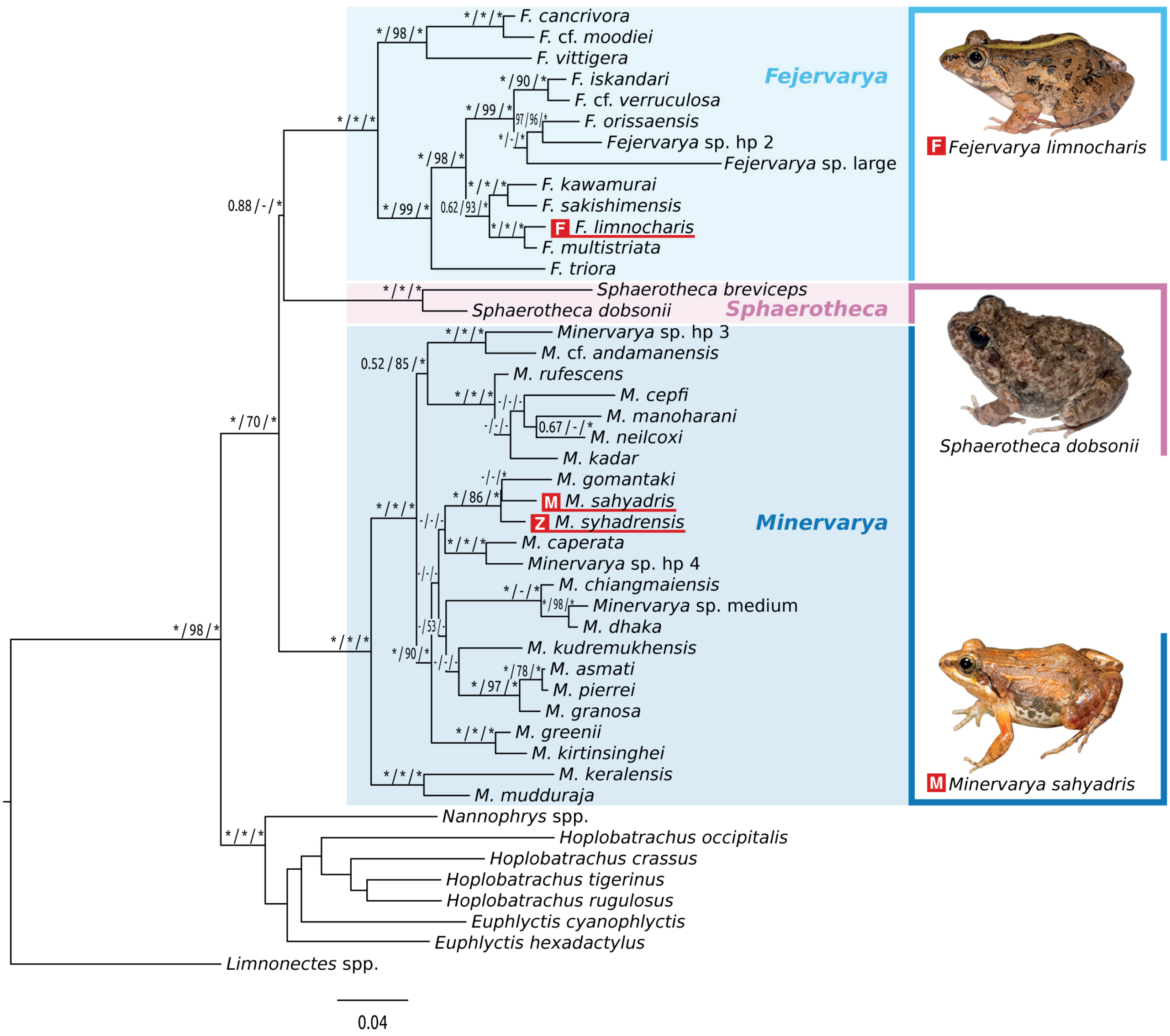

Figure 1. Maximum Likelihood tree of fejervaryan frogs based on a concatenated dataset of 12,752 bp of 14 mitochondrial and nuclear loci. The tree shown is the best tree recovered by ML analysis. Numbers at nodes are support values from separate analyses: BI posterior probabilities (asterisks denote 1.0), followed by MP and ML bootstrap percentages (asterisks denote 100%). Dashes denote instances in which a particular node was not recovered in the respective analyses. Variably-shaded boxes enclose species assigned to the three genera recognized here. Red underlined species names indicate type species of *Fejervarya* (F), *Minervarya* (M) and *Zakerana* (Z). For *Nannophrys* spp. and *Limnonectes* spp., included sequences are chimeric, corresponding to combined data from multiple species in these monophyletic genera.

Table 1. Summary of phylogenetic relationships inferred in individual single-gene trees. Table entries include BI posterior probabilities for various relationships recovered in single-gene tree analyses. SAC = South Asian clade; SEAC = Southeast Asian clade; Sph. = *Sphaerotheca*. Hyphens denote poorly supported clades.

Clade	SAC + SEAC + Sph.	SAC + SEAC	SAC monophyly	SEAC monophyly	SAC + Sph.	SEAC + Sph.
12S	–	–	–	0.96	–	–
16S	–	–	<0.5	<0.5	–	–
cxcr4	0.88	–	1	1	–	0.92
cytb	–	–	<0.5	<0.5	–	–
kiaa1239	1	0.54	1	1	–	–
ncx1	0.96	0.52	1	1	–	–
pomc	1	–	–	1	–	0.57
rag-1-3’	<0.5	–	<0.5	<0.5	–	<0.5
rag-1-5’	1	–	1	1	0.6	–
rag-2	1	–	1	1	–	0.85
rho	–	–	–	0.98	–	–
sacs	1	1	1	1	–	–
ttn	1	–	1	1	0.52	–
tyr	1	–	1	1	–	0.57
bdnf	1	–	–	–	–	–

to *Sphaerotheca*, albeit with low support (PP=0.88). Our ML analysis yielded a tree virtually identical to our BI estimate (Fig. SM17), whereas MP provided moderate support (bootstrap proportions, BS=64%) for *Fejervarya* sensu lato (with both South and Southeast Asian clades) as a monophyletic group, together constituting the group sister to *Sphaerotheca* (Fig. SM18). Also, the species tree analysis (with *BEAST) is different from the concatenated BI and ML analyses in providing strong support (PP=0.98) for monophyly of *Fejervarya* sensu lato (Fig. SM20).

To evaluate whether missing data might have influenced the placement of the two primary clades of *Fejervarya* (relative to *Sphaerotheca*), we analyzed a concatenated matrix reduced to eight taxa and a single outgroup, with only nuclear genes included, and pomc excluded. The topology of the resulting BI tree (Fig. SM1) was virtually identical to our preferred topology (Fig. 1), with an increased support for the placement of *Sphaerotheca* with the Southeast Asian clade (PP=0.9). In contrast, an additional analysis including only mtDNA sequences recovered *Sphaerotheca* closely related to the South Asian clade (PP=0.81; Fig. SM1). Nearly all single-gene trees (Figures SM2–16) recovered both South Asian and Southeast Asian fejervaryan clades (usually with weak support) and groupings of either of these clades with *Sphaerotheca*. Only a single individual gene tree (sacs) provided strong support for the monophyly of *Fejervarya* sensu lato relative to *Sphaerotheca* (Table 1).

Discussion

In this study, we assembled the largest dataset of mitochondrial and nuclear gene sequences compiled to date for the purpose of elucidating evolutionary relationships of fejervaryan frogs (*Fejervarya* sensu lato Frost 2017) and the related genus *Sphaerotheca*. Our results agree with previous studies by recovering three main subclades, corresponding to (1) genus *Sphaerotheca*, (2) South Asian clade, and (3) Southeast Asian clade (Frost et al. 2006, Kuramoto et al. 2007, Kotaki et al. 2008, 2010, Howlader 2011, Pyron & Wiens 2011, Hasan et al. 2014, Dinesh et al. 2015). Furthermore, our results unambiguously find support for a relationship in which taxa previously referred to *Minervarya* are nested within the South Asian clade (Kuramoto et al. 2007, Hasan et al. 2014, Dinesh et al. 2015). However, despite the inclusion of over 10 kbp of sequence data for 14 loci, relationships among the three subclades could not be satisfactorily resolved.

Although we anticipate that more extensive phylogenomic datasets may provide, in the future, robust estimates of topology and resolution of this persistent phylogenetic conundrum, we can also imagine that relationships and classifications proposed to accommodate them may remain controversial. At present, both Bayesian and likelihood analyses of concatenated nuclear and mitochondrial genes suggest the non-monophyly of fejervaryan frogs, whereas only the species tree found strong support for fejervaryan monophyly, and parsimony found moderate support for it. Consequently, the clade stability for *Fejervarya* sensu lato is weak, i.e., a clade including South Asian and South East Asian species and excluding species of *Sphaerotheca* is not consistently recovered by varying methods of analysis and datasets (Vences et al. 2013), necessitating a discussion of alternative classification strategies.

We consider the following: (1) should fejervaryan frog species all be contained within a single, maximally inclusive genus (*Fejervarya*) or (2) separated into two or more smaller, regionalized genera? Finally, (3) if splitting is shown to be the superior solution, which higher-level genus names should be applied to the monophyletic entities discovered here?

How many genera of fejervaryan frogs?

Clearly, reaching a consensus on the generic classification of *Fejervarya* could generate disagreement and debate, requiring a justified resolution of what could become a complex taxonomic issue; we acknowledge that any solution will necessarily remain subjective. In the following, we contribute to this discussion by evaluating the alternatives following the Taxon Naming Criteria (TNCs) of Vences et al. (2013). Of the originally conceived TNCs, three have been highlighted as particularly important (Vences et al. 2013): monophyly, robustness of clades to varying analysis methods and datasets ("clade stability"), and phenotypic diagnosability.

According to the data presented here, monophyly of fejervaryan frogs (South Asian taxa + Southeast Asian taxa), to the exclusion of *Sphaerotheca*, can neither be ascertained by concatenated multigene BI and ML analyses, single-gene trees, nor by separate concatenated analyses of mitochondrial and nuclear DNA sequences. However, the conceivable monophyly of a clade in which these two subclades are sister groups also cannot be refuted. In fact, some previous studies have supported such a monophyletic arrangement (Pyron & Wiens 2011) with strong nodal support, as did the MP analysis of our extensive dataset (Fig. SM18) and the species tree analysis (Fig. SM20). The Monophyly TNC, therefore, does not necessarily result in a need to change the existing classification—because in terms of a general economy of taxonomic change, unstable, back-and-forth changes in classification should be avoided (Vences et al. 2013). However, recent phylogenomic studies have shown that some controversial nodes of the Tree of Life are recalcitrant to unambiguous resolution even when millions of nucleotide positions are analyzed (e.g., Rodríguez et al. 2017). It is conceivable that the node that joins the two main clades of fejervaryan frogs, even if real, may never be unambiguously resolved and strongly supported in the foreseeable future.

The Phenotypic Diagnosability TNC also argues for the recognition of a single, more inclusive genus to accommodate all fejervaryan frogs. The species are morphologically very similar, and identification of a phenotypic distinction between South Asian versus Southeast Asian species has not been forthcoming (Ohler et al. 2014). One recognizable diagnostic character, a putative synapomorphy, shared by all fejervaryan species is their conspicuous ventrolateral lines (Fig. 2), whereas these structures are absent in other amphibians including *Sphaerotheca* (Dubois et al. 2001, Garg & Biju 2017).

On the contrary, classification of fejervaryan frogs into two genera, corresponding to South Asian and Southeast Asian regional clades, would be favored by the Clade Stability TNC of Vences et al. (2013). Each of the two clades received strong heuristic support and both were supported in nearly all single-gene analyses. If these three clades (when also considering *Sphaerotheca*) each are considered distinct genera, we would consider it unlikely that the monophyly of individual genera could be challenged in the near future.

Three further secondary TNCs should also be considered at this point, which would be most consistent with a two-genus classification scheme: first, the Time Banding (time calibration comparisons) TNC follows suggestions of Avise & Mitchell (2007), in which clades of similar evolutionary age might best be recognized at equivalent taxonomic "ranks". Our phylogeny generally demonstrates similar genetic scales of divergences among the branches separating the three clades; although we did not attempt an explicit dating analysis, this crude generalization suggests at least a generally comparable scale of temporal diversification among the main clades. Thus, we favor an interpretation resulting in the assignment of all three clades to equivalent rank, namely separate genera. Second, the Biogeography TNC favors classifications that maximize the biogeographic information. This criterion logically is consistent with a two-genus arrangement, which would facilitate discussion and analysis of distribution patterns of the primary respective clades. One of these contains a majority of South Asian (Indian subcontinent) taxa, but also a species from the Andaman Islands (*F.* cf. *andamanensis*), and some taxa from Thailand (e.g., an undescribed taxon previously named *F.* sp. hp3; Kotaki et al. 2010). In contrast, the Southeast Asian clade contains species primarily from Southeast Asia, but also extends to Bangladesh (*F.* cf.

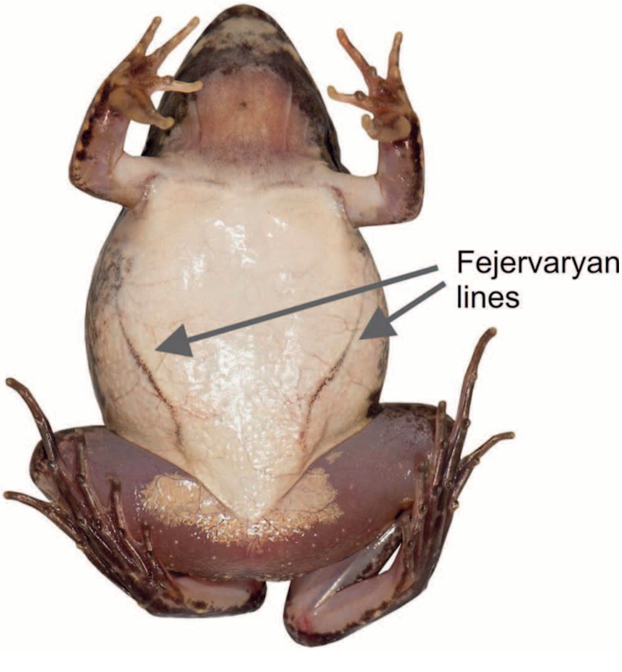

Figure 2. Ventral view of *Fejervarya limnocharis* from Bogor, Java, Indonesia, showing the presence of "fejervaryan lines," shared by members of *Fejervarya* and *Minervarya* (absent in *Sphaerotheca*).

moodiei) and India (*F. orissaensis*). Finally, third, although based on isolated evidence only, the Hybrid Viability TNC may also support classifying our primary clades as separate genera, as crossing experiments have revealed complete hybrid incompatibility between some species (Sumida et al. 2007, Islam et al. 2008). For example, Southeast Asian *Fejervarya* sp. "Large" produced viable hybrids when crossed with the equally Southeast Asian *F. iskandari*, whereas hybrids resulting from crosses with a representative of the South Asian clade, *Fejervarya* sp. "Medium", were not viable, i.e. complete hybrid inviability at embryonic stage (Islam et al. 2008).

Morphological variation and the phylogenetic position of *Minervarya*

Many species of fejervaryan frogs are morphologically similar; we suspect that many more morphologically cryptic (but genetically distinct) new species will be discovered and described in the future. However, despite this prevailing pattern, our phylogeny clarifies ranges of phenotypic variation in the clades defined here, and aids in the identification of morphologically distinct subgroups.

For instance, the phylogenetic position of *Minervarya* (as defined by Ohler et al. 2014), at first glance, is at odds with the definition of *Fejervarya* sensu lato. Its placement within the South Asian clade is confirmed by our multigene analyses (Fig. 1 and Fig. SM17–20) and by several single-gene trees (Table 1). In particular, molecular data are available for *M. sahyadris*, the type species of *Minervarya*, from Aralam, India (voucher RBRL 050714-01; Hasan et al. 2014), as well as for a specimen from the type series of *M. gomantaki* (voucher ZSI/WGRC/V/A/867 = CESF 2294; Dinesh et al. 2015), a phenotypically typical *Minervarya* species (Ohler et al. 2014). These small frogs are nested within the South Asian clade but are morphologically distinct from other dicroglossid frogs by their (1) smaller body, (2) white horizontal stripe on the upper lip, and (3) presence of a rictal gland (Dubois et al. 2001, Ohler et al. 2014). Substantial morphological variation in the South Asian clade also is conspicuously evident in five species of the *Fejervarya rufescens* subclade (*F. cepfi, F. kadar, F. manoharani, F. neilcoxi,* and *F. rufescens*; Garg & Biju 2017). These species notably resemble members of the genus *Sphaerotheca*, but differ by the presence of the fejervaryan lines and other morphological characters such as the presence of an outer metatarsal tubercle and smooth ventral body skin (Garg & Biju 2017).

Proposal for a classification of fejervaryan frogs in two genera

In this study, we compiled a large molecular phylogenetic dataset, yet were unable to provide unambiguous support for the monophyly of fejervaryan frogs. And although *Fejervarya* was paraphyletic with respect to *Sphaerotheca* in a subset of our individual gene trees, we likewise failed to identify unambiguous heuristic (bootstrap, posterior probabilities) support for such a relationship from all analyses. The respective nodes are, for the time being, best viewed as characterizing an unresolved polytomy. Identification of an unambiguous morphological synapomorphy (the derived presence of fejervaryan lines) which, apparently, is unique to fejervaryan taxa, serves to aid in the recognition and definition of the clade containing the South Asian + Southeast Asian taxa, as it is absent in *Sphaerotheca,* but might not reliably guide inference of relationships given the overall high amount of homoplasy observed in ranoid anuran morphology. After carefully evaluating relevant TNCs of Vences et al. (2013), we conclude that distinguishing between a single-genus versus two-genera solution for generic boundaries in fejervaryan frogs is hampered by ambiguous alternatives, guided solely by subjective assessment of the merits of TCNs and taxonomic distribution of character states and, thus, requires a somewhat arbitrary resolution.

Given past disagreements concerning the taxonomic arrangement of *Fejervarya*, we prefer an arrangement that treats South Asian and Southeast Asian taxa each as a separate genus. This is because, despite the clear ambiguity and anticipated remaining controversy (see comments by Frost 2017), we feel that a biogeographically sensible, regionally circumscribed arrangement has a higher probability of stabilizing the taxonomy of these frogs. We note that such a more atomized classification will not likely be challenged in future phylogenetic studies focusing on the question of monophyly versus paraphyly of fejervaryan taxa. We espouse this primary, geographically logical argument, based on the premise that recognition of two regionally defined and biogeographically delimited clades/genera of fejervaryan frogs, will result in stability and diminished controversy—and we feel that this scheme is in better agreement with the Time Banding, Biogeography, and Hybrid Viability TNCs (Vences et al. 2013).

The Southeast Asian species sampled here include *Rana limnocharis* Gravenhorst, 1829 (the type species of *Fejervarya*), which is the first-described genus-group name in the group (Frost, 2017). The second clade (primarily South Asian taxa) contains the type species of both *Minervarya* and *Zakerana* (*Minervarya sahyadris* Dubois, Ohler, and Biju, 2001; and *Rana limnocharis syhadrensis* Annandale, 1919), of which *Minervarya* was described earlier and, thus, has nomenclatural priority.

Of the 45 described species of *Fejervarya* (Frost 2017), 31 were included in our phylogenetic analysis and can definitively be assigned to either of the two proposed genera based on independent empirical results (genetic data, and species' positions in our phylogeny). For some species, morphological similarity-based arguments were presented by Ohler et al. (2009), allowing us to assert putative overall phenotypic assignments for selected taxa not sampled in our genetic dataset. We propose the following amended taxonomy, allocating all species of *Fejervarya* sensu lato Frost (2017) to either *Fejervarya* or *Minervarya*; we nonetheless are aware that in some cases, confirmation will be required to confidently place unsampled taxa in one of the two genera.

Individual problematic species' assignments may be challenging. It is also worth emphasizing that the identity of some of the historically described species (e.g., *M. brevipalmata*) will require additional scrutiny, due to apparently lost type specimens and doubtful type locality (Frost 2017). The identity and validity of numerous other taxa likewise require confirmation; for instance, *M. asmati* (Howlader, 2011) may be a junior synonym of *M. pierrei* (Dubois, 1975), judging from genetic similarity inferred here (Fig. 1).

Fejervarya Bolkay, 1915

Type species: *Rana limnocharis* Gravenhorst, 1829 by subsequent designation of Dubois (1981).

Content: *F. cancrivora* (Gravenhorst, 1829), *F. iskandari* Veith, Kosuch, Ohler, and Dubois, 2001, *F. kawamurai* Djong, Matsui, Kuramoto, Nishioka, and Sumida, 2011, *F. limnocharis* (Gravenhorst, 1829), *F. moodiei* (Taylor, 1920), *F. multistriata* (Hallowell, 1861), *F. orissaensis* (Dutta, 1997), *F. pulla* (Stoliczka, 1870), *F. sakishimensis* Matsui, Toda, and Ota, 2008, *F. schlueteri* (Werner, 1893), *F. triora* Stuart, Chuaynkern, Chan-ard, and Inger, 2006, *F. verruculosa* (Roux, 1911) and *F. vittigera* (Wiegmann, 1834). All these species are assigned on the basis of accompanying genetic data, except *F. pulla,* and *F. schlueteri* whose assignment is in need of confirmation.

Minervarya Dubois, Ohler & Biju, 2001

Type species: *Minervarya sahyadris* Dubois, Ohler, and Biju, 2001 by original designation.
Junior synonym: *Zakerana* Howlader, 2011
Type species of *Zakerana*: *Rana limnocharis syhadrensis* Annandale, 1919 by original designation.

Content: *M. andamanensis* (Stoliczka, 1870), *M. asmati* (Howlader, 2011), *M. brevipalmata* (Peters, 1871), *M. caperata* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008), *M. cepfi* (Garg and Biju, 2017), *M. chiangmaiensis* (Suwannapoom, Yuan, Poyarkov, Yan, Kamtaeja, Murphy, and Che, 2016), *M. chilapata* Ohler, Deuti, Grosjean, Paul, Ayyaswamy, Ahmed, and Dutta, 2009, *M. dhaka* (Howlader, Nair, and Merilä, 2016), *M. gomantaki* (Dinesh, Vijayakumar, Channakeshayamurthy, Torsekar, Kulkarni, and Shanker, 2015), *M. granosa* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008), *M. greenii* (Boulenger, 1905), *M. kadar* (Garg and Biju, 2017), *M. keralensis* (Dubois, 1981), *M. kirtisinghei* (Manamendra-Arachchi and Gabadage, 1996), *M. kudremukhensis* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008), *M. manoharani* (Garg and Biju, 2017), *M. modesta* (Rao, 1920), *M. mudduraja* (Kuramoto, Joshy, Kurabayashi, and Sumida, 2008), *M. murthii* (Pillai, 1979), *M. mysorensis* (Rao, 1922), *M. neilcoxi* (Garg and Biju, 2017), *M. nepalensis* (Dubois, 1975), *M. nicobariensis* (Stoliczka, 1870), *M. nilagirica* (Jerdon, 1854), *M. parambikulamana* (Rao, 1937), *M. pierrei* (Dubois, 1975), *M. rufescens* (Jerdon, 1853), *M. sahyadris* Dubois, Ohler, and Biju, 2001, *M. sauriceps* (Rao, 1937), *M. sengupti* (Purkayastha and Matsui, 2012), *M. syhadrensis* (Annandale, 1919), and *M. teraiensis* (Dubois, 1984). Species are assigned to the genus based on accompanying genetic data, except for the following species who are assigned based on their geographical occurrence in South Asia and/or morphological similarity to other *Minervarya*, and whose assignment is in need of confirmation: *M. brevipalmata*, *M.chilapata*, *M. modesta*, *M. murthii*, *M. mysorensis*, *M. nepalensis*, *M. nicobariensis*, *M. nilagirica*, *M. parambikulamana*, *M. sauriceps*, *M. sengupti*, *M. teraiensis*.

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References

Avise J. C. & D. Mitchell (2007): Time to standardize taxonomies. – Systematic Biology, **56**: 130–133.

Bolkay, S. J. (1915): Beiträge zur Osteologie einiger exotischer Raniden. – Anatomischer Anzeiger, Jena, **48**: 172–183.

Castresana, J. (2000): Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. – Molecular Biology and Evolution, **17**: 540–552.

Dinesh, K. P., S. P. Vijayakumar, B. H. Channakeshavamurthy, V. R. Torsekar, N. U. Kulkarni & K. Shanker (2015): Systematic status of *Fejervarya* (Amphibia, Anura, Dicroglossidae) from South and SE Asia with the description of a new species from the Western Ghats of Peninsular India. – Zootaxa, **3999**: 79–94.

Drummond, A. J., M. A. Suchard, D. Xie & A. Rambaut (2012): Bayesian phylogenetics with BEAUti and the BEAST 1.7. – Molecular Biology and Evolution, **29**: 1969–1973.

Dubois, A. (1981): Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du monde, avec identification de leurs espèces-types: conséquences nomenclaturales. Monitore Zoologico Italiano Supplemento, **15**: 225–284.

Dubois, A., A. Ohler & S. D. Biju (2001): A new genus and species of Ranidae (Amphibia, Anura) from south-western India. – Alytes, **19**: 53–79.

Frost, D. R. (2017): Amphibian Species of the World: an Online Reference. Version 6.0 (*accessed 22 July 2017*). – Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Frost, D. R., T. Grant, J. Faivovich, R. H. Bain, A. Haas, C. F. B. Haddad, R. O. De Sá, A. Channing, M. Wilkison, S. C. Donnelan, C. J. Raxworthy, J. A. Campbell, B. L. Blotto, P. Moler, R. C. Drewes, R. A. Nussbaum, J. D. Lynch, D. M. Green & W. C. Wheeler (2006): The amphibian tree of life. – Bulletin of the American Museum of Natural History, **297**: 11–291.

Garg, S. & S. D. Biju (2017): Description of four new species of Burrowing Frogs in the *Fejervarya rufescens* complex (Dicroglossidae) with notes on morphological affinities of *Fejervarya* species in the Western Ghats. – Zootaxa, **4277**: 451–490.

Hasan, M., M. M. Islam, M. M. R. Khan, T. Igawa, M. S. Alam, H. T. Djong, N. Kurniawan, H. Joshy, Y. H. Sen, D. M. Belabut, A. Kurabayashi, M. Kuramoto & M. Sumida (2014): Genetic divergences of South and Southeast Asian frogs: a case study of several taxa based on 16S ribosomal RNA gene data with notes on the generic name *Fejervarya*. – Turkish Journal of Zoology, **38**: 389–411.

Howlader, M. S. A. (2011): Cricket frog (Amphibia. Anura. Dicroglossidae): two regions of Asia are corresponding two groups. – Bonnoprani, **5**: 1–7.

Howlader, M. S. A., A. Nair & J. Merilä (2016): A new species of frog (Anura: Dicroglossidae) discovered from the mega city of Dhaka. – PLoS ONE, **11**: e0149597.

Islam, M. M., N. Kurose, M. M. R. Khan, T. Nishizawa, M. Kuramoto, M. S. Alam, M. Hasan, N. Kurniawan, M. Nishioka & M. Sumida (2008): Genetic divergence and reproductive isolation in the genus *Fejervarya* (Amphibia: Anura) from Bangladesh inferred from morphological observations, crossing experiments, and molecular analyses. – Zoological Science, **25**: 1084–1105.

Kotaki, M., A. Kurabayashi, M. Matsui, W. Khonsue, T. H. Djong, M. Tandon & M. Sumida (2008): Genetic divergences and phylogenetic relationships among the *Fejervarya limnocharis* complex in Thailand and neighboring countries revealed by mitochondrial and nuclear genes. – Zoological Science, **25**: 381–390.

Kotaki, M., A. Kurabayashi, M. Matsui, M. Kuramoto, T. H. Djong & M. Sumida (2010): Molecular phylogeny of the diversified frogs of genus *Fejervarya* (Anura: Dicroglossidae). – Zoological Science, **27**: 386–395.

Kurabayashi, A., M. Kuramoto, H. Joshy & M. Sumida (2005): Molecular phylogeny of the ranid frogs from Southwest India based on the mitochondrial ribosomal RNA gene sequences. – Zoological Science, **22**: 525–534.

Kuramoto, M., S. H. Joshy, A. Kurabayashi & M. Sumida (2007): The genus *Fejervarya* (Anura: Ranidae) in central Western Ghats, India, with description of four new cryptic species. – Current Herpetology, **26**: 81–105.

Lanfear, R., P. B. Frandsen, A. M. Wright, T. Senfeld & B. Calcott (2016): PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. – Molecular Biology and Evolution, **34**: 772–773.

Miller M. A., W. Pfeiffer, & T. Schwartz (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. – pp. 1–8 in: Proceedings of the Gateway Computing Environments Workshop (GCE); Nov. 14; New Orleans, LA.

Ohler, A., K. Deuti, S. Grosjean, S. Paul, A. K. Ayyaswamy, M. F. Ahmed & S. K. Dutta, (2009): Small-sized dicroglossids from India, with the description of a new species from West Bengal, India. – Zootaxa, **2209**: 43–56.

Ohler, A., S. Dutta & A. Dubois (2014): Morphological evolution in frogs of the genera *Fejervarya, Minervarya, Sphaerotheca* and *Zakerana* (Dicroglossidae). – Pranikee: journal of Zoological Society of Orissa, **26**: 1–12.

Pyron, R. A. & J. J. Wiens (2011): A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. – Molecular Phylogenetics and Evolution, **61**: 543–583.

Rambaut, A. & A. J. Drummond (2007): Tracer v1.5. Available from: http://beast.bio.ed.ac.uk/Tracer, accessed 30 May 2017.

Rodríguez, A., J. D. Burgon, M. Lyra, I. Irisarri, D. Baurain, L. Blaustein, B. Göçmen, S. Künzel, B. Mable, A. W. Nolte, M. Veith, S. Steinfartz, K. R. Elmer, H. Philippe & M. Vences (2017): Inferring the shallow phylogeny of true salamanders (*Salamandra*) by multiple phylogenomic approaches. – Molecular Phylogenetics and Evolution, **115**: 16–26

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard & J. P. Huelsenbeck (2012): MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – Systematic Biology, **61**: 539–542.

Shen, X. X., D. Liang & P. Zhang (2012): The development of three long universal nuclear protein-coding locus markers and their application to osteichthyan phylogenetics with nested PCR. – PLoS ONE, **7**: e39256

Stamatakis, A. (2006): RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. – Bioinformatics, **22**: 2688–2690.

Sumida, M., M. Kotaki, M. M. Islam, T. H. Djong, T. Igawa, Y. Kondo, M. Matsui, D. S. Anslem, W. Khonsue & M. Nishioka (2007): Evolutionary relationships and reproductive isolating mechanisms in the Rice Frog (*Fejervarya limnocharis*) species complex from Sri Lanka, Thailand, Taiwan and Japan, inferred from mtDNA gene sequences, allozymes, and crossing experiments. – Zoological Science, **24**: 547–562.

Suwannapoom, C., Z.-Y. Yuan, N. A. Poyarkov, Jr., F. Yan, S. Kamtaeja, R. W. Murphy & J. Che (2016): A new species of genus *Fejervarya* (Anura: Dicroglossidae) from northern Thailand. – Zoological Research, **37**: 1–11.

Swofford, D. L. (2002): PAUP* Phylogenetic Analysis using Parsimony *and other Methods. Version 4. – Sinauer Associates, Sunderland, Massachusetts.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei & S. Kumar (2011): MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. – Molecular Biology and Evolution, **28**: 2731–2739.

Thompson, J. D., D. G. Higgins & T. J. Gibson (1994): CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. – Nucleic Acids Research, **22**: 4673–4680.

Vences, M., J. M. Guayasamin, A. Miralles & I. de la Riva (2013): To name or not to name: Criteria to promote economy of change in Linnaean classification schemes. – Zootaxa, **3636**: 201–244.

Supplementary material

Supplementary Tables SM1–SM4.

Supplementary Figures SM1–SM20.

Supplementary material

Sanchez, E., S. D. Biju, M. M. Islam, M. Hasan, A. Ohler, M. Vences & A. Kurabayashi: Phylogeny and classification of fejervaryan frogs (Anura: Dicroglossidae). – Salamandra, 54(1): xx–xx.

Table SM1. Primer and conditions for PCRs. Thermal cycling schemes start with temperature (in °C) of each step, followed by the time in seconds between parentheses; number of cycles are indicated within brackets.

Marker	Primer name	Primer sequence	PCR conditions	Reference
KIAA	KIAA1239F1	CARCCTTGGGTNTTYCA	94(240), [94(45), 45(40), 72(120) x 45], 72(600)	Shen et al. (2011)
	KIAA1239R1	CMACAAAYTGGTCRTTR		Shen et al. (2012)
	KIAA1239NF1	GAGCCNGAYATHTTYTTYG	94(240), [94(45), 45(40), 72(120) x 35], 72(600)	Shen et al. (2012)
	KIAA1239NR1	TTCACRAANCCMCCNG		Shen et al. (2011)
SACS	SACSF2	AAYATHACNAAYGCNTGYTAYAA	94(240), [94(45), 45(40), 72(120) x 45], 72(600)	Shen et al. (2012)
	SACSR2	GCRAARTGNCCRTTNACRTGRAA		Shen et al. (2012)
	SACSNF2	TGYTAYAAYGAYTGYCCNTGGAT	94(240), [94(45), 45(40), 72(120) x 35], 72(600)	Shen et al. (2012)
	SACSNR2	CKGTGRGGYTTYTTRTARTTRTG		Shen et al. (2012)
POMC	POMC-DRV-F1	ATATGTCATGASCCAYTTYCGCTGGAA	94(120), [94(20), 60(50), 72(180) x 39], 72(600)	Vieites et al. (2007)
	POMC-DRV-R1	GGCRTTYTTGAAWAGAGTCATTAGWGG		Vieites et al. (2007)
TTN	TTN-F1	TATGCTGARAAYATNGCNGGNAT	94(240), [94(45), 45(40), 72(120) x 45], 72(600)	Shen et al. (2012)
	TTN-R1	CCMCCRTCAAAYARNGGYTT		Shen et al. (2012)
	TTN-NF1	GATGGNMGKTGGYTNAARTGYAA	94(240), [94(45), 45(40), 72(120) x 35], 72(600)	Shen et al. (2012)
	TTN-NR1	AGRTCRTANACNGGYTTYTTRTT		Shen et al. (2012)
RAG1-3’	Mart FL1	AGCTGCAGYCARTAYCAYAARATGTA	94(120), [94(20), 52-55(50), 72(180) x 40], 72(600)	Chiari et al. 2004
	Mart R6	GTGTAGAGCCARTGRTGYTT		Chiari et al. 2004
	Amp F2	ACNGGNMGICARATCTTYCARCC	94(120), [94(20), 52-55(50), 72(180) x 40], 72(600)	Chiari et al. 2004
	RAG1-DRV-UCR	TTGGACTGCCTGGCATTCAT		Chiari et al. 2004
RAG2	31.FN.Venk	TTYGGICARAARGGITGGCC	94(300), [94(30), 50(40), 68(180) x 35], 68(300)	Chiari et al. 2004
	Lung.460R	GCATYGRGCATGGACCCARTGICC		Chiari et al. 2004
	Lung.35F	GGCCAAAGAGRTCYTGTCCIACTGG	94(300), [94(30), 50(40), 68(180) x 35], 68(300)	Chiari et al. 2004
	Lung.320R	AYCACCCATATYRCTACCAAACC		Chiari et al. 2004

Primer references:

Chiari, Y., M. Vences, D. R. Vieites, F. Rabemananjara, P.Bora, O.Ramilijaona Ravoahangimalala, A.Meyer (2004): New evidence for parallel evolution of colour patterns in Malagasy poison frogs (Mantella). – Molecular Ecology, 13 3763–3774.

Shen, X.X., D.Liang, J. Z.Wen, P.Zhang (2011): Multiple genome alignments facilitate development of NPCL markers: A case study of tetrapod phylogeny focusing on the position of turtles. – Molecular Biology and Evolution, 28: 3237–3252.

Shen, X.X., D.Liang, P.Zhang (2012): The development of three long universal nuclear protein-coding locus markers and their application to 23 osteichthyan phylogenetics with nested PCR. –PLoS ONE 7, e39256. doi:10.1371/journal.pone.0039256.

Vieites, D.R., M. S.Min, D. B.Wake (2007): Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. – Proceedings of the National Academy of Sciences of the United States of America 104: 19903–19907.

Table SM2. Localities and voucher numbers of samples and accession numbers of DNA sequences.

ID	**Species**	**Voucher**	**Locality**	***12S***	***16S***	***cxcr4***	***cytb***	***kiaa1239***	***ncx1***	***pomc***	***rag2***	***rho***	***sacs***	***ttn***	***tyr***	***bdnf***	***rag1-3'***	***rag1-5'***
Fcn1	Fejervarya cancrivora	IABHU 19094	Indonesia: Cianjur		AB48882[p]	AB500240[q]	AB488817[p]	MG719867[*]	AB500246[q]	MG719880[*]			MG719891[*]	MG719903[*]		AB500232[q]		AB500226[q]
Fcn1	Fejervarya cancrivora	MVZ239403	Indonesia: Selatan: Sulawesi								HM163617[g]	EU979938[g]			EU980029[g]		HM163581[g]	
Fcn1	Fejervarya cancrivora	HW6	China: Guangxi: Beihai	EU652694[w]														
Fis1	Fejervarya iskandari	isolate = IABHU 18018	Indonesia: Cianjur	AB277287[q]	AB277303[q]	AB277316[q]	AB488813[p]	MG719868[*]	AB277328[q]	MG719881[*]	AB488981[p]	AB489021[q]	MG719892[*]	MG719904[*]	AB277355[q]	AB489045[q]	AB488954[p]	AB277342[q]
Fka1	Fejervarya kawamurai	isolate = MK2022	Japan: Hiroshima	AB488864[p]	AB488887[p]	AB488907[p]	AB488832[p]	MG719869[*]	AB488924[p]	MG719882[*]	AB488986[p]	AB489026[q]	MG719893[*]	MG719905[*]	AB489005[q]	AB489050[q]	AB488941[p]	AB488965[p]
Fli1	Fejervarya limnocharis	isolate = IABHU 18002	Indonesia: Bogor	AB277286[q]	AB277302[q]	AB277315[q]	AB488812[p]	MG719870[*]	AB277327[q]	MG719883[*]	AB488980[p]	AB489020[q]	MG719894[*]	MG719906[*]	AB277354[q]	AB489044[q]	AB488953[p]	AB277341[q]
Fmo1	Fejervarya moodiei	isolate = DFBGBAU Fmod 315	Bangladesh: Khulna	AB372082[o]	AB530508[l]		AB372069[o]											
Fmu1	Fejervarya multistriata	IABHU 34026 – 34031	China: Husa	AB488861[p]	AB488884[p]	AB500242[q]	AB488828[p]		AB500248[q]		AB500252[q]	AB500257[q]			AB500265[q]	AB500234[q]	AB500220[q]	AB500228[q]
For1	Fejervarya orissaensis	KU 197186	India: Orissa	AB277288[q]	AB277304[q]	AB277317[q]	AB488842[p]		AB277329[q]			AB500259[q]			AB277356[q]	AB500236[q]	AB500222[q]	AB277343[q]
Fsk1	Fejervarya sakishimensis	IABHU 32044	Japan: Iriomote	AB488863[p]	AB488886[p]	AB488906[p]	AB488831[p]		AB488923[p]		AB488985[p]	AB489025[q]			AB489004[q]	AB489049[q]	AB488940[p]	AB488964[p]
FTH1	Fejervarya sp. hp2	IABHU 32473 or 32474 or 32490 - 32492	Thailand: Bangkok	AB277281[q]	AB277299[q]	AB277307[q]	AB488821[p]		AB277321[q]		AB500254[q]	AB489023[q]			AB277350[q]	AB500238[q]	AB500224[q]	AB277340[q]
FBA2	Fejervarya sp. Large	DFBGBAU FspL 313	Bangladesh: Mymensingh	AB372019[o]	AB372009[o]		AB372046[o]											
Ftr1	Fejervarya triora	IABHU 266162 or 266164	Thailand: Ubon Ratchani	AB488860[p]	AB488883[p]	AB488905[p]	AB488820[p]		AB488922[p]		AB488982[p]	AB489022[q]			AB489003[q]	AB489046[q]	AB488939[p]	AB488963[p]
Fve1	Fejervarya verruculosa		Indonesia: Lesser Sunda: Ende		AB606421[r]													
Fvi1	Fejervarya vittigera	PNM7826	Philippines: Quezon Province	AY313683[i]	AY313683[i]													
Sbr1	Sphaerotheca breviceps			KJ725143[d]														
Sbr2	Sphaerotheca breviceps		Sri Lanka				AF249077[e]										DQ347214[e]	
Sbr2	Sphaerotheca breviceps	USNM 524017	Myanmar: Sagaing: Kanbular Township, near Chatthin Wildlife Sancturary	DQ283100[j]														
Sdb1	Sphaerotheca dobsonii	isolate = RBRL 060720-01 or 18-4-Jul-2004	India: Bajipe: Mangalore	AB277290[q]	AB277305[q]	AB277318[q]	AB488855[p]	MG719872[*]	AB277330[q]	MG719885[*]	AB488999[p]	AB489040[q]	MG719896[*]	MG719908[*]	AB277357[q]	AB489064[q]	AB488959[p]	AB277344[q]
FTH2	Fejervarya sp. hp-3	IABHU 18145 or 18156 or 18157	Thailand: Pilok		AB277300[q]	AB277312[q]	AB488822[p]		AB277325[q]			AB489024[q]			AB277352[q]	AB489048[q]	AB488956[p]	
ZNE1	Fejervarya sp. hp-4		Nepal: Chitwan	AB488866[p]	AB488889[p]	AB500245	AB488835[p]		AB500251[q]			AB500262[q]			AB500268[q]	AB500239[q]	AB500225[q]	AB500231[q]
Zba1	Fejervarya sp. Medium	IABHU 2097	Bangladesh: Mymensingh	MG719919[*]				MG719873[*]		MG719886[*]			MG719897[*]	MG719909[*]				
Zba2	Fejervarya sp. Medium		Bangladesh: Mymensingh	AB372077[o]	AB372011[o]		AB372054[o]											
Zku1	Minervarya kudremukhensis	isolate = BNHS 4653 or 4654	India: Kudermukh	AB488875[p]	AB488898[p]	AB488916[p]	AB488849[p]		AB488933[p]		AB488994[p]	AB489035[q]			AB489014[q]	AB489059[q]	AB488950[p]	AB488974[p]
Zan1	Minervarya andamanensis		India: Andaman	AB488876[p]	AB488899[p]	AB488917[p]	AB488850[p]		AB488934[p]		AB488995[p]	AB489036[q]			AB489015[q]	AB489060[q]	AB488951[p]	AB488975[p]
Zas1	Minervarya asmati	isolate = DFBGBAU FspS 11	Bangladesh: Cox's Bazar	AB372079[o]	AB372016[o]		AB372067[o]											
Zas2	Minervarya asmati	DFBGBAU FspS 31	Bangladesh: Mymensingh	AB372080[o]	AB372012[o]		AB372058[o]											
Zcp1	Minervarya caperata	isolate = BNHS 3066 or 5060	India: Mudigere	AB488871[p]	AB488894[p]	AB488912[p]	AB488843[p]	MG719874[*]	AB488929[p]		AB488990[p]	AB489031[q]	MG719898[*]	MG719910[*]	AB489010[q]	AB489055[q]	AB488946[p]	AB488970[p]
Fpf	Minervarya cepfi	SDBDU 2007.1561	India: Maharashtra: Koyna		KY447309[k]		KY820737[k]										KY820752[k]	
Fch	Minervarya chiangmaiensis	KIZ024057	Thailand: Omkoi		KX834135[z]													
Fdh	Minervarya dhaka	MZH-3371	Bangladesh: Dhaka		KP849817[n]													
Mgo1	Minervarya gomantaki	ZSI/WGRC/V/A/867 (CESF 2294)	India: Codal village		KT004440[h]										KR781085[h]			
Zga1	Minervarya granosa	isolate = BNHS 4651	India: Mudigere	AB488872[p]	AB488895[p]	AB488913[p]	AB488844[p]		AB488930[p]		AB488991[p]	AB489032[q]			AB489011[q]	AB489056[q]	AB488947[p]	AB488971[p]
Zge1	Minervarya greenii	MNHN 2000.617	Sri Lanka: Nuwara Eliya	AB488868[p]	AB488891[p]	AB488910[p]	AB488838[p]		AB488927[p]		AB488988[p]	AB489029[q]			AB489008[q]	AB489053[q]	AB488944[p]	AB488968[p]
Fkd	Minervarya kadar	ZSI/WGRC/V/A/940	India: Kerala: Thavalakuzhipara		KY447312[k]		KY820739[k]										KY820754[k]	
Zke1	Minervarya keralensis		India: Western Ghats	GQ478318[u]	GQ478322[u]		GQ478330[u]											
Zki1	Minervarya kirtisinghei	MNHN 2000.620	Sri Lanka: Laggalla	AB488867[p]	AB488890[p]	AB488909[p]	AB488836[p]		AB488926[p]		AB488987[p]	AB489028[q]			AB489007[q]	AB489052[q]	AB488943[p]	AB488967[p]
Fmn	Minervarya monoharani	ZSI/WGRC/V/A/950	India: Kerala: Chathankod-Bonnacad		KY447315[k]		KY820741[k]										KY820756[k]	
Zmd1	Minervarya mudduraja	isolate = BNHS 4646 or 20-7-June-2003	India: Madikeri	AB488873[p]	AB488896[p]	AB488914[p]	AB488845[p]	MG719875[*]	AB488931[p]		AB488992[p]	AB489033[q]	MG719899[*]	MG719911[*]	AB489012[q]	AB489057[q]	AB488948[p]	AB488972[p]

Table SM2. Localities and voucher numbers of samples and accession numbers of DNA sequences.

ID	Species	Voucher	Locality	*12S*	*16S*	*cxcr4*	*cytb*	*kiaa1239*	*ncx1*	*pomc*	*rag2*	*rho*	*sacs*	*ttn*	*tyr*	*bdnf*	*rag1-3'*	*rag1-5'*
Fnx	Minervarya neilcoxi	ZSI/WGRC/V/A/955	India: Kerala: Parambikulam		KY447317[k]		KY820743[k]										KY820758[k]	
Zpi1	Minervarya pierrei	IABHU 34056 or 34057	Nepal: Chitwan	AB488865[p]	AB488888[p]	AB488908[p]	AB48834[p]		AB488925[p]		AB490160[p]	AB489027[q]			AB489006[q]	AB489051[q]	AB488942[p]	AB488966[p]
Zru1	Minervarya rufescens	isolate = RBRL 040716-1 or 39-16-Jul-2004	India: Padil: Mangalore	AB488874[p]		AB488915[p]	AB488847[p]	MG719876[*]	AB488932[p]		AB488993[p]	AB489034[q]	MG719900[*]	MG719912[*]	AB489013[q]	AB489058[q]	AB488949[p]	AB488973[p]
Zru1	Minervarya rufescens	RBRL 030526-03	India: Bajipe		AB530601[m]													
Msh1	Minervarya sahyadris	RBRL 050714-02	India: Aralam		AB530605[m]													
Zsy1	Minervarya syhadrensis	10-Jul-04-19 or 20 or 21	India: Karnool	AB488870[p]		AB488911[p]	AB488840[p]		AB488928[p]		AB488989[p]	AB489030[q]			AB489009[q]	AB489054[q]	AB488945[p]	AB488969[p]
Zsy2	Minervarya syhadrensis	10-Jul-04-19 or 20 or 21	India: Karnool				AB488841[p]											
Ecy1	Euphlyctis cyanophlyctis	IABHU 3752	Bangladesh: Mymensingh	MG719917[*]				MG719866[*]		MG719879[*]	MG719889[*]			MG719902[*]			MG719914[*]	
Ecy2	Euphlyctis cyanophlyctis	IABHU 3752	Bangladesh: Mymensingh		AB488901[p]	AB488919[p]			AB488936[p]		AB488997[p]	AB489038[q]			AB489017[q]	AB489062[q]	AB488957[p]	AB488977[p]
Ecy2	Euphlyctis cyanophlyctis		India: Assam				AB290611[a]											
Ecy2	Euphlyctis cyanophlyctis		Sri Lanka	AB290433[a]														
Ehx1	Euphlyctis hexadactylus	isolate = IABHU 3685	Bangladesh: Khulna	MG719921[*]				MG719878[*]		MG719888[*]							MG719916[*]	
Hcr1	Hoplobatrachus crassus											AF249109[e]						
Hcr1	Hoplobatrachus crassus	IABHU 3973					AB671196[l]											
Hcr1	Hoplobatrachus crassus	IABHU 3859	Bangladesh: Sandwip: Chittagong		AB543601[l]													
Hcr1	Hoplobatrachus crassus		Bangladesh: Khulna	AB273158[a]														
Hcr1	Hoplobatrachus crassus														AF249172[e]			
Hoc1	Hoplobatrachus occipitalis	KU 290425	Ghana: Winneba: Muni Lagoon									DQ283787[j]						
Hoc1	Hoplobatrachus occipitalis		Tanzania	AB273162[a]			AB274148[a]											
Hoc1	Hoplobatrachus occipitalis				AF261263[x]													
Hoc1	Hoplobatrachus occipitalis	MVZ 234146	Tanzania: Mwanza Region: Lamadi												EU980026[f]			
Hru1	Hoplobatrachus rugulosus	FMNH 255191	Laos: Mounlapamok District: Dong: Khanthung Nat Biodiv Conservation Area									DQ283842[j]						
Hru1	Hoplobatrachus rugulosus						KC196066[v]											
Hru1	Hoplobatrachus rugulosus		Thailand: Nong khai		AB636618[c]													
Hru1	Hoplobatrachus rugulosus	isolate = IABHU 4101	Thailand	MG719920[*]				MG719877[*]		MG719887[*]			MG719901[*]	MG719913[*]				
Hru1	Hoplobatrachus rugulosus	MVZ 224079	Vietnam: Vinh Phuc: Vinh Yen Dist: Tam Dao												EU980024[f]			
Hti1	Hoplobatrachus tigerinus			MG719918[*]				MG719871[*]		MG719884[*]	MG719890[*]		MG719895[*]	MG719907[*]			MG719915[*]	
Hti2	Hoplobatrachus tigerinus	IABHU 20006	Bangladesh: Mymensingh			AB277319[p]			AB277331[q]		AB488998[p]	AB489039[q]			AB277358[q]	AB489063[q]	AB488958[p]	AB277345[q]
Hti2	Hoplobatrachus tigerinus		Bangladesh: Mymensingh	NC014581[b]			NC014581[b]											
Hti2	Hoplobatrachus tigerinus				AB636620[c]													
Lsp1	Limnonectes khasianus	KUHE 23158	Thailand: Narathiwat: Bala	AB981414[s]														
Lsp1	Limnonectes laticeps		Malaysia: Kuala Lumpur		AB277306[q]	AB277320[q]	AB488856[p]		AB277332[q]		AB489000[q]	AB489041[q]			AB277359[q]	AB489065[q]	AB488960[p]	AB277346[q]
Nsp1	Nannophrys ceylonensis	WHTCEY	Sri Lanka				GQ204546[t]									GQ204480[t]	GQ204610[t]	
Nsp1	Nannophrys ceylonensis											AF249112[e]						
Nsp1	Nannophrys ceylonensis	VUB 0172							AY948809[y]									
Nsp1	Nannophrys ceylonensis		Sri Lanka	AF249016[e]	AF249047[e]										AF249175[e]			

Sequences from the following publications: [a]Alam et al. 2008, [b]Alam et al. 2010, [c]Alam et al. 2012, [d]Bahuguna, Chowdhary and Bahuguna submitted 2014, [e]Bossouyt and Milinkovitch 2000, [f]Che et al. 2009, [g]Che et al. 2010, [h]Dinesh et al. 2010, [i]Evans et al. 2003, [j]Frost et al. 2006, [k]Garg and Biju 2017, [l]Hasan et al. 2012, [m]Hasan et al. 2014, [n]Howlader et al. 2016, [o]Islam et al. 2008, [p]Kotaki et al. 2008, [q]Kotaki et al. 2010, [r]Kurniawan et al. 2014, [s]Matsui et al. 2014, [t]Meegaskumbura and Schneider (Unpublished), [u]Meenakshi et al. 2010, [v]Pan et al. (Unpublished), [w]Ren et al. 2009, [x]Richards (Unpublished), [y]Roelants et al. 2007, [z]Suwannapoom et al. 2016, [*]This study.

Institutional abbreviations: BNHS = Bombay Natural History Society; CESF = Centre for Ecological Sciences, Frogs; DFBGBAU = Department of Fisheries Biology & Genetics, Bangladesh Agricultural University; FMNH = Field Museum of Natural History ; HW6 = voucher specimen of School of Life Sciences, Fudan University; IABHU = Institute for Amphibian Biology,Hiroshima university; KIZ = KIZ: Kunming Institute of Zoology, Chinese Academy of Sciences, China; KU = University of Kansas, Museum of natural History, USA; KUHE = Graduate School of Human and Environmental studies, Kyoto university; MK = National Museum of Kenya, Nairobi, Kenya; MNHN = Museum National d'Histoire Naturelle, Paris; MVZ = Museum of Vertebrate Zoology, Berkeley ; MZH = Finnish Museum of Natural History, Finland; PNM = Philippine National Museum, Manila, Philippines; RBRL = Rondano Biodiversity Research Laboratory, St. aloysius College; SDBDU = Systematics Lab, University of Delhi; USNM = National Museum of Natural History, Division of Amphibians and Reptiles, USA; VUB = Vrije Universiteit Brussel, Belgium ; WHT = Wildlife Heritage Trust, 95 Cotta Road, Colombo 8, Sri Lanka; ZSI/WGRC = Zoological Survey of India, Western Ghats Regional Centre, Calicut.

In the 'Voucher' column, isolate denotes that there is only tissue available.

References referred in Table SM2:

Alam, M. S., Igawa, T., Khan, M. M. R., Islam, M. M., Kuramoto, M., Matsui, M., ... & Sumida, M. (2008). Genetic divergence and evolutionary relationships in six species of genera *Hoplobatrachus* and *Euphlyctis* (Amphibia: Anura) from Bangladesh and other Asian countries revealed by mitochondrial gene sequences. Molecular Phylogenetics and Evolution, 48(2), 515-527.

Alam, M. S., Kurabayashi, A., Hayashi, Y., Sano, N., Khan, M. M. R., Fujii, T., & Sumida, M. (2010). Complete mitochondrial genomes and novel gene rearrangements in two dicroglossid frogs, *Hoplobatrachus tigerinus* and *Euphlyctis hexadactylus*, from Bangladesh. Genes & genetic systems, 85(3), 219-232.

Alam, M. S., Islam, M. M., Khan, M. M. R., Hasan, M., Wanichanon, R., & Sumida, M. (2012). Postmating isolation in six species of three genera (*Hoplobatrachus*, *Euphlyctis* and *Fejervarya*) from family Dicroglossidae (anura), with special reference to spontaneous production of allotriploids. Zoological science, 29(11), 743-752.

Bossuyt, F., & Milinkovitch, M. C. (2000). Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. Proceedings of the National Academy of Sciences, 97(12), 6585-6590.

Che, J., Hu, J. S., Zhou, W. W., Murphy, R. W., Papenfuss, T. J., Chen, M. Y., ... & Zhang, Y. P. (2009). Phylogeny of the Asian spiny frog tribe Paini (Family Dicroglossidae) sensu Dubois. Molecular Phylogenetics and Evolution, 50(1), 59-73.

Che, J., Zhou, W. W., Hu, J. S., Yan, F., Papenfuss, T. J., Wake, D. B., & Zhang, Y. P. (2010). Spiny frogs (Paini) illuminate the history of the Himalayan region and Southeast Asia. Proceedings of the National Academy of Sciences, 107(31), 13765-13770.

Dinesh, K. P., Vijayakumar, S. P., Channakeshavamurthy, B. H., Torsekar, V. R., Kulkarni, N. U., & Shanker, K. (2015). Systematic status of *Fejervarya* (Amphibia, Anura, Dicroglossidae) from South and SE Asia with the description of a new species from the Western Ghats of Peninsular India. Zootaxa, 3999(1), 79-94.

Evans, B. J., Brown, R. M., McGuire, J. A., Supriatna, J., Andayani, N., Diesmos, A., ... & Cannatella, D. C. (2003). Phylogenetics of fanged frogs: testing biogeographical hypotheses at the interface of the Asian and Australian faunal zones. Systematic Biology, 52(6), 794-819.

Frost, D. R., T. Grant, J. Faivovich, R. H. Bain, A. Haas, C. F. B. Haddad, R. O. De Sá, A. Channing, M. Wilkison, S. C. Donnelan, C. J. Raxworthy, J. A. Campbell, B. L. Blotto, P. Moler, R. C. Drewes, R. A. Nussbaum, J. D. Lynch, D. M. Green & W. C. Wheeler (2006). The amphibian tree of life. Bulletin of the American Museum of Natural History 297: 11–291.

Garg, S. & Biju, S.D. (2017). Description of four new species of Burrowing Frogs in the *Fejervarya rufescens* complex (Dicroglossidae) with notes on morphological affinities of Fejervarya species in the Western Ghats. Zootaxa 4277: 451–490.

Hasan, M., Islam, M. M., Khan, M. M. R., Alam, M. S., Kurabayashi, A., Igawa, T., ... & Sumida, M. (2012). Cryptic anuran biodiversity in Bangladesh revealed by mitochondrial 16S rRNA gene sequences. Zoological Science, 29(3), 162-172.

Hasan, M., Islam, M. M., Khan, M. M. R., Igawa, T., Alam, M.S., Djong, H.T., Kurniawan, N., Joshy, H., Sen, Y.H., Belabut, D.M., Kurabayashi, A., Kuramoto, M. & Sumida, M. (2014). Genetic divergences of South and Southeast Asian frogs: a case study of several taxa based on 16S ribosomal RNA gene data with notes on the generic name *Fejervarya*. Turkish Journal of Zoology, 38:389–411.

Howlader, M. S. A., A. Nair & Merilä, J. (2016). A new species of frog (Anura: Dicroglossidae) discovered from the mega city of Dhaka. PLoS ONE 11: e0149597.

Islam, M. M., Kurose, N., Khan, M. M. R., Nishizawa, T., Kuramoto, M., Alam, M. S., Hasan, M., Kurniawan, N., Nishioka, M. & Sumida, M. (2008). Genetic divergence and reproductive isolation in the genus *Fejervarya* (Amphibia: Anura) from Bangladesh inferred from morphological observations, crossing experiments, and molecular analyses. Zoological Science, 25: 1084–1105.

Kotaki, M., A. Kurabayashi, M. Matsui, W. Khonsue, T.H. Djong, M. Tandon & Sumida, M. (2008). Genetic divergences and phylogenetic relationships among the *Fejervarya limnocharis* complex in Thailand and neighboring countries revealed by mitochondrial and nuclear genes. – Zoological Science, 25: 381–390.

Kotaki, M., A. Kurabayashi, M. Matsui, M. Kuramoto, T.H. Djong & Sumida, M. (2010). Molecular phylogeny of the diversified frogs of genus *Fejervarya* (Anura: Dicroglossidae). Zoological Science, 27: 386–395.

Kurniawan, N., Djong, T. H., Maideliza, T., Hamidy, A., Hasan, M., Igawa, T., & Sumida, M. (2014). Genetic divergence and geographic distribution of frogs in genus *Fejervarya* from Indonesia inferred from mitochondrial 16S rRNA gene analysis. Treubia, 41, 1-16.

Matsui, M., Nishikawa, K., & Eto, K. (2014). A new burrow-utilizing fanged frog from Sarawak, East Malaysia (Anura: Dicroglossidae). Raffles Bulletin of Zoology, 62, 679-687.

Meenakshi, K., Suraj, T., Bhagwati, S. S., Sujith, V. G., Santhoshkumar, K., & Sanil, G. (2010). Molecular resolution of four Species from Western Ghats (India) with their intrageneric phylogeny based on COI, Cyt B, 12S and 16S rRNA genes. Asian Journal of Experimental Biological Sciences, 1(4), 782-786.

Ren, Z., Zhu, B., Ma, E., Wen, J., Tu, T., Cao, Y., ... & Zhong, Y. (2009). Complete nucleotide sequence and gene arrangement of the mitochondrial genome of the crab-eating frog *Fejervarya cancrivora* and evolutionary implications. Gene, 441(1), 148-155.

Roelants, K., Gower, D. J., Wilkinson, M., Loader, S. P., Biju, S. D., Guillaume, K., ... & Bossuyt, F. (2007). Global patterns of diversification in the history of modern amphibians. Proceedings of the National Academy of Sciences, 104(3), 887-892.

Suwannapoom, C., Z.-Y. Yuan, N. A. Poyarkov, Jr., F. Yan, S. Kamtaeja, R. W. Murphy & Che, J. (2016). A new species of genus *Fejervarya* (Anura: Dicroglossidae) from northern Thailand. Zoological Research, 37: 1–11.

Table SM3. Flank positions of blocks selected by Gblocks.

Gene	Original positions	No. blocks	Flank positions	New positions
12S	1007	12	[499 521] [523 567] [569 641] [644 703] [709 743] [751 765] [772 790] [811 822] [824 836] [838 862] [864 882] [884 894]	350 (34%)
16S	1422	8	[855 878] [888 1077] [1079 1088] [1093 1110] [1113 1176] [1179 1191] [1193 1247] [1255 1382]	502 (35%)

Table SM4. Partitions and substitution models for the phylogenetic analysis identified using PartitionFinder.

Gene	Taxa	bp	Best Model for MrBayes		
			1st Position	2nd Position	3rd Position
12S	41	347	GTR+I+G		
16S	44	502	GTR+I+G		
CXCR4	25	705	HKY+I+G	GTR+I	GTR+I+G
CytB	41	1146	SYM+I+G	GTR+I+G	GTR+G
KIAA	13	830	HKY+I+G	GTR+I	HKY+G
NCX1	26	943	GTR+I	GTR+I	HKY+G
POMC	10	449	GTR+G	GTR+G	GTR+I+G
RAG2	24	1153	HKY+I+G	HKY	HKY+G
RHO	29	343	HKY+I+G	GTR+I	HKY+G
SACS	11	807	GTR+G	GTR+I	HKY+G
TTN	12	1433	HKY+G	F81+I	F81+G
TYR	30	702	HKY+I+G	GTR+I+G	GTR+I+G
BDNF	27	742	GTR+G	JC	K80+G
RAG1-3'	35	1503	GTR+I+G	GTR+I	GTR+G
RAG1-5'	24	1148	SYM+G	HKY+I+G	HKY+I+G
TOTAL	53	12753			

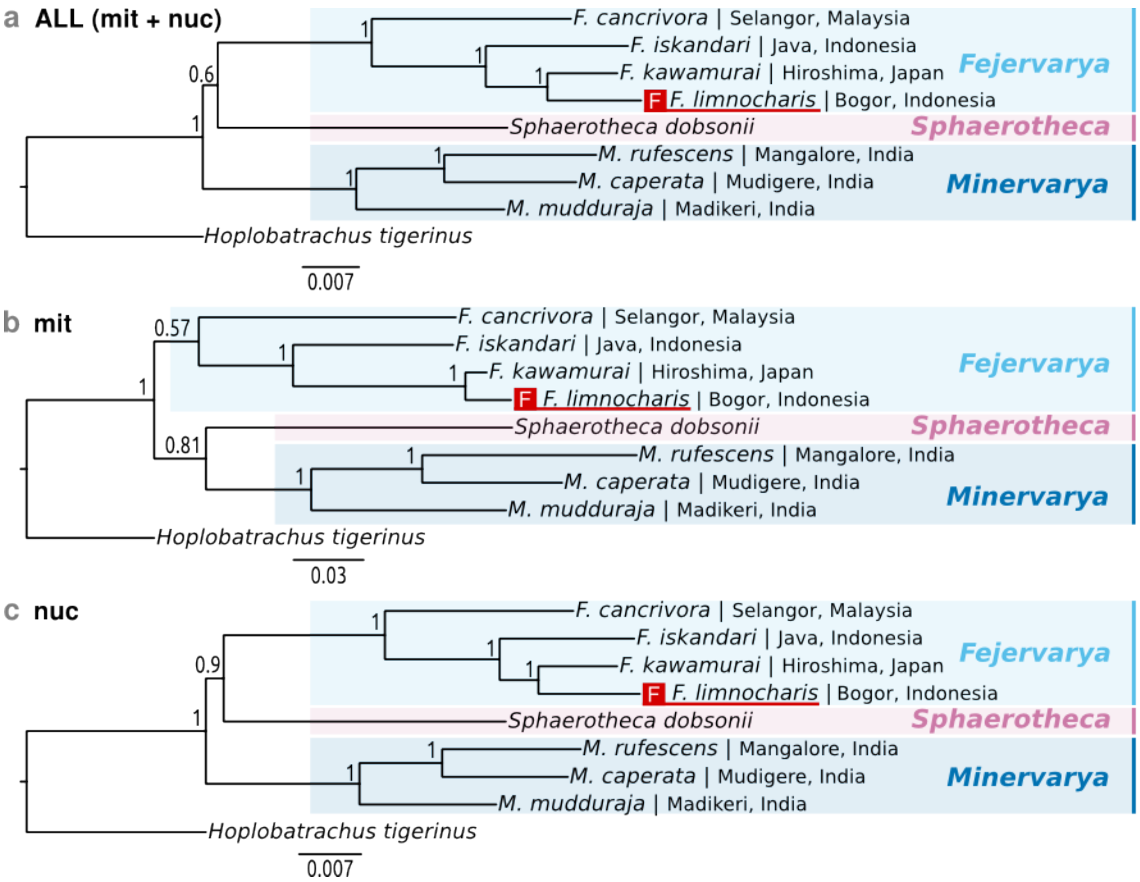

Figure SM1. Majority-rule consensus trees from the Bayesian Inference analysis using a matrix excluding sites with missing data. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). Red boxes indicate the type species of *Fejervarya* (F). **a** Tree inferred using the complete matrix (9,173 bp) **b** Tree inferred including only mitochondrial genes (662 bp) **c** Tree inferred including only nuclear genes (8,511 bp).

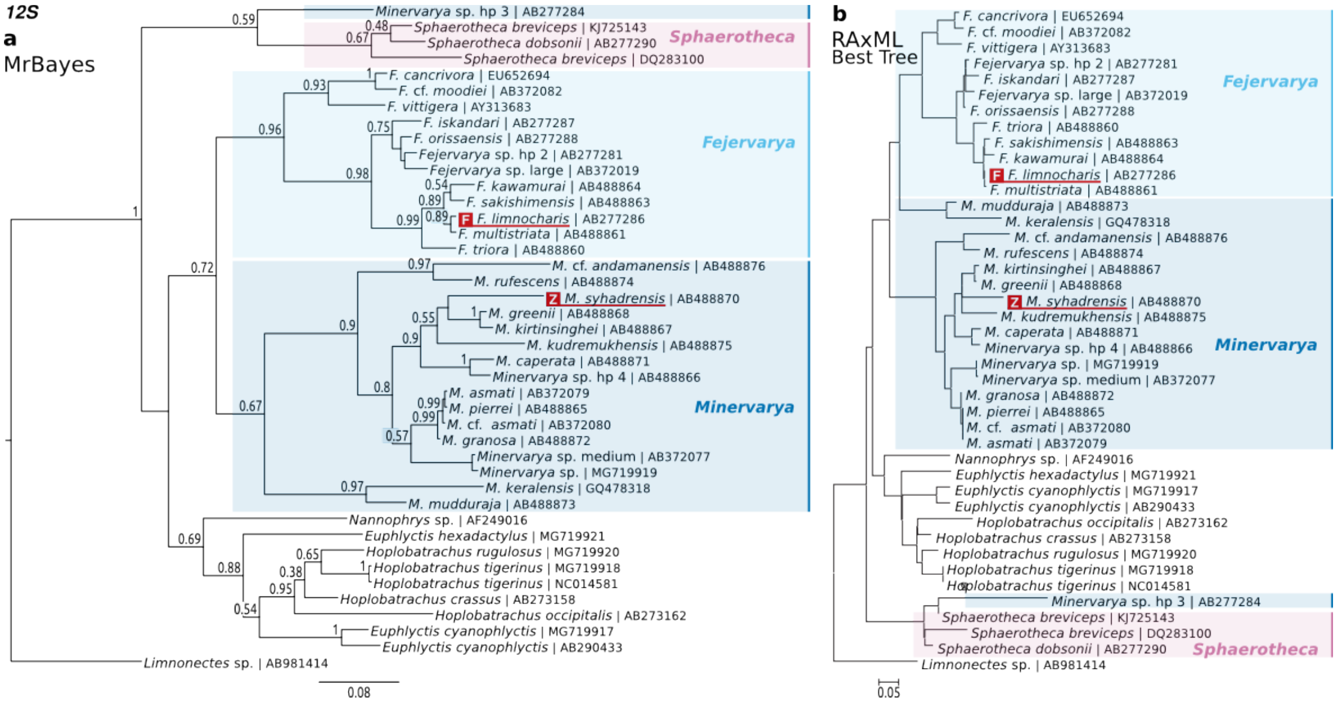

Figure SM2. *12S* (347 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

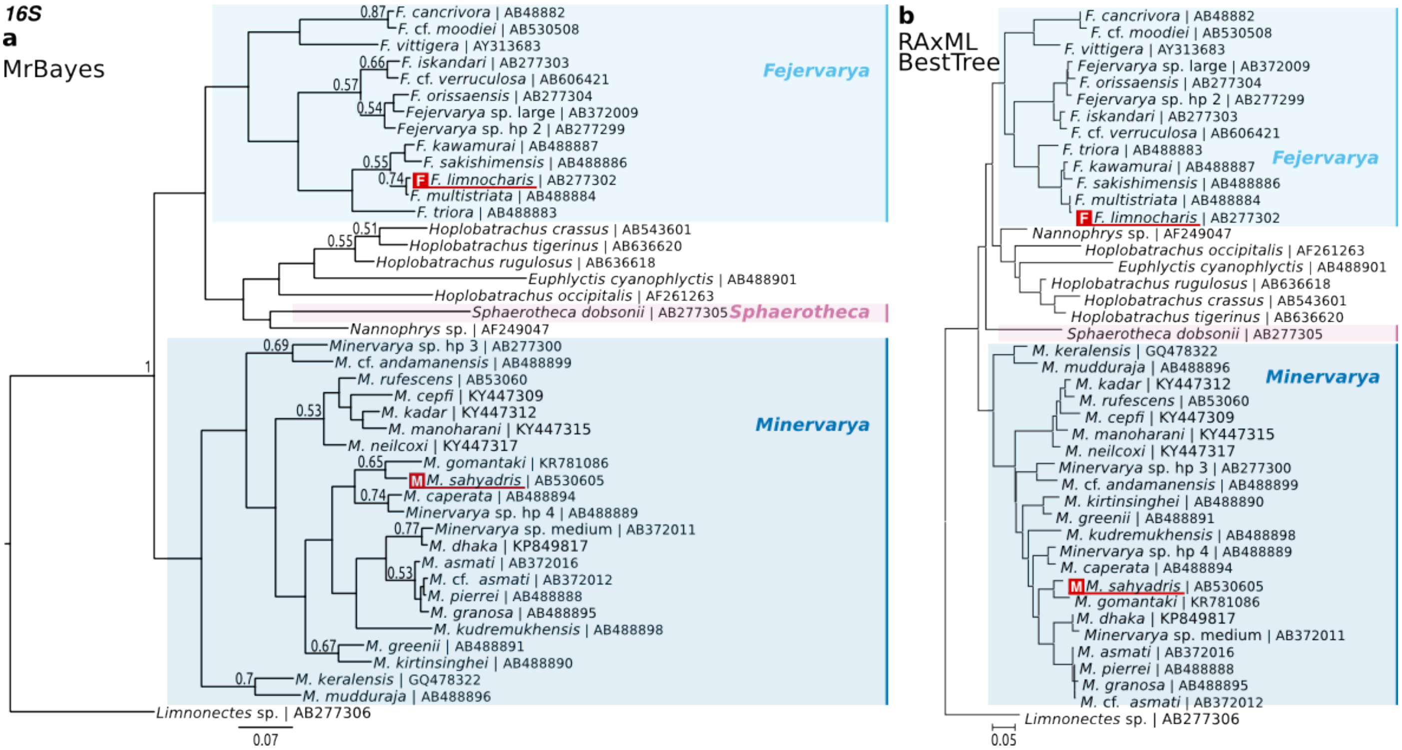

Figure SM3. *16S* (502 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Minervarya* (M).

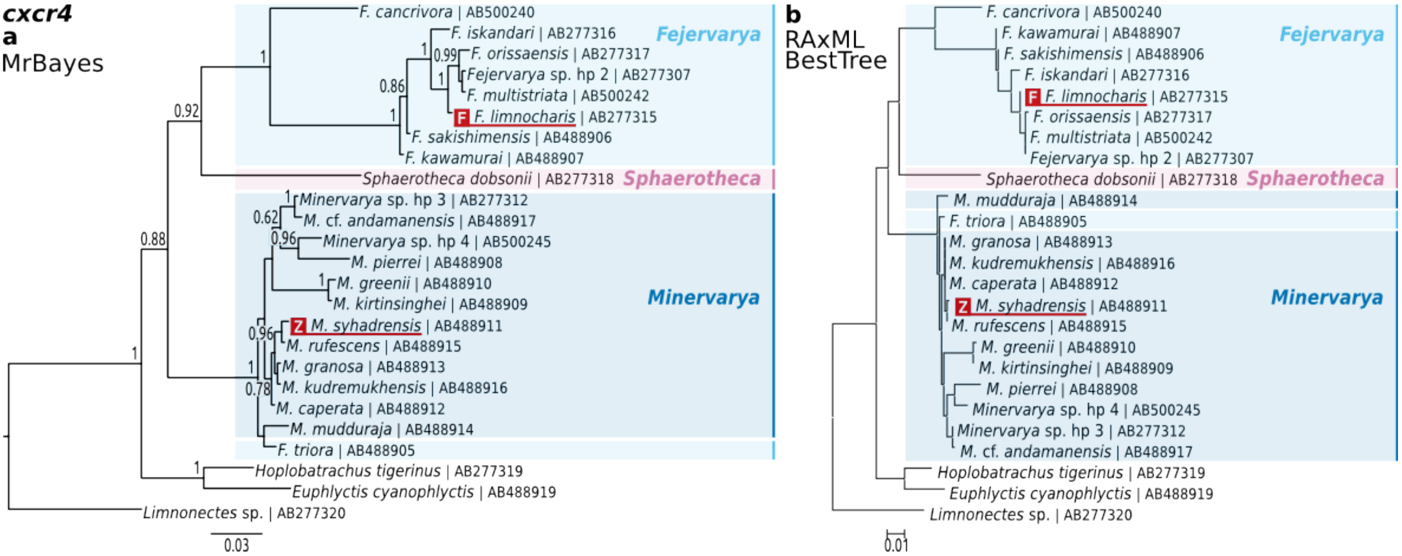

Figure SM4. c*xcr4* (705 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

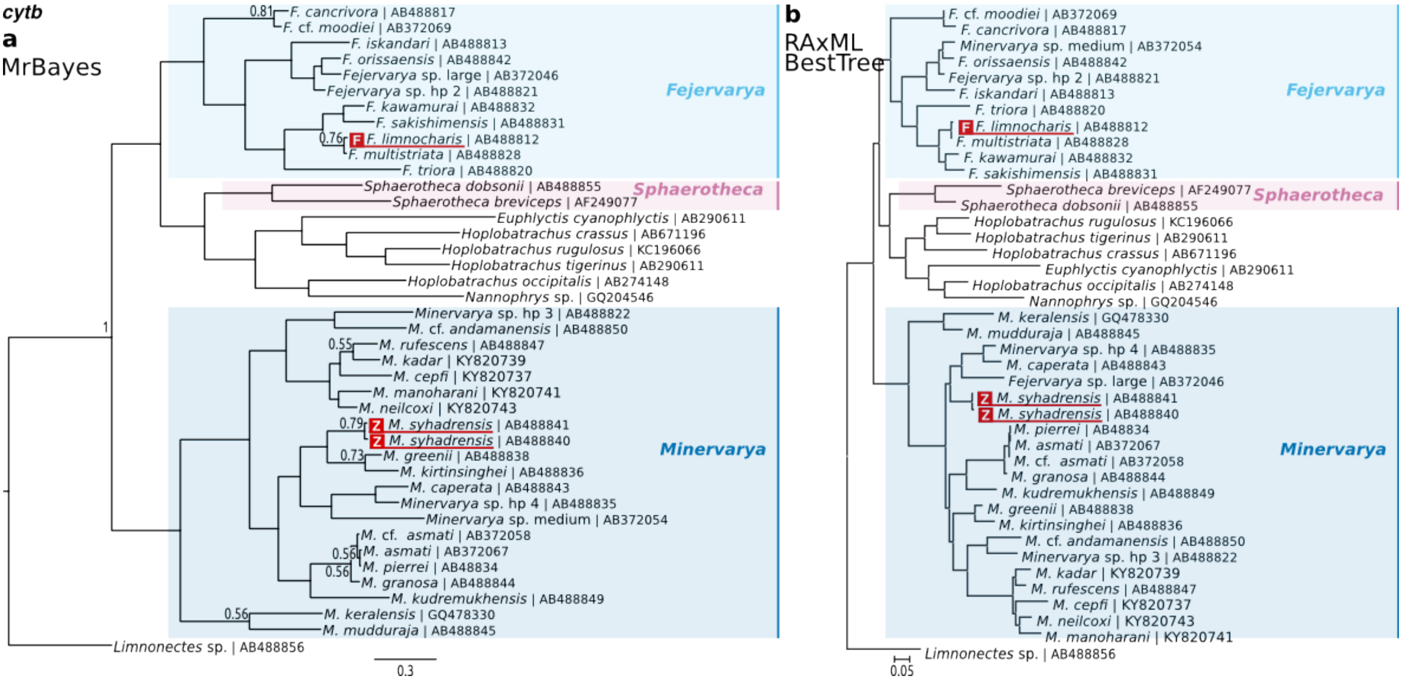

Figure SM5. ***cytb*** **(1146 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

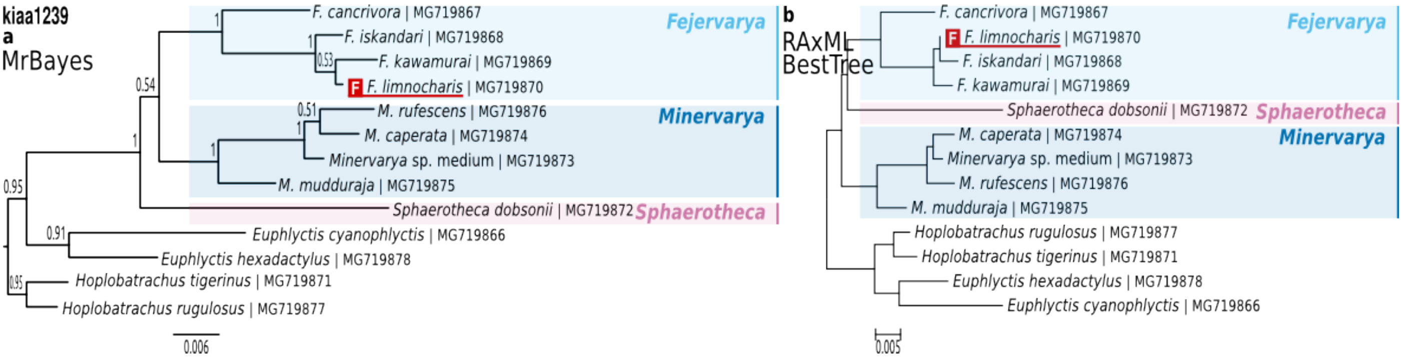

Figure SM6. ***kiaa1239*** **(854 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red box indicates the type species of *Fejervarya* (F).

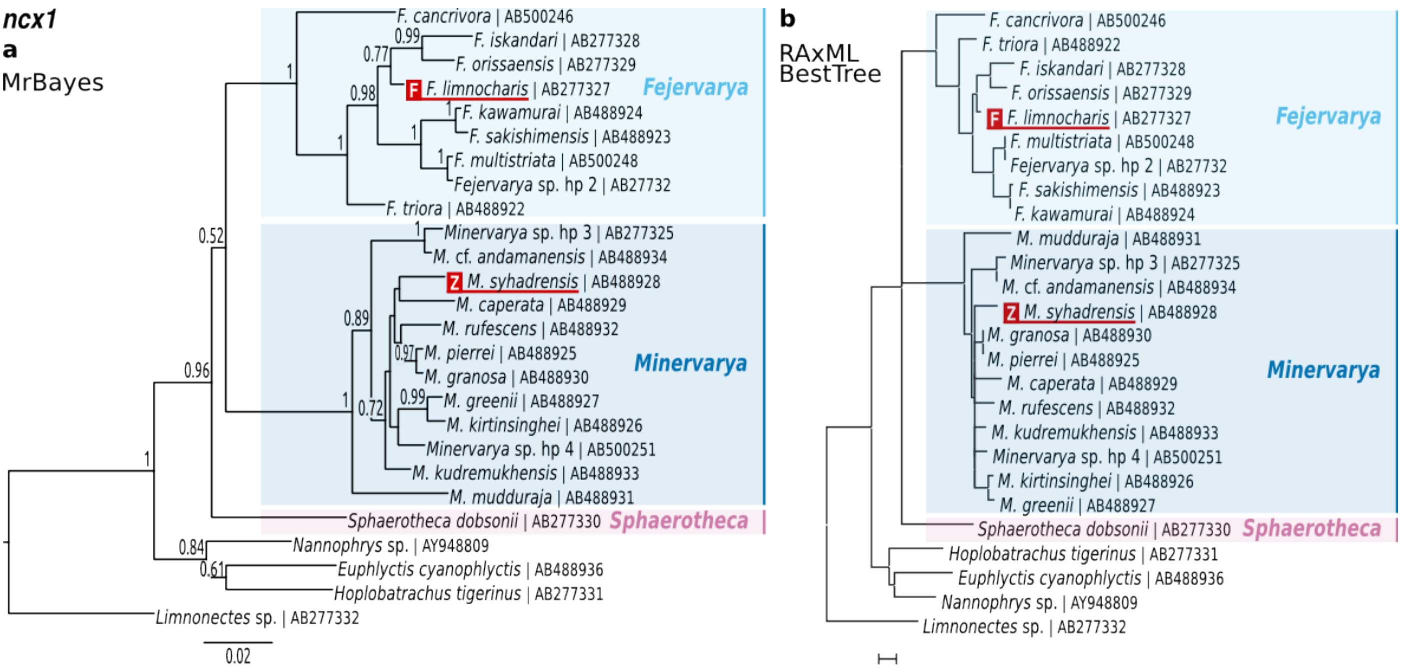

Figure SM7. *ncx1* (988 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

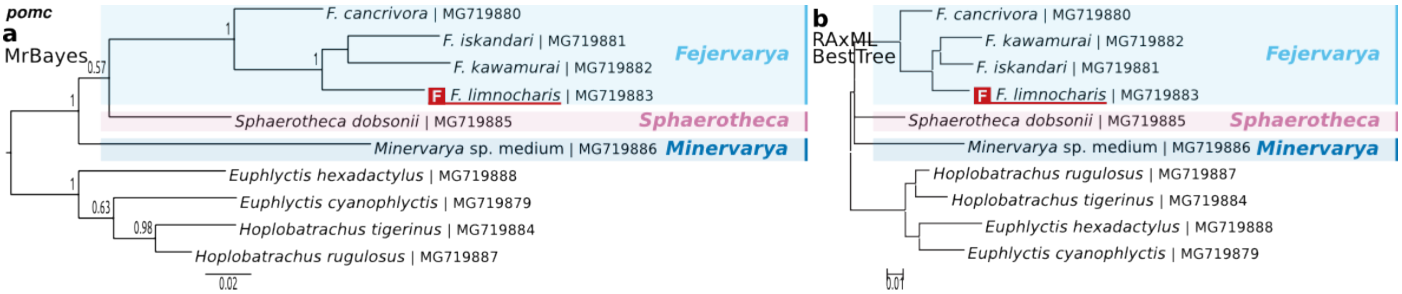

Figure SM8. *pomc* (449 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red box indicates the type species of *Fejervarya* (F).

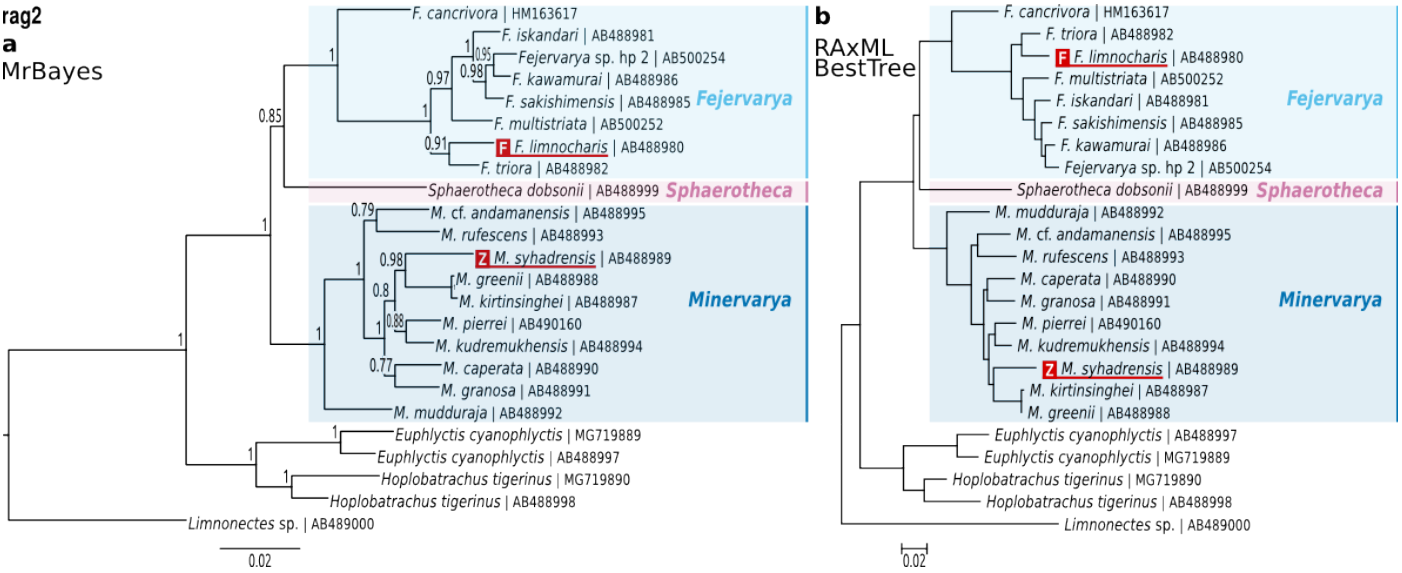

Figure SM9. *rag2* (1153 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

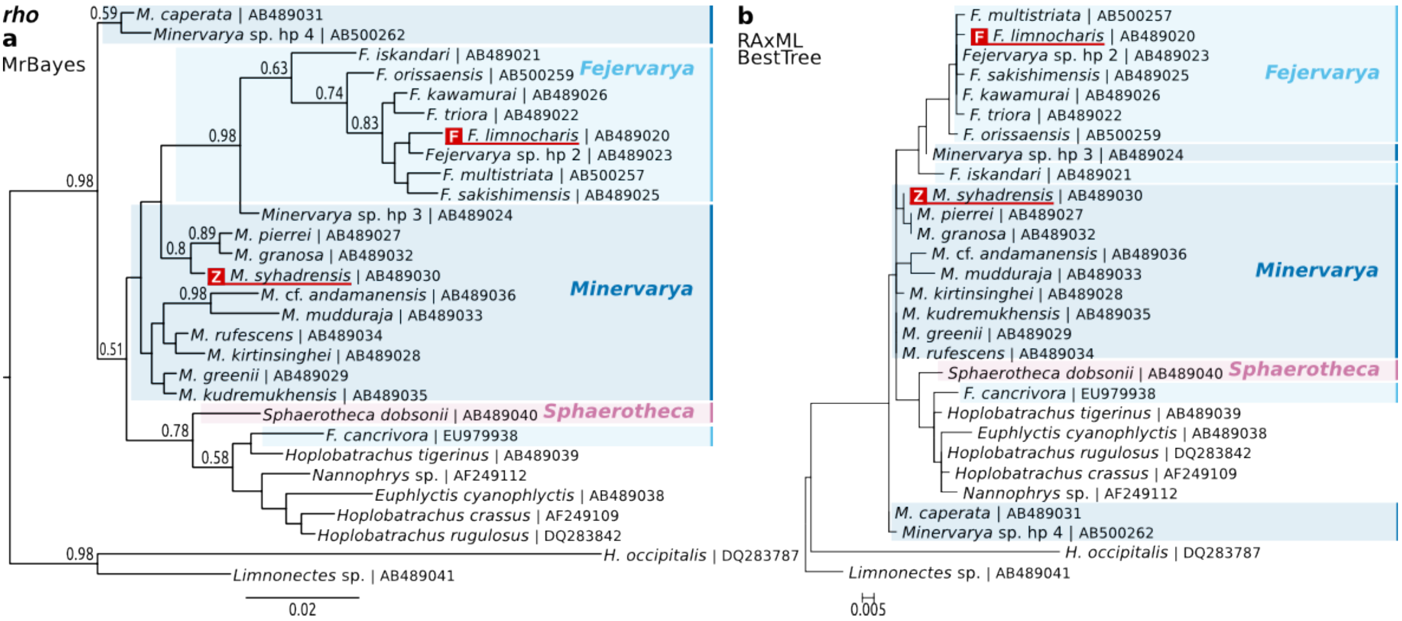

Figure SM10. ***rho*** **(343 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

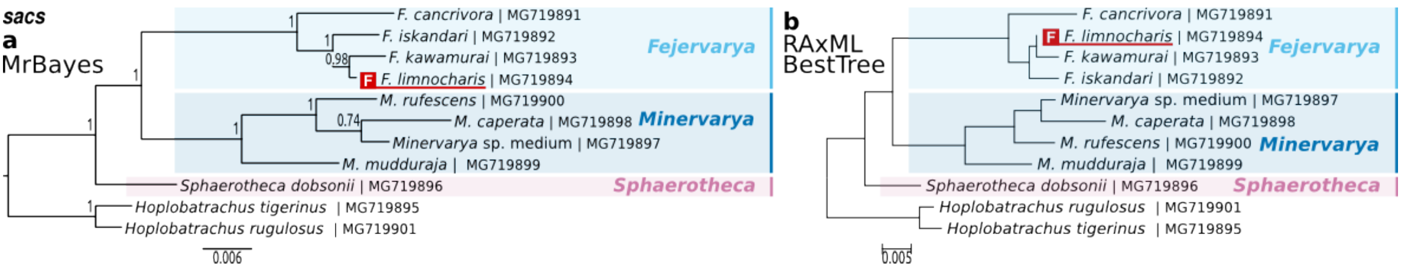

Figure SM11. ***sacs*** **(807 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red box indicates the type species of *Fejervarya* (F).

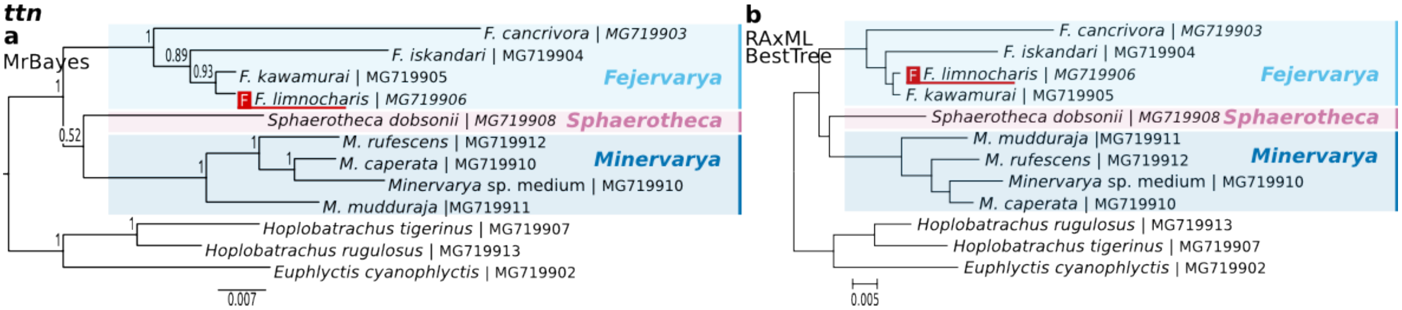

Figure SM12. ***ttn*** **(1501 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red box indicates the type species of *Fejervarya* (F).

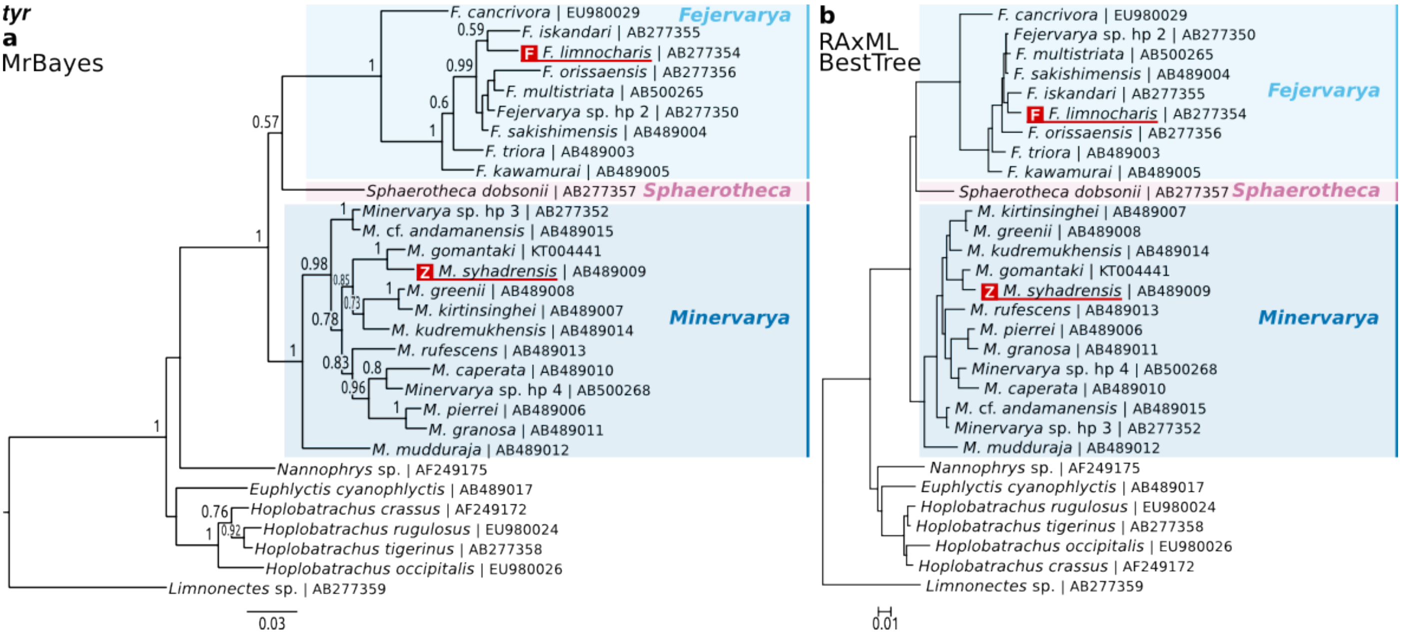

Figure SM13. ***tyr* (702 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

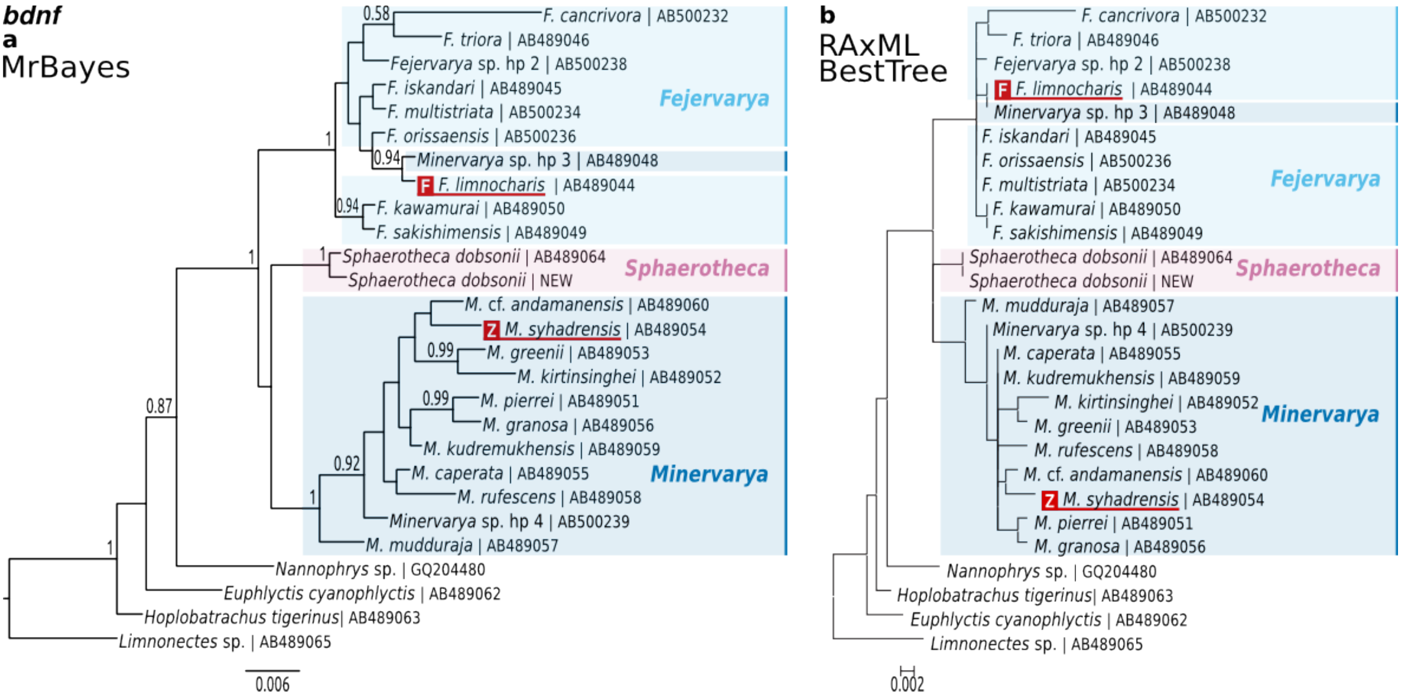

Figure SM14. ***bdnf* (742 bp) gene trees. a** Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

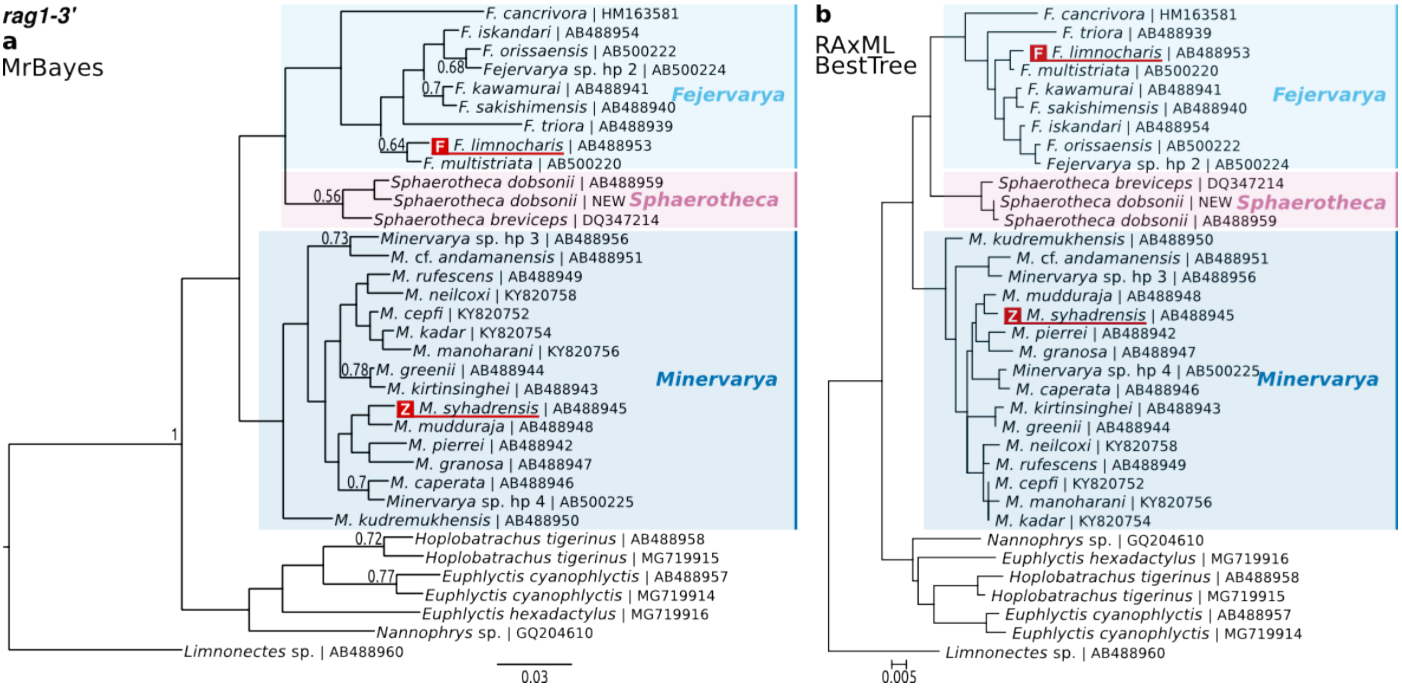

Figure SM15. *rag1*-3’ (1503 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

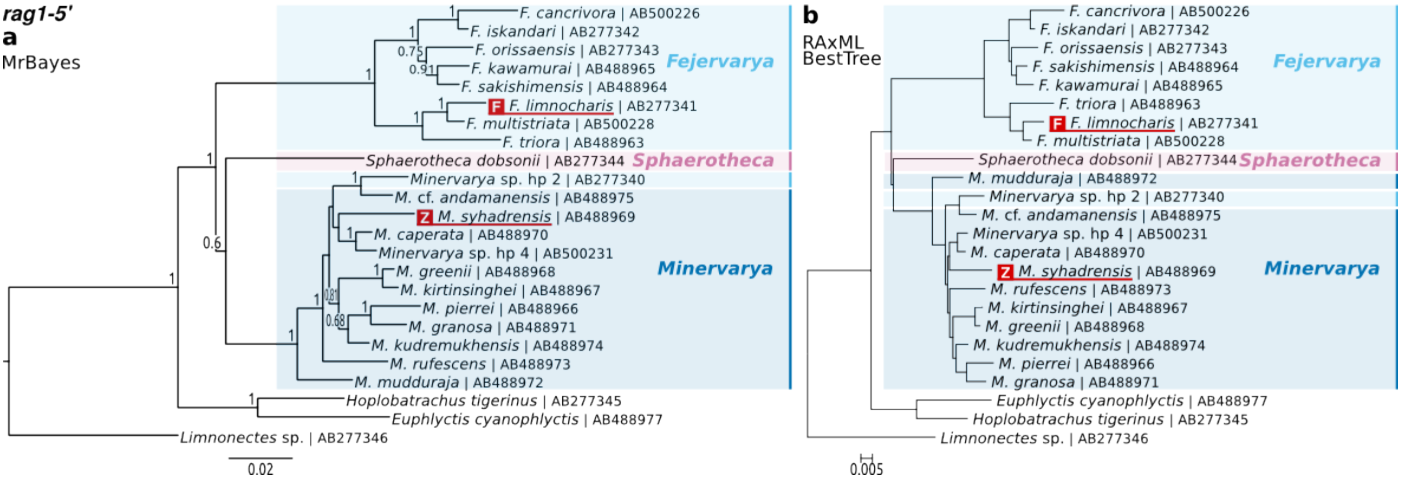

Figure SM16. *rag1*-5’ (1148 bp) gene trees. a Majority-rule consensus tree from the Bayesian Inference analysis. Numbers at nodes are posterior probabilities (only values ≥ 0.50 are shown). **b** Best tree inferred under under the Maximum Likelihood optimality criterion. In both trees, red boxes indicate the type species of *Fejervarya* (F) and *Zakerana* (Z).

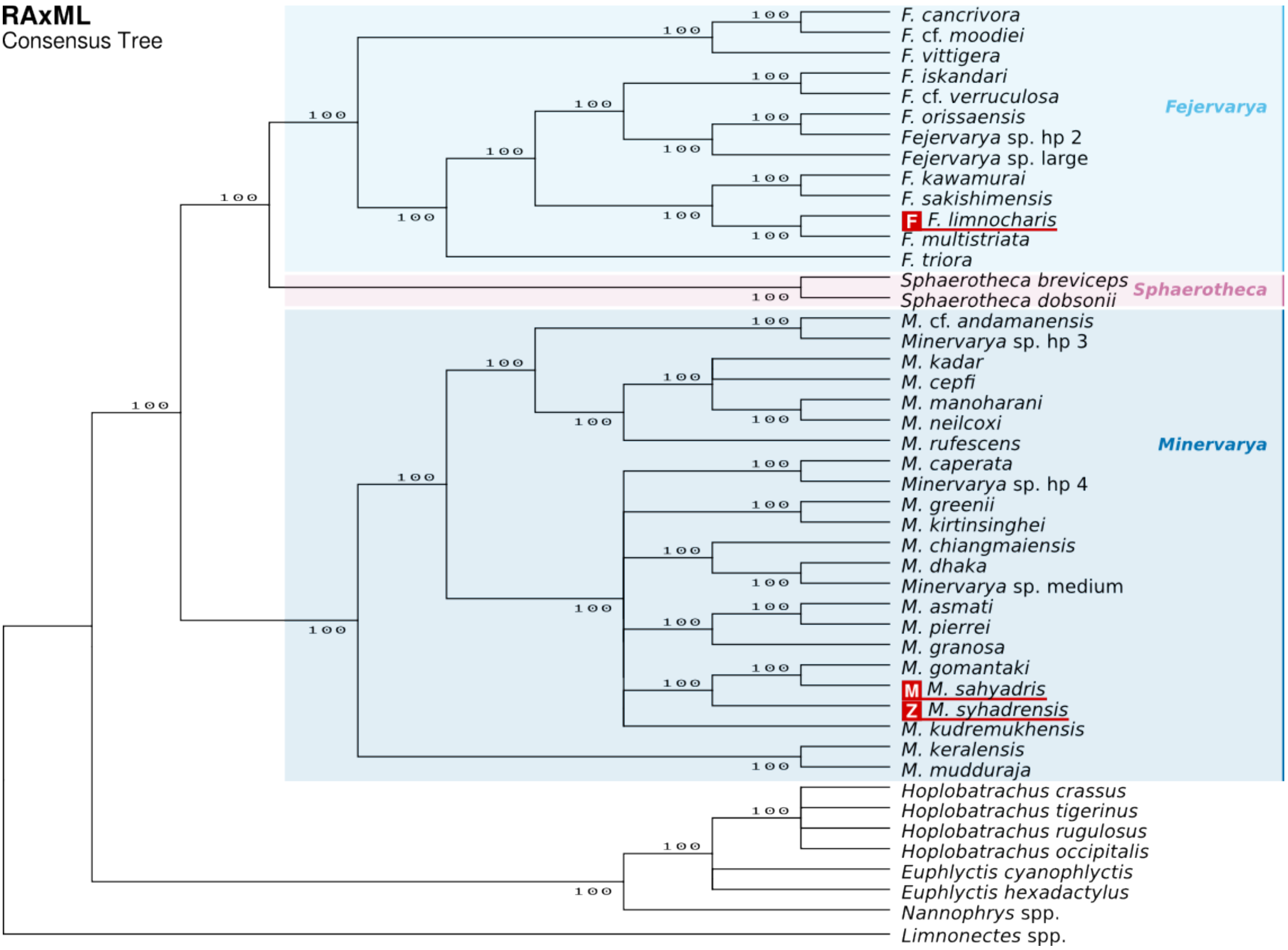

Figure SM17. Majority rule bootstrap consensus tree from the Maximum Likelihood analysis (12,752 bp). Numbers at nodes are bootstrap values. Genus classification follows the suggestion herein. Red boxes indicate the type species of *Fejervarya* (F), *Minervarya* (M) and *Zakerana* (Z). For *Nannophrys* spp. and *Limnonectes* spp. the sequences are chimeric, corresponding to different species of these monophyletic genera.

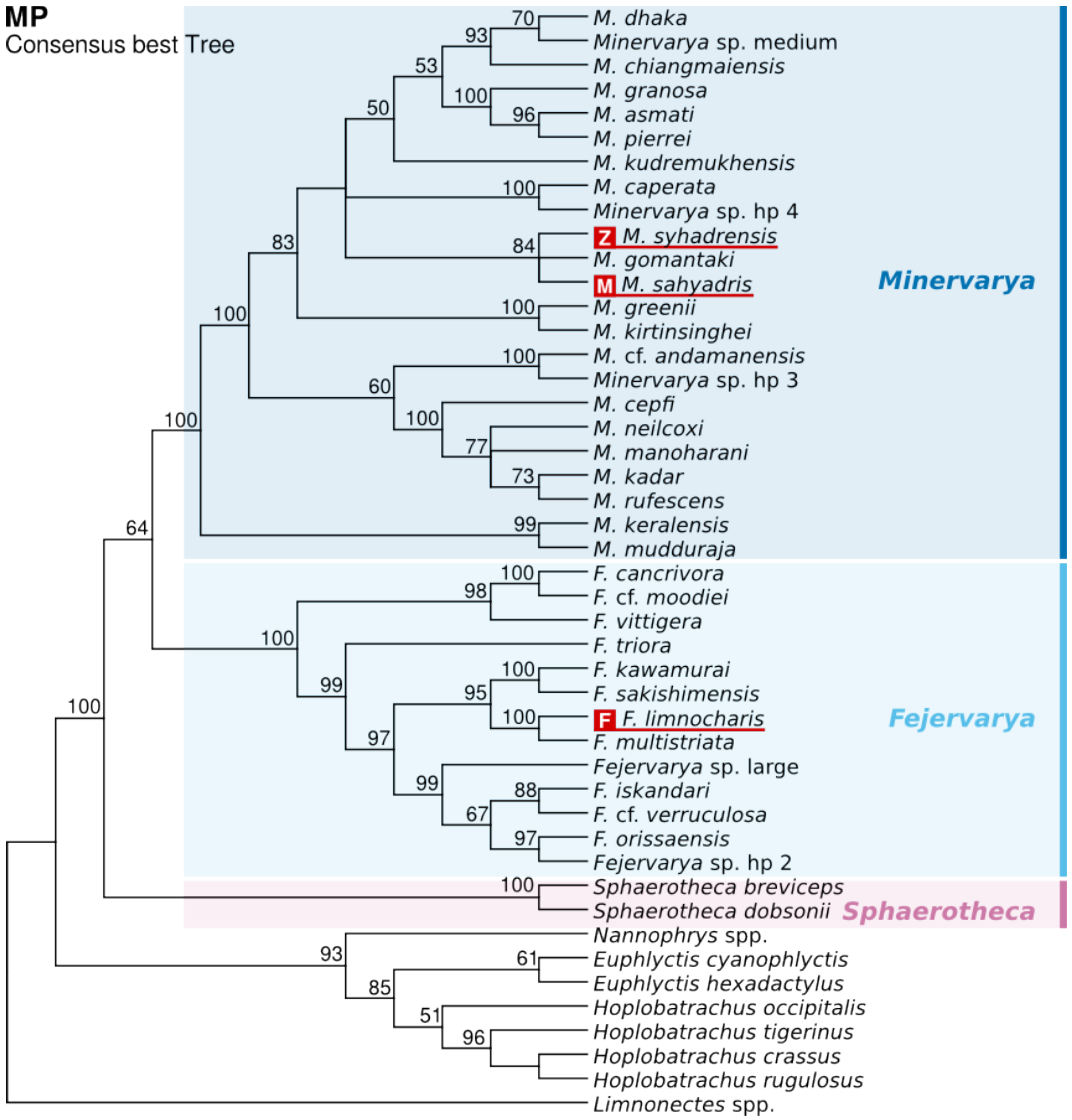

Figure SM18. Maximum Parsimony tree (12,752 bp). The analysis under the MP optimality criterion resulted in 12 equally most parsimonious trees (7455 steps), of which the strict consensus is shown here. Numbers at nodes are bootstrap values from a separate bootstrap analysis, with 2000 replicates. Genus classification follows the suggestion herein. Red boxes indicate the type species of *Fejervarya* (F), *Minervarya* (M) and *Zakerana* (Z). For *Nannophrys* spp. and *Limnonectes* spp. the sequences are chimeric, corresponding to different species of these monophyletic genera.

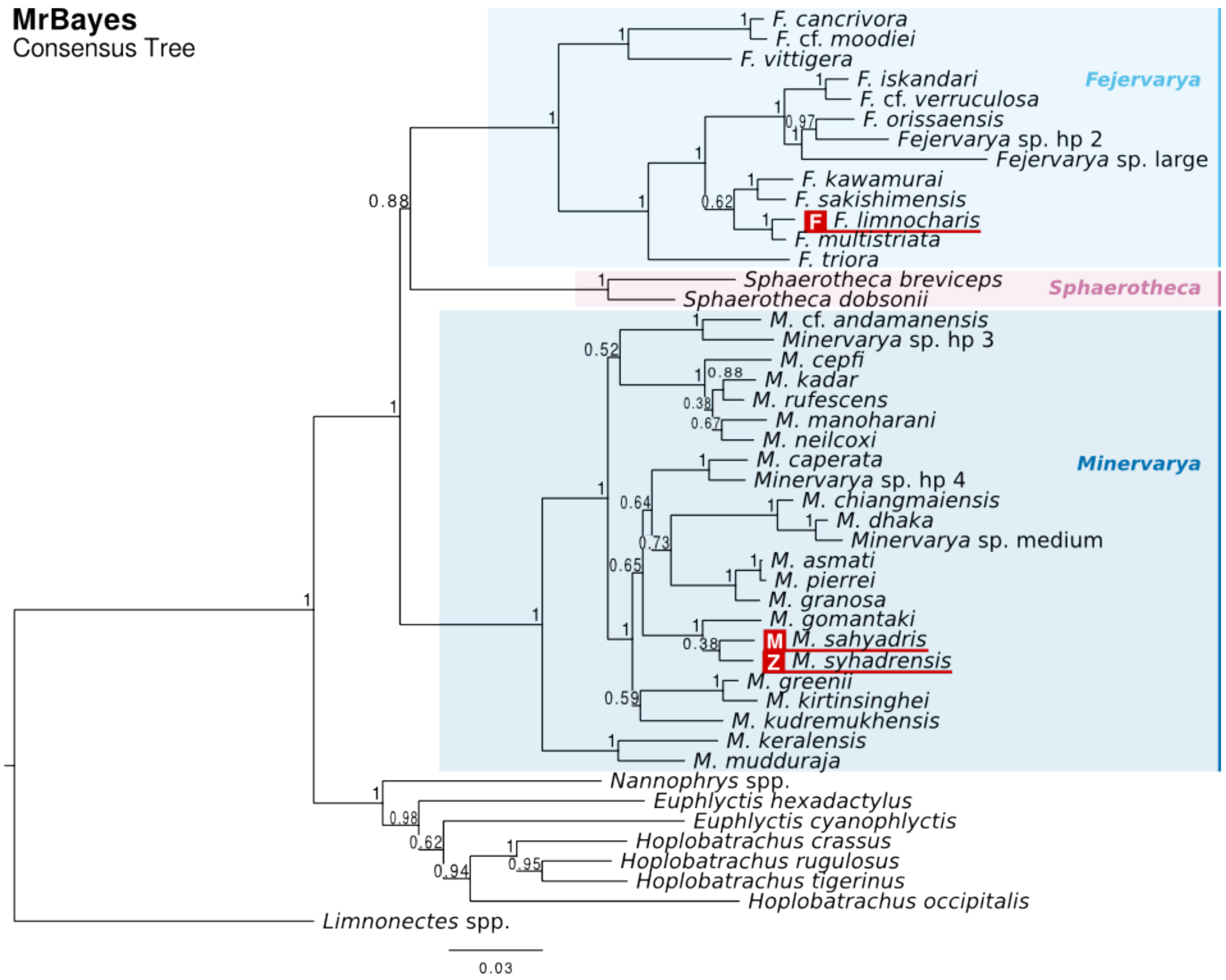

Figure SM19. Majority consensus tree from a Bayesian Inference analysis (12,752 bp). Numbers at nodes are posterior probabilities. Genus classification follows the suggestion herein. Red boxes indicate the type species of *Fejervarya* (F), *Minervarya* (M) and *Zakerana* (Z). For *Nannophrys* spp. and *Limnonectes* spp. the sequences are chimeric, corresponding to different species of these monophyletic genera.

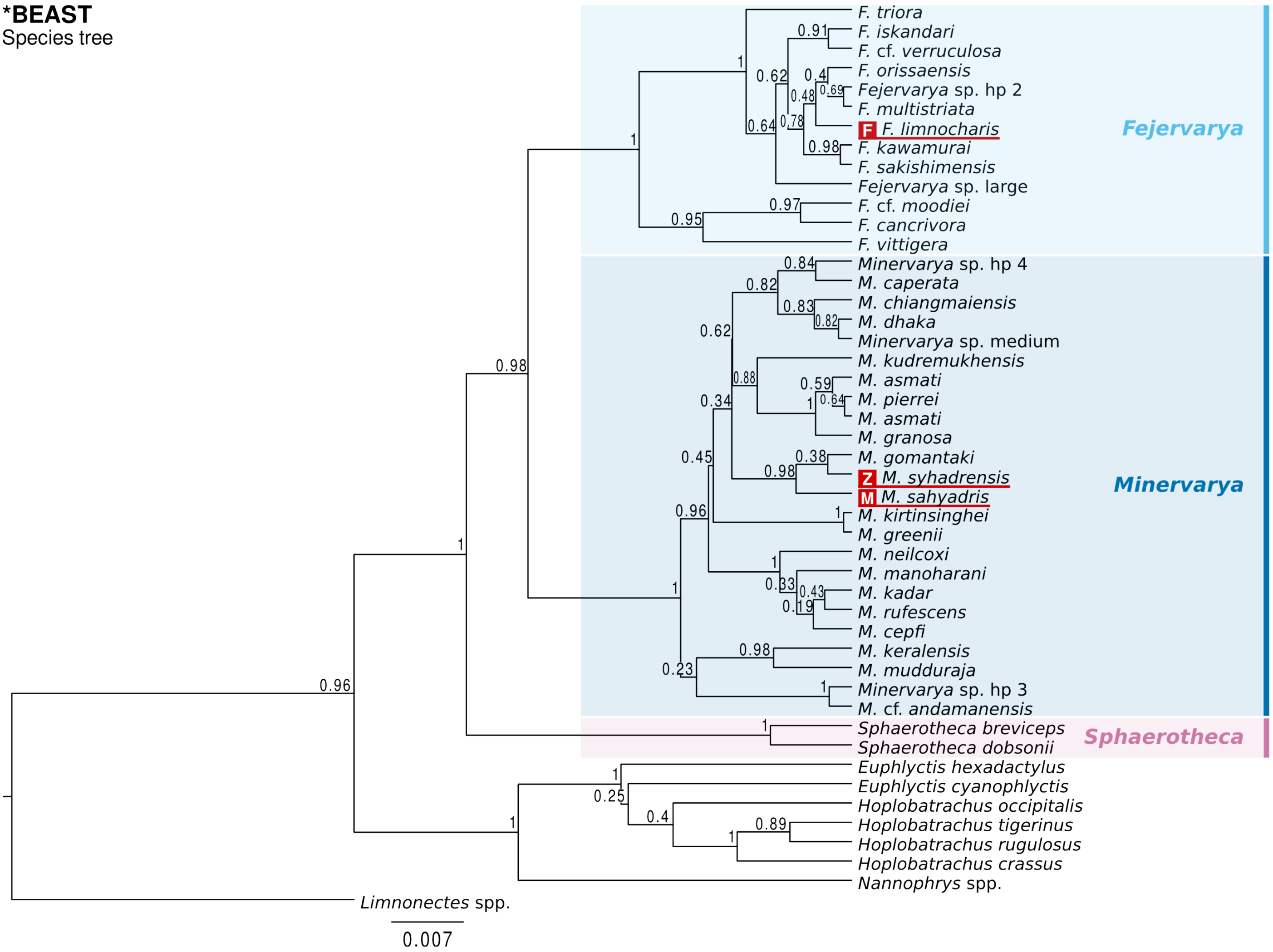

Figure SM20. Species tree inferred using *BEAST. Numbers at nodes are posterior probability values. Genus classification follows the suggestion herein. Red boxes indicate the type species of *Fejervarya* (F), *Minervarya* (M) and *Zakerana* (Z).