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Nomenclatural stability does not justify recognition of paraphyletic taxa: A response to Scherz et al. (2016)

Pedro L.V. Peloso [a,b,*], Christopher J. Raxworthy [b], Ward C. Wheeler [c], Darrel R. Frost [b]

[a] Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Avenida Perimetral, 1901, Terra Firme, CEP 66077-530 Belém, Pará, Brazil[1]
[b] Division of Vertebrate Zoology (Herpetology), American Museum of Natural History, Central Park West at 79th Street, 10024 New York, NY, USA
[c] Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, 10024 New York, NY, USA

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ABSTRACT

Peloso et al. (2015: PELOSO) published a comprehensive phylogenetic study of the frog family Microhylidae, which resulted in the discovery that several taxa were not monophyletic. To remedy this, a series of nomenclatural changes were proposed (several generic synonymies and two new subfamilies named). A recent study published in this journal by Scherz et al. (2016: SCHERZ), provided a novel phylogeny for the Malagasy subfamily Cophylinae. SCHERZ dispute the analyses and taxonomic conclusions of PELOSO. Their study is, however, based on *substantial* reduction of data from the PELOSO study, limited addition of new data, and different analytical methods. In spite of the fact that their own results are consistent with the taxonomy of PELOSO, SCHERZ reject that conservative taxonomy and suggest the revalidation of *Platypelis* (from the synonymy of *Cophyla*), the revalidation of *Stumpffia* (from the synonymies of *Rhombophryne*), and the creation of at least two new genera (only one named therein). In doing so, SCHERZ accept the recognition of likely paraphyletic taxa, with *Stumpffia* paraphyletic in their parsimony analysis. Herein, we provide a response to several points raised in SCHERZ: (1) we discuss issues with their interpretation (and selective use) of available phylogenetic and phenotypic evidence; (2) and provide a new phylogenetic analysis of all the data in PELOSO and SCHERZ combined. In the new analysis *Stumpffia* is paraphyletic with respect to *Rhombophryne*, whereas *Cophyla* and *Platypelis* are both monophyletic and sister taxa. We provide a case for the use of the taxonomy suggested in PELOSO.

1. Introduction

Microhylidae represent approximately 8.8% of the global frog diversity and are found in almost every tropical landmass on earth. Despite dense sampling and repeated attempts to infer phylogenetic relationships among members of the family (e.g., de Sá et al., 2012; Peloso et al., 2015; van der Meijden et al., 2007), relationships, particularly among the nominal subfamilies, are largely unstable, and several genera and subfamilies are still suspected to be para- or polyphyletic.

Peloso et al. (2015: hereafter PELOSO) performed a sensitivity analyses (sensu Wheeler, 1995) on a variety of combinations of taxa (up to 142 taxa) and genomic data (up to 73 loci) to infer the phylogeny of microhylids. Based on their phylogenetic results, PELOSO reviewed the classification of Microhylidae suggesting several taxonomic updates to generic classification, and also naming two new subfamilies in the process. After PELOSO, Microhylidae was considered to be composed of 13 subfamilies.

1.1. The generic content in Cophylinae

Cophylinae is endemic to Madagascar and is composed of 72 named species (third largest microhylid subfamily), plus an apparent high number of unnamed taxa (Köhler et al., 2010; Perl et al., 2014; Scherz et al., 2016; Wollenberg et al., 2008). The phylogeny of Cophylinae has received considerable attention compared to most other subfamilies (Andreone et al., 2005; Blommers-Schlösser and Blanc, 1993; Scherz et al., 2016; Wollenberg et al., 2008); hence, multiple alternate hypotheses of relationships have been suggested. PELOSO sampled 32 cophyline taxa in their analyses, including six of the seven genera recognized at the time (excepting *Madecassophryne*, for which tissue samples are unavailable). The results in PELOSO corroborated previous suspicions that some cophyline genera are not monophyletic: *Platypelis* (paraphyletic with respect to *Cophyla*), *Stumpffia*, and *Rhombophryne* (with respect to each other). To remedy this, PELOSO suggested,

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* Corresponding author at: Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Avenida Perimetral, 1901, Terra Firme, CEP 66077-530 Belém, Pará, Brazil.

E-mail address: pedropeloso@gmail.com (P.L.V. Peloso).

[1] Present Address.

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among other things: (1) *Platypelis* Boulenger, 1882 should be treated as a synonym of *Cophyla* Boettger, 1880; and (2) *Stumpffia* Boettger, 1881 should be treated as a synonym of *Rhombophryne* Boettger, 1880.

1.2. Scherz et al. (2016)

A recent study published in this journal, by Scherz et al. (2016: hereafter SCHERZ), disputed the data, results and taxonomic conclusions of PELOSO. The principal taxonomic actions of SCHERZ were to: (1) reject the synonymy of *Platypelis* with *Cophyla*, (2) reject the synonymy of *Stumpffia* with *Rhombophryne*, and (3) create a new genus (*Anilany*).

In support of their taxonomic decisions, SCHERZ provided novel phylogenetic analyses (with many added analytical assumptions) of Cophylinae, which also purported to constitute "a re-analysis of the cophyline members of the PELOSO dataset". However, when doing so, SCHERZ inexplicably excluded a large fraction of the PELOSO dataset. 75% of the taxa and 97% of the genetic data from PELOSO were completely discarded without much discussion or justification. Despite the availability of up to 73 loci from the PELOSO study, data for 71 loci were discarded. Only data from the mitochondrial genes *16S ribosomal RNA* (*16S*) and *Cytochrome Oxidase Subunit I* (COI) generated by PELOSO were included by SCHERZ. A substantial amount of data available for outgroup taxa were also ignored—SCHERZ deleted all data for non-Malagasy microhylids.

SCHERZ employed two methods for phylogenetic inference: Bayesian inference (via MrBayes) and parsimony (via TNT)—their implementations based on a two-step procedure (multiple sequence alignment + phylogenetic inference: i.e., similarity-alignment). Nevertheless, SCHERZ largely ignored the results from their own parsimony analysis (which do not support their preferred taxonomy) in favor of the Bayesian topology (which marginally supports their preferred taxonomy).[2] Furthermore, SCHERZ never discussed the fact that their discovery operations (similarity-alignment) are based on conspicuously different theoretical foundations than that of PELOSO (direct optimization: Sankoff, 1975; Wheeler, 1996—tree-alignment). Several authors have discussed the issue of assessing DNA sequence homology, whereas many of them agree that multiple-sequence alignment is best performed with explicit reference to the phylogeny (Felsenstein, 1988, p. 525; Sankoff, 1975; Sankoff and Cedergren, 1983; Wheeler, 1996).

SCHERZ's arguments for the rejection of the taxonomic review of PELOSO are largely based on: (1) sample misidentifications in the dataset of PELOSO; (2) the claim that the changes are unnecessary to attain a monophyletic classification; and (3) that SCHERZ's classification promotes taxonomic stability. We discuss these topics below.

2. A response to Scherz et al. (2016)

SCHERZ "re-analysis" of PELOSO, and the conclusions drawn from it, are questionable. In this section, we address several logical, analytical, and theoretical issues in SCHERZ's study.

2.1. Sample misidentifications and their impact in the proposed taxonomy

SCHERZ provided a series of corrections and updates to identifications of samples used in PELOSO. The authors claim that these identification mistakes "caused erroneous genus-level changes within the Cophylinae", but fail to recognize that most of these changes were not a result of misidentifications. Rather, the changes proposed by PELOSO stem from the fact that paraphyletic taxa have been historically recognized in the subfamily.

SCHERZ thoroughly reviewed the identification of the genetic samples of cophyline taxa used in PELOSO. This was accomplished by direct comparisons with new (published with SCHERZ) and legacy (GenBank) sequences. The potential sources of the identification errors were discussed in SCHERZ (Supplementary Material). SCHERZ's co-author Miguel Vences (MV), through the Technische Universität Braunschweig, supplied many (almost 30%) of the mislabeled samples used in PELOSO. Some of these mislabeled samples included tissues supposedly taken from type specimens of species collected and described by MV (and colleagues). A sample labeled *Rhombophryne matavy* D'Cruze, Köhler, Vences, and Glaw, 2010 in PELOSO, turned out to represent a tissue of the holotype of *Plethodontohyla fonetana* Glaw, Köhler, Bora, Rabibisoa, Ramilijaona, and Vences, 2007, whereas a sample labeled as one of the paratypes of *Rhombophryne mangabensis* Glaw, Köhler, and Vences, 2010, was re-identified as an unnamed species of *Stumpffia*. This, however, does not exempt PELOSO from the responsibility of actually incorporating these samples into their work. Clearly, however, future workers should beware of identifications of frog tissue samples provided by the Technische Universität Braunschweig (including type specimens).

Regardless of the source of the misidentifications, SCHERZ's statement that these mistakes are the main source of erroneous changes to the taxonomy is misleading. Contrary to their claim, the evidence reported by PELOSO was not the sole argument for the taxonomic changes proposed. Fig. 1 shows the cophyline section of the optimal tree from PELOSO with updated and corrected sample IDs (as corrected in SCHERZ)—this reevaluation shows that even with updated sample identifications (assuming the identifications provided in SCHERZ are 100% correct), the taxonomy proposed in PELOSO is monophyletic, whereas the one suggested by SCHERZ is still not—i.e., after sample identification corrections *Cophyla* is still nested within *Platypelis* (rendering the latter paraphyletic), and *Stumpffia* is nested within *Rhombophryne* (rendering the latter paraphyletic).

Finally, we emphasize that there is abundant phylogenetic evidence supporting the taxonomy advocated in PELOSO—this comes not only from the dataset and analyses in PELOSO itself (Fig. 1), but also from previously published papers, many by the authors in SCHERZ (e.g., Perl et al., 2014; Pyron and Wiens, 2011; Rakotoarison et al., 2015; Scantlebury, 2013; Wollenberg et al., 2008). The sample identification errors are, therefore, insufficient to reject the taxonomy proposed in PELOSO.

2.2. To name or not to name?

SCHERZ argued that their taxonomy is formalized based on the *Taxon-Naming Criteria* (TNC) proposed by Vences et al. (2013). However, the criteria were applied inconsistently. When advocating for the TNCs, Vences et al. (2013) established a series of considerations and priorities to be addressed when suggesting name changes in a given group's classification.

Vences et al. (2013) suggested that economy of change should be "a main priority for biological classification". Vences et al. (2013) further considered that monophyly, clade stability, and phenotypic diagnoses should also receive high priority in taxonomic decisions. SCHERZ allegedly follow these priorities, but favor a taxonomy that (i) created a monotypic genus (*Anilany*) of unstable relationships (possibly rendering *Stumpffia* paraphyletic, even according to their own parsimony analyses), and (ii) will likely require further generic changes in the near future—at least two additional new genera are already necessary (one for *Stumpffia tri-*

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[2] Their Bayesian topology does support the monophyly of *Cophyla, Platypelis, Rhombophryne*, and *Stumpffia*, albeit with very low posterior probability.