A 21ST-CENTURY VISION FOR NEOTROPICAL SNAKE SYSTEMATICS

UNA VISIÓN DEL SIGLO XXI SOBRE LA SISTEMATICA DE LAS SERPTIENTES NEOTROPICALES

R. Alexander Pyron^{1*}

¹Dept. of Biological Sciences, The George Washington University, Washington DC, USA 20052. *correspondence author: rpyron@colubroid.org

We live in an unprecedented age for systematics and biodiversity studies. Ongoing global change is leading to a future with reduced species richness and ecosystem function (Pereira, Navarro & Martins, 2012). Yet, our knowledge about biodiversity is increasing exponentially. For squamates in particular, we have range maps for all species (Roll et al., 2017), phylogenies containing estimates for all species (Tonini, Beard, Ferreira, Jetz & Pyron, 2016), and myriad ecological and natural-history datasets for a large percentage of species (Meiri et al., 2013; Mesquita et al., 2016). For neotropical snakes, a recent synthesis of museum specimens and verified localities offers a fine-grained perspective on their ecogeographic distribution in Central and South America, and the Caribbean (Guedes et al., 2018).

More than anything, however, what these datasets reveal is our lack of knowledge; of the true number of species, of their geographic distribution, ecological interactions, lifehistory traits, threat status, etc. A recent study summarizing phylogenetic and threat data for squamates revealed that 4,340 species lacked genetic data, and 6,459 species were data deficient or unassessed for extinction risk (Tonini et al., 2016). Another study showed that 927 lizards are known only from their type locality, while 213 are known only from a single specimen (Meiri et al., 2018). The Reptile Database shows that species descriptions had plummeted by 1950, but that the last two decades have seen all-time highs in new taxa described yearly (Uetz & Stylianou, 2018), implying that just 20 years ago we had no knowledge of thousands of species from throughout the world. Clearly, our knowledge is limited, and its gaps are vast.

As daunting as our ignorance may be, we stand on the cusp of a 21st century renaissance in systematics and biodiversity research, integrating both classical fields such as morphology and taxonomy, and modern advances in genomics and molecular systematics. I suggest that there are three major facets underpinning this new research program that will require the focus and cohesion of the global research community. They are: (i) renewed attention to classical taxonomic and nomenclatural practices, (ii) more focused attention on filling out the Tree of Life, and (iii) increasing integration of systematics and natural history studies. Positive trends in these areas are arising organically in research groups throughout the neotropics and the world; I seek here to highlight specific avenues of research that might be pursued.

First is the description of new species. Almost no progress can be made in any comparative field of biological sciences without an accurate accounting of species' true diversity. This is particularly relevant for systematics, evolution, ecology, behavior, and conservation (Mace, 2004; Will, Mishler & Wheeler, 2005). The 21st century has seen an almost exponential rise in the description of new reptile species (Uetz & Stylianou, 2018), and the same trend likely holds for most groups of plants and animals. In Brazil and Mexico, two of the most diverse neotropical countries, new descriptions peaked in 1758 and the mid-19th century, but show a moderate, consistent output since the late 1990's (Fig. 1). At the same time, taxonomic expertise is fading worldwide (Hopkins & Freckleton, 2002). How do we reconcile this?

One possible explanation is simply booms in the population of both citizens and scientists in those countries, with larger numbers of people describing fewer species per person but maintaining a baseline yearly output. In Brazil, 58 unique author sets described 69 species from 2000 to 2018; in Mexico, 24 described 32; and in Argentina, 3 described 3. In comparison, Cope leads in having described 69 species from Mexico, and Linnaeus leads in Brazil and Argentina with 33 and 19 (Cope is in second with 28 and 15), respectively. As a side note, it seems clear that undiscovered and undescribed biodiversity is much higher in tropical regions, though certainly not zero in temperate areas. While Argentina may be plateauing in the rate of descriptions, neither Brazil nor Mexico show any signs of slowing down (Fig. 2); who knows what their true diversity may actually be?

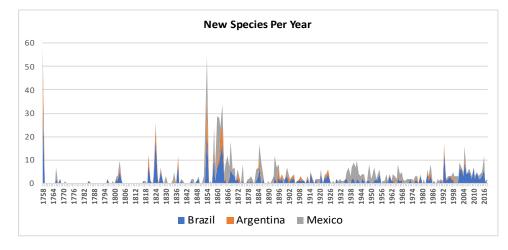


Figure 1. Number of new species described per year in the three largest neotropical countries: Brazil, Argentina, and Mexico. Note major spikes in 1758 and the mid-19th century, and moderate but consistent volume since the 1990's. Data from the Reptile Database (http://www.reptile-datatabase.org/; accessed 22 March 2018).

Answering this question will require both modern systematics methods and traditional taxonomic expertise (Dayrat, 2005; Fujita, Leaché, Burbrink, McGuire & Moritz, 2012; Renner, 2016).

At least anecdotally, molecular phylogenies are now often replete with "aff.," "cf., "gr.," and "sp." in the labels of terminal taxa, particularly for poorly-known groups from tropical areas. Similarly, museum curators are readily induced to speak of the tremendous backlog of candidate species in their collections. Though species descriptions are increasing rapidly, one suspects that they drastically lag the real discovery rate of new taxa, as dwindling expertise and low rewards dis-incentivize high productivity in taxonomy. Similarly, issues with nomenclature frequently arise due to incomplete familiarity with the ICZN (Dubois, 2017), causing problems with the availability and validity of new names. While numerous researchers are undoubtedly engaged in life-long good-faith efforts to turn "sp. 1" into "sp. nov.", it seems clear that renewed community commitments and dedication to the less-glamorous work of taxonomy and nomenclature are still needed (Wheeler, 2004).

The sociological remedies needed for large-scale reinvigoration of traditional taxonomy are beyond the scope of this editorial, and likely beyond the individual efforts of most researchers. But every practicing biologist should keep in mind the desperate importance of making some progress on any apparently new taxa they discover through the course of their studies, and not perpetually overlook them in favor of more glamorous or better-incentivized research programs. The literature on species concepts & delimitation is massive (see De Queiroz, 2007), and no one set of recommendations can cover how best to go about describing new species. But in the most general sense, if you know you have a new lineage, do your best to describe it and tell the world. Few single actions in science have as immediate and permanent an impact as describing a new species, transcending disciplines and political boundaries.

Second is increasing phylogenetic coverage. The largest analysis of squamate phylogeny to date included only 56% of described, extant species, and 152 genera (108 in snakes) were completely absent. While some missing genera have been added in recent studies (Figueroa, McKelvy, Grismer, Bell & Lailvaux, 2016; Pyron, Guayasamin, Peñafiel, Bustamante & Arteaga, 2015; Weinell & Brown, 2018), the following neotropical genera are still unknown on GenBank: Amnesteophis, Anomalepis, Cercophis, Chapinophis, Chersodromus, Coronelaps, Ditaxodon, Emmochliophis, Enuliophis, Enulius, Eutrachelophis, Geagras, Helminthophis, Lioheterophis, Omoadiphas, Plesiodipsas, Rhadinella, Rhadinophanes, Saphenophis, Simophis, Tantillita, and Uromacerina. At least 25 species were unsampled for Atractus (128 missing), Micrurus (57), Tantilla (56), Geophis (42), Erythrolamprus (34), Dipsas (30), and Apostolepis (25). While some of these are rare, others are not. Even historical specimens can now often be sequenced using nextgeneration technologies (Ruane & Austin, 2017).

As with accurate alpha taxonomy and describing new species, the creation of a fully-sampled Tree of Life estimate is a crucial foundation for analyses in systematics and evolutionary biology (Jetz, Thomas, Joy, Hartmann & Mooers, 2012), and conservation assessments (Isaac, Turvey, Collen, Waterman & Baillie, 2007). Few tasks in the early 21st century have as much urgency as sequencing unsampled species and including them in larger phylogenies. Tensions arise from this imperative, though, as researchers rarely have the time and money needed to sequence

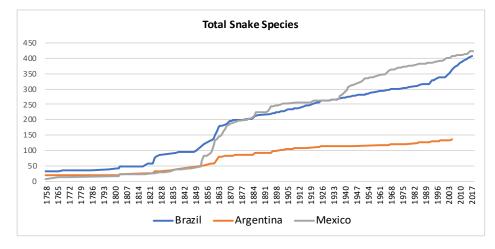


Figure 2. The total number of snake species described since 1758 in the three largest neotropical countries: Brazil, Argentina, and Mexico. Note the sharp upticks in mid-19th century Mexico, and in 21st century Brazil, and the lack of a plateau for descriptions from those countries.

random species that might be lying around in their freezer. Thus, constructing larger projects involving more complete sampling of a clade, and a biological focus for the study beyond simple phylogeny and taxonomy, often delay publication of new data. As with species descriptions, there are no simple, blanket prescriptions to alleviate these roadblocks and increase the flow of phylogenetic knowledge. Nevertheless, the list above can at least serve as a reminder that these gaps exist, that they need to be filled, and that perhaps you can help fill them. If you have *Amnesteophis* or *Atractus* in your tissue collection, consider what you might do to include them in the Tree of Life as quickly as possible.

Third is the collection and collation of trait data. This is likely the most high-profile and active area of research of the three, with numerous existing databases covering thousands of species from numerous groups (Chave et al., 2009; Kattge et al., 2011; Kleyer et al., 2008; Oliveira, São-Pedro, Santos-Barrera, Penone & Costa, 2017). Trait datasets were less easily combined prior to the internet, as raw measurements weren't commonly included in published papers, or required laborious transcription from appendices or tables. Numerous challenges still remain, such as standardized observation formats and data structures, missing data when combining studies, and small or non-representative samples for many species. Yet efforts and support for large-scale initiatives is strong, such as the NSF-funded VertLife project (DEB-1441737; http://www.vertlife.org/), which is gathering dozens of traits for all terrestrial vertebrates, and the TRY plant database (http://www.try-db.org/), which boasts "7 million trait records for 1,800 traits of 2.6 million individual plants, representing 140,000 plant taxa."

There are several major paths forward for trait data. One is simply continuing and increasing the massive expenditure of time and money required to gather high-quality natural-history data in the field. No amount of sophistication in genomic sequencing or computer modelling will ever remove the need to observe species in their natural habitats (Barrows, Murphy-Mariscal & Hernandez, 2016). The second is dredging the literature, where centuries of meticulous observations are often trapped in distant libraries and foreign languages (Faulwetter et al., 2016). Initiatives such as the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/) offer increasing coverage of historical sources, as do digitization efforts of societies such as the SSAR for natural-history-rich journals like Herpetological Review (https://ssarherps.org/herpetological-review-pdfs/). In the interim, methods exist for dealing with missing data in a phylogenetic context (Swenson, 2014),

The insights from phylogenetic analysis of large-scale trait datasets in squamates have been manifold (Dunham & Miles, 1985; Garland Jr & Losos, 1994; Pyron & Burbrink, 2014; Wiens, Brandley & Reeder, 2006). Yet there are numerous additional avenues of investigation. Even after common traits such as body size, microhabitat, diet preference, etc., have been filled in and analyzed, we might wonder about other, more abstract traits. Daily activity periods and seasonal variation therein, ontogenetic shifts in diet and microhabitat preference, species interactions, physiology and metabolic processes, the list goes on. Such traits are valuable across scales, from the individual to the community to the global assemblage (McGill, Enquist, Weiher & Westoby, 2006). Robust data can be synthesized from independent collections of single traits (Weiher et al., 1999), while others will only emerge after long periods of numerous groups laboring away to measure them using new, sophisticated technologies in groups of species (Diele-Viegas et al., 2018). While decades of dedicated study may be needed to fully document the life history of just a few taxa, knowledge of species' attributes can only increase in time, and the value of these data will never diminish.

As scientists, we are committed to generating and sharing data. Sometimes, this leads quickly to new paradigms, radical insights, and seismic shifts in perception. Other times, it involves long struggles for incremental gains in knowledge. The former is predicated on the latter, however, and scientific revolutions only intermittently punctuate the progress of normal science (Kuhn, 1963). The path such revolutions take can often seem meandering, desultory, and lacking in the kind of methodological coherence that typically lends meaning to ordinary investigations (Feyerabend, 1993). Describing species, building phylogenies, and constructing trait databases are not the most glamorous endeavors in biology. But they are crucial, and even if one does not devote their career solely to these aims, we can all participate, at least occasionally, as a community. If a conscious, consistent effort is made to do so, we can close out the 21st century with a significantly enhanced knowledge not just of neotropical snakes, but of all global biodiversity. Few if any of us will live to see the 22nd century. It will be a drastically different world, biologically, politically, and socially. But individual contributions to our collective knowledge of taxonomy, phylogeny, and traits have a unique persistence and relevance through time and will serve to make that world a richer place. These data will undoubtedly set the stage for future biological breakthroughs that are unimaginable at present.

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