Review

How not to describe a species: lessons from a tangle of anacondas (Boidae: *Eunectes* Wagler, 1830)

Wolfgang Wüster[1,*] (iD), Hinrich Kaiser[2,3] (iD), Marinus S. Hoogmoed[4], Luis M. P. Ceríaco[5,6,7] (iD), Lutz Dirksen[8], Christophe Dufresnes[9] (iD), Frank Glaw[10] (iD), Axel Hille[11], Jörn Köhler[12] (iD), Thore Koppetsch[13] (iD), Konstantin D. Milto[14] (iD), Glenn M. Shea[15,16] (iD), David Tarkhnishvili[17] (iD), Scott A. Thomson[18,19] (iD), Miguel Vences[20] (iD) and Wolfgang Böhme[3] (iD)

[1]Molecular Ecology and Evolution at Bangor, School of Environmental and Natural Sciences, Bangor University, Bangor, LL57 2UW, Wales, United Kingdom
[2]Department of Biology, Victor Valley College, 18422 Bear Valley Road, Victorville, CA 92395, United States
[3]Department of Vertebrate Zoology, Sektion Herpetologie, Leibniz-Institut zur Analyse des Biodiversitätswandels, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 127, 53113 Bonn, Germany
[4]Museu Paraense Emilio Goeldi, COZOO, Caixa postal 399, 66017-970 Belém, PA, Brazil
[5]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
[6]Associação BIOPOLIS, Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661, Vairão, Portugal
[7]Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, 20940-040 Rio de Janeiro, RJ, Brazil
[8]Neukirchstraße 37a, 13089 Berlin, Germany
[9]Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE-PSL, Université des Antilles, Paris, France
[10]Zoologische Staatssammlung München (ZSM-SNSB), Münchhausenstraße 21, 81247 München, Germany
[11]Altheider Weg 13, 32805 Horn-Bad Meinberg, Germany
[12]Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany
[13]Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, 0138 Oslo, Norway
[14]Zoological Institute, Russian Academy of Sciences, Universitetskaya emb., 1, 199034, St. Petersburg, Russia
[15]Sydney School of Veterinary Science B01, University of Sydney, NSW 2006, Australia
[16]Australian Museum Research Institute, Australian Museum, 1 William St, Sydney, NSW 2010, Australia
[17]Institute of Ecology, Ilia State University, 3/5 Cholokashvili Avenue, Tbilisi, 0162, Georgia
[18]Centro de Estudos dos Quelônios da Amazônia - CEQUA, 69055-010 Manaus, AM, Brazil
[19]Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0909, Australia
[20]Zoological Institute, Technische Universität Braunschweig, Mendelssohnstraße 4, 38106 Braunschweig, Germany

*Corresponding author. Molecular Ecology and Evolution at Bangor, School of Environmental and Natural Sciences, Bangor University, Bangor, LL57 2UW, Wales, United Kingdom. E-mail: w.wuster@bangor.ac.uk

ABSTRACT

A recent revision of the anacondas (Serpentes: Boidae: *Eunectes*), with the description of a new species of green anaconda, generated extensive publicity, but also provoked considerable controversy due to inadequacies of the evidence used and errors in nomenclature. We here use the case of this problematic publication to: (i) highlight common issues affecting species delimitations, especially an over-reliance on mitochondrial DNA data, and reiterate best practices; (ii) reanalyse the data available for anacondas to establish the true current state of knowledge and to highlight lines of further research; and (iii) analyse the nomenclatural history and status of the genus. While our analysis reveals significant morphological variation in both green and yellow anacondas, denser sampling and an analysis of informative nuclear markers are required for meaningful species delimitation in *Eunectes*. Tracing the history of name-bearing types establishes Trinidad as the type locality for *Boa murina* Linnaeus, 1758 and allows identification of the extant lectotype for the species. Finally, we emphasize the responsibility of both journals and authors to ensure that published taxonomic work meets the burden of evidence required to substantiate new species descriptions and that species are named in compliance with the rules of zoological nomenclature.

Keywords: *Eunectes*; species delimitation; new species; mitochondrial DNA; lectotype; type locality; nomenclature; *International Code of Zoological Nomenclature*

INTRODUCTION

In mid-February 2024, nature enthusiasts around the world were captivated by news of a sensational discovery: a new species of one of the world's largest snakes, the green anaconda, *Eunectes murinus* (Linnaeus, 1758), had been described from northern South America by a multinational author team, led by the well-known anaconda natural historian, conservationist, ecologist, and behaviourist Jesús A. Rivas, and including among its members a number of prominent names in herpetology as well as in documentary television (Rivas *et al.* 2024a). Yet within a month of its publication, the discovery was shown to be deeply flawed: two teams of scientists (Dubois *et al.* 2024, Vásquez-Restrepo *et al.* 2024) provided conclusive evidence that the proposed scientific name of the northern anaconda, '*Eunectes akayima*', was at best a junior synonym of a previously coined name, and Dubois *et al.* provided evidence that this nomen was unavailable for the purposes of zoological nomenclature, the system governing species names, and could not be used at all. These authors critiqued a number of other aspects of the Rivas *et al.* paper in sometimes harshly antagonistic terms.

How could such an important, sensationalized discovery be so problematic that, in a matter of weeks, it became relegated to the archives of science, returning anaconda taxonomy to the *status quo ante* amidst significant acrimony in online discussions? In this paper, we disentangle the 'northern green anaconda' case by providing additional analyses that allow us to identify some common problems found in both the scientific approach (taxonomy) and the proposal of the new scientific name (nomenclature). On that basis, we then generalize and suggest guidelines towards better, more convincing species delimitations and descriptions that lead to widely accepted species with correctly proposed, nomenclaturally available scientific names.

Taxonomy and nomenclature in scientific practice

The science of taxonomy, and its methodology for delimiting species in particular, forms one of the cornerstones of systematic biology, on which biodiversity research and the diverse community of taxonomy users subsequently rely. These delimitations generally result in the publication of species diagnoses and descriptions, a process through which a species is officially named following a set of standard and globally accepted nomenclatural rules. These rules have been elaborated by the International Commission on Zoological Nomenclature (hereafter ICZN) into a social contract known as the *International Code of Zoological Nomenclature* (ICZN 1999; hereafter 'the *Code*'), a set of guidelines in the form of Articles of the *Code* (hereafter abbreviated as 'Art.') to ensure that the taxon-naming process is supported by proper accounting of the resultant scientific names. This document, currently in its 4th edition, is almost universally adhered to by the global zoological community. Taxon names (formally called nomina; Dubois 2000) are fundamental to scientific communication as they provide a direct link/reference to any newly described species, which can then be part of the catalogue of known life on Earth. They link science and society and underpin multiple lines of downstream research, including ecological and biogeographical studies, *in situ* and *ex situ* conservation efforts, and regulatory frameworks. In this regard it is critical that users of taxonomy are able to depend on science done right. Erroneous species delimitations and errors in the scientific process of taxonomy not only affect the fate of overlooked taxa (May 1990) and waste resources on the conservation of erroneously recognized species, but ignorance and complacency in nomenclatural practice lead to instability and difficulties in scientific communication. Consequently, the act of describing and defining species carries a significant burden of responsibility (Hillis 2019) for both authors and publishers.

The potential consequences of unfounded or misleading species delimitations are especially acute in high-profile or iconic taxa that are not only more likely to be targeted for conservation action but also generate public interest. As scientists in the 2020s, we believe that any opportunity for raising the awareness of the contributions of science to society is an asset, and this is one of the reasons why science must be done particularly well and why all scientists owe it to their discipline to highlight and countermand work whose conclusions are not supported by the evidence.

How anacondas became tangled

In their revision of anacondas, Rivas *et al.* (2024a) (hereafter Rivas *et al.*) provided selected molecular data, specifically an expanded mitochondrial DNA (mtDNA) phylogeny, and then pursued taxonomic decisions, including the description of a new species ('*Eunectes akayima*') and the synonymization of two others. Unfortunately, instead of producing a solid basis for their taxonomic decisions, the authors' errors in data interpretation and a lack of nomenclatural acuity produced a publication that raised a remarkable number of taxonomic and nomenclatural issues. Some of these have already been discussed elsewhere (Dubois *et al.* 2024, Vásquez-Restrepo *et al.* 2024), and the speed and the verve with which these critiques have appeared are a measure of how seriously the deficiencies in Rivas *et al.* have been perceived by the scientific community.

Given the iconic nature of anacondas and the publicity accompanying the description of the new species, the publication by Rivas *et al.* provides a teachable moment to review current taxonomic and nomenclatural practices. We here revisit the requirements for credible species delimitation and description, including the responsibilities of authors, journal editors, and publishers, and provide a commentary on commonly observed scientific shortfalls, as exemplified by the work of Rivas *et al.*

A common factor underlying many problematic species descriptions is, in the first instance, an insufficient appreciation of the evidence needed to support species delimitation. Beyond that, there appears to be lack of understanding of the workings of zoological nomenclature, and in particular the requirements of the *Code* (ICZN 1999). The need for reinforcement of these requirements outside the pages of the *Code*, also evidenced by other recent problematic species descriptions in high-profile taxa (Dubois *et al.* 2021, Wüster and Kaiser 2023), is due to the lack of training in basic taxonomic methods in standard university biology curricula and the concomitant decline in the availability of taxonomic expertise and specialist taxonomists (Drew 2011, Britz *et al.* 2020, Coleman and Radulovici 2020, Löbl *et al.* 2023). This problem has recently been exacerbated by an emerging trend of challenging globally established nomenclatural rules and practices over societal and ethical concerns (e.g.

Mosyakin 2022, Ceríaco *et al.* 2023). The Rivas *et al.* paper also showcases a shortcoming of peer-review processes in non-specialized taxonomic journals, in this case the MDPI journal *Diversity*, where Rivas *et al.* were able to publish their manuscript with remarkable speed (32 days from submission to publication for an article of > 10 000 words in length).

We here re-emphasize and elaborate on the proposals made a decade ago by Kaiser *et al.* (2013) and provide guidance on the best practices for species description in the 21ˢᵗ century. We do this by reanalysing the evidence, methods, and interpretations of Rivas *et al.* and by presenting recommendations on how to avoid these unfortunate mistakes.

We wish to highlight from the outset that none of our criticisms of Rivas *et al.* are in any way intended to diminish the standing of the paper's authors in their respective fields. The lead author, Jesús A. Rivas, is a leading authority on anacondas and his work is internationally acclaimed (Rivas 2020, Ineich 2021). The same applies to his co-authors in their respective fields of expertise, which include evolution, ecology, ethology, conservation, toxinology, and systematics. We regret that the necessity to issue a critical appraisal of this particular work has arisen. Nonetheless, we feel that the combination of methodological and epistemological problems of their paper and its potential negative consequences for both science and conservation, as well as the failures of the peer-review process, oblige us to comment on the study's deficiencies and highlight ways of avoiding similar issues in future.

A very brief introduction to anacondas (genus *Eunectes*) and Rivas *et al.* (2024a)

The genus *Eunectes* comprises a small group of large, semiaquatic boid snakes from the tropical and subtropical regions of South America east of the Andes. Due to their large body size, anacondas have become some of the most iconic South American snakes, immortalized by a Hollywood movie with three sequels, and their considerable size combined with an existence largely hidden from human view have fascinated naturalists since the early dawn of natural history as a science. This interest led to a number of early scientific descriptions of anacondas, resulting in multiple taxon names to refer to the different species (see Strimple *et al.* 1997, Dubois *et al.* 2024). During the course of the 19ᵗʰ and 20ᵗʰ centuries many of these older names were synonymized, but since the synonymization of *Eunectes barbouri* Dunn and Conant, 1936 with *E. murinus* (Strimple *et al.* 1997) and the description of *E. beniensis* by Dirksen (2002), the taxonomy of the genus has been stable, with four recognized species: the widespread, large-bodied 'green anaconda' (*E. murinus*), and the smaller-bodied 'yellow anacondas', *Eunectes beniensis* Dirksen, 2002 (Bolivia), *Eunectes deschauenseei* Dunn and Conant, 1936 (Lower Amazon and French Guiana), and *Eunectes notaeus* Cope, 1862 (Paraguay Basin). This was the departure point for Rivas *et al.* and for our analysis.

Rivas *et al.* reconstructed the phylogeny of *Eunectes* using mitochondrial gene sequence analysis. Their results revealed small genetic distances between the three nominal species of yellow anacondas (the *E. notaeus* group), and paraphyly of *E. notaeus* in the mitochondrial gene tree (see also Tarkhnishvili *et al.* 2022). This led Rivas *et al.* to synonymize *E. deschauenseei* and *E. beniensis* with *E. notaeus*. The authors also identified a

relatively deep north/south phylogeographic split within the green anacondas (*E. murinus*), which led them to describe the northern lineage as a new species of green anaconda using the binomen '*Eunectes akayima*'. Despite the limitations imposed by sample availability, their paper certainly represents a significant contribution to our knowledge of genetic structuring and phylogeography among green anacondas, suggesting that there could indeed exist cryptic diversity in the widespread *E. murinus*. However, Rivas *et al.* did not make sufficient time for the usual critical scrutiny and evaluation that befits a complex taxonomic situation. As it turns out, their methodological approach, the genetic results and conclusions, as well as the taxonomic and nomenclatural treatment raise a number of problems we discuss below.

PART I—WHAT WENT WRONG IN RIVAS *ET AL.* (2024A)?

Species concept and delimitation criteria

There is today widespread agreement that species delimitation should be treated as a hypothesis-testing exercise (de Queiroz 1998, Padial *et al.* 2010, Puillandre *et al.* 2012, Miralles *et al.* 2024), where species are defined as independently evolving metapopulation lineages and criteria for species delimitation must be firmly established. The hypothesis that a biological entity constitutes a species, derived from morphological differences or a distinct mtDNA haplotype clade, can then be tested using additional evidence or alternative approaches (Padial *et al.* 2010). Since all species delimitation methods inevitably rely on a certain amount of simplification, Carstens *et al.* (2013) emphasized the need to apply a diversity of delimitation methods and criteria to arrive at robust species delimitations. The clear implication of this is that species delimitation requires in the first instance a clear statement of the species concept being used, a statement of what evidence would cause the authors to either accept or reject the hypothesis that a putative lineage constitutes a separate species, and ideally the use of a range of methods and sources of evidence. Unfortunately, the revision of the anacondas by Rivas *et al.* fulfilled none of these requirements, lacking a clear species hypothesis, eschewing clear delimitation criteria, and relying on insufficient evidence. As a result of this conceptual void, it is difficult to retrace the basis for their taxonomic decisions on the status of putative taxa, and their attempted revision remains largely unconvincing.

The basis of evidence for taxonomic conclusions: mtDNA is not enough

Scientifically, a key problem of Rivas *et al.* is their complete reliance on mtDNA to the exclusion of all other data types. While mtDNA can help reveal historical evolutionary lineages, its clonal, matrilinear mode of inheritance precludes the discovery of introgression and admixture between populations. Moreover, as a result of processes such as introgression or incomplete lineage sorting, mtDNA may follow an evolutionary trajectory that does not reflect the evolutionary history of the associated organismal lineages, a phenomenon variously known as cytonuclear or mitonuclear discordance (Toews and Brelsford 2012, Bonnet *et al.* 2017, Després 2019).

Speciation is usually seen as the point of the diversification process where tokogenetic patterns of genetic exchange between incipient lineages cease and are replaced by divergent evolution (phylogenesis; Hillis 2019). Consequently, controlling for gene flow between nascent species lineages is a fundamental part of the species delimitation process. Integrative species delimitation approaches, where multiple sources of evidence are treated as independent tests of species status (Padial *et al.* 2010), are key to inferring species boundaries. There are numerous examples in the literature where more integrative analyses have shown mtDNA phylogeography to be misleading (Galtier *et al.* 2009), by inflating the number of putative species (Harrington and Burbrink 2022), missing taxa due to complete mtDNA introgression (Babik *et al.* 2005, Dufresnes *et al.* 2019), suggesting ghost lineages (Chan *et al.* 2020, Dufresnes *et al.* 2024), or misrepresenting the nature and position of contact zones between lineages (Dufresnes *et al.* 2019, Burbrink *et al.* 2021, Hillis and Wüster 2021, Marshall *et al.* 2021, Hillis 2022). Therefore, describing new species based solely on mitochondrial divergence is inappropriate and may even be considered scientific malpractice (e.g. Ahrens *et al.* 2021).

Padial *et al.* (2010) and Puillandre *et al.* (2012) provided excellent workflow suggestions whereby distinct mtDNA clades are treated as Primary Species Hypotheses or Candidate Species, which act as hypotheses that can be further tested with additional evidence from, for instance, nuclear genetic markers or morphology (see also Miralles *et al.* 2024). Where independent markers support the mtDNA clades as organismal lineages on independent evolutionary trajectories, these are then upgraded to Confirmed Candidate Species that can then be described, named, and recognized in nomenclature.

Against this background, the reliance by Rivas *et al.* on mtDNA alone for their taxonomic decisions is highly problematic. They justified the splitting of green anacondas based on ostensibly relatively high (> 5%) p-distances across three different, fast-evolving mitochondrial genes (but see comments on mtDNA-based genetic distances below). The authors also described amplifying and sequencing six single-copy nuclear genes but stated that these markers did not yield 'sufficient numbers of variable sites [...] to distinguish lineages' and that they were therefore 'not included in phylogenetic analyses'. However, in their discussion, Rivas *et al.* only mentioned having attempted to use TATA-binding protein (*TBP*) and intron sequence data but gave no details in the results; only a single nuclear locus tree is shown in their supplementary materials. None of their nuclear gene sequences are available on GenBank, making it impossible to verify their claims.

While finding informative single-copy nuclear loci can be challenging, a wide variety of loci potentially suitable for species delimitation in snakes have been identified and used successfully in a number of taxa (e.g. Townsend *et al.* 2008, Anderson and Greenbaum 2012), including at low taxonomic ranks among boids (e.g. Rivera *et al.* 2011, Reynolds *et al.* 2013). Sequences publicly available from GenBank do in fact show low-level variation (1–3 variable base pair positions) in green anacondas in the nuclear genes neurotrophin 3 (*NT3*), recombination-activating gene 1 (*RAG1*), and brain-derived neurotrophic factor (*BDNF*).

Very low levels of sequence divergence in conserved nuclear genes are of little help in phylogenetic reconstruction. However,

since the main aim of species delimitation is to determine where genetic exchange between lineages ceases, and not phylogenetic tree construction, low divergence in individual loci does not undermine their usefulness. Even highly conserved loci with only a handful of variable sites can provide valuable information on allele sharing and hence represent a clear independent test of mtDNA-defined Candidate Species (e.g. Ratnarathorn *et al.* 2023). Moreover, a set of nuclear haplotype networks or analyses seeking to determine overall patterns of genomic variation in multilocus datasets, such as *STRUCTURE* (Pritchard *et al.* 2000) and analogous methods, or *POFAD* (Joly and Bruneau 2006), can generate highly informative overall summaries of genetic distinctiveness from such data and detect ongoing genetic exchange between lineages (Zancolli *et al.* 2016).

An alternative approach would have been testing for congruence between morphology and mtDNA, where morphology serves as a proxy for overall genomic variation. Species status for different mitochondrial lineages would predict a clear break in phenotypic similarity coinciding with mitochondrial clade membership. Rivas *et al.* relied on tabulated morphological data taken from Dirksen (2002), but without adding morphological data from the specimens they sampled for their molecular data or any formal analysis of existing data. Instead of producing their own evidence to allow an informed decision, Rivas *et al.* appear to have avoided specimen work and declared, based on a very superficial scanning of other researchers' data, that *E. murinus* and the new species were 'truly cryptic, and there is no way to tell from morphological data which species the type belongs to'. Careful reanalysis of the publicly available data of Tarkhnishvili *et al.* (2022) would have constituted an appropriate test for their mitochondrial Candidate Species (*sensu* Padial *et al.* 2010). A summary dismissal of morphology based on published, tabulated data without further analysis avoids a key aspect of taxonomic science (i.e., specimen work) and is likely to miss important evidence (see below).

Taxonomic decisions based on an overreliance on mtDNA and a lack of critical analysis of additional data are a common and major problem in herpetology (Hillis 2019, Dufresnes and Jablonski 2022). As shown by the example of Rivas *et al.*, the lack of independent evidence for species limits has major consequences. In particular, the close geographic proximity of mtDNA haplotypes of the northern and southern clades of green anacondas in the Guianas could be due to sympatry or narrow parapatry between two separate species, or alternatively it could reflect the presence of two older mtDNA haplotype clades within a single organismal lineage (Irwin 2002, Schield *et al.* 2015, Harrington and Burbrink 2022). Without independent evidence from nuclear loci or rigorously analysed morphological data, it is impossible to distinguish between these hypotheses, yet they fundamentally affect the taxonomic conclusions.

Even with informative nuclear DNA data, any inference of species limits provided by Rivas *et al.* would be further impeded by their very limited geographical sampling of green anacondas throughout the Amazon Basin. In particular, the low sampling density in or around likely contact zones between the mtDNA clades (e.g. in the Guianas) would preclude any accurate assessment of the nature of contact zones (e.g. Marshall *et al.* 2021). While the low sampling density is understandable in such a large and logistically difficult region, this cannot lower the threshold

of evidence required for convincing species delimitation (Hillis 2019). Consequently, the data presented by Rivas *et al.* cannot support their taxonomic conclusions on multiple levels.

In summary, the case of the 'northern anaconda' demonstrates the need to critically test species boundaries, particularly when these are first hypothesized based only on a mtDNA phylogeography.

Genetic distances and flawed divergence time estimates

Rivas *et al.* relied heavily on pairwise genetic distances and divergence time estimates to draw taxonomic conclusions and develop biogeographic scenarios. In this context, it is important to re-iterate that genetic divergences by themselves are not taxonomic characters. The statement for green anacondas that a 'high level of genetic divergence and geographic separation justifies the recognition of [...] a distinct species' is therefore misleading from a taxonomic perspective. It is also insufficient from a speciation perspective. Genomic divergence increases roughly proportionally with time, eventually leading to an accumulation of mutations that then triggers postzygotic reproductive incompatibility (RI). Overall genomic divergence thus offers an uncontroversial indicator for the completion of speciation ('the mass of genes' model for the build-up of RI in allopatric speciation; Dufresnes *et al.* 2021). In the absence of cytonuclear discordance (see above), mitochondrial divergence is roughly correlated with overall genomic divergence, and both increase with time. Hence, the build-up of RI and consequently the probability of speciation increase with increasing sequence divergence in mitochondrial genes. However, it is essential to understand that in most taxa, a wide range of divergences can be consistent with both conspecificity and separate species status. To re-evaluate the taxonomic status of candidate lineages in anacondas, we here re-examine their genetic distances alongside their divergence times.

The genetic divergences in anacondas revealed by Rivas *et al.* are unexceptional. The three highly variable mitochondrial protein-coding genes (cytochrome *b*: *Cytb*; NADH-Dehydrogenase subunit 2, *ND2*; and NADH-Dehydrogenase subunit 4, *ND4*) analysed together (concatenated alignment) yielded uncorrected pairwise distances of 5.5% between the two main green anaconda clades and 0.7–2.4% between the three yellow anaconda clades. For *Cytb*, a gene that is often used to assess genetic divergences in snakes and other vertebrate groups, distances were reported as 5.2% between the two main green anaconda clades, and 0.7–2.6% between the three yellow anaconda clades.

The *Cytb* divergence level of 5.2% between northern and southern green anacondas is compatible with both conspecificity and separate species status. While some clearly distinct or even sympatric snake species differ by < 5% in their *Cytb* sequences, such as *Naja nigricollis* Reinhardt, 1843, *N. ashei* Wüster and Broadley, 2007, and *N. mossambica* Peters, 1854 (Wüster and Broadley 2007), considerably higher divergences are found among demonstrably conspecific lineages. For instance, *Pantherophis emoryi slowinskii* (Burbrink, 2002) and *P. emoryi emoryi* (Baird and Girard, 1853) differ by nearly 7.5% (Marshall *et al.* 2021), and the Central and the Mississippi and Eastern lineages of *Lampropeltis getula* (Linnaeus, 1766) of Pyron and Burbrink (2009), shown to be conspecific by Harrington and Burbrink (2022), differ by 5.8–6.0%. In conclusion, while a *Cytb*

divergence of 5% among green anacondas may indeed indicate species-level divergence, that is by no means a foregone conclusion.

Because genetic distances at individual mitochondrial loci can be affected by variation in substitution rates between loci and lineages, divergence times may provide a more reliable measure of divergence and of the probability of speciation than simple genetic distances in a single gene. However, divergence times are inherently difficult to infer from molecular data due to possible analytical artefacts and a scarcity of reliable calibration points. Rivas *et al.* used their mitochondrial data in combination with a set of relatively ancient fossil and biogeographic calibrations. In three of their four calibration schemes, the most informative calibration was that of the root, in this case the split between Sanziniidae and Boidae, for which they applied minimum and maximum bounds of 80 and 145 Mya, respectively. Their fourth calibration scheme used maximum bounds for three fossil calibrations at 64–113 Mya. This analytical strategy is problematic in two respects: (1) at such ancient divergences, the hyper-variable mitochondrial protein-coding genes Rivas *et al.* used (in particular third codon positions) are likely to be largely saturated, leading to overestimates of divergence times among the distal nodes of the tree relative to more basal nodes (Lukoschek *et al.* 2012, Near *et al.* 2012); (2) the biogeographic root calibration age presented by Rivas *et al.* is higher than the vast majority of published timetree estimates for the Sanziniidae-Boidae split (e.g. 61 Mya—Crottini *et al.* 2012, 64 Mya with a 95% confidence interval (CI) of 40.8–86.3 Mya according to www.timetree.org—Kumar *et al.* 2022; accessed on 29 Feb 2024).

Consequently, the timetree of Rivas *et al.* suggests older ages for many nodes than shown by most other estimates, including those done with nuclear genes and a large number of fossil calibration points. For instance, Rivas *et al.* estimated the *Epicrates-Eunectes* split at 35–46 Mya, which, as the authors discussed themselves, is much older than other published estimates (27.8 Mya with 95% CI 15.8–37.3 Mya according to www.timetree.org). This suggests that they may also have overestimated lineage divergence times for anacondas (e.g. the split between yellow and green species at 20–26 Mya). Equally, these results call into question the biogeographical scenarios invoked by Rivas *et al.*, which rely on older geological events such as the formation of the Vaupés Arch (Winemiller and Willis 2011).

Population genetics and paraphyletic species

Three further aspects of molecular differentiation in anacondas warrant comment. The first is the use by Rivas *et al.* of the term and the concept of paraphyly in a taxonomic context. Besides their erroneous use of the term 'paraphyletic clade' (a clade is monophyletic by definition), the main concern is their statement that recognizing *beniensis* and *deschauenseei* as subspecies of *E. notaeus* 'would make *E. notaeus* a paraphyletic species, which is not desirable in modern taxonomy'. This statement is problematic because (1) on an operational level, it confuses gene tree and species tree: just because a mitochondrial tree suggests paraphyly, it does not necessarily follow that the same is true for the underlying evolutionary relationships among lineages, especially considering the possibility of phenomena such as introgression or incomplete lineage sorting (e.g. Marshall *et al.* 2021); (2) on a conceptual level, there is no need at all for

a species to be monophyletic: a species is a segment of a population lineage that does not equal a clade (de Queiroz 1998, Hillis 2022, Vences *et al.* 2024); and (3) recognition of a subspecies cannot make a species paraphyletic, only potentially one of the other subspecies of that species.

A second aspect is the need to consider biological phenomena that could explain the claimed lack of nuclear gene divergence among reasonably diverged mitochondrial lineages. Unfortunately, in the absence of access to their data on GenBank, this claim cannot be verified. The only information on nuclear loci provided by Rivas *et al.* is the tree for the TBT gene in their figure S2. Two samples, from Trinidad and the Venezuelan llanos, appear to display divergent haplotypes. However, notably, only two of the green anaconda samples in that tree are from the southern clade, making it difficult to interpret this result.

Taking the claim of little or no divergence in the nuclear loci at face value, one plausible explanation is simply that the genes are too slow-evolving to show any divergence in this taxon. While not impossible, this seems unlikely for all of them since several of the mentioned genes have proven useful in other species-level studies in snakes (e.g. *CMOS*—Ratnarathorn *et al.* 2023, melanocortin-1 receptor, *NT3*, *RAG1*—Jablonski *et al.* 2023, *BDNF*, *NT3*, ornithine decarboxylase, *RAG1*—Doniol-Valcroze 2021). Another explanation could be an overall large effective population size and insufficient divergence time for population structure to be reflected in nuclear allele sorting. Finally, male-biased dispersal in anacondas could maintain admixture and gene flow in nuclear genes while allowing for the emergence of mitochondrial phylogeographic structure (Irwin 2002). Male-biased dispersal has been documented for large boids, including anacondas (Rivera *et al.* 2006, Smaniotto *et al.* 2020). Given the presence of large male breeding aggregations in green anacondas (Rivas and Burghardt 2001), the low dispersal capacity of female individuals and the reported male-biased dispersal for congeneric species, male-biased dispersal might also affect the nuclear genetic variation in green anacondas, potentially leading to multiple mitochondrial lineages coexisting within a single organismal lineage (Irwin 2002). With the increased implementation of multilocus approaches in phylogeography, such situations of cytonuclear discordance are now being unveiled as more common than previously anticipated (Harrington and Burbrink 2022, Dufresnes *et al.* 2024).

The third population genetics aspect is the potential presence of a hybrid zone. Although Rivas *et al.* stated that their two species of green anacondas were geographically distinct, both mitochondrial lineages appear to occur together in at least one location on the northeastern coast of South America. This points to the existence of a contact or hybrid zone between the two mitochondrial lineages, which must be investigated in depth to assess the amount of admixture between them, ideally using a population genomics approach, and thereby to test their status as distinct species.

Data management: keeping the data F.A.I.R.

In many fields of science, scientific findings have a relatively short half-life and are quickly superseded by new studies using more advanced methods and/or larger datasets. This can rapidly turn the underlying raw data into almost a 'niche interest', most relevant to historians of science or for verification of the accuracy of the experimental results. In contrast, taxonomy and nomenclature are cumulative disciplines, where an 18th century study can be as relevant as one from the previous year. Due to the permanence of taxonomic decisions in the context of nomenclature, there is an enduring need to know which specimens were examined, which methods were used, and which data were generated by our predecessors to derive their taxonomic decisions and the resultant nomenclature. This reality is very particular to taxonomic studies, but almost 'exotic' to other sciences, where a publication more than a decade old might be considered outdated and irrelevant (Arbesman 2012, Davis 2013). Therefore, making taxonomic data permanently available using the F.A.I.R principles of findability, accessibility, interoperability, and reusability constitutes a crucial best practice (Miralles *et al.* 2020). This includes, for instance, making raw morphometric measurements and meristic counts for each specimen, as well as all DNA sequences, publicly accessible at the time of publication.

In the case of Rivas *et al.*, the raw data underlying the authors' conclusions are mostly not available to the scientific community: (1) raw morphological data are only made available for a small subset of specimens, for which not even the sex is stated; (2) sequences of nuclear markers were not published in GenBank, despite the authors' claim that they were studied and revealed no differences between lineages, and despite the presentation of a gene tree for one of the six loci (their figure S2). This makes it impossible to verify the conclusions of Rivas *et al.* or re-interpret their data, and leaves the authors open to accusations of having excluded data inconsistent with their preferred narrative (Kok 2023). Finally, apart from being poor practice, withholding these data represents a lost resource for science more widely. Nuclear loci are almost invariably badly underrepresented in databases compared to mitochondrial genes (see Zaher *et al.* 2019: table S3), so the nuclear sequences generated by Rivas *et al.* would be useful to a wider user community; (3) those sequences the authors did deposit in GenBank lack precise locality data. In their supporting information, table S1, Rivas *et al.* only provided general country- or state-level information for each sample, even though they mapped these localities more precisely in their figure 5. Re-analysis and verification of lineage distribution with these data is thus impossible, as is combining their data with additional future sequences.

Nomenclature: the consequences of not following the *Code*

A key facet of the process of species description is the allocation of scientific names to the taxa delimited during the taxonomic process. For animals, the *Code* presents a set of rules on how names should be attached to biological entities. The rules are intended to ensure a universal, stable, and unambiguous system of biodiversity labelling to facilitate information retrieval and communication.

One of the first steps required to properly allocate nomina to newly defined taxa is a thorough review of the existing literature to identify any older available taxon names, perhaps in the synonymy of another taxon, that might be applicable and should be given to a proposed new taxon. As a perfect example of the historical and continuous nature of natural history studies, our review of anaconda nomenclature (see below) needs to extend back in time to what has been defined as the founding event of

nomenclatural availability for animals, the publication in 1758 of the 10th edition of Carolus Linnaeus's *Systema Naturae* (Linnaeus 1758), as well as even earlier literature, when pre-Linnaean works are cited as sources of data for defining Linnaean-era nomina. As decreed by the Principle of Priority of the *Code*, the correct scientific name that must be applied to a taxon is the oldest available Linnaean or post-Linnaean name. Due to previous taxonomic interpretations (using different methods, concepts, data, etc.), such an available nomen may have been relegated to the synonymy of another taxon in the past, but synonymy does not affect availability. If new data lead to a new taxonomic interpretation, creation of a new nomen is inappropriate if a synonym exists for the taxon in question; the older available nomen must then be used.

The assignment of a nomen to a taxon is determined and safeguarded by the assignment of a name-bearing type specimen (or *onymophoront sensu* Dubois 2005). The one or more name-bearing types, known as syntypes if more than one specimen was used or implied when a nomen was proposed by the author(s) in the original description, are the crucial specimens to which the nomen is anchored. Where a nomen is based on an illustration, the type is deemed to be the specimen used for that illustration, not the illustration itself (Art. 72.5.6). In any taxonomic treatment, data from name-bearing types are therefore a key component: whatever the affinities of the type turn out to be, the nomen follows that specimen. This means that the authors of any study comparing newly defined or redefined taxa must examine the information from type specimens, ideally first-hand (Denzer and Kaiser 2023), to determine unequivocally to which proposed taxon a type belongs. If an existing nomen is the oldest one available, even for a newly delimited taxon, then it becomes the valid scientific name for that taxon. Other subsequently coined taxon names, whose type specimens are members of the same taxon, become synonyms of the older nomen. It is only if type specimen examination and a thorough review of the literature reveal that no existing available names can be linked to a redefined taxon that an entirely new nomen should be coined for this entity.

Naming a new species needs to follow the rules and steps prescribed in the *Code*. Rivas *et al.* did not follow several of these provisions, which led to the outcome that the name of their new species, '*Eunectes akayima*', is at best a junior synonym of older nomina and, in reality, as a *nomen nudum*, unavailable for the purposes of zoological nomenclature (Dubois *et al.* 2024).

Ignored synonyms

One of the first nomenclatural issues affecting the Rivas *et al.* paper is their lack of an appropriate and comprehensive nomenclatural review. In their response to Rivas *et al.*, Dubois *et al.* (2024) (hereafter Dubois *et al.*) presented such a review of all available scientific names with relevance to taxonomic decisions among green anacondas, with a total of six potentially applicable available names. Such nomenclatural reviews are fundamental in any revision and should have been performed by Rivas *et al.* Instead, those authors did not even mention the existing available nomina *Boa scytale* Linnaeus, 1758, *Boa gigas* Latreille in Sonnini and Latreille, 1801, *Boa aboma* Daudin, 1803, *Boa anacondo* Daudin, 1803, *Boa aquatica* Wied-Neuwied, 1823, and *Eunectes barbouri* Dunn and Conant, 1936, and omitted any

consideration of whether any of these older binomina might apply to their putative new taxon. This caused Rivas *et al.* to propose a new scientific name for a taxon for which older nomina were in fact available.

Availability of the name 'akayima'

A complicated question with respect to the new taxon named by Rivas *et al.* is the nomenclatural availability of their newly proposed name. Availability is defined in Chapter 4 of the *Code*, in which articles define the criteria to make a name nomenclaturally available. Dubois *et al.* dissected the issues surrounding the name '*akayima*' at some length. Here we summarize their points and comment where appropriate.

The very first of the *Code's* criteria for taxonomic decisions is whether a work is actually published (Arts. 7–9). In papers published in an online-only journal, specific strictures have to be observed to ensure a species name is published in compliance with the *Code* (ICZN 2012). One firm requirement is the immutability of the publication where a nomen is introduced: it must have a fixed content and layout (Art. 8.1.3.2). Dubois *et al.* noted, as we did, that the online version of Rivas *et al.* was updated on numerous occasions after its first appearance. Thus, in violation of the *Code*, both content and layout have been in flux and it is not certain whether or when a final, definitive version will be produced. From a nomenclatural perspective, all versions that precede a final version are deemed preliminary and not considered published for the purposes of zoological nomenclature. As pointed out by the Linz ZooCode Committee (Dubois *et al.* 2022a, b), the inability to clearly identify when an electronically published article has reached the definitive version is problematic.

As long as the issue of the final version has not been clarified, it is not possible to state unequivocally when or whether the paper by Rivas *et al.* has actually met the requirements of Art. 8.1.3.2. This brings up a second important point: the date of publication. Under Art. 21.1 the date of publication should be the date shown in the publication itself, unless this is determined to be in error. As per Dubois *et al.*, the date of publication claimed on the publisher's website and in the pdf files of all published versions is 16 February 2024, but this cannot be correct since additional, edited versions appeared until at least March 2024. Therefore, the actual date is not yet known and must be determined once the publication finally meets the requirements of Art. 8 and is not excluded by Art. 9. At present, following Art. 21 of the *Code*, the corrected date of publication would be 31 March 2024. Clearly, there are problems with the *Code's* rules on electronic publication. We join Dubois *et al.* (2022a) in urging the ICZN to consider amendments that address the issue of identifying the final online version and final date of publication.

An additional concern is that the type of document downloadable from the publisher is a PDF/A-2 document instead of the currently preferred standard of PDF/A-1. The difference is subtle but, in essence, a PDF/A-2 can be edited by anyone with Adobe Acrobat Pro whereas the more recent PDF/A-1 cannot be edited by just anyone. We would therefore recommend to the ICZN that they clearly state which type of documents can be considered as published for the purposes of nomenclature, and that for online publications the industry gold standard of PDF/A-1 is the only acceptable format. This does not impact

the availability of '*Eunectes akayima*' but is a noteworthy point for further development of the *Code*.

In practical terms, the most pressing nomenclatural issue of the Rivas *et al.* species description is not the mode of publication but whether the new nomen even meets the requirements of Art. 13.1 of the *Code*, which states that a new name must 'be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon' (Art. 13.1.1). In most species descriptions authors rely on morphological diagnoses to meet the provisions of Art. 13.1, but molecular diagnoses are becoming more common (Renner 2016, Rheindt *et al.* 2023). Although Vázquez-Restrepo *et al.* (2024) considered the description by Rivas *et al.* to meet the requirements of Art. 13.1, we agree with Dubois *et al.* that simply stating genetic distances as grounds for separating *E. murinus* into two species, as done by Rivas *et al.*, does not meet the requirements of Art. 13.1. Even though their tables 4 and 6 present a series of morphological characters, along with definitions of some character states, there are no differences between their new species and *E. murinus* in any of the characters listed and, moreover, Rivas *et al.* explicitly stated that the two species were 'truly cryptic' and that 'the northern and southern clades are indistinguishable morphologically'. Rivas *et al.* also did not provide a *Code*-compliant molecular diagnosis, which should be both state-specific and contrastive (Rheindt *et al.* 2023) and needs to state 'in words characters that are purported to differentiate the taxon' (Art. 13.1.1). Rivas *et al.* only described levels and times of divergence between the populations, and therefore did not use words to describe characters. Molecular divergence levels alone do not meet the conditions of Art. 13.1.1. Because Rivas *et al.* did not refer to any differences published elsewhere, they also did not meet Art. 13.1.2. Consequently, the name '*Eunectes akayima*' Rivas *et al.* 2024a is objectively a *nomen nudum* and hence unavailable under Arts. 13.1.1 and 13.1.2 of the *Code*.

Finally, we agree with Dubois *et al.* that the designation of specimen MPEG 27428 as a lectotype of *Boa murina* Linnaeus, 1758 by Rivas *et al.* is invalid, since the specimen is not part of the original series seen or referred to by Linnaeus in his original description (Art. 74.1).

Politics and the Code

The dominance of scientific names coined by 'Western' scientists and their associated cultural baggage have recently become a topic of much discussion. Proposals including the replacement of current names with pre-existing indigenous names (Gillman and Wright 2020) or even the wholesale renaming of all eponymous nomina (Guedes *et al.* 2023) have generated considerable debate, with substantial opposition from many practising taxonomists (Palma and Heath 2021, Ceríaco *et al.* 2023, Pethiyagoda 2023, Jablonski and Dufresnes 2024, Jiménez-Mejías *et al.* 2024). Rivas *et al.* provided another example of such a mingle of politics and science. With a declared political motive, the authors affirmed that they deliberately ignored the letter of the *Code*'s Principle of Priority and considered the use of the name '*akayima*' as having priority over other names coined by what they called 'Western science'. In their own words: 'the word "*akayima*" has been indigenously used to designate this species for at least hundreds (and perhaps thousands) of years

before the use of any other synonyms. […] This is admittedly an unorthodox position regarding the International Code of Zoological Nomenclature, which prefers the names that have been published in Western science as 'valid'. However, it is well due time that Western science starts recognizing the ancestral knowledge and cultural legacy of non-Westernized society. If we respect and honor the culture of these original nations, accepting *akayima* as the senior synonym is unavoidable'.

This last statement is not only 'unorthodox' in respect to the *Code* but has been shown to be misguided: several authors (e.g. Palma and Heath 2021) have already explained the issues related to confusing local indigenous names with scientific names. We reiterate that scientific names represent explicit hypotheses, published as such in the scientific literature, in contrast to the utilitarian use of vernacular names as labels for categories of life useful or apparent to the users of the relevant language.

To be available, and hence subject to the Principle of Priority, a scientific name must be published in accordance with Arts. 8 and 11. Vernacular names may have a long history of usage, but they have not been published in accordance with the *Code*, they have not been used as valid scientific names in their initial publications (Art. 11.5), and they have not been published in unambiguous combination with a valid genus name (Art. 11.9). The indigenous word *akayima* is also a vernacular name that was never published in accordance with the *Code* and is therefore not subject to the Principle of Priority, the claims of Rivas *et al.* notwithstanding. If it were available, it would be a junior synonym of any conspecific name published prior to 2024. Somewhat ironically, as noted by Dubois *et al.*, one of the 'Western' names casually ignored by Rivas *et al.* is an indigenous name itself: *Boa aboma*, described by Daudin (1803), who adopted the indigenous Surinamese name reported by Stedman (1796).

PART II. FIXING THE ANACONDAS

Where are we now and where do we need to go?

The attempted revision of the anacondas by Rivas *et al.* has left in its wake a situation of uncertainty over the taxonomy and the nomenclature of the green anaconda complex. In the following paragraphs, we reassess and reanalyse the currently available morphological and molecular genetic data on anacondas to better understand the extent and limits of our current knowledge of the systematics of this iconic genus. We also resolve remaining questions on the nomenclature of the green anacondas, and we identify the way forward to a robustly supported body of evidence for the systematics of these giant snakes.

Understanding the origin of *Eunectes*: re-evaluating the timeline of anaconda evolution

The age of the splits among anacondas was a key reason cited by Rivas *et al.* for their taxonomic decisions. To evaluate their results and to illustrate the uncertainties associated with timetree calibrations based on the limited data at hand, we carried out a series of re-analyses of the available data, analysing nuclear protein-coding genes (concatenated *RAG1*, *BDNF*, *CMOS*, *NT3*) and mitochondrial sequences (*Cytb*) separately. On both datasets, we used two approaches for timetree calculation: a Bayesian Inference using MCMCtree (Rannala and Yang 2007) and the
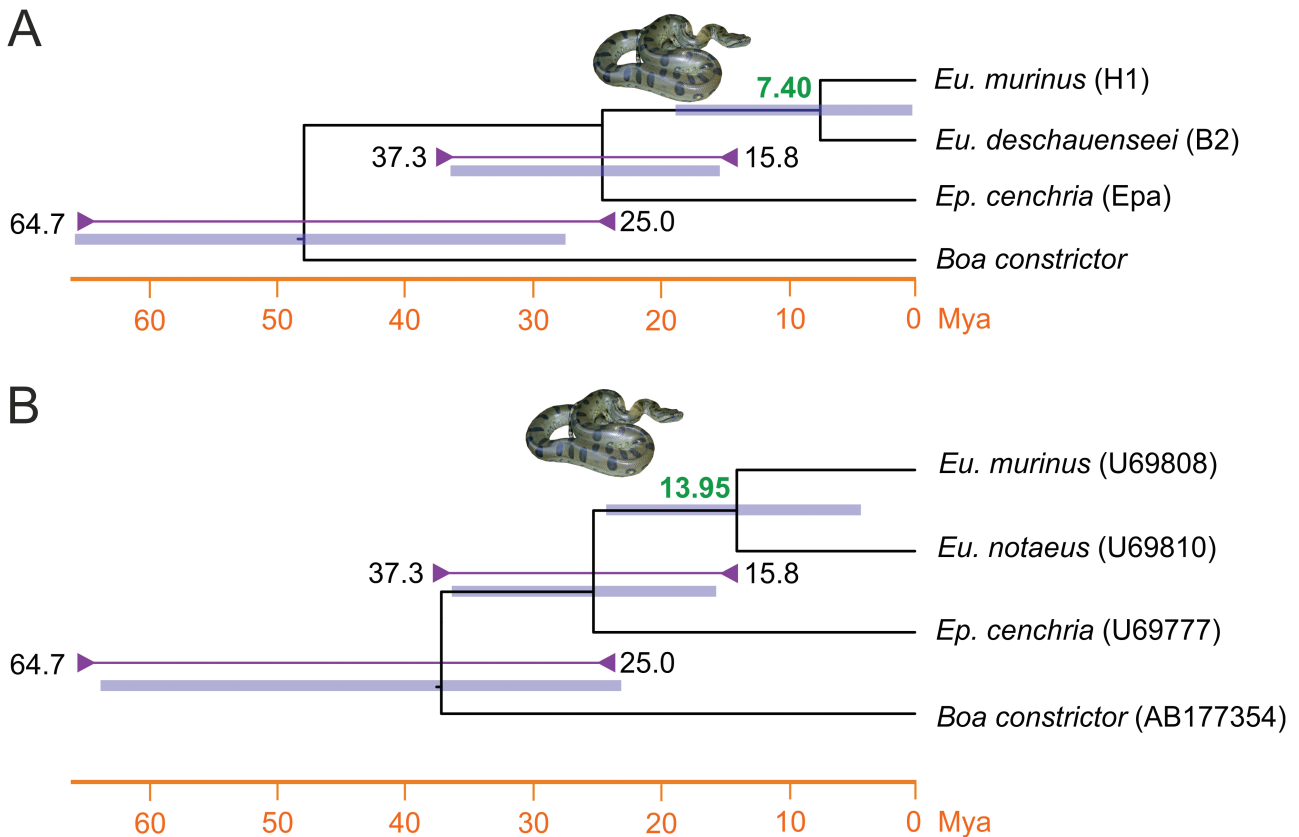
Figure 1. Timetrees inferred with MCMCtree, estimating the split between yellow and green anaconda lineages (genus *Eunectes*). We show these to illustrate the considerable uncertainties surrounding the evolutionary age of anacondas with the limited data available and the large differences between inferences from nuclear-encoded vs. mitochondrial DNA sequences. Analyses are based on 2150 bp of four fragments of nuclear-encoded protein-coding genes (A) and 1098 bp of the mitochondrial cytochrome *b* gene (B), constraining the *Epicrates-Eunectes* split to 15.8–37.3 Mya (secondary calibration obtained from www.timetree.org). Constraints are shown in purple, credibility intervals in light blue. Preferred age estimates of the split between yellow and green anacondas are shown in green. See Supporting information for additional analyses and detailed methods. Photo of *Eunectes murinus* by Frank Glaw.

RELTIME approach implemented in MEGA v.11 (Tamura *et al.* 2021), each with two alternative sets of secondary calibrations taken either from www.timetree.org (Kumar *et al.* 2022) or from Rivas *et al.* For details of the calibrations and timetrees resulting from the nine separate analyses, see Supporting information, Section S1.

The timetrees we obtained (Fig. 1; Supporting information, Figs. S1, S2) illustrate the large differences among approaches based on mitochondrial and nuclear genes, where the preferred estimates for the divergence of yellow and green anacondas ranged between 3.95 and 22.88 Mya. While we do not claim that any of these timetrees provides an accurate estimate of the evolutionary age of anacondas, it is worth noting that almost all of them are younger than the 20.81 Mya estimate of Rivas *et al.* in their preferred scenario. Even our RELTIME tree, based on the secondary calibration derived from Rivas *et al.* (37.7 Mya for the *Epicrates-Eunectes* split), suggests a split between green and yellow anacondas slightly younger than 20 Mya, probably due to the removal of third codon positions. Notably, the estimates based on the protein-coding nuclear genes, which are less affected by saturation, recover a very young split between green and yellow anacondas, varying between 4 and 11 Mya. This would in turn imply even younger divergences between the two green lineages and between the three yellow lineages.

Low genetic distances and the relatively young lineage divergence ages obtained by our reanalyses do not rule out that the various mitochondrial lineages of anacondas (both green and yellow) may represent distinct species. They do however raise the bar for the level of additional evidence required to justify that conclusion. This highlights the requirement for robust, complementary, integrative evidence to support their species status. But such evidence remains scant for anaconda lineages.

The presence of two relatively distant mitochondrial haplogroups in *E. murinus* presumably reflects a period of geographic isolation between green anaconda populations, and it is probable that this isolation period started earlier (but also finished earlier) than the isolation period between the three species of yellow anacondas. However, it remains possible that these populations later merged (failed speciation; Schield *et al.* 2015), and there is no evidence that the differences aggregated in the period of isolation are maintained.

Morphological reanalysis

Rivas *et al.* made much of the lack of morphological distinction between *E. murinus* and their new species but provided no analysis to support that conclusion beyond tabulated data from the literature. Moreover, there are inconsistencies in their data compilation. For instance, while their table 4 ostensibly shows

a 'comparison of different species of green anaconda', the two columns of data for the new species actually only show data for three specimens collected by the authors, and a summary of data from Dirksen (2002). The holotype and paratype of the new species designated by Rivas *et al.* show values outside of those shown in their table 4 for several characters (their table 6). This makes a meaningful comparison of morphological variation between their putative species even more difficult.

Surprisingly, Rivas *et al.* did not attempt to reanalyse or even compile the large, publicly available morphological dataset of Tarkhnishvili *et al.* (2022). The latter authors provided the raw data underlying their morphological analysis in the supplementary materials to their paper and, moreover, found evidence of morphological divergence between different green anaconda populations, especially between those from Peru and the remaining populations. We here re-analyse these data with the aim of testing the conclusions of Rivas *et al.*

We combined the data on green anacondas from the morphological data matrix of Tarkhnishvili *et al.* (2022) with additional data in table 6 of Rivas *et al.* for the types of their new species and their intended 'lectotype' of *E. murinus*. Preliminary analyses showed that sexual dimorphism in meristic counts has little impact on the outcome of the analyses; moreover, information on sex was not available for many specimens; we therefore combined data for male and female specimens for our analysis. We divided the data of the green anacondas into the following Operational Taxonomic Units (OTUs): Cerrado (the Cerrado biome south of the Amazon), S. of Amazon (Amazonian forests south of the Amazon River), N. Peru (northern Peru and adjoining Colombia), and N. of Amazon (north of the Amazon—Guianas, Venezuela and adjoining parts of Brazil). In the case of the yellow anacondas, we treated each named species as an individual OTU. Each meristic character was then subjected to a one-way ANOVA to test for significant differences between the four green anaconda OTUs and between the three yellow anaconda OTUs, and a Principal Component Analysis (PCA) was then run on those meristic characters that showed significant variation. We then carried out a discriminant function analysis (DFA) to test the extent to which specimens of the different OTUs could be differentiated and assigned to their own populations. For further details, including PCA matrices and results of ANOVAs, see Supporting information, Section S2; Supporting information, Tables S1–S7.

The resulting ordination of specimens of green anacondas along the first two principal components (Fig. 2) broadly separates specimens from north and south of the Amazon along the first principal component, whereas specimens from northern Peru (Iquitos region and adjoining Leticia, Colombia), attributed to the southern mtDNA clade by Rivas *et al.*, constitute a third distinct group, displaying higher PC-2 scores than other specimens. The ANOVA revealed statistically significant differences among the four OTUs in six of the eight characters examined (Supporting information, Table S1).

The DFA revealed few 'misclassifications' across the Amazon River (6.25%), with the vast majority of specimens being correctly classified into their original OTU, suggesting that the four populations do represent distinct morphological groupings (Supporting information, Tables S3, S4).

In summary, the reanalysis of the morphological data of Tarkhnishvili *et al.* (2022) reveals considerable morphological variation among green anaconda populations, including across the Amazon, contrary to the assertions of Rivas *et al.* Our reanalysis also reveals discrepancies compared to the pattern predicted by the mitochondrial phylogeography, in particular the very distinct morphology of the material from northern Peru and the absence of evidence of two species in the Guianas, which would have been predicted from the co-existence of two species in the region claimed by Rivas *et al.* This is particularly relevant to the question of the origin of the types of *E. murinus* and some of its synonyms (see below).

For the yellow anacondas, the ANOVAs revealed statistically significant differences between the species in five of the nine meristic characters from Tarkhnishvili *et al.* (Supporting information, Table S5). The PCA indicates reasonable degrees of separation between *E. notaeus* and *E. deschauenseei*, whereas *E. beniensis* forms a distinct, discrete cluster from the two other yellow anacondas (Fig. 3; see Supporting information, Table S6, for the principal component matrix). The DFA (Table 1) shows that the classification function successfully classified the overwhelming majority of specimens to their correct species, further emphasizing the distinctness of the three taxa. While the minimal mtDNA sequence divergences between the three yellow anacondas suggest a recent common ancestry, the morphological differences, extensive distribution gaps, and lack of additional nuclear DNA evidence suggest that continued recognition of the three species would be the preferable alternative until additional evidence sheds new light on their systematics.

Anaconda systematics: the current status

Our re-analyses of the available evidence show that many of the claims of Rivas *et al.* are poorly supported or depend on questionable priors. The mitochondrial divergence levels among green anacondas are inconclusive and the age of the divergence of the anacondas was likely greatly overestimated due to the use of extreme calibration points and saturated mitochondrial sequences. Contrary to Rivas *et al.*, there is considerable geographic variation in morphology among green anacondas, but this only very partially reflects their preferred narrative of two species separated by the Amazon. In our view, the burden of proof lies with those proposing taxonomic changes. Since Rivas *et al.* did not support their claims with adequate evidence, and in the absence of convincing evidence for change, we suggest that taxonomic treatises should apply the principle of taxonomic parsimony (Scherz *et al.* 2017) and return to the *status quo* before Rivas *et al.*: recognition of the long-recognized four anaconda species (*E. beniensis*, *E. deschauenseei*, *E. murinus*, *E. notaeus*).

PART III. FIXING THE NOMENCLATURE

A first review of the nomenclature: Dubois *et al.* (2024)

In response to the problems of nomenclature contained in Rivas *et al.*, Dubois *et al.* provided a comprehensive revision of all previously published nomina used for anacondas. These authors selected specimens believed to be lost as lectotypes for *Boa murina* Linnaeus, 1758, *Boa gigas* Latreille in Sonnini and Latreille, 1801, *Boa aboma* Daudin, 1803, *Boa anacondo* Daudin,
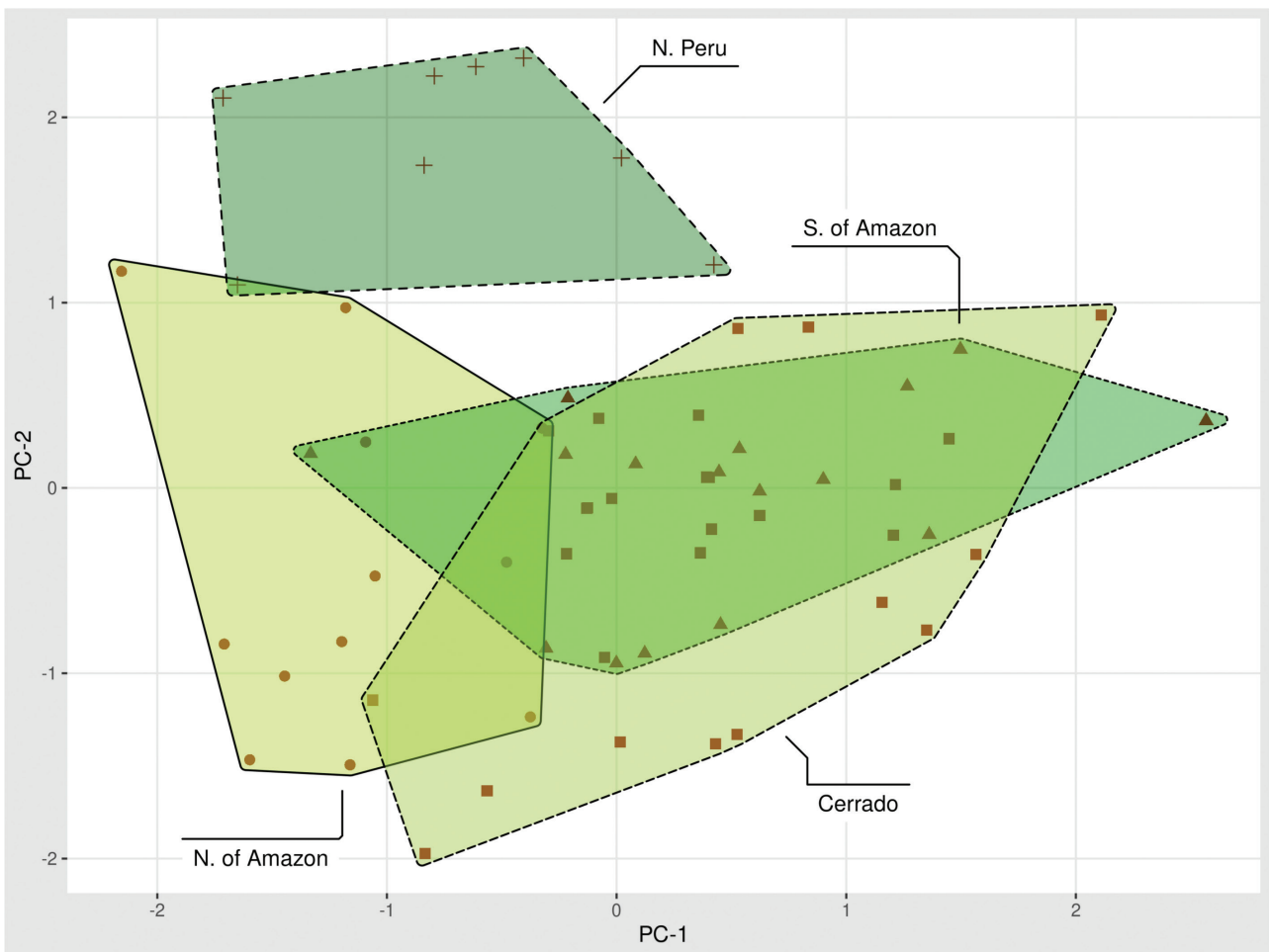
Figure 2. Ordination of green anaconda (*Eunectes murinus*) specimens along axes displaying the first two principal components (PC) of a principal component analysis. PC-1 and PC-2 explain 28.8% and 19.2% of the total variance in the data, respectively. See Supporting information, Table S2 for the principal components table.

1803, and *Boa aquatica* Wied-Neuwied, 1823, and also considered the status of all other nomina used for the species of the genus. However, despite the depth of their analysis, unanswered questions remain, especially regarding the type series of *Boa murina* used by Linnaeus (1758) to establish the species. It is therefore important to delve into this specific topic here.

There has been extensive discussion about the type series of *Boa murina* in the past, and Dubois *et al.* provided a summary that led them to designate a specimen figured in the *Thesaurus* of Albertus Seba (1665–1736) as the lectotype of *Boa murina*. The second volume of the *Thesaurus* (Seba 1735: 30, plate 29, fig. 1) features an illustration of an anaconda, which Dubois *et al.* labelled 'ONID Sm2'; they then designated the specimen represented by this illustration as the lectotype of *Boa murina*. Dubois *et al.* justified this selection on the grounds that the illustrated animal was the only syntype with a stated type locality consistent with the known range of the species (although rather broad in geographical terms). They further argued that since the specimen was believed lost, their lectotype assignment would pave the way for the designation of a genetically characterized specimen as a neotype for *Boa murina*, which would resolve questions of species affinities if there were indeed several species of green anaconda.

The selection of a 'lost' specimen as lectotype to allow future designation of a neotype is an unconventional but *Code*-compliant trick to re-establish stability in a taxon where the origins of extant types may be murky. In this case, the only likely extant syntype of *Boa murina* appeared to be an old, fluid-preserved specimen in the Stockholm collection accessioned as NRM-9. Both Rivas *et al.* and Dubois *et al.* considered this specimen likely to be unsuitable for molecular analysis due to its age and preservation. However, that assessment may have been premature, as many recent studies have successfully retrieved molecular data from old specimens, type specimens included. For example, Kehlmaier *et al.* (2019) successfully sequenced the entire mitogenomes of 19 of 20 type specimens of chelonians preserved using various fixation and preservation techniques, and several other studies obtained mitochondrial and nuclear DNA sequence data from fluid-preserved museum samples of reptiles more than a century old (Ruane and Austin 2017, Rancilhac *et al.* 2020, Zacho *et al.* 2021, Bernstein and Ruane 2022, Fong *et al.* 2023). While these techniques may not always be successful, there is no a priori reason to discount them. Besides, contrary to Rivas *et al.*, it is certainly incorrect to assume that an 18th century specimen was formalin-fixed, since that method of preservation was only discovered in 1893 (Musiał *et al.* 2016). It is
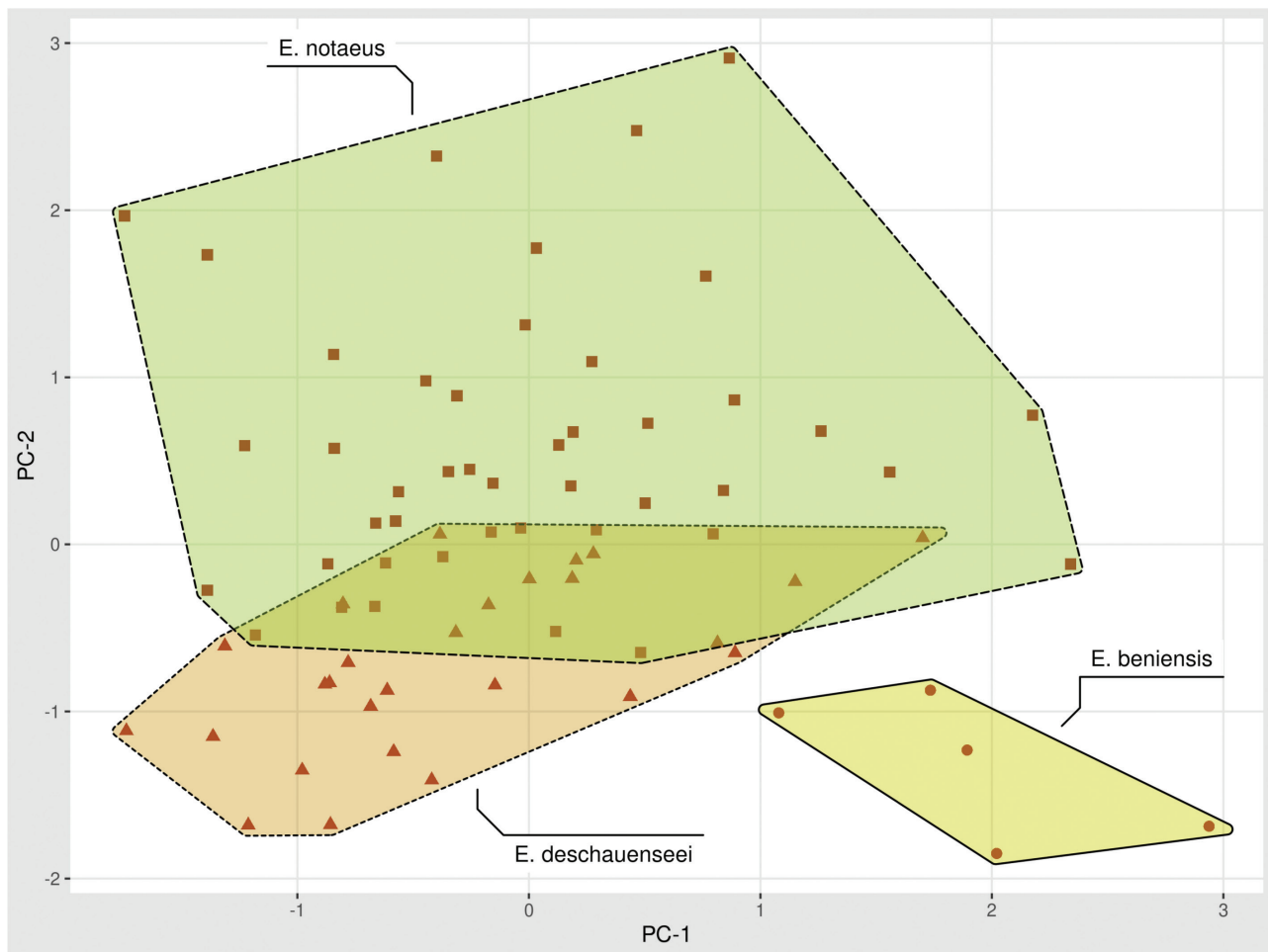
Figure 3. Ordination of specimens of yellow anacondas (*E. beniensis, E. deschauenseei, E. notaeus*) along axes displaying the first two principal components (PC) of a principal component analysis. PC-1 and PC-2 explain 29.0% and 19.5% of the total variance in the data, respectively. See Supporting information, Table S6 for the principal components table.

Table 1. Output of classification function of a DFA of yellow anacondas, comparing original and predicted species membership. See Supporting information, Table S7, for the pooled discriminant scores table

		Predicted species			
		E. beniensis	*E. deschauenseei*	*E. notaeus*	N
Original species	*E. beniensis*	100%	0	0	5
	E. deschauenseei	0	96.3%	3.7%	27
	E. notaeus	0	11.4%	88.6%	44

thus entirely possible that NRM-9 could be genotyped, although there is now little reason to do so, given the designation of the specimen depicted by Seba (1735) as a lectotype.

However, one of the pitfalls of designating as a lectotype a specimen believed to be lost is the possibility that it may later be found, thereby invalidating any subsequent neotype designation (Art. 75.8). This is especially topical here as a number of Seba specimens have recently been identified in European collections (Milto and Barabanov 2011, Bauer and Günther 2013, Pereyra *et al.* 2021, Wüster and Tillack 2023). In the following paragraphs, we re-evaluate the history of typification of the green anacondas

and attempt to trace the history of the lectotype designated by Dubois *et al.*

Re-evaluating the typification of *Eunectes*

Origin of the lectotype of *Boa murina*

The suggestion of Rivas *et al.* that there may be two species of green anaconda renders the determination of types and type localities for existing green anaconda nomina a priority, since their affinities will determine the correct names to be used for the different taxa in the event of a split. On p. 215 of the 10th

edition of *Systema Naturae*, Linnaeus (1758) introduced the name *Boa murina* by including one set of unattributed ventral and subcaudal counts (254 and 65, respectively) for a specimen apparently examined by him as well as by referencing a specific, descriptive passage in Gronovius (1756) and an illustration (plate 29, fig. 1) in Seba (1735). In the former work, a specimen listed as No. 44 has scale counts of 254 ventral scales and 69 subcaudal scales. Gronovius further cited two other references, one with a specimen (now lost; Bauer and Wahlgren 2013) illustrated by Scheuchzer (1735) from the Linck collection in Leipzig, Germany, the other a second plate (plate 23, fig. 1) in Seba (1735). Seba's illustrations are accompanied by brief textual accounts that do not include scale counts or measurements.

By 1758, Linnaeus had also seen a green anaconda specimen in what was then the collection of the Swedish king Adolph Frederick (1710–1771). Dubois *et al.* were uncertain about whether this specimen had been seen prior to 1758. However, Linnaeus reportedly conducted his study of the king's collection between 1752 and 1754 (Fernholm and Wheeler 1983) or at least by 1755 (Wahlgren 2012). Linnaeus (1754) published the first part of his account of this collection, but the second part (Linnaeus 1764), containing a description of the anaconda, was delayed by a decade for financial reasons, although it had been completed by the time of publication of the first part (Fernholm and Wheeler 1983). Under Art. 72.4.1.1, such specimens seen by Linnaeus and identified prior to the publication of the name, even if not explicitly mentioned in the formal description of the species, are considered to be part of the type series. Thus, NRM-9 in the Stockholm collection, described by Andersson (1899), is also a syntype of *Boa murina*, and despite their expressed doubts, Dubois *et al.* rightly listed it in their table 1 as 'PL' (paralectotype). Minor differences in scale counts between Linnaeus (1758) and Andersson (1899) may be due to different ways of counting ventral and subcaudal scales.

Thus, at least five specimens formed the original type series of *Boa murina*. As a result of the lectotype designation by Dubois *et al.*, the name of the taxon *Eunectes murinus* now rests with the specimen illustrated on plate 29, figure 1 in the second volume of Seba's *Thesaurus*. This volume was issued in 1735 in two simultaneously published versions (Engel 1937, Holthuis 1969), one in Latin and Dutch and the other in Latin and French. It is critical to note that Seba himself wrote the Dutch text of this volume (Engel 1937, Wallach 2011), and this text must therefore be accepted as the original, authoritative version when it comes to specimen information, including localities. The translations from the Dutch were not done by Seba himself (Engel 1937), but the Dutch text was translated into Latin by the German physician Hieronymus David Gaub (1705–1780) and the resulting Latin text was translated into French by the French scholar Louis de Jaucourt (1704–1779).

In Seba's own words, as printed in the Dutch version of the *Thesaurus*, the following description on page 30 accompanies his illustration of the anaconda:

"*Serpens, Testudinea, Americana, murium insidiator.
Schildpad-slang uit de Spaansche West-Indiën, op muizen azende.*"
[Tortoise snake from the Spanish West-Indies, hunting for mice.]
In the Latin/French version, the translated text is:

"*Serpens, Testudinea, Americana; murium insidiator.
Serpent d'Amerique, à moucheture de Tortue; Mangeur de Rats.*"
[Snake from America, with tortoise-like spotting; rat eater]

Critically, in the translations the important specific geographic information found in the Dutch version was reduced to only the continent. Wallach (2011: 19) already noted that during the translation of the original Dutch text into Latin and French, many mistakes were made.

In Seba's time in the early 18th century Netherlands, the broad term West Indies was used for all Caribbean islands south to Trinidad as well as for all the mainland areas surrounding the Caribbean Sea and the Gulf of Mexico (i.e. Central America, the southern USA, Colombia, and Venezuela; Benjamins and Snelleman 1914). In his accounts, Seba (1735) used several names for localities in the general Caribbean area, including 'Westindien' (West Indies), 'Spaansche West-Indiën' (Spanish West Indies), 'Nieuw Spanjen' (the Vice Kingdom of New Spain, from Costa Rica north to California, Arizona, New Mexico, and Texas), and 'Westindische Zee' (Caribbean Sea). In Volume I of the *Thesaurus* (e.g. Seba 1734: 127) he also specified that a tortoise that occurred throughout the 'Ports des Espagnols' [the Spanish ports] was received from Curaçao. Thus, it seems clear that Seba tried to differentiate between localities in the Caribbean Region and included detailed information when it was available to him. During this time, the term 'Spanish West Indies' was applied to an historical administrative unit that included only the Spanish island possessions in the Caribbean (Cabrera Bosch 1993). In its administration, including governance and trade, this loose assemblage of islands was distinct from all mainland colonies (the 'Spanish Main'; Sauer 1966), which had their own administrative units. Thus, Seba's 'Spaansche West-Indiën' locality turns out to be quite specific since the only part of the Spanish West Indies within the range of anacondas is the island of Trinidad, now part of the nation of Trinidad and Tobago (Newson 1976, Murphy, 1996, 1997, Boos 2001). We therefore can safely assume that the specimen described and figured by Seba (1735: plate 29, fig. 1) hailed from Trinidad and is assignable to the northern mitochondrial haplotype group of Rivas *et al.*

The Trinidad connection was missed by Dubois *et al.*, who had only the French-Latin version of Seba (1735) at their disposal. While Dubois *et al.* noted that Wallach (2011) listed the specimen as from the 'West Indies', in his table 1, Wallach interpreted Seba's 'Spaansche West-Indiën' as the 'Greater Antilles (Cuba, Hispaniola, Puerto Rico, Jamaica)', an area outside the range of *Eunectes*. In his table 2, Wallach listed the locality of Seba's specimen simply as 'West Indies', without mention of the Spanish connection. As a result, Dubois *et al.* remained unaware that a more detailed locality could be assigned to the illustrated anaconda specimen based on the Dutch-Latin version of the *Thesaurus* and, crucially, that this included Trinidad, an island harbouring anacondas to this day. As a consequence, both Rivas *et al.* and Dubois *et al.* (their table 1) agreed that the species name *murinus* should apply to the so-called 'southern mitochondrial lineage of green anacondas': our identification of Trinidad as the type locality shows this to be in error, since Rivas *et al.* provided mitochondrial sequences for five specimens from Trinidad

that all clustered within their northern mitochondrial lineage. Consequently, the Trinidadian origin of the specimen selected as lectotype for *E. murinus* by Dubois *et al.* firmly attaches that nomen to the northern lineage of green anacondas.

ZISP 1441: the extant lectotype

Stabilizing the nomenclature of the green anacondas requires first and foremost to establish the fate of the lectotype of *Boa murina*. Bauer *et al.* (2024) reviewed the dispersion routes of Seba's specimens throughout Europe. For green anacondas they concluded that 'each of the plausible pathways of the anaconda illustrated on plate 29 by Seba (1735) and selected by us (Dubois *et al.* 2024) as the lectotype of *Boa murina* leads to a dead end'. They further noted that they found 'no evidence of the agreement of both documentary data and specimen similarity that would unambiguously point to any surviving specimens as being the model for Seba's (1735) plate' and concluded that 'Seba's illustrated anaconda should be considered as lost'. They argued that this would allow the designation of a well-documented and genetically characterized neotype to settle the status of the name *E. murinus*. While Bauer *et al.* (2024) diligently traced the paper trail associated with the several collectors and agents who purchased specimens at the auction of Seba's material in 1752 (e.g. Anonymous 1752, Boeseman 1970), and while they identified a number of gaps in the record, particularly when it comes to snakes, we disagree with their conclusion that the lectotype is lost.

Three extant anaconda specimens attributable to Seba's collections are in the holdings of the Zoological Institute of the Russian Academy of Sciences (ZISP), St. Petersburg, Russian Federation. The first of these (ZISP 3363), a stuffed and mounted specimen illustrated by Bauer and Wahlgren (2013), is thought to originate from Seba's first collection, purchased by Tsar Peter the Great in 1717 (Holthuis 1969), and is excluded as the possible model for plate 29 because specimens illustrated in the *Thesaurus* came from Seba's second collection, established *de novo* after the sale to the Tsar. The remaining two specimens (ZISP 1441–42) are alcohol-preserved and may potentially have been obtained from Seba's second collection, thus requiring further attention.

Both specimens are identified in the collection's catalogue as having been obtained from the Kunstkamera, an exhibition of Peter the Great's collection (Driessen-Van het Reve 2006), in the 1780s via the estate of Th. Sluyter, a known broker for specimens sold at the 1752 auction of Seba's collection (Engel 1961, Boeseman 1970, Juriev 1981, Driessen-Van het Reve 2006, Milto and Barabanov 2011, Bauer *et al.* 2024), after Sluyter's death (Juriev 1981). While Sluyter's own cabinet was reported to have been sold in 1757, 5 years after Seba's collection (Engel 1939), it is possible that some specimens were retained or remained unsold. Bauer *et al.* (2024) did not have the opportunity to examine these two anaconda specimens but noted that 'It remains to be seen if these can be demonstrated to have come from Seba's second collection or if either corresponds to Seba's (1735) pl. 29 fig. 1'. One of the specimens, ZISP 1442, could not be located in the ZISP collection in March 2024. However, ZISP 1441 remains available in the collection and shows a remarkable resemblance to the illustrated snake and, in conjunction with its documented history, we consider it highly likely that

this specimen is indeed the basis for Seba's plate and hence the lectotype for *Boa murina.*

ZISP 1441 (Fig. 4) is in excellent condition and agrees in pattern with the snake in Seba's plate 29. Within the limits of the accuracy of Seba's figures, the position, shape, size, and number of black spots on the middle of the back and on the flanks, and the shape and position of the temporal stripes, especially the elongated dark stripe under the pale temporal band on the left side of ZISP 1441, entirely agree with those in Seba's illustration (see Fig. 4). It is important to note that many, but not all, of Seba's illustrators drew the specimens on printing plates without reversal, so that the resulting printed plates are often mirror-images of the specimen (Engel 1937). In the case of ZISP 1441, we note a seeming contradiction between the correspondence of the body pattern of the type with Seba's illustrations without reversal, whereas the lengthened lower temporal stripe seen on the left side only of ZISP 1441 corresponds to the illustration of the right-hand side of the head in Seba's plate. We suspect that the artist positioned the specimen in a manner similar to that depicted in Figure 4A, with the left side of the body visible to them, but, because of the sharply angled position of the head of ZISP 1441, and as part of their efforts to create an aesthetically pleasing illustration (most of Seba's illustrations depict specimens in idealized positions rather than as faithful depictions of their preserved state—e.g. see Bauer and Günther 2013, Wüster and Tillack 2023), illustrated the left side of the head in mirror image, as this would have been visible to them while maintaining their position vis-à-vis the specimen. This 'mixed-view modelling' can also explain the inaccuracy around the neck, where the illustrator appears to have used some artistic licence to get from Blotch 12 to the head. Given that the curved position of the snake in Seba's illustration approximates well that of the actual specimen, and that most of the details in dorsal patterning are readily accounted for, we consider it most likely that the snake was indeed drawn in mirror image (resulting in a non-reversed final plate), with the exception of the head that was not mirrored because of its preserved position relative to the rest of the body.

ZISP 1441 is an adult male with 253 ventrals, 66 unpaired subcaudals, an undamaged tail tip, 47-61-37 dorsal scale rows around the body one head length behind the head, at mid-body, and one head length before the cloaca, a single cloacal plate, 17-17 upper labials (with the 14th on the left side consisting of a small scale below and a larger one above, and the 4th on the right side distinctly smaller than the adjacent ones), 21-19 lower labials, one preocular, one supraocular, three postoculars, two suboculars, scales on top of the head small, irregularly arranged, with the exception of two enlarged supranasals and two enlarged interoculars.

Measurements of this specimen include a snout–vent length of 1467 mm, tail length 225 mm, and head length 58 mm. On each side of the head is a light, broad temporal band, running from the posterior corner of the eye towards the corner of the mouth, widening posteriorly, bordered ventrally by a broad dark brown band, narrower than the temporal band. Tellingly, the broad dark band under the temporal band extends much further back than the pale temporal band itself on the left side of the head, corresponding to Seba's figure if illustrated as explained above. The top of head has an arrow-shaped brown spot, starting with a sharp tip at the posterior border of the supranasals and
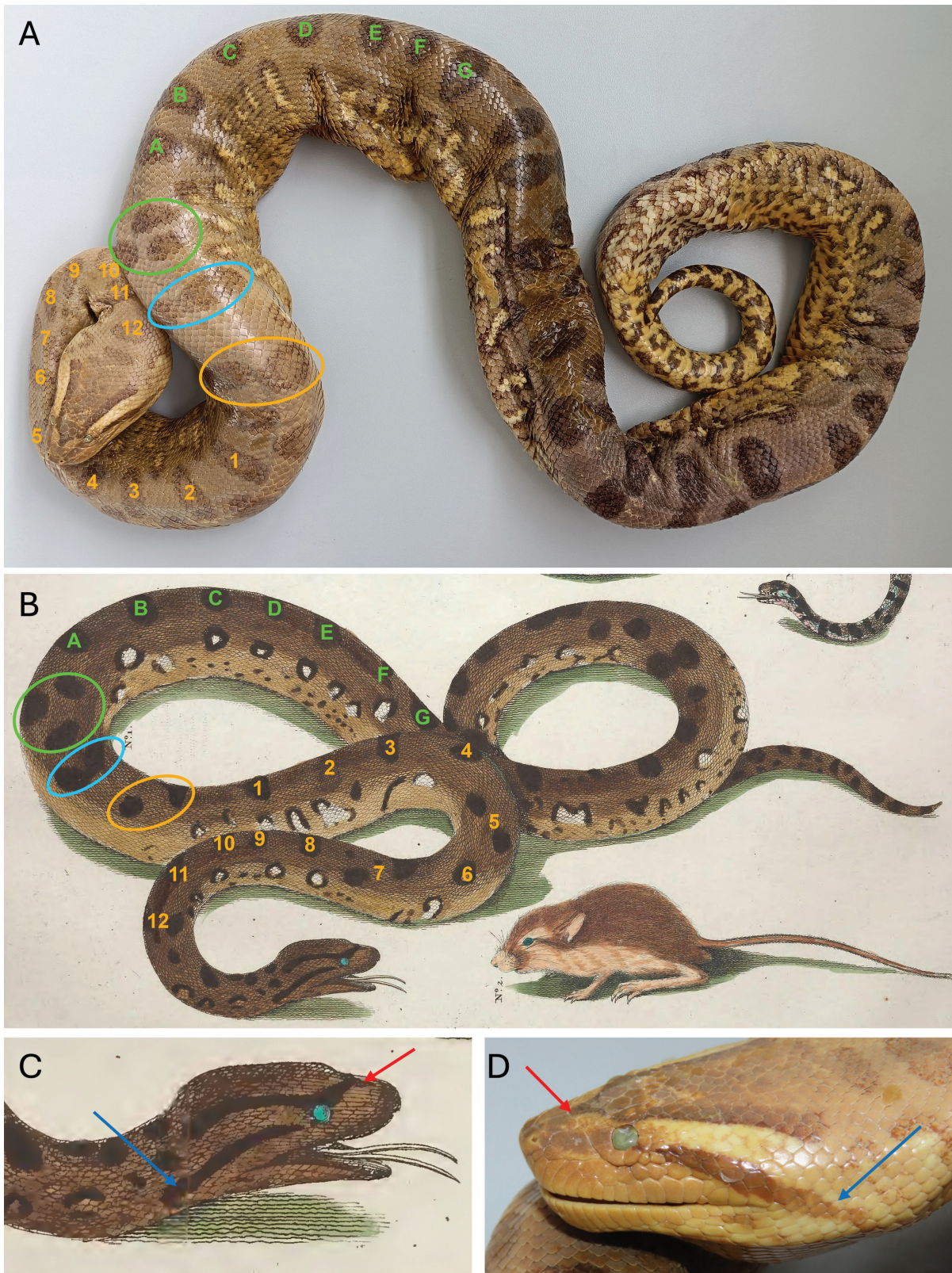
Figure 4. Comparison of ZISP 1441, the lectotype of *Boa murina* Linnaeus, 1758, with plate 29, fig. 1 in Seba (1735). A, photograph of ZISP 1441. Numbering, lettering and coloured ovals refers to equivalent blotches and pattern features for comparison with Seba's figure. B, plate 29, fig. 1 from Seba (1735) with pattern features equivalent to those in (A) highlighted. C, D, detail of head in Seba's plate 29, fig. 1 and of ZISP 1441. Note the posterior extension of the lower postocular stripe and the arrow-shape of the dark mark on top of the head. Photos of ZISP 1441 by Konstantin Milto. The high-resolution illustration of Seba's anaconda were downloaded from the Biodiversity Heritage Library, contributed by Smithsonian Libraries and Archives.

widening posteriorly to occupy the entire area between the temporal bands of both sides and outlined with a dark brown line separating it from the light temporal bands. The dorsum has large, black, round to oval blotches, sometimes in pairs, that may be in contact or sometimes single, totalling 107 including the tail; where two blotches were partly fused across the middorsal line, we counted them as separate blotches. Distances between spots are irregular. The sides of the body have irregular dark rings with a light centre, many merging with each other or the ventral surface.

The concerns expressed by Bauer *et al.* (2024) regarding the identity of the two fluid preserved ZISP specimens stem from the fact that these specimens only reached St. Petersburg in the late 1780s, three decades after Sluyter had purchased 70 of Seba's snakes in 1752 (lots 10, 24–27, 37–41, 62–67, 101–110, 121–126, 136–144, 145–152, 302–312, 391–400; see Anonymous 1752, Juriev 1981, Bauer *et al.* 2024). However, part of Sluyter's collection was sold to St. Petersburg in 1757 (Engel 1939, 1986, Bauer *et al.* 2024) and therefore there was 'opportunity for confusion of the pedigrees of individual specimens'. However, Bauer *et al.* (2024) did not examine the specimens in question. In our opinion, the shared pattern motifs between ZISP 1441 and Seba's plate 29 (Fig. 4) provide the necessary additional evidence that ZISP 1441 is indeed the assumed 'lost' lectotype of *Boa murina*.

In a discussion of material obtained by the British Museum from the Cabinet of Theodoor van Lidth de Jeude (1788–1863), Thomas (1892) suggested that a specimen of *E. murinus* (NHMUK 66.8.14.308) and a fish in that collection agreed so well with Seba's (1735) plates that 'it appears very probable that these specimens are Seba's originals, and that they escaped Peter the Great, and passed with the Mammals into the hands of Prof. Lidth de Jeude'. We have been able to examine photos of NHMUK 66.8.14.308 and have come to the conclusion that the pattern of dorsal spots in the neck region of the specimen is different from that in the cited figure. Besides, if the specimen indeed 'escaped Peter the Great', who purchased only Seba's first collection, then it would not have been illustrated in the *Thesaurus*. Thus, we confidently exclude the possibility that NHMUK 66.8.14.308 could be the specimen that served as basis for the cited figure, and we concur with Bauer *et al.* (2024) to exclude this specimen from further consideration.

Assessing the affinities of ZISP 1441

While we consider the case for Trinidad as the type locality of the specimen illustrated in Seba's plate 29 to be strong and are convinced by the resemblance between ZISP 1441 and Seba's figure, we nevertheless consider it essential to further verify the affinities of the specimen using the morphological analyses described above. To achieve this, we included the morphological data from this specimen (see above) in the DFA of green anacondas described earlier. Instead of assigning the specimen to an OTU, we left it unassigned so that the classification function of the DFA could assign it to one of the existing OTUs. The ordination of specimens along the first two discriminant axes is shown in Figure 5, and the output of the classification function in Table 2. As can be seen, ZISP 1441 groups robustly with the specimens from north of the Amazon in the ordination and is equally robustly assigned to that OTU in the classification function. In terms of its morphology, the specimen is thus consistent with an

origin on Trinidad, as per the stated type locality in Seba (1735, Dutch-Latin edition).

Towards taxonomizing anacondas: what evidence and approaches do we need?

As part of our reanalysis of the existing evidence, we have highlighted the inadequacies of the molecular evidence underlying the conclusions of Rivas *et al.*, noted the fragility of their molecular dating analyses, and established the presence of considerable morphological variation among green anacondas that is at least partly incongruent with the taxonomic hypothesis Rivas *et al.* established. We also determined that the *de facto* type locality of *Boa murina* Linnaeus, 1758 is the island of Trinidad and identified ZISP 1441 as the extant lectotype of the species, previously designated by Dubois *et al.*

Our reanalysis revealed the many remaining open questions in anaconda systematics. The resolution of these questions will ultimately require two things: much denser sampling than is currently available, and the use of informative nuclear loci. For green anacondas, the Guianas appear to represent a relatively accessible contact zone where the southern and northern mitochondrial haplotypes can be found in close proximity. Extensive sampling in this region, coupled with the use of appropriate nuclear loci, may provide the required evidence to determine whether the mitochondrial lineages identified by Rivas *et al.* correspond to independently evolving organismal lineages or represent relicts of past range fragmentation retained within a single gene pool. Among yellow anacondas, the use of appropriate nuclear markers is again required to determine whether the three named taxa represent organismal lineages on independent evolutionary trajectories or geographic variation within a single such lineage. Given the difficulties of sampling across the enormous, remote, and logistically difficult range of the genus *Eunectes*, we recommend the use of next generation sequencing methods to maximize the information content of each sample and generate a sufficient number of markers to help overcome the inevitable difficulty of dense sampling. We also hope that samples and data will be shared in a collegial manner among all interested parties to allow the open taxonomic questions affecting the genus to be resolved without unnecessary duplication of effort.

The typification of *Eunectes murinus* also requires additional work. While our enquiries have traced the geographical origin of the *Boa murina* lectotype to Trinidad and thus the northern mitochondrial clade *sensu* Rivas *et al.*, and while we have identified ZISP 1441 as that specimen, the status of other older nomina remains unresolved despite the efforts of Dubois *et al.* The missing lectotype of *Boa gigas* Latreille in Sonnini and Latreille, 1801 selected by Dubois *et al.* was from Cayenne, French Guiana, from where Rivas *et al.* reported both their northern and southern haplotype clades. The same appears to be true of *Boa aboma* Daudin, 1803: the type locality of the non-extant lectotype chosen by Dubois *et al.* was given as near Wanhatti, northeastern Suriname. Rivas *et al.* (their fig. 5) showed a southern haplotype from central Suriname but the only Surinamese specimens in their table of genetic samples (their supporting information, table S1) are both listed as '*Eunectes akayima*'. Unfortunately, due to this lack of attention to detail, the distribution of the two haplotype lineages in the Guianas remains largely unclear, and there is no possibility of assigning these names to either lineage
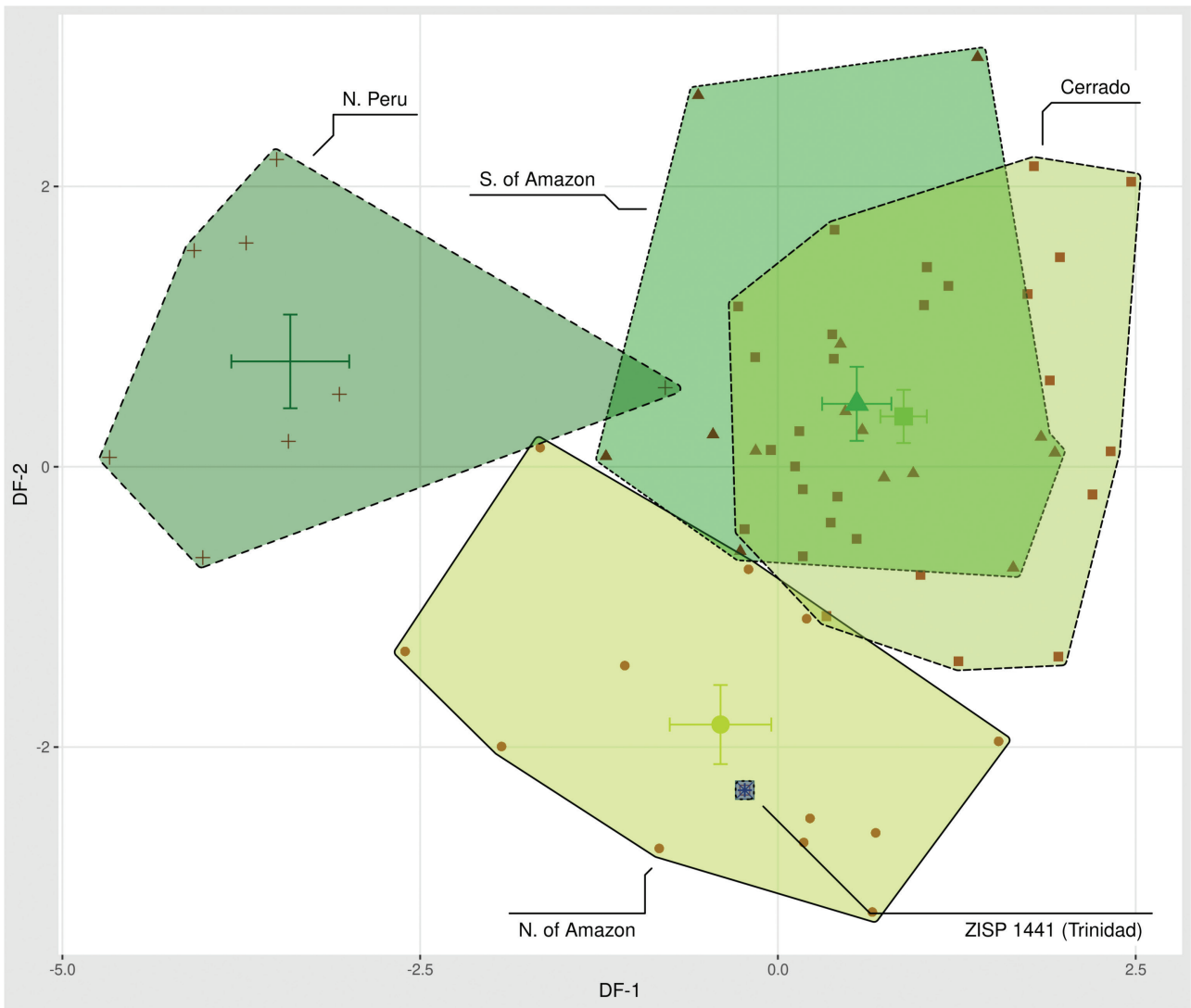
Figure 5. Ordination of green anaconda (*Eunectes murinus*) specimens along the first two discriminant axes of a Discriminant Function Analysis. Enlarged symbols indicate group centroids. The first and second discriminant function account for 70.2% and 25.2% of total variance, respectively. See Supporting information, Table S7, for the pooled discriminant scores table of this analysis.

Table 2. Percent probability of assignment of ZISP 1441 to the four green anaconda OTUs in the classification function of the DFA

	Predicted OTU			
	Cerrado	*S. Amazon*	*N. Peru*	*N. Amazon*
Assignment probability of ZISP 1441	1.2%	3.6%	0%	95.2%

based on the evidence currently available. We therefore consider the assignment of *Boa gigas* and *Boa anacondo* to the southern lineage and of *B. aboma* to the northern lineage by Dubois *et al.* (their table 1) premature.

An additional complication regarding the collecting localities of the lectotypes chosen by Dubois *et al.* for Latreille's and Daudin's anaconda taxa is that the presence of both mitochondrial haplotype clades in the Guianas may be indicative of a zone of introgression between two putative lineages. A binomen based on a topotypical neotype that turns out to be a hybrid would not be available for either parental species (Art. 23.8). This reinforces the need for careful genetic analysis of potential

neotypes, using a multilocus dataset and analyses suitable for discovering introgression between species.

Dubois *et al.* selected as the lectotype of *Boa aquatica* (Wied-Neuwied, 1823) the non-extant specimen from the 'River Belmonte', southern Bahia, illustrated in Wied-Neuwied (1823). They erroneously attributed the locality to the Brazilian state of Pará and provided the coordinates of the Belo Monte hydroelectric dam on the Xingu River, in the Amazon Basin. However, Wied-Neuwied (1820, 1823) only visited eastern Brazil and never collected in the Amazon. His 'River Belmonte' refers to the Rio Grande do Belmonte, which is an alternative name for the lower reaches of the Rio Jequitinhonha in eastern Minas

Gerais and southern Bahia, Brazil, approximately 2000 km to the southeast of the locality indicated by Dubois *et al.* The green anacondas of the Atlantic forest biome appear to be geographically isolated from populations in the Cerrado and Amazon Basin (Nogueira *et al.* 2019). It would therefore be premature to assume that they can be assigned to the southern mtDNA haplotype clade. Given the isolation of this population in a separate centre of endemism and their hydrological separation from the Amazon and Paraná Basins, additional and hitherto undocumented diversity in green anacondas along the eastern Brazilian coast cannot be excluded and requires urgent further research.

The resolution of the status of these names, and thus the nomenclature of the green anacondas, will require the designation of neotypes from localities of origin 'as near[ly] as practicable from the original type locality' (Art. 75.3.6), with appropriate molecular data to fix the affinities of these names in case that future data do indeed support the existence of multiple species of green anaconda, as intended by Dubois *et al.* Importantly, molecular data will be required for material from the region of Cayenne (for *Boa gigas* and its objective synonym *Boa anacondo*), northeastern Suriname (*Boa aboma*), and southern Bahia (*Boa aquatica*) to settle the nomenclature of the southern lineage of green anacondas, if future data warrant its taxonomic recognition.

For additional comments on the typification of anacondas, see Supporting information, Section S3.

WHAT CAN WE LEARN FROM THE ANACONDA DEBACLE?

The attempted revision of the anacondas by Rivas *et al.* is not the first high-profile taxonomic revision to generate controversy, and it will undoubtedly not be the last. Often, differences of opinion on concepts and the appropriateness of data types and methods of analysis can lead to heated but legitimate debate (Burbrink and Ruane 2021, Hillis *et al.* 2021). In other cases, otherwise sound works inadvertently violate a technical provision of the *Code*, resulting in names that are unavailable (Krell 2009). Unfortunately, Rivas *et al.* accumulated such a large number of objectively definable problems, both scientific and nomenclatural, that we felt obliged to dissect their work in the previous paragraphs. We have done so in the hope that this high-profile case concerning an iconic element of the South American megafauna can also serve as a high-profile lesson on the importance of getting taxonomy right. Moreover, since earlier critiques (Dubois *et al.* 2024, Vásquez-Restrepo *et al.* 2024) focussed primarily on the nomenclatural defects of the paper, we also wanted to dissect the science underlying the conclusions of Rivas *et al.*, to ensure that lack of published critique thereof is not mistaken for agreement. Over the following paragraphs, we summarize some of the key lessons to be learned and suggest steps to be taken to ensure that taxonomic studies, and in particular works of species delimitation, result in scientifically convincing and nomenclaturally valid publications that add value to the body of scientific knowledge on the biodiversity of our planet.

Responsible taxonomy: responsibilities of journals, editors, and reviewers

In order to maintain a reliable and stable taxonomy, we would like to appeal to the responsibilities of all involved parties.

To act responsibly in a taxonomic context includes not only the role of authors, but also those of reviewers, editors, and publishers.

Journals need to ensure that the expertise of editors matches the content of the manuscript they are editing. We note that among the three listed editors of the Rivas *et al.* paper, two are not taxonomists and the third is a Crustacean specialist.

Editors should always select reviewers with appropriate taxonomic and nomenclatural expertise. Reviews from such experienced peers would very likely have prevented most of the problems highlighted here. Assuming such an adequate peer review process, editors handling these manuscripts have the obligation to take taxonomically critical points of reviews seriously. Where critical reviewers' objections concern matters of taxonomy and nomenclature, these cannot be ignored, or the authors spared from argumentation to justify their actions. It should also be noted that it would ordinarily take a considerable amount of time and effort on the part of a reviewer to complete a suitably comprehensive review for a submission like the one by Rivas *et al.*, which involves a complex analysis of a high-profile group of animals. Their paper documents that only 25 days (15 Jan–9 Feb 2024) elapsed from first submission to the arrival of the authors' revision at the journal, and we wonder to what degree the speed of the review process contributed to the failure to uncover the many issues in taxonomy and nomenclature we and others have identified. This is of course not a unique occurrence in the case of this paper, but seems standard for the publisher, MDPI (Crosetto 2021), leading to concern about the scientific and reviewing standards of the affected journals (Brainard 2023).

Scientific journals (and their publishers) publishing articles on taxonomy and nomenclature, especially those working exclusively with online publication, have the responsibility to respect and implement established and essential rules in this regard. In the case of species descriptions, type designations, and other taxonomic measures, publishers must comply fully with the *Code* to ensure the validity of the action. This includes, among other responsibilities, that there must only be one final version of the published article and that the publication is not subsequently changed for any reason (see also Dubois *et al.* 2024). If a certain journal was proven not to follow defined criteria of the *Code* in a series of cases (i.e. failing to fulfil its responsibilities) and if, as a consequence, published articles threaten the stability of classification and nomenclature, we recommend that professional taxonomists avoid these journals as an outlet for their research. This should apply particularly in cases where a journal or publisher refuses to accept responsibility for failings (Wüster and Kaiser 2023). Ultimately, editors and publishers concerned about the reputation of their journals will benefit from respecting the provisions of the *Code*, thereby avoiding unnecessary errata, republication, or corrections.

Responsible taxonomy: responsibilities of authors

While journal editors and publishers have a responsibility towards their readers and the broader integrity of the scientific enterprise, authors are ultimately responsible for the content of their publications. It is their reputations that will suffer as a result of work containing major flaws. Some simple principles can help avoid the collection of problems presented by Rivas *et al.*

Understand the nature of taxonomy as a complex, sophisticated, independent scientific discipline

Taxonomy is neither a service industry providing names on demand (Jackson *et al.* 2017), nor is it a conceptually simple discipline that anyone can 'dabble' in. It has its own concepts, philosophies, and rules (Thomson *et al.* 2018), and its conclusions have a far-reaching impact on all the biodiversity-related sciences. The evidence required to justify species delimitations and the rules governing the naming of taxa may be complex and multifaceted. We stress that these statements are not aimed at deterring young scientists from venturing into the discipline of taxonomy, as delimiting and naming a new species is not per se a particularly complex process. However, non-taxonomists intending to delve into taxonomic studies need to ensure that they acquire the necessary expertise or collaborate with suitably experienced colleagues. The rules of the *Code* are complex and can result in seemingly minor taxonomic acts, perhaps perpetrated as a side-line to other research ('*en passant*' taxonomy; Wüster and Tillack 2023), having significant, unintended consequences for the nomenclature of a larger group. Moreover, errors, misleading information and unwarranted changes, once in the literature, can spread and persist easily and for inordinate lengths of time, leading to parallel nomenclatures and impeding comprehensive information retrieval and communication (Wüster and Bérnils 2011). This is of particular importance in prominent organisms such as anacondas, whose distribution area spans multiple countries and where premature taxonomic changes may disrupt not only scientific communication but also international legislation and conservation management.

Ensure the data justify the conclusions

One of the most frequent causes of unconvincing or controversial species descriptions is a lack of awareness of the limitations of different data types (Hillis 2019, Hillis *et al.* 2021). Probably the most frequently overinterpreted data type is mtDNA (Dufresnes and Jablonski 2022, Ahrens 2024). Due to its matrilineal, clonal, non-recombining mode of inheritance, mtDNA on its own is not an appropriate marker for species delimitation. While mtDNA is used quite legitimately to generate species hypotheses ('Candidate Species' or 'Primary Species Hypotheses'—Padial *et al.* 2010, Miralles *et al.* 2024), additional evidence from, for instance, morphology or nuclear markers must be used to explicitly and critically test whether mtDNA clades represent organismal lineages, and not just used post-hoc to confirm them. When single-copy nuclear gene sequence data are used, this should involve approaches that test for genetic exchange and differentiation, such as networks of phased haplotypes, clustering algorithms implementing admixture models, such as *STRUCTURE* or equivalent, PCoA of standardized multilocus distances, or others. Such methods should use '*de novo*' (Ahrens 2024) or 'exploratory' (Miralles *et al.* 2024) species discovery approaches that allow independent comparison with mtDNA-derived candidate species, rather than validatory approaches that are often intrinsically biased towards confirming the candidate species designated as priors (Ahrens 2024). Most notably, phylogenetic analyses of concatenated nuclear and mitochondrial sequence data would not be suitable for this purpose since this approach cannot test for tokogenetic rather than phylogenetic processes.

For species delimitation, a phylogenetic analysis of concatenated sequences of highly variable mitochondrial genes and a few conserved nuclear genes is for most intents and purposes a mitochondrial analysis with added noise, not a multilocus analysis (Folt *et al.* 2019). Generating both phylogenies separately is in fact more informative, as instances of cytonuclear discordance can potentially inform on past hybridization events.

Where morphology is used to test mitochondrially inferred Candidate Species, unless the mitochondrial clades differ obviously in discrete morphological characters, analyses should rigorously test whether the candidate species correspond to phenotypically distinct morphological groupings, using prospective approaches such as PCA, multiple factor analysis, or similar procedures. In contrast, post-hoc approaches that compare pre-designated groups corresponding to the mitochondrial candidate species, such as Discriminant Function Analysis (if all specimens of a candidate species are grouped into a single OTU), comparisons of the candidate species using ANOVA, and similar approaches, assume what should be tested, namely the phenotypic homogeneity of the candidate species.

Nomenclature: do your homework!

Doing one's 'homework' in a nomenclature context includes carrying out a rigorous and thorough survey of the existing taxonomic literature, perhaps going back centuries, to assess the status of previously published names and their types and to achieve a thorough understanding of the relevant parts of the *Code*. Due to the complexities of the *Code*, it is easy to either contravene relatively unintuitive rules or to inadvertently generate a series of complications that then fall to others to deal with.

Types: do your homework!

Our analysis of the typification of *Boa murina* and its junior synonyms demonstrates the need for extreme care in assessing the status of types for a given nomen. While the attempt at lectotype designation by Rivas *et al.* was not *Code*-compliant, Dubois *et al.* attempted to use the trick of designating as lectotypes specimens believed to be lost in order to free taxonomists from onerous enquiries and research into the origins and affinities of poorly documented ancient types, allowing instead the designation of newer, better-documented and genetically characterized specimens as neotypes. While the 'fetishisation' of older specimens (Dubois *et al.*) can indeed generate considerable complications, we caution against hasty assumptions as to the status of types believed lost. As we have shown here, the designation of a 'lost' lectotype had a series of unintended consequences, including affixing the name *Boa murina* to the northern mtDNA lineage, which will matter if the green anacondas do indeed comprise more than one species. Given the possibility of other Seba specimens lurking in collections across Europe (Boeseman 1970, Bauer and Günther 2013, Bauer *et al.* 2024, Valencia-Zuleta *et al.* 2024), authors need to carefully evaluate the potential consequences of a type presumed to be lost being rediscovered in the future (Bauer *et al.* 2024).

If you don't know, ask

For non-specialists in particular, the requirements of the *Code* can seem arcane and difficult to understand (Braby *et al.* 2024). The nomenclatural histories of some taxa, especially high-profile,

widespread and geographically variable groups, can be exceedingly complex and require extensive research and intimate familiarity with the *Code* to unravel (Fritz and Schmidtler 2020). Asking knowledgeable colleagues for advice and collaborating with suitable specialists will avoid later embarrassment and unnecessary perturbation of the literature.

Politics and nomenclature

One of the current global statement buzz phrases is that 'everything is political' and therefore science, as an integrative part of human culture, should also be political. While everyone recognizes that politics and societal norms affect the scientific enterprise—as active researchers we feel this every day in our jobs, whose funding is highly dependent on political choices of governments and other funding agencies—it is abusive to assume that politics can or should affect the *scientific method* or such objective rules as those governing zoological nomenclature. That is probably the greatest strength of the scientific method—it is universal and can be used, applied, and followed by anyone regardless of political and religious preferences, societal background, geographic origin, sexual orientation, etc. But for the scientific method and nomenclatural rules to remain effective and globally accepted, politics and ethical debates need to remain outside its realms. However, recent political and societal debates have now reached the realms of taxonomy and zoological nomenclature (Gillman and Wright 2020, Hammer and Thiele 2021, Palma and Heath 2021, Ceríaco *et al.* 2023, Guedes *et al.* 2023, Pethiyagoda 2023, Jiménez-Mejías *et al.* 2024). With their choice of the indigenous name '*akayima*' and their claims that its use in indigenous languages confers priority over existing synonyms within the purview of the *Code*, Rivas *et al.* joined this debate and generated a disconcerting mingle of politics and science.

Rivas *et al.* made much of the need for 'Western Science' to recognize indigenous culture and knowledge. Leaving aside the question of what indigenous knowledge suggested that southern and northern anacondas may be different species, their argument falls within a wider discussion of the heritage of scientific names reflecting the values, cultural norms, and geopolitical realities of Western culture through the ages, some of which many would now deplore with the benefit of hindsight. The current debate concerns whether and to what extent naming practices or even objectionable existing names should be changed (Gillman and Wright 2020, Hammer and Thiele 2021, Smith and Figueiredo 2022, Guedes *et al.* 2023) or not (Palma and Heath 2021, Mosyakin 2022, Ceríaco *et al.* 2023, Pethiyagoda 2023, Jablonski and Dufresnes 2024, Jiménez-Mejías *et al.* 2024).

It is not our intention to contribute to this broader debate at the interface between science and society. However, we must point out that if one wished to follow the argumentation of Rivas *et al.*, one should also acknowledge the cultural heritage of European history. Ancient Greek and Roman authors had their own names for the Mediterranean snake species, with more than 15 centuries 'priority' over the current 'Western', post-Linnaean names (Böhme and Koppetsch 2021). In contrast to the vague origin of *akayima* from a tribal tradition, in Ancient Greece or Rome we even have identified individuals as 'taxon authors' such as Nicandros of Kolophon (*c.* 197–*c.* 130 BC) or Pliny the Elder (AD 23/24–79), whose snake names have two millennia

of 'priority' over Linnaean and post-Linnaean ones. 'Boa' (literally 'cow snake') would antedate *Elaphe*, 'Aspis' would antedate *Naja [haje]*, Pliny's binominal 'Aspis Ptyas' would antedate the names of spitting cobras in the *N. nigricollis* complex, 'Echis/Echidna' would antedate [male and female] *Vipera*, and so on. The only antique snake name retaining its original meaning is 'Kerastes' [= *Cerastes*]. One can only imagine the number of well-documented pre-Linnaean names in numerous languages for a widespread species such as the adder (*Vipera berus*) across its immense range. We think and hope that nobody will be interested in replacing the current system by this multicultural heritage.

In view of these ongoing discussions, we stress what we regard as three key self-evident truths that should govern the conversation about taxonomy and scientific nomenclature:

(i) Scientists must subscribe to a universal, global system of registering and labelling the planet's biodiversity, in a manner that ensures unique, universal, and stable (subject to development of knowledge) names for all taxa. Such a system is indispensable for communication, information retrieval, research, conservation and regulation globally, and benefits all of humanity.

(ii) The Linnaean system of nomenclature is the only such system currently in existence and, while not perfect, it has provided a global standard giving each species its own unique, universal classification and scientific name. It underpins virtually all of our collective global knowledge about our planet's biodiversity.

(iii) Any global bookkeeping system requires a set of unambiguous rules that ensures for each taxon a unique, universal scientific name. Those are the rules provided by the zoological, botanical, and microbial *Codes*.

We therefore caution against arbitrary disregard for the rules of the *Code* in formulating nomenclatural decisions. While, in extreme circumstances and with large-scale community consensus, agreed breaches of the *Code's* rules can enhance the stability of zoological nomenclature (Kaiser *et al.* 2013, Wüster *et al.* 2021), individual maverick decisions to override the *Code* should be strongly discouraged (e.g. Kaiser *et al.* 2020). There are mechanisms to lobby for change in the biological *Codes*, and these mechanisms should be followed by those who wish to see the *Codes* reflect the changing values of society. Engaging with ongoing consultations on future editions of the *Codes* and making the case for changes in appropriate journals, such as *Taxon* or the *Bulletin of Zoological Nomenclature* would be the way forward, as is happening already (e.g. Hammer and Thiele 2021).

We also emphasize that there is nothing new about the establishment of an indigenous name as a scientific name by Rivas *et al.* – there is ample precedent going all the way back to Linnaeus (e.g. *Coluber naja*, whose specific epithet is the Sinhalese word for cobra). In fact, many taxonomists transform suitable vernaculars into scientific names within the rules of the *Code* and with due regard for prior nomina. A listing of recently described reptile taxa (e.g. through the Reptile Database; Uetz *et al.* 2024) will reveal how much more of this is happening at present, with clearly 'Western' names restricted to a small minority of new nomina. Moreover, with at least 80% of the world's biodiversity

(Mora *et al.* 2011), but possibly vastly more (Larsen *et al.* 2017, Li and Wiens 2023), still to be named and catalogued, there is ample scope for redressing the balance in favour of indigenous names, and for greater inclusion of underrepresented minorities through a renewed global effort to document the diversity of our planet. However, crucially, this needs to happen within the rules of biological nomenclature, rather than by undermining the one global biodiversity cataloguing and information retrieval system we have.

CONCLUSION

As scientists in the 21ˢᵗ century, we have many technological advantages over our colleagues from bygone times, and we have assembled a vast amount of knowledge about the natural environment. We now have at our finger tips incredible analysis tools, as well as broad, nearly instant access to our colleagues' expertise and to printed materials all across the globe. That is how lucky we are, and in our discipline of taxonomy, these advantages are documented by the progress we are making every year as we continue to identify our fragile planet's biodiversity. However, it behoves us to remember that to produce meaningful, lasting taxonomy, we must not only *know* about the information at our disposal, we must *use* it. Indeed, we must look back to recognize whose shoulders we need to stand on (and whose taxon names we need to consider) to reach our research goals. As we continue to engage with the various animal groups in our respective zoological disciplines, we encourage our fellow taxonomists and users of taxonomy to acknowledge that taxonomy is a scientific process requiring expertise and training, to keep a set of best practices firmly in mind as we proceed with our analyses, and to stand firm in a commitment to place the interests of science before our personal gratification.

NOTE ADDED IN PROOF

While our paper was in press, Rivas *et al.* (2024b) published a follow-up to their original paper, where they made the name *Eunectes akayima* available under the *Code* (ICZN 1999) by providing a diagnosis compliant with Article 13.1.1, and they designated a neotype for *Boa murina* Linnaeus, 1758. They also provided evidence of differences in sexual size dimorphism (SSD) between northern and southern green anacondas.

Many of the other points raised in the new paper are reiterations and elaborations of earlier claims in Rivas *et al.* (2024a) and have been fully discussed above. This includes issues concerning their use of molecular divergences, molecular dating, the lack of analysis of contact zones and of critical testing of their mitochondrially defined candidate species, and the lack of distinction between scientific and vernacular names. While the differences in SSD described by Rivas *et al.* (2024b) add weight to the suggestion that northern and southern anacondas may be different species, the use of validatory rather than exploratory analyses means that the possibility of broad admixture still cannot be excluded.

However, two points require further comment:

1. The status of *nomina dubia* from the zone of overlap of the mtDNA haplotype clades in the Guianas should be resolved through the selection of appropriate, genetic-

ally characterised neotypes (Dubois *et al.* 2024), as their persistence as *nomina dubia* will continue to threaten nomenclatural stability. However, this will first require a resolution of the systematics of the green anacondas and the status of populations in the contact zone.

2. Neotype designation: Dubois *et al.* (2024) suggested that the specimen depicted in Plate 29, fig. 1 of Seba (1735), which they designated as the lectotype of *Boa murina*, was lost. On that basis, Rivas *et al.* (2024b) designated MPEG 27428 as the neotype of *Boa murina*. However, as detailed above, Seba's specimen remains extant as ZISP 1441, and is thus the name-bearing type of *Boa murina*; therefore MPEG 27428 loses that status (*Code*, Article 75.8). Moreover, since we have shown that the type locality of *Boa murina* is Trinidad and that ZISP 1441 is clearly a northern anaconda (neither of which Rivas *et al.* could have known), the choice of a southern anaconda from Pará as neotype is invalid on both taxonomic and geographical grounds (*Code*, Art. 75.3). *Eunectes akayima* Rivas *et al.*, 2024b is thus a junior subjective synonym of *Boa murina* Linnaeus, 1758, and if there are indeed two species of green anaconda, *Eunectes murinus* would be the name of the northern green anaconda, while the name of the southern green anaconda would require clarification.

Rivas *et al.* (2024b) make much of the importance of familiarity with the study organism over familiarity with the *Code*. The continuing uncertainty over the number of anaconda species and their nomenclatural instability emphasise that neither is enough on its own: the most enduring taxonomic revisions will be generated by multidisciplinary teams encompassing expertise on the organisms, on best practices in taxonomy and species delimitation, and on the *Code*. We hope that our paper will raise awareness of the need for collaborative and truly integrative taxonomy that follows best practices in both science and nomenclature.

SUPPORTING INFORMATION

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Wolfgang Wüster (conceptualization, methodology, formal analysis, investigation, writing—original draft, writing—review and editing), Hinrich Kaiser (conceptualization, investigation, writing—original draft, writing—review and editing), Marinus S. Hoogmoed (conceptualization, investigation, writing—original draft, writing—review and editing), Luis M. P. Ceríaco (conceptualization, writing—original draft, writing—review and editing), Lutz Dirksen (writing—original draft, writing—review and editing), Christophe Dufresnes (writing—original draft, writing—review and editing), Frank Glaw (writing—original draft, writing—review and editing), Axel Hille (methodology, formal analysis), Jörn Köhler (writing—original draft, writing—review and editing), Thore Koppetsch (methodology, formal analysis,

DATA AVAILABILITY

Datasets used for morphological (re)analysis, as well as molecular alignments and tree files are available from the Zenodo repository (https://doi.org/10.5281/zenodo.11581482).

REFERENCES

Anonymous. *Catalogus van de Uitmuntende Cabinetten, met Allerley Soorten van Ongemeene Schoone Gepolyste Hoorns, Dubletschelpen, Coraal- en Zeegewassen; Benevens het Zeldzame en Vermaarde Cabinet van Gediertens in Flessen en Naturalia, en Veele Raare Anatomische Preparata van den Professor Ruysch: als Mede een Verzameling van Diverse Mineralen Versteende Zaaken, Agaate Boomsteenen, Edele Gesteentens, en Verscheidene Andere Rariteiten. Met Veel Moeite en Kosten in een Reeks van Jaaren Vergadert. En Nagelaten door Wylen den Heere Albertus Seba, Lid van de Keizerlyke Leopoldische Carolinische en Koningl. Engelsche Societeit der Wetenschappen, alsook der Academie van Boloniën. Dewelke Verkogt Sullen Worden door de Makelaars Th. Sluyter, J. Schut en N. Blinkvliet, op Vrydag den 14. April 1752. En Volgende Dagen, 's Morgens ten 9, en 's Namiddags ten 3 Uuren, te Amsterdam, ten Huize van Huybert de Wit, Casteleyn in 't Oudezyds Heeren Logement. Zullende alles des Woensdags voor de Verkooping van een Ieder Kunnen Gezien werden. De Catalogus is te Bekomen by de Voornoemde Makelaars. Catalogus van Diverse Slangen. Volgens Tab. & N. van het 2e Deel*, 1752, 1–13. [With 12 handwritten pages inserted, listing the buyers of lots]

Ahrens D. Species diagnosis and DNA taxonomy. In: DeSalle R (ed.). *Methods in Molecular Biology. DNA Barcoding.* New York, NY: Springer, 2024, 33–52. https://doi.org/10.1007/978-1-0716-3581-0_2

Ahrens D, Ahyong ST, Ballerio A *et al.* Is it time to describe new species without diagnoses? A comment on Sharkey *et al.* (2021). *Zootaxa* 2021;**5027**:151–9. https://doi.org/10.11646/zootaxa.5027.2.1

Anderson CG, Greenbaum E. Phylogeography of northern populations of the black-tailed rattlesnake (*Crotalus molossus* Baird and Girard, 1853), with the revalidation of *C. ornatus* Hallowell, 1854. *Herpetological Monographs* 2012;**26**:19–57. https://doi.org/10.1655/herpmonographs-d-11-00012.1

Andersson LG. Catalogue of Linnean type-specimens of snakes in the Royal Museum in Stockholm. *Bihang till Kongliga Svenska Vetenskaps-Akademiens. Handlingar* 1899;**24**:1–35.

Arbesman S. *The Half-life of Facts: Why Everything we Know has an Expiration Date.* New York, NY: Penguin, 2012.

Babik W, Branicki W, Crnobrnja-Isailović J *et al.* Phylogeography of two European newt species — discordance between mtDNA and morphology. *Molecular Ecology* 2005;**14**:2475–91. https://doi.org/10.1111/j.1365-294x.2005.02605.x

Baird SF, Girard C. *Catalogue of North American Reptiles in the Museum of the Smithsonian Institution. Part I. Serpents.* Washington, DC: Smithsonian Institution, 1853.

Bauer AM, Günther R. Origin and identity of the von Borcke collection of amphibians and reptiles in the Museum für Naturkunde in Berlin: a cache of Seba specimens? *Zoosystematics and Evolution* 2013;**89**:167–85. https://doi.org/10.1002/zoos.201300005

Bauer AM, Wahlgren R. On the Linck collection and specimens of snakes figured by Johann Jakob Scheuchzer (1735) – the oldest fluid-preserved herpetological collection in the world? *Bonn Zoological Bulletin* 2013;**62**:220–52.

Bauer AM, Denzer W, Dubois A *et al.* The specimens of green anaconda, *Boa murina* Linnaeus, 1758 (Squamata, Serpentes, Boidae, *Eunectes*), from the collection of Albertus Seba, and recommendations for tracing historical specimens. *Bionomina* 2024;**38**:7–29. https://doi.org/10.11646/bionomina.38.1.2

Benjamins HD, Snelleman JF (eds). *Encyclopaedie van Nederlandsch West-Indie: West-Indië.* 's-Gravenhage, The Netherlands: Martinus Nijhoff / Leiden, The Netherlands: N.V. v. h. E.J. Brill, 1914.

Bernstein JM, Ruane S. Maximizing molecular data from low-quality fluid-preserved specimens in natural history collections. *Frontiers in Ecology and Evolution* 2022;**10**:893088. https://doi.org/10.3389/fevo.2022.893088

Boeseman M. The vicissitudes and dispersal of Albertus Seba's zoological specimens. *Zoologische Mededelingen* 1970;**44**:177–206.

Böhme W, Koppetsch T. Snake names in the Greek-Roman antiquity: old characterizations, identity in current zoology, and change of their original meaning in post-Linnean herpetology. *Salamandra* 2021;**57**:475–501.

Bonnet T, Leblois R, Rousset F *et al.* A reassessment of explanations for discordant introgressions of mitochondrial and nuclear genomes. *Evolution* 2017;**71**:2140–58. https://doi.org/10.1111/evo.13296

Boos HEA. *The Snakes of Trinidad and Tobago.* College Station, TX: Texas A & M University Press, 2001.

Braby MF, Hsu YF, Lamas G. How to describe a new species in zoology and avoid mistakes. *Zoological Journal of the Linnean Society* 2024;zlae043. https://doi.org/10.1093/zoolinnean/zlae043

Brainard J. Fast-growing open-access journals stripped of coveted impact factors. *Science* 2023;**379**:1283–4. https://doi.org/10.1126/science.adi0092

Britz R, Hundsdörfer A, Fritz U. Funding, training, permits – the three big challenges of taxonomy. *Megataxa* 2020;**1**:49–52. https://doi.org/10.11646/megataxa.1.1.10

Burbrink F. Phylogeographic analysis of the cornsnake (*Elaphe guttata*) complex as inferred from maximum likelihood and Bayesian analyses. *Molecular Phylogenetics and Evolution* 2002;**25**:465–76. https://doi.org/10.1016/s1055-7903(02)00306-8

Burbrink FT, Ruane S. Contemporary philosophy and methods for studying speciation and delimiting species. *Ichthyology & Herpetology* 2021;**109**:874–94. https://doi.org/10.1002/ece3.9069

Burbrink FT, Gehara M, McKelvy AD *et al.* Resolving spatial complexities of hybridization in the context of the gray zone of speciation in North American ratsnakes (*Pantherophis obsoletus* complex). *Evolution* 2021;**75**:260–77. https://doi.org/10.1111/evo.14141

Cabrera Bosch MI. *El Consejo Real de Castilla y la Ley.* Madrid, Spain: Consejo Superior de Investigaciones Científicas, 1993.

Carstens BC, Pelletier TA, Reid NM *et al.* How to fail at species delimitation. *Molecular Ecology* 2013;**22**:4369–83. https://doi.org/10.1111/mec.12413

Ceríaco LMP, Aescht E, Ahyong ST *et al.* Renaming taxa on ethical grounds threatens nomenclatural stability and scientific communication. *Zoological Journal of the Linnean Society* 2023;**197**:283–6. https://doi.org/10.1093/zoolinnean/zlac107

Chan KO, Hutter CR, Wood PL Jr *et al.* Gene flow creates a mirage of cryptic species in a Southeast Asian spotted stream frog complex. *Molecular Ecology* 2020;**29**:3970–87. https://doi.org/10.1111/mec.15603

Coleman CO, Radulovici AE. Challenges for the future of taxonomy: talents, databases and knowledge growth. *Megataxa* 2020;**1**:28–34. https://doi.org/10.11646/megataxa.1.1.5

Cope ED. Synopsis of the species of *Holcosus* and *Ameiva*, with diagnoses of New West Indian and South American Colubridæ. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1862;**14**:60–82.

Crosetto P. *Is MDPI a Predatory Publisher?* 2021. https://paolocrosetto.wordpress.com/2021/04/12/is-mdpi-a-predatory-publisher (7 May 2024, date last accessed).

Crottini A, Madsen O, Poux C *et al*. Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. *Proceedings of the National Academy of Sciences* 2012;**109**:5358–63. https://doi.org/10.1073/pnas.1112487109

Daudin FM. *Histoire Naturelle, Génerale et Particulière des Reptiles; Ouvrage Faisant Suite aux Oeuvres de Leclerc de Buffon, et Partie du Cours Complet d'Histoire Naturelle Rédigé par C.S. Sonnini, Membre de Plusieurs Sociétés Savantes. Tome Sixième.* Paris, France: F. Dufart, 1803.

Davis PM. *Journal Usage Half-Life.* 2013. https://www.infodocket.com/wp-content/uploads/2013/12/Journal-Usage-Half-Life-Study.pdf (17 April 2024, date last accessed).

Denzer W, Kaiser H. Naming and gaming: the illicit taxonomic practice of 'nomenclatural harvesting' and how to avoid it. *Journal of Zoology* 2023;**320**:161–8. https://doi.org/10.1111/jzo.13061

de Queiroz K. The general lineage concept of species, species criteria, and the process of speciation. A conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH (eds), *Endless Forms. Species and Speciation*. New York, NY: Oxford University Press, 1998, 57–75.

Després L. One, two or more species? Mitonuclear discordance and species delimitation. *Molecular Ecology* 2019;**28**:3845–7. https://doi.org/10.1111/mec.15211

Dirksen L. *Anakondas: Monographische Revision der Gattung Eunectes Wagler, 1830 (Serpentes, Boidae).* Münster, Germany: Natur und Tier-Verlag, 2002.

Doniol-Valcroze P, Ursenbacher S, Mebert K *et al*. Conflicting relationships of *Vipera walser* inferred from nuclear genes sequences and mitochondrial DNA. *Journal of Zoological Systematics and Evolutionary Research* 2021;**59**:2307–20. https://doi.org/10.1111/jzs.12543

Drew LW. Are we losing the science of taxonomy? *BioScience* 2011;**61**:942–6. https://doi.org/10.1525/bio.2011.61.12.4

Driessen-Van het Reve JJ. *De Kunstkamera van Peter de Grote: de Hollandse Inbreng, Gereconstrueerd uit Brieven van Albert Seba en Johann Daniel Schumacher uit de Jaren 1711–1752.* Hilversum, The Netherlands: Verloren, 2006.

Dubois A. Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia* 2000;**4**:33–98.

Dubois A. Proposed rules for the incorporation of nomina of higher-ranked zoological taxa in the International Code of Zoological Nomenclature. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema* 2005;**27**:365–426.

Dubois A, Aneesh PT, Bauer AM *et al*. The Linz Zoocode project. Third report of activities (2020). Nomenclatural availability. 2. Work availability. *Bionomina* 2022a;**28**:18–49. https://doi.org/10.11646/bionomina.28.1.2

Dubois A, Aneesh PT, Bauer AM *et al*. The Linz Zoocode project. Fifth report of activities (2022). Nomenclatural availability. 4. Electronic publication. *Bionomina* 2022b;**28**:71–119. https://doi.org/10.11646/bionomina.28.1

Dubois A, Denzer W, Entiauspe-Neto OM *et al*. Nomenclatural problems raised by the recent description of a new anaconda species (Squamata, Serpentes, Boidae), with a nomenclatural review of the genus *Eunectes*. *Bionomina* 2024;**37**:8–58. https://doi.org/10.11646/bionomina.37.1.2

Dubois A, Frétey T, Ineich I. It is high time that taxonomists follow the Code. 3. The *Bungarus romulusi* case (Serpentes, Elapidae). *Bionomina* 2021;**21**:120–2. https://doi.org/10.11646/bionomina.21.1.8

Dufresnes C, Jablonski D. A genomics revolution in amphibian taxonomy. *Science* 2022;**377**:1272. https://doi.org/10.1126/science.ade5002

Dufresnes C, Brelsford A, Jeffries DL *et al*. Mass of genes rather than master genes underlie the genomic architecture of amphibian speciation. *Proceedings of the National Academy of Sciences of the United States of America* 2021;**118**:e2103963118. https://doi.org/10.1073/pnas.2103963118

Dufresnes C, Ghielmi S, Halpern B *et al*. Phylogenomic insights into the diversity and evolution of Palearctic vipers. *Molecular Phylogenetics and Evolution* 2024;**197**:108095. https://doi.org/10.1016/j.ympev.2024.108095

Dufresnes C, Mazepa G, Jablonski D *et al*. Fifteen shades of green: the evolution of *Bufotes* toads revisited. *Molecular Phylogenetics and Evolution* 2019;**141**:106615. https://doi.org/10.1016/j.ympev.2019.106615

Dunn ER, Conant R. Notes on anacondas, with descriptions of two new species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1936;**88**:503–6.

Engel H. The life of Albert Seba. *Svenska Linné Sällskapets Arsskrift* 1937;**20**:75–100.

Engel H. Alphabetical list of Dutch zoological cabinets and menageries. *Bijdragen tot de Dierkunde* 1939;**27**:247–346. https://doi.org/10.1163/26660644-02701011

Engel H. The sale-catalogue of the Cabinets of Natural History of Albertus Seba (1752). A curious document from the period of the naturae curiosi. *Bulletin of the Research Council of Israel. Section B. Zoology* 1961;**10B**:119–31.

Engel H. Hendrik Engel's Alphabetical List of Dutch Zoological Cabinets and Menageries, prepared by P. Smit, A.P.M. Sanders & J.P.F. van der Veer. *Nieuwe Nederlandse bijdragen tot de geschiedenis der geneeskunde en der natuurwetenschappen* 1986;**19**:i–x, 1–340

Fernholm B, Wheeler A. Linnaean fish specimens in the Swedish Museum of Natural History, Stockholm. *Zoological Journal of the Linnean Society* 1983;**78**:199–286. https://doi.org/10.1111/j.1096-3642.1983.tb00867.x

Folt B, Bauder J, Spear S *et al*. Taxonomic and conservation implications of population genetic admixture, mito-nuclear discordance, and male-biased dispersal of a large endangered snake, *Drymarchon couperi*. *PLoS One* 2019;**14**:e0214439. https://doi.org/10.1371/journal.pone.0214439

Fong JJ, Blom MPK, Aowphol A *et al*. Recent advances in museomics: revolutionizing biodiversity research. *Frontiers in Ecology and Evolution* 2023;**11**:1188172. https://doi.org/10.3389/fevo.2023.1188172

Fritz U, Schmidtler JF. The fifth labour of Heracles: cleaning the Linnean stable of names for grass snakes (*Natrix astreptophora, N. helvetica, N. natrix* sensu stricto). *Vertebrate Zoology* 2020;**70**:621–65. https://doi.org/10.26049/VZ70-4-2020-07

Galtier N, Nabholz B, Glémin S *et al*. Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology* 2009;**18**:4541–50. https://doi.org/10.1111/j.1365-294X.2009.04380.x

Gillman LN, Wright SD. Restoring indigenous names in taxonomy. *Communications Biology* 2020;**3**:609. https://doi.org/10.1038/s42003-020-01344-y

Gronovius LT. *Amphibiorum Animalium Historia Zoologica Exhibens Amphibiorum qui in Museo Laurentii Theorodi Gronovii, J.U.D. Adservantus, Descriptiones Ordine Systematico. Musei Ichthyologici Tomus Secundus sistens Piscium Indigenorum & Nonnullorum Exoticorum, quorum Maxima Pars in Museo Laurentii Theorodi Gronovii, J.U.D. Adservatur, nec non Quorundam in Aliis Museis Observatorum Descriptionis. Accedunt Nonnullorum Exoticorum Piscium Icones Aeri Incisae, et Amphibiorum Animalium Historia Zoologica.* Lugduni Batavorum [Leiden], The Netherlands: Theodorum Haak, 1756, 47–88.

Guedes P, Alves-Martins F, Arribas JM *et al*. Eponyms have no place in 21st-century biological nomenclature. *Nature Ecology & Evolution* 2023;**7**:1157–60. https://doi.org/10.1038/s41559-023-02022-y

Hammer TA, Thiele KR. Proposals to amend Articles 51 and 56 and Division III, to allow the rejection of culturally offensive and inappropriate names. *Taxon* 2021;**70**:1392–4. https://doi.org/10.1002/tax.12620

Harrington S, Burbrink FT. Complex cycles of divergence and migration shape lineage structure in the common kingsnake species complex.

Journal of Biogeography 2022;**50**:341–51. https://doi.org/10.1111/jbi.14536

Hillis DM. Species delimitation in herpetology. *Journal of Herpetology* 2019;**53**:3–12. https://doi.org/10.1670/18-123

Hillis DM. Species, clades, and their relationship to paraphyly and monophyly: examples from the *Pantherophis obsoletus* complex. *Herpetological Review* 2022;**53**:47–53.

Hillis DM, Wüster W. Taxonomy and nomenclature of the *Pantherophis obsoletus* complex. *Herpetological Review* 2021;**52**:51–2.

Hillis DM, Chambers EA, Devitt TJ. Contemporary methods and evidence for species delimitation. *Ichthyology & Herpetology* 2021;**109**:895–903. https://doi.org/10.1643/h2021082

Holthuis LB. Albertus Seba's 'Locupletissimi Rerum Naturalium Thesauri...'. (1734–1735) and the 'Planches de Seba' (1827–1831). *Zoologische Mededelingen* 1969;**43**:239–252 + 3 plates.

ICZN. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Bulletin of Zoological Nomenclature* 2012;**69**:161–9.

ICZN. *International Code of Zoological Nomenclature: Fourth Edition.* London, UK: The International Trust for Zoological Nomenclature, 1999.

Ineich I. Analyses d'ouvrage. *Anaconda. The Secret Life of the World's Largest Snake* de Jesús A. Rivas. *Bulletin de la Société Herpétologique de France* 2021;**178**:106–12. https://doi.org/10.48716/BULLSHF.178-13

Irwin DE. Phylogeographic breaks without geographic barriers to gene flow. *Evolution* 2002;**56**:2383–94. https://doi.org/10.1111/j.0014-3820.2002.tb00164.x

Jablonski D, Dufresnes C. Nomenclatural censorship puts biodiversity conservation and taxonomic science at risk. *Alytes* 2024;**41**:1–4.

Jablonski D, Ribeiro-Júnior MA, Simonov E *et al.* A new, rare, small-ranged, and endangered mountain snake of the genus *Elaphe* from the Southern Levant. *Scientific Reports* 2023;**13**:4839. https://doi.org/10.1038/s41598-023-30878-4

Jackson MD, Scherz MD, Zona S. Taxonomy is not beholden to its dependencies: a rebuttal to Garnett and Christidis (2017). *PeerJ Preprints* 2017;**5**:e3060v1. https://doi.org/10.7287/peerj.preprints.3060v1

Jiménez-Mejías P, Manzano S, Gowda V *et al.*; 1543 additional coauthors. Protecting stable biological nomenclatural systems enables universal communication: a collective international appeal. *BioScience* 2024;biae043. https://doi.org/10.1093/biosci/biae043

Joly S, Bruneau A. Incorporating allelic variation for reconstructing the evolutionary history of organisms from multiple genes: an example from *Rosa* in North America. *Systematic Biology* 2006;**55**:623–36. https://doi.org/10.1080/10635150600863109

Juriev KB. Albert Seba and his contribution to the development of herpetology. *Proceedings of the Zoological Institute of the Academy of Sciences of the USSR* 1981;**101**:109–20.

Kaiser H, Crother BI, Kelly CMR *et al.* Best practices: in the 21st century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. *Herpetological Review* 2013;**44**:8–23.

Kaiser H, Thomson SA, Shea GM. *Nawaran* Esquerré, Donnellan, Brennan, Lemmon, Lemmon, Zaher, Grazziotin & Keogh, 2020 is an invalid junior synonym of *Nyctophilopython* Wells & Wellington, 1985 (Squamata, Pythonidae): simple priority without ZooBank pre-registration. *Bionomina* 2020;**20**:47–54. https://doi.org/10.11646/bionomina.20.1.4

Kehlmaier C, Zhang X, Georges A *et al.* Mitogenomics of historical type specimens of Australasian turtles: clarification of taxonomic confusion and old mitochondrial introgression. *Scientific Reports* 2019;**9**:5841. https://doi.org/10.1038/s41598-019-42310-x

Kok PJR. Special issue: a few steps back, several steps forward. *Journal of Vertebrate Biology* 2023;**72**:1–3. https://doi.org/10.25225/jvb.E2303

Krell FT. ZooBank and the next edition of the Code – challenges and new developments in the 250th year of zoological nomenclature. *Aquatic Insects* 2009;**31**:269–82. https://doi.org/10.1080/01650420903083393

Kumar S, Suleski M, Craig JM *et al.* TimeTree 5: an expanded resource for species divergence times. *Molecular Biology and Evolution* 2022;**39**:msac174. https://doi.org/10.1093/molbev/msac174

Larsen BB, Miller EC, Rhodes MK *et al.* Inordinate fondness multiplied and redistributed: the number of species on Earth and the new Pie of Life. *The Quarterly Review of Biology* 2017;**92**:229–65. https://doi.org/10.1086/693564

Li X, Wiens JJ. Estimating global biodiversity: the role of cryptic insect species. *Systematic Biology* 2023;**72**:391–403. https://doi.org/10.1093/sysbio/syac069

Linnaeus C. *Museum S:æ R:æ M:tis Adolphi Friderici Regis Svecorum, Gothorum, Vandalorumque. Hær. Norv. Duc. Slesv. Hols. Storm. Ditm. Com. Oldenb. Delmenhorstiæ. &c. &c. Animalia Rariora Imprimis, et Exotica: Quadrupedia, Aves, Amphibia, Pisces, Insecta, Vermes Describuntur et Determinantur, Latine et Svetice cum Iconibus.* Holmiæ [Stockholm, Sweden]: Kongliga Tryckeriet, 1754.

Linnaeus C. *Systema Naturæ per Regna Tria Naturæ, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* Editio Decima, Reformata. Holmiæ [Stockholm, Sweden]: Laurentii Salvii [Lars Salvius, printer], 1758.

Linnaeus C. *Museum S:æ R:æ M:tis Adolphi Friderici Regis Svecorum, Gothorum, Vandalorumque &c. &c. &c. in quo Animalia Rariora Imprimis & Exotica: Aves, Amphibia, Piscis describuntur. Tomi Secundi Prodromus.* Holmiæ [Stockholm, Sweden]: Laur. Salvii [Lars Salvius, printer], 1764.

Linnaeus C. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Editio Duodecima, Reformata. Holmiae [Stockholm, Sweden]: Laurentii Salvii [Lars Salvius, printer], 1766.

Löbl I, Klausnitzer B, Hartmann M *et al.* The silent extinction of species and taxonomists – an appeal to science policymakers and legislators. *Diversity* 2023;**15**:1053. https://doi.org/10.3390/d15101053

Lukoschek V, Keogh JS, Avise JC. Evaluating fossil calibrations for dating phylogenies in light of rates of molecular evolution: a comparison of three approaches. *Systematic Biology* 2012;**61**:22–43. https://doi.org/10.1093/sysbio/syr075

Marshall TL, Chambers EA, Matz MV *et al.* How mitonuclear discordance and geographic variation have confounded species boundaries in a widely studied snake. *Molecular Phylogenetics and Evolution* 2021;**162**:107194. https://doi.org/10.1016/j.ympev.2021.107194

May RM. Taxonomy as destiny. *Nature* 1990;**347**:129–30. https://doi.org/10.1038/347129a0

Milto KD, Barabanov AV. An annotated catalogue of the amphibian types in the collection of the Zoological Institute, Russian Academy of Sciences, St. Petersburg. *Russian Journal of Herpetology* 2011;**18**:137–53. https://doi.org/10.30906/1026-2296-2011-18-2-137-153

Miralles A, Bruy T, Wolcott K *et al.* Repositories for taxonomic data: where we are and what is missing. *Systematic Biology* 2020;**69**:1231–53. https://doi.org/10.1093/sysbio/syaa026

Miralles A, Puillandre N, Vences M. DNA barcoding in species delimitation: from genetic distances to integrative taxonomy. In: DeSalle R (ed.), *Methods in Molecular Biology. DNA Barcoding.* New York, NY: Springer US, 2024, 77–104.

Mora C, Tittensor DP, Adl S *et al.* How many species are there on Earth and in the ocean? *PLoS Biology* 2011;**9**:e1001127. https://doi.org/10.1371/journal.pbio.1001127

Mosyakin SL. If "*Rhodes-*" must fall, who shall fall next? *Taxon* 2022;**71**:249–55. https://doi.org/10.1002/tax.12659

Murphy JC. Crossing Bond's Line: the herpetofaunal exchange between the eastern Caribbean and mainland South America. In: Powell R, Henderson RW (eds), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz.* Ithaca, NY: Society for the Study of Amphibians and Reptiles, 1996, 207–16.

Murphy JC. *Amphibians and Reptiles of Trinidad and Tobago.* Melbourne, FL: Krieger, 1997.

Musiał A, Gryglewski RW, Kielczewski S *et al.* Formalin use in anatomical and histological science in the 19th and 20th centuries. *Folia Medica Cracoviensia* 2016;**56**:31–40.

Near TJ, Eytan RI, Dornburg A *et al.* Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America* 2012;**109**:13698–703. https://doi.org/10.1073/pnas.1206625109

Newson LA. *Aboriginal and Spanish Colonial Trinidad: a Study in Culture Contact*. London, UK: Academic Press, 1976.

Nogueira CC, Argôlo AJS, Arzamendia V *et al*. Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South American Journal of Herpetology* 2019;**14**:1–274. https://doi.org/10.2994/SAJH-D-19-00120.1

Padial JM, Miralles A, De la Riva I *et al*. The integrative future of taxonomy. *Frontiers in Zoology* 2010;**7**:16. https://doi.org/10.1186/1742-9994-7-16

Palma RL, Heath ACG. Science versus vernacular: should some taxa of animals and plants be renamed according to 'indigenous' practices? *Bionomina* 2021;**22**:32–8. https://doi.org/10.11646/bionomina.22.1.1

Pereyra MO, Blotto BL, Baldo D *et al*. Evolution in the genus *Rhinella*: a total evidence phylogenetic analysis of neotropical true toads (Anura: Bufonidae). *Bulletin of the American Museum of Natural History* 2021;**447**:1–156. https://doi.org/10.1206/0003-0090.447.1.1

Peters WCH. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. *Berichte über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen Preußischen Akademie der Wissenschaften zu Berlin* 1854;**1854**:614–28.

Pethiyagoda R. Policing the scientific lexicon: the new colonialism? *Megataxa* 2023;**10**:20–5. https://doi.org/10.11646/megataxa.10.1.4

Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. *Genetics* 2000;**155**:945–59. https://doi.org/10.1093/genetics/155.2.945

Puillandre N, Modica MV, Zhang Y *et al*. Large-scale species delimitation method for hyperdiverse groups. *Molecular Ecology* 2012;**21**:2671–91. https://doi.org/10.1111/j.1365-294X.2012.05559.x

Pyron RA, Burbrink FT. Systematics of the common kingsnake (*Lampropeltis getula*; Serpentes: Colubridae) and the burden of heritage in taxonomy. *Zootaxa* 2009;**2241**:22–32. https://doi.org/10.1111/j.1365-294X.2009.04292.x

Rancilhac L, Bruy T, Scherz MD *et al*. Target-enriched DNA sequencing from historical type material enables a partial revision of the Madagascar giant stream frogs (genus *Mantidactylus*). *Journal of Natural History* 2020;**54**:87–118. https://doi.org/10.1080/00222933.2020.1748243

Rannala B, Yang Z. Inferring speciation times under an episodic molecular clock. *Systematic Biology* 2007;**56**:453–66. https://doi.org/10.1080/10635150701420643

Ratnarathorn N, Nadolski B, Sumontha M *et al*. An expanded description, natural history, and genetic variation of the recently described cobra species *Naja fuxi* Shi *et al*., 2022. *Vertebrate Zoology* 2023;**73**:257–76. https://doi.org/10.3897/vz.73.e89339

Reinhardt JT. Beskrivelse af nogle nye Slangearter. *Kongelige Danske Videnskabernes Selskabs, Naturvidenskabelige og Mathematiske Afhandlinger* 1843;**10**:233–79.

Renner SS. A return to Linnaeus's focus on diagnosis, not description: the use of DNA characters in the formal naming of species. *Systematic Biology* 2016;**65**:1085–95. https://doi.org/10.1093/sysbio/syw032

Reynolds RG, Niemiller ML, Hedges SB *et al*. Molecular phylogeny and historical biogeography of West Indian boid snakes (*Chilabothrus*). *Molecular Phylogenetics and Evolution* 2013;**68**:461–70. https://doi.org/10.1016/j.ympev.2013.04.029

Rheindt FE, Bouchard P, Pyle RL *et al*. Tightening the requirements for species diagnoses would help integrate DNA-based descriptions in taxonomic practice. *PLoS Biology* 2023;**21**:e3002251. https://doi.org/10.1371/journal.pbio.3002251

Rivas JA. *Anaconda: the Secret Life of the World's Largest Snake*. Oxford, UK: Oxford University Press, 2020.

Rivas JA, Burghardt GM. Understanding sexual size dimorphism in snakes: wearing the snake's shoes. *Animal Behaviour* 2001;**62**:F1–6. https://doi.org/10.1006/anbe.2001.1755

Rivas JA, De La Quintana P, Mancuso M , *et al*. Disentangling the anacondas: revealing a new green species and rethinking yellows. *Diversity* 2024a;**16**:127. https://doi.org/10.3390/d16020127

Rivas JA, Terra JS, Roosen M *et al*. Description of the Northern green anaconda (*Eunectes akayima* sp. nov. Serpentes; Boidae): what is in a name? *Diversity* 2024b;**16**: 418. https://doi.org/10.3390/d16070418

Rivera PC, Di Cola V, Martínez JJ *et al*. Species delimitation in the continental forms of the genus *Epicrates* (Serpentes, Boidae) integrating phylogenetics and environmental niche models. *PLoS One* 2011;**6**:e22199. https://doi.org/10.1371/journal.pone.0022199

Rivera PC, Gardenal CN, Chiaraviglio M. Sex-biased dispersal and high levels of gene flow among local populations in the Argentine boa constrictor, *Boa constrictor occidentalis*. *Austral Ecology* 2006;**31**:948–55. https://doi.org/10.1111/j.1442-9993.2006.01661.x

Ruane S, Austin CC. Phylogenomics using formalin-fixed and 100+ year-old intractable natural history specimens. *Molecular Ecology Resources* 2017;**17**:1003–8. https://doi.org/10.1111/1755-0998.12655

Sauer CO. *The Early Spanish Main*. Cambridge, UK: Cambridge University Press, 1966.

Scherz MD, Vences M, Rakotoarison A *et al*. Lumping or splitting in the Cophylinae (Anura: Microhylidae) and the need for a parsimony of taxonomic changes: a response to Peloso *et al*. (2017). *Salamandra* 2017;**53**:479–83.

Scheuchzer JJ. *Physica Sacra. Iconibus Æneis Illustrata, Procurante & Sumtus Suppeditante Johanne Andrea Pfeffel, Augustano, Sacræ, Cæsaræ Majestatis Chalcographo Aulico*. Augustæ Vindelicorum & Vlmae [Augsburg and Ulm, Germany]: Christian Ulrich Wagner, 1735.

Schield DR, Card DC, Adams RH *et al*. Incipient speciation with biased gene flow between two lineages of the western diamondback rattlesnake (*Crotalus atrox*). *Molecular Phylogenetics and Evolution* 2015;**83**:213–23. https://doi.org/10.1016/j.ympev.2014.12.006

Seba A. *Locupletissimi Rerum Naturalium Thesauri Accurata Descriptio, et Iconibus Artificiosissimis Expressio, per Universam Physices Historiam. Opus, Cui, in hoc Rerum Genere, Nullum par Exstitit. Ex Toto Terrarum Orbe Collegit, Digessit, Descripsit, et Depingendum Curavit. Tomus I.* Amsteraedami [Amsterdam, The Netherlands]: J. Wetstenium, & Gul. Smith, & Janssonio-Waesbergios, 1734.

Seba A. *Locupletissimi Rerum Naturalium Thesauri Accurata Descriptio, et Iconibus Artificiosissimis Expressio, per Universam Physices Historiam. Opus, Cui, in hoc Rerum Genere, Nullum par Exstitit. Ex Toto Terrarum Orbe Collegit, Digessit, Descripsit, et Depingendum Curavit. Tomus II.* Amsterlaedami [Amsterdam, The Netherlands]: J. Wetstenium, & Gul. Smith, & Janssonio-Waesbergios, 1735.

Smaniotto NP, Moreira LFB, Rivas JA *et al*. Home range size, movement, and habitat use of yellow anacondas (*Eunectes notaeus*). *Salamandra* 2020;**56**:159–67.

Smith GF, Figueiredo E. "*Rhodes-*" must fall: some of the consequences of colonialism for botany and plant nomenclature. *Taxon* 2022;**71**:1–5. https://doi.org/10.1002/tax.12598

Sonnini CS, Latreille PA. *Histoire Naturelle des Reptiles, avec Figures Dessinées d'après Nature. Tome III.* Paris, France: Imprimerie de Crapelet, 1801.

Stedman JG. Narrative, *of a Five Years' Expedition, Against the Revolted Negroes of Surinam, in Guiana, on the Wild Coast of South America, from the Year 1772, to 1777: Elucidating the History of that Country, and Describing its Productions, viz. Quadrupedes, Birds, Fishes, Reptiles, Trees, Shrubs, Fruits, & Roots: with an Account of the Indians of Guiana, & Negroes of Guinea.* London, UK: J.J. Johnson & J. Edwards, 1796.

Strimple PD, Puorto G, Holmstrom WF *et al*. On the status of the anaconda *Eunectes barbouri* Dunn & Conant. *Journal of Herpetology* 1997;**31**:607–9. https://doi.org/10.2307/1565623

Tamura K, Stecher G, Kumar S. MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 2021;**38**:3022–7. https://doi.org/10.1093/molbev/msab120

Tarkhnishvili D, Hille A, Waller T *et al*. Morphological trends and genetic divergence in anacondas, genus *Eunectes* Wagler, 1830 (Serpentes: Boidae). *Amphibia-Reptilia* 2022;**43**:379–93. https://doi.org/10.1163/15685381-bja10114

Thomas O. On the probable identity of certain specimens, formerly in the Lidth de Jeude collection, and now in the British Museum, with

those figured by Albert Seba in his 'Thesaurus' of 1734. *Proceedings of the Zoological Society of London* 1892;**60**:309–48. https://doi.org/10.1111/j.1469-7998.1892.tb06833.x

Thomson SA, Pyle RL, Ahyong ST *et al.* Taxonomy based on science is necessary for global conservation. *PLoS Biology* 2018;**16**:e2005075. https://doi.org/10.1371/journal.pbio.2005075

Toews DPL, Brelsford A. The biogeography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* 2012;**21**:3907–30. https://doi.org/10.1111/j.1365-294X.2012.05664.x

Townsend TM, Alegre RE, Kelley S *et al.* Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles. *Molecular Phylogenetics and Evolution* 2008;**47**:129–42. https://doi.org/10.1016/j.ympev.2008.01.008

Uetz P, Freed P, Aguilar R *et al.* (eds). *The Reptile Database.* http://www.reptile-database.org (28 April 2024, date last accessed).

Valencia-Zuleta A, Milto KD, Maciel NM. Redescription of the holotype of the cane toad *Rana marina* Linnaeus, 1758 (Anura: Bufonidae). *Zootaxa* 2024;**5453**:135–43. https://doi.org/10.11646/zootaxa.5453.1.10

Vásquez-Restrepo JD, Alfonso-Rojas A, Palacios-Aguilar R. On the validity of the recently described northern green anaconda *Eunectes akayima* (Squamata, Serpentes). *Bionomina* 2024;**37**:1–7. https://doi.org/10.11646/bionomina.37.1.1

Vences M, Miralles A, Dufresnes C. Next-generation species delimitation and taxonomy: implications for biogeography. *Journal of Biogeography* 2024;jbi.14807. https://doi.org/10.1111/jbi.14807

Wahlgren R. Carl Linnaeus and the Amphibia. *Bibliotheca Herpetologica* 2012;**9**:5–38.

Wallach V. Synonymy and preliminary identification of the snake illustrations of Albertus Seba's 'Thesaurus' (1734–1735). *Hamadryad* 2011;**35**:1–190.

Wied-Neuwied M Prinz zu. *Reise nach Brasilien in den Jahren 1815 bis 1817. Erster Band.* Frankfurt a.M., Germany: H.L. Brönner, 1820.

Wied-Neuwied M Prinz zu. *Abbildungen zur Naturgeschichte Brasiliens. 2. Lieferung.* Weimar, Germany: Verlag des Grossherzogl. Sächs. priv. Landes-Industrie-Comptoirs, 1823.

Winemiller KO, Willis SC. The Vaupes Arch and Casiquiare Canal. In: Albert JS, Reis RE (eds), *A Historical Biogeography of Neotropical Freshwater Fishes.* Berkeley, CA: University of California Press, 2011, 225–42.

Wüster W, Bérnils RS. Bérnils RS. On the generic classification of the rattlesnakes, with special reference to the neotropical *Crotalus durissus* complex (Squamata: Viperidae). *Zoologia (Curitiba)* 2011;**28**:417–9. https://doi.org/10.1590/s1984-46702011000400001

Wüster W, Broadley DG. Get an eyeful of this: a new species of giant spitting cobra from eastern and north-eastern Africa (Squamata: Serpentes: Elapidae: *Naja*). *Zootaxa* 2007;**1532**:51–68. https://doi.org/10.11646/zootaxa.1532.1.4

Wüster W, Kaiser H. Bungled *Bungarus*: lessons from a venomous snake complex illustrate why taxonomic decisions belong in taxonomy-competent journals. *Zootaxa* 2023;**5297**:139–43. https://doi.org/10.11646/zootaxa.5297.1.9

Wüster W, Tillack F. On the importance of types and the perils of 'en passant' taxonomy: a brief history of the typification of *Coluber naja* Linnaeus, 1758 (Serpentes: Elapidae) and its implications, with the designation of a lectotype. *Zootaxa* 2023;**5346**:403–19. https://doi.org/10.11646/zootaxa.5346.4.3

Wüster W, Thomson SA, O'Shea M *et al.* Confronting taxonomic vandalism in biology: conscientious community self-organization can preserve nomenclatural stability. *Biological Journal of the Linnean Society* 2021;**133**:645–70. https://doi.org/10.1093/biolinnean/blab009

Zacho CM, Bager MA, Margaryan A *et al.* Uncovering the genomic and metagenomic research potential in old ethanol-preserved snakes. *PLoS One* 2021;**16**:e0256353. https://doi.org/10.1371/journal.pone.0256353

Zaher H, Murphy RW, Arredondo JC *et al.* Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS One* 2019;**14**:e0216148. https://doi.org/10.1371/journal.pone.0216148

Zancolli G, Baker TG, Barlow A *et al.* Is hybridization a source of adaptive venom variation in rattlesnakes? A test, using a *Crotalus scutulatus* x *viridis* hybrid zone in southwestern New Mexico. *Toxins* 2016;**8**:188. https://doi.org/10.3390/toxins8060188