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**Lumping or splitting in the Cophylinae (Anura: Microhylidae)
and the need for a parsimony of taxonomic changes:
a response to PELOSO et al. (2017)**

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PELOSO et al. (2016) published a phylogenomic study on the anuran family Microhylidae, in which they used sequences from previous work (e.g., VAN DER MEIJDEN et al. 2007, DE SÁ et al. 2012) together with newly generated DNA sequences of seven gene fragments for 142 microhylids, plus genomic data (66 loci) for a selection of 48 taxa. Although the study was mainly focussed on inter-subfamily relationships, they took taxonomic action at genus-level in three subfamilies (Asterophryinae, Cophylinae, and Microhyliinae). In the Madagascar-endemic subfamily Cophylinae, they proposed to synonymise the genus *Platypelis* BOULENGER, 1882 with *Cophyla* BOETTGER, 1880, and *Stumpffia* BOETTGER, 1881 with *Rhombophryne* BOETTGER, 1880, four genera with stable and separate nomenclature for the past 135 years.

SCHERZ et al. (2016) found that several of the terminals in PELOSO et al. (2016) were misidentified, i.e. 10 out of 32 cophylines. After correcting these misidentifications, SCHERZ et al. (2016) tested the PELOSO et al. (2016) paraphyly hypotheses, based on the cophyline portion of the PELOSO et al. (2016) dataset (limited to the 16S rRNA and COI gene fragments) plus 52 newly produced sequences and several already published sequences from previous work by SCHERZ et al. (2016) co-authors for nine additional genes, for an almost complete taxon sampling within the subfamily Cophylinae. Phylogenomic data from PELOSO et al. (2016) were available from just three of the eight cophyline genera, which was considered insufficient to assess relationships within Cophylinae, so they were discarded.

The Bayesian Inference (BI) phylogeny of SCHERZ et al. (2016) showed that (1) *Platypelis* and *Cophyla* are monophyletic genera; (2) one lineage of *Stumpffia* (*S. helenae* VALLAN, 2000) rendered *Stumpffia* paraphyletic with respect to *Rhombophryne*; this species was transferred to the new genus *Anilany* SCHERZ, VENCES, RAKOTOARISON, ANDREONE, KÖHLER, GLAW & CROTTINI, 2016 described in SCHERZ et al. (2016), rendering *Stumpffia* monophyletic; and (3) several undescribed species thought to possibly represent *Stumpffia* based on gross morphology (mostly due to their extremely reduced size but not yet analysed morphologically) probably represent undescribed genera. The Maximum Parsimony (MP) tree of SCHERZ et al. (2016) supported most of these findings, but also placed *S. tridactyla* GUIBÉ, 1975 and an unnamed candidate species (*'Rhombophryne'* sp. Cao7) next to *Anilany*, but with low support. This result disagreed with the BI trees, but was considered artefactual and thus was not discussed in detail. SCHERZ et al. (2016) argued, based on external morphology, osteology, and phylogenetic evidence, founded on the Taxon Naming Criteria (TNCs) of VENCES et al. (2013), that the genera synonymised by PELOSO et al. (2016) were distinct, and advocated for their continued treatment as separate, valid genera.

PELOSO et al. (2017) re-analysed the dataset of SCHERZ et al. (2016) with more extensive outgroup sampling and all of the PELOSO et al. (2016) genetic loci, under MP only. Their phylogeny largely supports the BI tree of SCHERZ et

al. (2016), and is almost identical in gross topology to the MP tree of that study (incongruences are reported below). PELOSO et al. (2017) found 98% jackknife support for the reciprocal monophyly of *Platypelis* and *Cophyla*, contradicting the results of PELOSO et al. (2016) and supporting those of SCHERZ et al. (2016). As with the MP tree of SCHERZ et al. (2016), *Stumpffia tridactyla* was found to cluster with *Anilany*, but now with '*Rhombophryne*' sp. Ca07 nested deep inside *Rhombophryne* and sister to '*Stumpffia*' sp. Ca34. The latter two candidate taxa formed the sister group of *Stumpffia* in the BI tree of SCHERZ et al. (2016), and were placed in a clade with *S. tridactyla* plus *Anilany*, and inside *Rhombophryne*, respectively, in the MP tree of SCHERZ et al. (2016), making it clear that the relationships of these three species (*S. tridactyla*, '*Rhombophryne*' sp. Ca07 and '*Stumpffia*' sp. Ca34) are still unstable. All analyses are consistent in recovering *Rhombophryne* and *Stumpffia* without *S. tridactyla* (and *Anilany*) as monophyletic units (albeit with moderate support), contradicting the general paraphyly found in PELOSO et al. (2016). The relationship of *S. tridactyla* with *Anilany* received very low support (40% jackknife support) and the position of *S. tridactyla* falling outside the *Stumpffia*+*Rhombophryne* clade received extremely low support (18% jackknife support) in PELOSO et al. (2017). Due to the low support for the position of *S. tridactyla* in the MP analyses of PELOSO et al. (2017), and the instability of the position of *S. tridactyla* as evidenced by the disagreement between MP and BI phylogenies in its placement, we consider this poor evidence for the paraphyly of *Stumpffia*, and suggest that it possibly represents an artefact resulting from, for example, long-branch attraction or missing data.

Corrections to claims made in PELOSO et al. (2017)

There are several statements in PELOSO et al. (2017) that we consider misleading or inaccurate, to which we here reply directly:

(1) PELOSO et al. (2017) pointed out that "SCHERZ[16]'s co-author MIGUEL VENCES (MV), through the Technische Universität Braunschweig, supplied many (almost 30%) of the mis-labeled samples used in PELOSO[16]", and warned that "future workers should beware of identifications of frog tissue samples provided by the Technische Universität Braunschweig (including type specimens)." To be precise, MV provided 44% (14 out of 32) of the cophyline samples used in PELOSO et al. (2016). Of these, two samples (14% of the provided samples, or precisely 20% of the ten misidentified samples) were mislabelled. The remaining 80% of the mislabelled samples (eight out of ten) were supplied by co-authors of PELOSO et al. (2016), from collections catalogued and hosted in the American Museum of Natural History.

(2) PELOSO et al. (2017) stated that "SCHERZ[16] inexplicably excluded a large fraction of the PELOSO[16] dataset. 75% of the taxa and 97% of the genetic data from PELOSO[16] were completely discarded without much discussion or justification. Despite the availability of up to 73 loci from the PELOSO[16] study, data for 71 loci were discarded." These

data were indeed discarded from the dataset analysed by SCHERZ et al. (2016). However, the 66 loci obtained with an anchored phylogenomic approach were only available for five samples belonging to three of the eight cophyline genera (*Anodonthyla* – 1 species, *Platypelis* – 2 species, and *Stumpffia* – 2 species) and therefore were not informative for the testing of paraphyly of the genera of interest (additional data of at least one *Cophyla* species and of at least one *Rhombophryne* species would have been necessary); the genomic regions of the data matrix for the other taxa of course contained only missing data. Other (non-cophyline) taxa were discarded because they were irrelevant to the questions pertaining to the reconstruction of the phylogenetic relationships within the Cophylinae. It is true that at least 5 loci obtained through Sanger sequencing and available for all 32 cophylines sampled in PELOSO et al. (2016) could have been analysed as well, but we decided against this due to our a priori doubts on the identity of the analysed samples, and added these for just the 16S and COI genes, which were available for comparative specimens from our own work, allowing direct comparison and verification.

(3) PELOSO et al. (2017) misinterpreted the results of RAKOTOARISON et al. (2015) by referring to the less robust tree (fewer genes, more taxa, barcoding tree for species identification) which indicated paraphyly, rather than to the more robust tree (more genes, fewer taxa, robust phylogeny for phylogenetic conclusions) specifically created in that study to address deeper phylogenetic relationships within and between *Cophyla* and *Platypelis*. A similar misunderstanding led them to repeatedly cite the DNA barcoding tree of PERL et al. (2014) as evidence of paraphyly. That tree is based on a single mitochondrial marker (COI), has low support throughout, and was never published as a hypothesis of deep phylogeny. This and other barcoding trees have the goal of showing which terminals are separated from others by substantial branch lengths, indicating genetic divergence and potential taxonomic distinctness, rather than revealing deep phylogenetic relationships.

(4) PELOSO et al. (2017) claim multiple times "some members of *Stumpffia* and *Rhombophryne* [are] impossible to place in one genus or the other based on morphology alone (therefore the large number of misidentified specimens in museum collections and of sequences in GenBank)." In reality these two genera are in almost all cases easily diagnosable (SCHERZ et al. 2016). It is possible that the authors are intending to refer instead to the trouble diagnosing between *Rhombophryne* and *Plethodontohyla*, a topic that was discussed by SCHERZ et al. (2016), and that remains difficult without osteological data, but that has no bearing on genus-level taxonomy in this subfamily as it pertains to two distantly related but morphologically similar genera.

Phylogeny-taxonomy dissonance in PELOSO et al. (2017) and the principle of parsimony in taxonomic decisions

Despite agreement in many aspects between the favoured phylogeny of PELOSO et al. (2017) and those of SCHERZ et

al. (2016), and numerous disagreements between it and that of PELOSO et al. (2016), PELOSO et al. (2017) continue to advocate for the lumping of genera proposed in PELOSO et al. (2016), and indeed proposed to synonymise *Anilany* and *Stumpffia* with *Rhombophryne* once more. This proposal is largely based on the unusual position of *S. tridactyla*, as the two undescribed species ‘*Stumpffia*’ sp. Ca34 and ‘*Rhombophryne*’ sp. Cao7 have yet to be assigned to a genus and do not constitute paraphyly. This may be artefactual, as the position of *S. tridactyla* is certainly not yet stable. Contrary to MP analyses, BI analyses placed *S. tridactyla* sister to all other *Stumpffia* sensu stricto in SCHERZ et al. (2016). Debates as to whether parsimony or likelihood-based tree reconstruction methods are more appropriate, especially in the analysis of sparse supermatrices (DUNN et al. 2003, FULTON & STROBECK 2006, WOLSAN & SATO 2010, SIMMONS 2012), including considerable philosophical discussions (PADIAL et al. 2014), are still on-going, but are clearly beyond the scope of our present comment. A detailed investigation into the affiliations of *S. tridactyla* is obviously necessary, and is indeed underway, and the erection of additional genera might be warranted.

PELOSO et al. (2017) reanalysed the morphological dataset for the distinction of *Stumpffia* and *Rhombophryne* provided by SCHERZ et al. (2016) with more objective classification criteria. Their non-metric multidimensional scaling (NMDS) analysis supports *Rhombophryne* and *Stumpffia* as having non-overlapping dimension space, but the confidence intervals of the genera do overlap to some degree. In our opinion, this overlap is likely due to the relatively small sample sizes involved in the morphological dataset. Additional taxa would likely diminish the confidence intervals and thus the degree of overlap. We note, however, that these data still support all the analysed species of *Rhombophryne* and *Stumpffia* as being different. This is reflected in the taxonomic history of the species of these two genera; no species of *Stumpffia* or *Rhombophryne* has ever mistakenly been described in the other genus. PELOSO et al. (2017) included *Anilany* in their NMDS analysis, and found it to fall within *Stumpffia*. This is obviously to be expected because the morphological characters in the original analysis by SCHERZ et al. (2016) were chosen to provide distinction between *Rhombophryne* and *Stumpffia*, and did not include those characters in which *Anilany* clearly differs from both these genera (e.g., dilated finger tips, shorter parasphenoid cultriform process, different organisation of the vomer and the neopalatine). However, we note that it is also partly because PELOSO et al. (2017) miscoded the clavicles of *Stumpffia* as curved and those of *Rhombophryne* as straight (the reverse is true), while those of *Anilany* are correctly coded as curved; rectifying this error leads to *A. helenae* falling clearly outside of the minimum convex hull around the sampled *Stumpffia* species (Fig. 1).

In summary, the decision to synonymise *Stumpffia* and *Anilany* with *Rhombophryne* was based on unstable relationships that are currently inconclusive, and the morphospace of those species sampled for morphological characters remain completely distinct, despite overlap of confi-

dence intervals (Fig. 1). Furthermore, treating these taxa as a single genus represents a significant decrease in informativeness, as we discuss below. We therefore formally reject the PELOSO et al. (2017) proposal to synonymise these genera, and resurrect *Stumpffia* and *Anilany* as valid genera.

The argument to retain *Platypelis* as a synonym of *Cophyla* is less understandable. As in SCHERZ et al. (2016) and RAKOTOARISON et al. (2015), and in direct contradiction of PELOSO et al. (2016), PELOSO et al. (2017) found these two genera to be reciprocally monophyletic, and appear to have proposed to re-synonymise them on principle alone. These two taxa have remained unambiguously separate for 135 years, and only one of their combined 19 nominal species has ever been mistakenly described in one genus when it belongs to the other (*Cophyla occultans*). As discussed by SCHERZ et al. (2016), morphological and osteological datasets remain too incomplete to unambiguously say whether or not diagnostic features exist between these two monophyletic groups, but at least provisionally some differences seem to exist, especially at the osteological level (RAKOTOARISON et al. 2012, 2015, SCHERZ et al. 2016). We do not exclude that in the future, once complete osteological and morphological data sets have become available, synonymy of *Platypelis* with *Cophyla* will be warranted; however, in light of the high support for monophyly of each of the two taxa, the existence of some informative osteological characters, and the historical stability of the two names, we also remove *Platypelis* from the synonymy of *Cophyla*.

PELOSO et al. (2016, 2017) advocate for the use of parsimony criteria in the reconstruction of phylogeny. As said before, whether parsimony- or likelihood-based methods are superior for tree-building with supermatrices is a discussion far beyond this reply. However, we feel that another point needs to be made: if parsimony is to be used as a general principle, then it should apply not only to tree reconstruction, but also to taxonomy; that is to say, taxonomic change should be economized (VENCES et al. 2013). This applies at two levels:

(1) We fully agree that in the case of well-supported phylogeny unambiguously supporting paraphyly of a higher taxon, there is a need for changing the taxonomy of the taxa involved. Yet, well-established taxonomies should not be deliberately changed as soon as a new, poorly supported tree indicates paraphyly. Such a procedure is non-parsimonious because multiple future corrections and changes are likely to be needed as the phylogeny stabilizes. We instead argue that minimizing the total number of forth-and-back changes of a taxonomy is a procedure in line with the principle of parsimony, and is important because poorly supported and later reverted taxonomic changes cause confusion in the end-users of taxonomy, e.g., the conservation community that relies on species lists to prioritize their efforts.

(2) When the priority criteria for changing a classification are fulfilled (e.g., well-supported paraphyly), and after taking into account other taxon naming criteria (VENCES et al. 2013), often a taxonomic decision remains to be made between (a) lumping two speciose genera because a clade of unusual members jumps out, and (b) naming a new ge-

nus for that clade of unusual members and retaining the classification of all other taxa. Here the principle of parsimony may be applied again. If other arguments for either decision are weak or inconclusive, then the fewest possible overall taxonomic changes may be preferred (i.e., the fewest species changes from one genus to another). Option (a) requires n_j steps, where n_j is the number of species included in the junior genus, whereas option (b) requires n_n steps, where n_n is the number of species in the phylogenetically separate lineage. Where $n_n < n_j$, parsimony argues for the erection of a new genus – the fewest steps. As n_n approaches n_j , the argument for synonymy increases.

In the case of *Stumpffia* and *Anilany*, it can be argued that the most parsimonious option was to erect a new genus, rather than rename the 15 nominal *Stumpffia* species to *Rhombophryne*. The existence of *Anilany* as a lineage separated from *Stumpffia* had been known for almost a decade (WOLLENBERG et al. 2008), but taxonomic action was only taken once sufficient morphological and molecular support became available (SCHERZ et al. 2016). This argument will hold for the treatment of *S. tridactyla* as well. This is especially true as there is strong morphological support for the distinction of *Rhombophryne* and *Stumpffia*, as

shown in SCHERZ et al. (2016), PELOSO et al. (2017), and the NMDS study herein.

Obviously, there are multiple other criteria besides parsimony to be taken into account when deciding among alternative taxonomic schemes to reach a phylogenetically stable classification. One further important criterion is diagnosability of the resulting taxonomic units (VENCES et al. 2013). Having units identifiable by external morphology is not just a trivial service to field biologists; it also can feed back into the progress of taxonomic knowledge. For example, taxonomic inventories based on field surveys often contain unidentified taxa requiring taxonomic revision, identified to the genus level only (e.g., by using species names such as *Rhombophryne* sp. or *Stumpffia* sp.; see for example RAXWORTHY & NUSSBAUM 1996). Biogeographers, ecologists and taxonomists can use such information to understand that in the site surveyed, unidentified and possibly undescribed species of small, terrestrial, leaf-litter dwelling frogs (*Stumpffia*), or of larger, burrowing frogs (*Rhombophryne*, in the cited study still referred to as *Plethodontohyla*), exist. Much less information is conveyed in a ‘lumping’ classification in which all these findings are subsumed under *Rhombophryne* sp., which would indicate

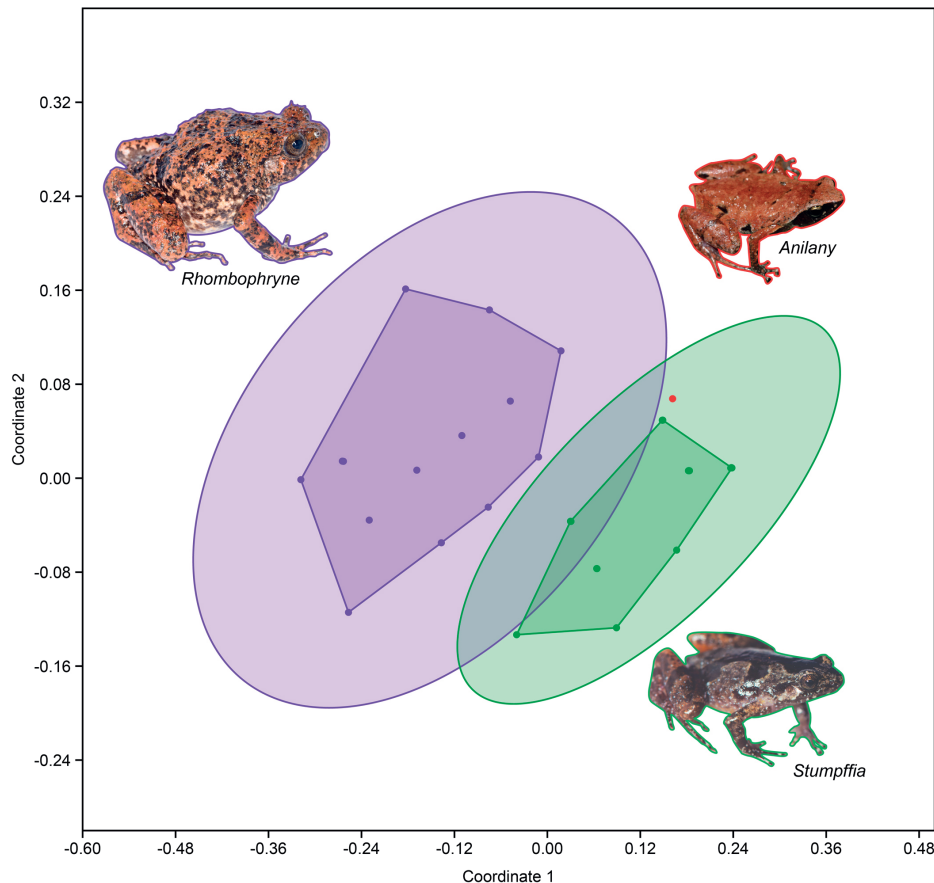


Figure 1. Non-metric multidimensional scaling (NMDS) ordination of *Rhombophryne*, *Stumpffia*, and *Anilany* after correcting the coding of clavicle states of *Stumpffia* and *Rhombophryne*. Otherwise, coding is identical to that used in PELOSO et al. (2017). Original data and methods were presented in SCHERZ et al. (2016).

only that a microhylid frog of either terrestrial or fossorial habits has been recorded.

PELOSO et al. (2017) state that ‘the consensus among authors working on Malagasy fauna is that the phenotypic diagnosis of most cophyline genera is extremely difficult, if at all possible.’ While this is true of some genera (especially *Rhombophryne* and *Plethodontohyla*, and to a lesser degree *Cophyla* and *Platypelis*), it is possible to unambiguously classify all cophyline species into genera using a dichotomous key of morphological characters (as provided by SCHERZ et al. 2016). We therefore advocate for the continued use of *Cophyla*, *Platypelis*, *Stumpffia*, *Anilany*, and *Rhombophryne* as valid genera, and urge other researchers working on the herpetofauna of Madagascar to do likewise (as recently done by e.g. FENG et al. 2017), in order to avoid unnecessary confusion and loss of information. As more taxa are described and more data become available, keys to the subfamily Cophylinae, and our understanding of its supraspecific taxonomy, will need to be continuously updated, but applying changes to a large number of names without adequate or stable evidence is no true progress.

The taxonomic status of the phylogenetically distant miniaturized specimens that superficially resemble *Stumpffia* and *Anilany*, and especially the status of *S. tri-dactyla*, will obviously require further study, as will the placement of *Madecassophryne*, recently rediscovered and genetically documented (RAKOTOARISON et al. in press). A revision based on more extensive molecular and morphological data, currently underway, will lead to an improved classification of cophylines, with the priority of recognizing genus-level units that are (1) well supported as monophyletic groups, (2) morphologically diagnosable, and (3) obtained in a taxonomically parsimonious manner, i.e., by applying as few changes as possible to the established taxonomy to attain stability going forward. Genus-level stability is even more important in light of the extremely rapid rate of alpha-taxonomic progress on this subfamily in recent years (14 species described since 2014), with many species currently in description.

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