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Brygophis coulangesi (Domergue, 1988) (Serpentes: Pseudoxyrhophiidae) and its taxonomic relationship with respect to *Compsophis* (Günther, 1882)

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Abstract

Described in 1988, the monotypic Malagasy snake *Brygophis coulangesi* (Domergue, 1988) has rarely been seen, with only two vouchered specimens in collections and never before included in any molecular phylogenetic studies. Here, using recently collected tissue samples from two *Brygophis coulangesi* from northeastern Madagascar, we sequenced the commonly used barcoding gene cytochrome oxidase subunit I to determine placement of these two *Brygophis* specimens with respect to the similar and more well-known genus *Compsophis* (Günther, 1882). Unsurprisingly, given its previously noted morphological similarity to *Compsophis*, we find that *Brygophis* is deeply nested within *Compsophis* and thus should be referred to as *Compsophis coulangesi* **comb. nov**.

Key words: Gemsnakes, Madagascar, Malagasy, snakes, Compsophis coulangesi comb. nov., Squamata

Introduction

Worldwide, certain snake species are considered rare and hard to find, with just a few voucher specimens, or even the holotype alone representing an entire species, such as *Geophis dunni* Schmidt, 1932 from Nicaragua, *Gongylosoma nicobariensis* (Stoliczka, 1870) from the Nicobar Islands, and *Madagascarophis lolo* Ruane, Burbrink, Randriamahatantsoa, and Raxworthy, 2016 from Madagascar. Comparative materials, (i.e., type series material and/or additional vouchered specimens) provide key information for systematic studies; a lack of specimens for any given species makes it impossible to determine the extent of intraspecific morphological variation, including sexual dimorphism. While limited specimens may not be as problematic for identifying taxa that possess distinct morphological characters (e.g., *Pseudocerastes urarachnoides* Bostanchi, Anderson, Kami, and Papenfuss, 2006), in other cases a lack of specimens may result in erroneous taxonomic assignment of species or even genera. The use of molecular data, which are objective more so than are some morphological characters, may be better used to parse out the validity of taxonomic assignment (e.g., *Lampropeltis extenuata* (Brown, 1890) see Pyron & Burbrink 2009), especially when comparative materials are limited.

Many of the pseudoxyrhophiid snakes of Madagascar fall into the realm of just a few specimens representing an entire species due to a variety of reasons. These include the likely extinct *Pseudoxyrhopus ankafinaensis* Raxworthy and Nussbaum, 1994 known only from a forest on Ankanfina Mountain that has since been deforested (Raxworthy & Nussbaum 1994), the rarely seen *Alluaudina mocquardi* Angel, 1939 from the hard-to-access tsingy karst systems of Ankarana and its preference for karst caves as a habitat, and *Langaha pseudoalluaudi* Domergue, 1988 which bears such a similar and subjective description to *L. alluaudi* that the identification for this species is unclear at best. Similarly, *Brygophis coulangesi* (Domergue, 1988) has been reported as collected in the literature only twice

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before. It was first described as a distinct genus by Domergue (1988) from an individual collected in 1968 from the Fiherenana humid forest in east-central Madagascar (initially as genus *Perinetia* but replaced by *Brygophis* due to *Perinetia* being used previously within Insecta; Domergue & Bour 1989).

Domergue (1988) based this new genus on the specimen having an additional postocular scale and posterior gular scales that were "divergent" when compared to other Malagasy snake genera, namely *Lycodryas*, *Madagascarophis*, and *Compsophis*, but how the gulars differed from any other genera is not further explained in the description. A second individual was later found during a survey in February 1996 from the Anjanaharibe-Sud Chain wet forest in northeastern Madagascar (Andreone & Raxworthy 1998). The description of this additional specimen closely matches the meristics and scale counts of the holotype (see Table 1 in Andreone & Raxworthy 1998). It is worth pointing out that the number of postoculars, deemed important by Domergue (1988) is variable for this second specimen, with three on the left side of the head and two on the right. In their description of the second *B. coulangesi* specimen, the authors note the morphological similarities of *Brygophis* to *Compsophis* (Günther, 1882), a more commonly seen genus composed of seven described taxa which are found across the eastern half of the island in low and mid-elevation humid forest. Other authors have also noted similarities between these two genera (Ziegler *et al*. 1997; Glaw & Vences 2007; Glaw *et al*. 2007; Cadle *et al*. 2022) with respect to scale counts, coloration, and pupil shape (broadly elliptical which is not widespread among Malagasy snakes), suggesting that *Brygophis* and *Compsophis* may be closely related.

TABLE 1. Morphological data from four specimens of *Brygophis coulangesi*; also see Andreone & Raxworthy (1998) for additional details of the measurements and meristics used. Abbreviations are Muséum National d'Histoire Naturelle, France (MNHN), Museo Regionale di Scienze Natural (MRSNR), Mention Zoologie et Biodiversité Animale of the University of Antananarivo (UADBA) and APR (Achille P. Raselimanana field series).

	Holotype MNHN 1977.817	MRSNR 1617	UADBA 73004 (APR 13404)	UADBA 73005 (APR 14116)
Genbank ID	N/A	N/A	PV976157	PV976158
Year Collected	1968	1998	2020	2021
Sex	Female	Male	Female	Female
Total Length	970	420	568	466
Tail Length	230	90	114	85
Total Length/Tail Length	4.22	4.67	4.98	5.48
Snout-vent-length	740	330	454	381
Snout-vent Length/Tail Length	3.22	3.67	3.98	4.48
Supraoculars	1/1	1/1	1/1	1/1
Preoculars	1/1	1/1	1/1	1/1
Primary Temporals	1/1	1/1	1/1	1/1
Secondary Temporals	2/2	2/2	2/2	2/2
Tertiary Temporals	4/4	4/3	4/4	4/4
Scales Surrounding Parietals	12/11	10/9	12/12	12/12
Scales Surrounding the Eye	6/6	6/6	6/6	6/6
Postoculars	3/3	3/2	3/3	3/3
Supralabials	7/7	7/7	7/7	7/7
Supralabials in Contact with the Eye	3rd, 4th	3rd, 4th	3rd,4th	3rd,4th
Infralabials	9/9	10/10	9/9	9/9
Infralabials in Contact with Anterior Inframaxillaries	4	4	4	4
Dorsal Scale Rows (ant/mid/post)	19/19/17	19/19/17	19/19/19	19/19/19
Ventral Scales	204	196	195	197
Subcaudal Scales	72-73	72	74	75
Anal Scale	Single	Single	Single	Single

Here we use a fragment of the barcoding gene cytochrome c oxidase subunit I (CO1) to generate reference sequences and determine the phylogenetic affinity of two specimens of *B. coulangesi* collected in 2020 and 2021 from northeastern Madagascar, near the locality of the individual collected by Andreone & Raxworthy (1998). We infer a gene tree that includes all described species of the likely closely related genus *Compsophis* as well as representatives for all other available Malagasy pseudoxyrhophiid genera and species. We discuss the taxonomic revisions necessary to resolve the placement of this species in the context of our molecular results.

Methods

The two new *Brygophis coulangesi* specimens were collected at the Simpona Camp within the Marojejy National Park (-14.4367, 49.7434). The first specimen (Achille P. Raselimanana field series; APR 13404) was collected on 18 November, 2020 by APR. The snake was active on a branch, descending from the top of a tree and about to cross over a pitfall line in a closed canopy humid forest on a ridge (1335 m) at 20:45 hours. The snake was found ~2m high and was observed using its tail to anchor its body as it extended the anterior part of the body to reach towards a tree covered by moss and lichens. The second specimen (APR 14116) was collected a year later, on 26 November, 2021 in the same general location at ~21:00 hours by APR and FR. The Simpona Camp is ~50 km northeast of the location of the individual collected by Andreone & Raxworthy (1998) at Anjanaharibe-Sud (-14.7667, 49.4333), and ~470 km further north and slightly east from the holotype locality of Fiherenana (-18.4667, 48.4000; Domergue, 1988) (Fig.1).

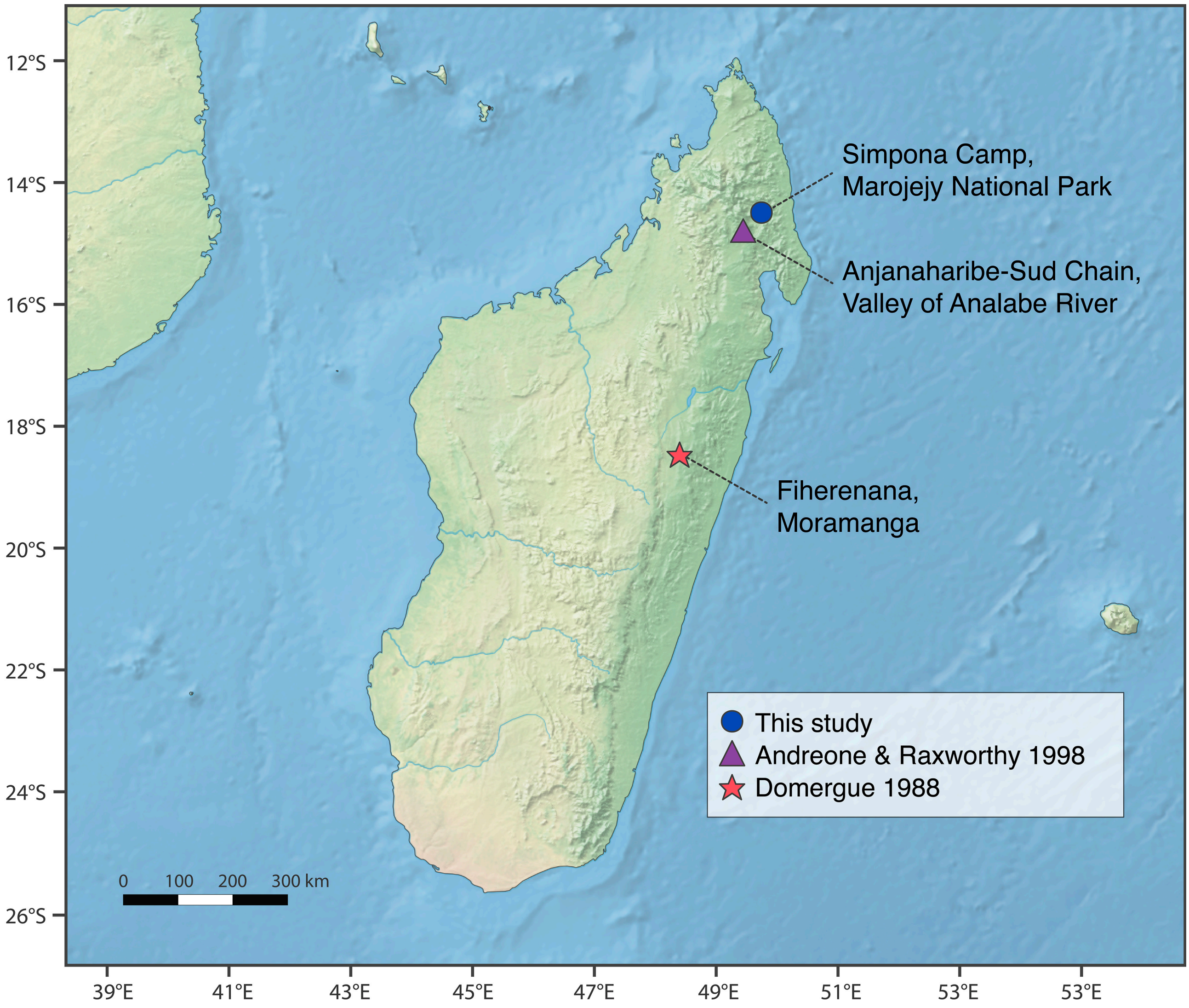

FIGURE 1. Map of Madagascar showing all collection localities for *Brygophis coulangesi*.

FIGURE 2. Photo of the snake *Brygophis coulangesi* in life, as found in situ (UADBA 73004/APR 13404); photo taken by APR.

The two specimens were initially identified in the field as *B. coulangesi* based on morphological characters similar to those of the holotype (Muséum National d'Histoire Naturelle, France; MNHN 1977.817) and the second collected specimen (Museo Regionale di Scienze Natural, Italy; MRSNR 1617) as described in Andreone & Raxworthy (1998), including the dorsal scale number and the pattern/coloration as it is the only reddish-orange colored snake that looks similar to *Compsophis* (Fig. 2; Table 1). The snakes were euthanized on site, fixed with 10% formalin, and deposited at the collection of the Mention Zoologie et Biodiversité Animale of the University of Antananarivo (UADBA) prior to fixation, liver tissue was removed from each individual and stored in EDTA buffer. For comparative purposes with the other two individuals collected prior, morphological characters used in Andreone & Raxworthy (1998) were examined and compiled from these new specimens (Table 1).

Subsamples of the liver tissues from the two *B. coulangesi* specimens were exported to the Field Museum of Natural History (USA) for DNA extraction and sequencing. A fragment of the barcoding gene cytochrome oxidase subunit I (CO1) was chosen to help determine the genetic distinctiveness of *B. coulangesi* and its placement with respect to *Compsophis* and other Malagasy pseudoxyrhophiid genera and species. The DNA was extracted using the Qiagen(R) DNEasy Blood and Tissue Kit, amplified via the polymerase chain reaction for CO1 using standard PCR protocols and universal primers (COI-C02 and COI-C04, Che *et al*. 2012), and Sanger-sequenced in each direction in the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution.

The *B. coulangesi* contigs were assembled and examined by-eye for premature stop codons in Geneious Prime 2025.0.3.These two new sequences were combined with a previously published Sanger-sequenced dataset (Burbrink *et al*. 2019) that included four loci: the aforementioned CO1 barcoding gene and three nuclear loc (oocyte maturation factor mos gene (CMOS), recombination activating 2 gene (RAG-2), and Nav1.4 intron 5 (NAV5) (see Burbrink *et al.* 2019 doi.org/10.5061/dryad.07h0n14 for alignments for each locus in directory "2_Phylogenies_comparative_data", and sample metadata in "6_Sample_Data_Names_Sanger_AHA.xlsx"). Using these published alignments from Burbrink *et al*. (2019), our alignment included 57 individual *Compsophis* sequences representing all seven described species plus seven *Compsophis* lineages identified as potentially new taxa, and these were combined with the additional available Malagasy pseudoxyrhophiid sequences spanning all described genera (535 individuals), plus the outgroup taxa across major snake families (29 individuals).

To determine the taxonomic affinity of the *B. coulangesi* samples with respect to other Malagasy pseudoxyrhophiids, we performed a maximum likelihood (ML) analysis using RAxML-NG 1.0.2 (Kozlov *et al.* 2019). We used Modeltest-NG (Darriba *et al.* 2020) as implemented in RAxML-NG to select the best models for each partitioned locus, as determined by the Akaike information criterion (Akaike 1974). Each protein coding locus was also partitioned by codon position, resulting in 10 total partitions. We ran 100 independent searches for the best tree and 1,000 bootstrap replicates to estimate support values. Using CO1, we calculated the mean pairwise uncorrected genetic distance (p-distances) between *B. coulangesi* and all other *Compsophis* in MEGA 12 (Kumar *et al.* 2024) All files associated with these analyses can be accessed via the Dryad data repository (doi.org/10.5061/dryad.05qfttfg3).

Results

Morphological examination of the new specimens found most characters identical or comparable to the two previously collected individuals, especially with respect to the holotype for *Brygophis coulangesi* (Table 1). For example, the mid-body dorsal scale rows of all four individuals is 19, the numbers of ventral scales are similar to that of the type specimen MRSN R1617 (196 in MRSN R1617, 195 in UADBA 73004 (APR 13404), 197 in UADBA 73005 (APR 14116), and the number of subcaudals similar for all four specimens (from 72–75). The most obvious difference in the new specimens is the lack of reduction in dorsal scale rows from 19 to 17 in the posterior of the body as is found in the two older specimens. Generally, these characters are also quite similar to the morphological diagnostics and/or within the ranges for *Compsophis infralineatus* (Günther, 1882).

For each *B. coulangesi* sample, the fragment of CO1 was successfully sequenced (674 base pairs) and the two newly generated sequences are accessioned on GenBank (APR 13404/UADBA 73004: PV976157; APR 14116/UADBA 73005: PV976158). The final resulting alignment thus included 623 individuals total and 2,476 sites. The best models selected for our partitions were GTR+I+B for COI and JC+B for all nuclear loci with the best tree from our ML analysis resulting in a logLikelihood of -47988.049063. Our concatenated gene tree is similar to the species tree of Burbrink *et al*. (2019) which uses the same taxa, with the exception of our two newly added *B. coulangesi* CO1 samples. All genera are monophyletic with moderate to high support (except for the placement of *Heteroliodon fohy*, which has the same incongruence and low support as seen across gene trees in Burbrink *et al*. 2019) and the concatenated gene tree is largely congruent for the generic relationships across Malagasy pseudoxyrhophiids with respect to the trees presented in Burbrink *et al*. (2019) (see the Dryad Dataset DOI: 10.5061/dryad.05qfttfg3 for the concatenated alignment raw tree file and other intermediate data files). Here we find that *Brygophis coulangesi* renders the genus *Compsophis* paraphyletic. Within *Compsophis*, *B. coulangesi* is the sister taxon to a clade of *Compsophis infralineatus* + two potentially undescribed species of *Compsophis* (both referred to as "*Compsophis* sp. 1" following Burbrink *et al*., 2019) (Fig. 3).

The mean uncorrected p-distance between *B. coulangesi* sequences and all other *Compsophis* = 0.10 and the range between *B. coulangesi* and *Compsophis* species (range: 0.60–0.12) is comparable to that found between other *Compsophis* species or lineages (range: 0.9–0.12) (see the Dryad Dataset DOI: 10.5061/dryad.05qfttfg3 for the complete p-distance matrix).

Discussion

Following the International Code of Zoological Nomenclature, our results indicate that the monotypic genus *Brygophis* should be synonymized with *Compsophis* and thus the sole species of *Brygophis* is henceforth referred to as *Compsophis coulangesi* **comb. nov**. While a gene tree using CO1 is not enough to confidently state more about overall generic relationships or detailed intraspecific relationships, our work suggests that *C. coulangesi* could be considered a valid species but that it does not warrant placement in a monotypic genus and is best described as a species of *Compsophis*, preserving the monophyly of the genus. It is worth noting that the position of *C. coulangesi*

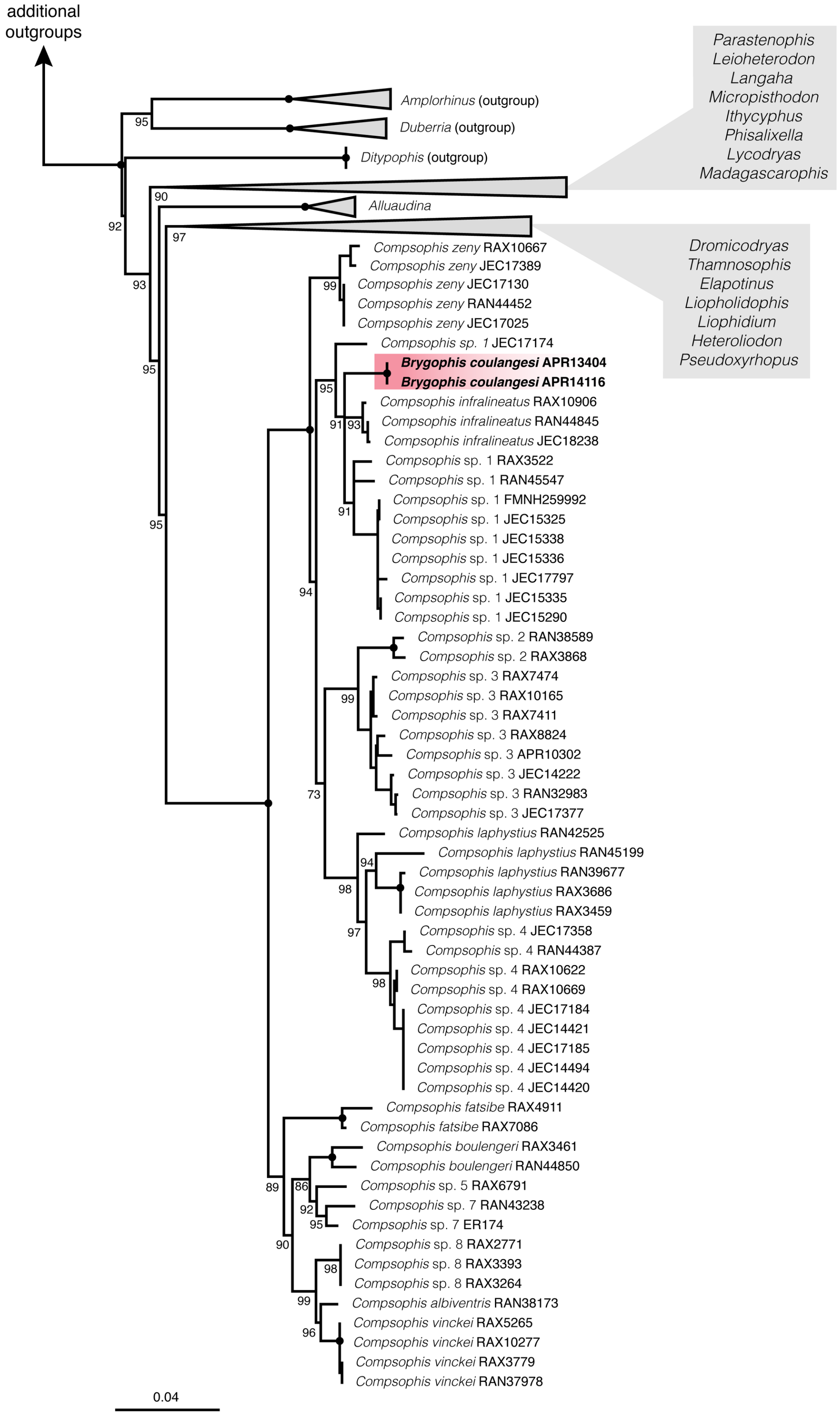

FIGURE 3. The best tree resulting from a maximum likelihood analysis of four concatenated loci, with outgroups pruned for clarity. Two monophyletic clades of Malagasy pseudoxyrhophiids are collapsed with embedded genera listed in grey boxes. Node support values represent 1,000 bootstrap (BS) replicates; support values = 100 represented with black circles, (APR 13404 = UADBA 73004; APR 14116 = UADBA 73005).

within the concatenated gene tree is in a clade with *C. infalineatus*, and Glaw & Vences (2007) specifically mention *C. infralineatus* as a similar species with respect to *C. coulangesi*. A more detailed molecular examination of *Compsophis*, ideally from a genomic-level perspective and with some focus on species delimitation with respect to *C. infralineatus*, *C. coulangesi*, and the many potentially cryptic and undescribed *Compsophis* spp. (e.g., "*Compsophis* sp. 1", Burbrink *et al*. 2019), is certainly warranted. We also note that the gene tree produced here as well as the phylogeny of Burbrink *et al*. (2019) does not support the use of the subgenus *Geodipsas* as suggested by Glaw *et al*. (2007), as the proposed subgenera (*Compsophis* and *Geodipsas*) are not monophyletic in either tree. Our work here only highlights the need for continuing with more detailed revisions for the genus.

Given the historic taxonomic uncertainty of *C. coulangesi*, as expressed by previous authors as far as noting its overall similarity to *Compsophis* (Andreone & Raxworthy 1998; Ziegler *et al*. 1997; Glaw *et al*. 2007; Glaw & Vences 2007; Cadle *et al*. 2022), our results are unsurprising. When comparative material is lacking, naming species or genera may be a disservice to stable taxonomy. Across snakes, it is well known that polymorphic traits such as color pattern or morphological characters such scale counts can vary greatly within a species (Lourdais *et al*. 2004; Olsson *et al*. 2013; Goldenberg *et al*. 2024). Even within the two previously collected specimens of *C. coulangesi*, characters such as the numbers of postoculars and infralabial scales vary (Table 1). In some cases, the presence of sexual dimorphism is another issue when the two sexes are not on hand during the description (e.g., *Langaha* spp.). This natural intraspecific variation of commonly used morphological characters for snakes underscores that datasets that are based on only very limited amounts of morphological material should be approached with caution when making taxonomic decisions.

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Literature cited

Akaike, H. (1974) Markovian representation of stochastic processes and its application to the analysis of autoregressive moving average processes. *Annals of the Institute of Statistical Mathematics*, 26, 363–387.
https://doi.org/10.1007/BF02479833

Andreone, F. & Raxworthy, C.J. (1998) The colubrid snake *Brygophis coulangesi* (Domergue 1988) rediscovered in north-eastern Madagascar. *Tropical Zoology*, 11, 249–257.
https://doi.org/10.1080/03946975.1998.10539368

Angel, F. (1939). Reptiles et Batraciens de Madagascar et de Réunion. Description d`un serpent nouveau du genre *Alluaudina*. *Bulletin Museìum National d'Histoire Naturelle*, 11, 536–538.

Bostanchi, H., Anderson, S., Kami, H. & Papenfuss, T. (2006) A new species of *Pseudocerastes* with elaborate tail ornamentation from Western Iran (Squamata: Viperidae). *Proceedings of the California Academy of Sciences*, 57, 443–450.

Brown, A.E. (1890) On a new genus of Colubridae from Florida. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 42, 199–200.

Burbrink, F.T., Ruane, S., Kuhn, A., Rabibisoa, N., Randriamahatantsoa, B., Raselimanana, A.P., Andrianarimalala, M.S., Cadle, J.E., Lemmon, A.R., Lemmon, E.M. & Nussbaum, R.A., (2019) The origins and diversification of the exceptionally rich gemsnakes (Colubroidea: Lamprophiidae: Pseudoxyrhophiinae) in Madagascar. *Systematic Biology*, 68, 918–936.
https://doi.org/10.1093/sysbio/syz026

Cadle, J.E., Scherz, M.D., Ruane, S., Burbrink, F.T., Raxworthy, C.J. & Glaw, F. (2022) Pseudoxyrhophiidae and Psammophiidae, Colubroid snakes, Bibilava. *In*: Goodman, S.M. (Ed.) *The New Natural History of Madagascar*. *Vol. 2.* Princeton University Press, Princeton, New Jersey, pp. 1525–1531.
https://doi.org/10.2307/j.ctv2ks6tbb.220

Che, J., Chen, H.-M., Yang, J.-X., Jin, J.-Q., Jiang, K., Yuan, Z., Murphy, R. & Zhang, Y.-P. (2012) Universal COI primers for DNA barcoding amphibians. *Molecular Ecology Resources*, 12, 247–258.
https://doi.org/10.1111/j.1755-0998.2011.03090.x

Darriba, D., Posada, D., Kozlov, A.M., Stamatakis, A., Morel, B. & Flouri, T. (2020) ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution*, 37, 291–294.
https://doi.org/10.1093/molbev/msz189

Domergue, C.A. (1988) Notes sur les serpents de la région malgache. 8. Colubridae nouveaux. *Bulletin du Museum National D'histoire Naturelle*, 10, 135–146.
https://doi.org/10.5962/p.287500

Domergue, C.A. & Bour, R. (1989) *Brygophis* nom nouveau pour *Perinetia* Domergue, 1988, préemployé (Reptilia, Colubridae). *Bulletin du Museum National D'histoire Naturelle*, 10, 805–806.
https://doi.org/10.5962/p.287605

Glaw, F. & Vences, M. (2007) *A Field Guide to the Amphibians and Reptiles of Madagascar*. Vences & Glaw Verlag, Köln, 496 pp.

Glaw, F., Nagy, Z.T., & Vences, M. (2007) Phylogenetic relationships and classification of the Malagasy pseudoxyrhophiine snake genera *Geodipsas* and *Compsophis* based on morphological and molecular data. *Zootaxa*, 1517 (1), 53–62.
https://doi.org/10.11646/zootaxa.1517.1.2

Goldenberg, J., Bisschop, K., Bruni, G., Di Nicola, M.R., Banfi, F. & Faraone, F.P. (2024) Melanin-based color variation in response to changing climates in snakes. *Ecology and Evolution*, 14, e11627.
https://doi.org/10.1002/ece3.11627

Kozlov, A.M., Darriba, D., Flouri, T., Morel, B., & Stamatakis, A. (2019), RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics*, 35, 4453–4455.
https://doi.org/10.1093/bioinformatics/btz305

Kumar, S., Stecher, G., Suleski, M., Sanderford, M., Sharma, S. & Tamura, K. (2024), Molecular Evolutionary Genetics Analysis Version 12 for adaptive and green computing. *Molecular Biology and Evolution*, 41, 1–9.
https://doi.org/10.1093/molbev/msae263

Lourdais, O., Shine, R., Bonnet, X., Guillon, M. & Naulleau, G. (2004) Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos*, 104, 551–560.
https://doi.org/10.1111/j.0030-1299.2004.12961.x

Olsson, M., Stuart-Fox, D. & Ballen, C. (2013) Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology*, 24, 529–541.
https://doi.org/10.1016/j.semcdb.2013.04.001

Pyron, R.A. & Burbrink, F.T. (2009) Neogene diversification and taxonomic stability in the snake tribe Lampropeltini (Serpentes: Colubridae). *Molecular Phylogenetics and Evolution*, 52, 524–529.
https://doi.org/10.1016/j.ympev.2009.02.008

Raxworthy, C.J. & Nussbaum, R.A. (1994) A review of the Madagascan snake genera *Pseudoxyrhopus*, *Pararhadinaea*, and *Heteroliodon* (Squamata: Colubridae). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 182, 1–37.

Ruane, S., Burbrink, F.T., Randriamahatantsoa, B. & Raxworthy, C.J. (2016) The cat-eyed snakes of Madagascar: Phylogeny and description of a new species of *Madagascarophis* (Serpentes: Lamprophiidae) from the Tsingy of Ankarana. *Copeia*, 104, 712–721.
https://doi.org/10.1643/CH-15-346

Schmidt, K.P. (1932) Stomach contents of some American coral snakes, with the description of a new species of *Geophis*. *Copeia*, 1932 (1), 6–9.
https://doi.org/10.2307/1437020

Stoliczka, F. (1870) Observations on some Indian and Malayan Amphibia and Reptilia. *Journal Asiatic Society of Bengal*, 39, 134–228.
https://doi.org/10.1080/00222937008696209

Ziegler, T., Vences, M., Glaw, F. & Bohme, W. (1997) Genital morphology and systematics of *Geodipsas* Boulenger, 1896 (Reptilia: Serpentes: Colubridae), with description of a new genus. *Revue Suisse de Zoologie*, 104, 95–114.
https://doi.org/10.5962/bhl.part.79992