



# Phylogenomic analyses reveal novel relationships among snake families



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## ABSTRACT

Snakes are a diverse and important group of vertebrates. However, relationships among the major groups of snakes have remained highly uncertain, with recent studies hypothesizing very different (and typically weakly supported) relationships. Here, we address family-level snake relationships with new phylogenomic data from 3776 nuclear loci from ultraconserved elements (1.40 million aligned base pairs, 52% missing data overall) sampled from 29 snake species that together represent almost all families, a dataset ~100 times larger than used in previous studies. We found relatively strong support from species-tree analyses (NJst) for most relationships, including three largely novel clades: (1) a clade uniting the boas, pythons and their relatives, (2) a clade placing cylindrophiids and uropeltids with this clade, and (3) a clade uniting bolyeriids (Round Island boas) with pythonids and their relatives (xenopeltids and loxocemids). Relationships among families of advanced snakes (caenophidians) were also strongly supported. The results show the potential for phylogenomic analyses to resolve difficult groups, but also show a surprising sensitivity of the analyses to the inclusion or exclusion of outgroups.

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## 1. Introduction

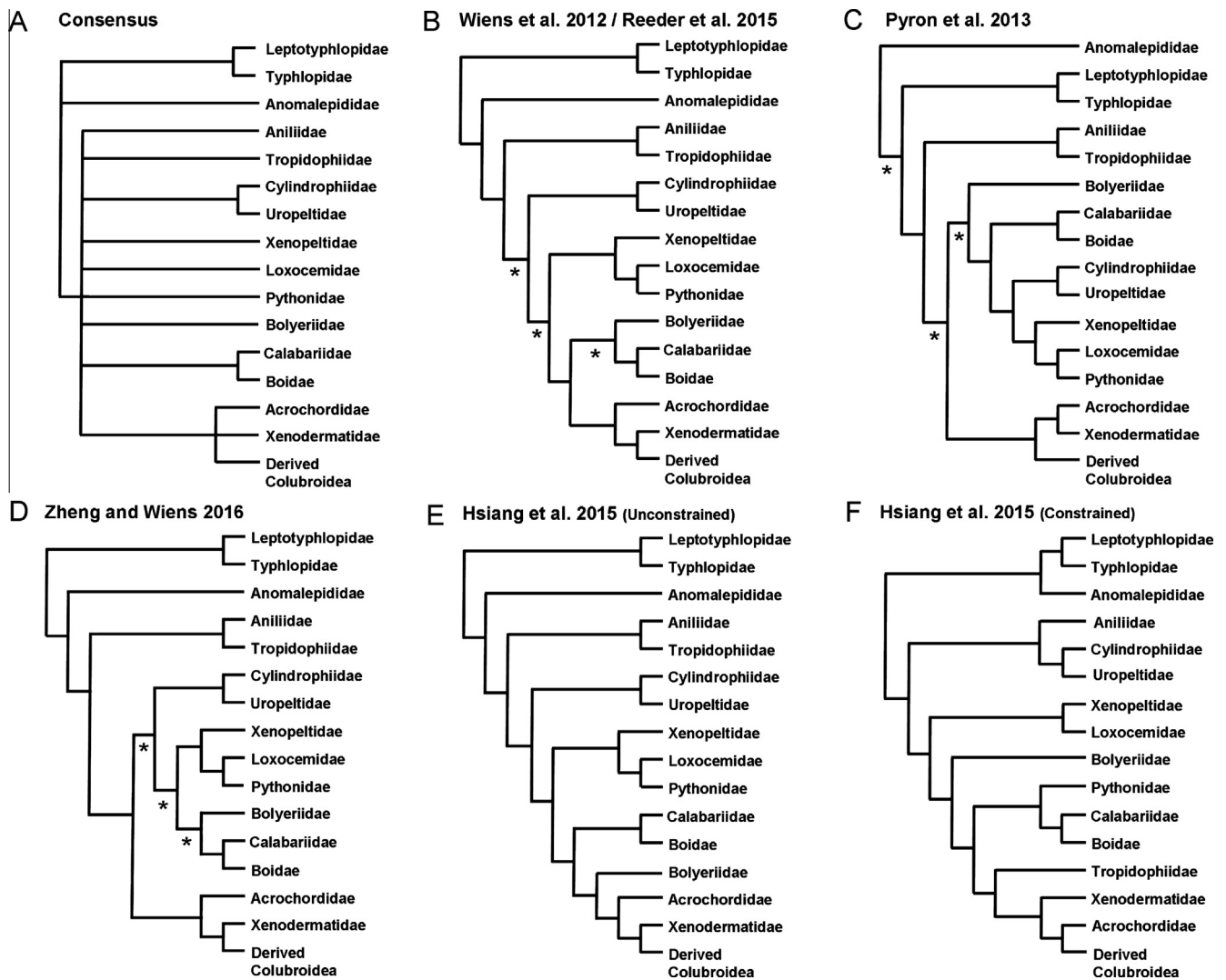
Snakes are a diverse and important group of vertebrates. They include ~3500 described species (Uetz et al., 2014), currently distributed among 24 families (taxonomy from Pyron et al., 2013). Snakes are particularly important to humans because they include many dangerously venomous species. These species are responsible for tens of thousands of human deaths per year (Kasturiratne et al., 2008). Yet, at the same time, snake venoms are also a valuable resource for medicine (Fox and Serrano, 2007). Additionally, snakes are a model system for many researchers across many fields, and have been the focus of comparative studies (i.e. among species) of molecular evolution, behavior, physiology, functional morphology, and ecology (e.g. Fry and Wüster, 2004; Gartner et al., 2009; Colston et al., 2010; Castoe et al., 2013; Vonk et al., 2013; Byrnes and Jayne, 2014; Senter et al., 2014; Bellini et al., 2015). These comparative studies generally require a phylogenetic framework.

The relationships among the major groups of snakes have proved to be surprisingly difficult to resolve. Among recent studies, very few relationships are universally agreed upon (Fig. 1A). This is surprising because recent studies have applied relatively large

amounts of genetic and phenotypic data to these relationships. For example, Wiens et al. (2012) analyzed 44 nuclear loci for most snake families (Fig. 1B), but still found only weak support for some relationships (e.g. placement of boids, pythonids, bolyeriids, cylindrophiids, and uropeltids to each other). Reeder et al. (2015) added 2 loci, 691 morphological characters, and many fossil taxa to that dataset, but still found weak support for relationships among these same major snake clades (Fig. 1B). Pyron et al. (2013) analyzed a smaller number of mitochondrial and nuclear genes (12 total) but many extant snake species (1262 sp.), and found several relationships (Fig. 1C) that contradicted these two studies, with varying levels of support. For example, they weakly placed anomalopids as sister to all other snakes (instead of leptotyphlopids and typhlopids), and bolyeriids (Round Island boas) as sister to a clade including calabariids, boids, cylindrophiids, uropeltids, xenopeltids, loxocemids, and pythonids. They also found some unusual relationships within advanced snakes (caenophidians), including the placement of acrochordids and xenodermatids as sister taxa (Fig. 1C) and placement of homalopsids with elapids and lamprophiids. An analysis by Zheng and Wiens (2016) combined the molecular datasets of Wiens et al. (2012) and Pyron et al. (2013), to yield a dataset of 52 genes with extensive taxon sampling (1262 species). The resulting maximum likelihood estimate for snake families (Fig. 1D) was similar to that of Wiens et al. (2012) and Reeder et al. (2015). However, the estimate of Zheng and Wiens (2016) was similar to that of Pyron et al. (2013) in weakly

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**Fig. 1.** Summary of recent hypotheses of higher-level snake phylogeny (B–F), including a strict consensus tree (A) of these hypotheses. Asterisks indicate relatively weakly supported nodes (support values less than 70%). The tree of [Wiens et al. \(2012\)](#) matches that of [Reeder et al. \(2015\)](#) for snake families. The trees in B, C, and D are based on concatenated maximum likelihood analyses. E and F are based on Bayesian analyses of [Hsiang et al. \(2015\)](#), their Figs. 2 and 4, respectively), where E is the molecular-only analysis and F is the constrained, combined analysis of molecular and morphological data. A few families were not included in all analyses, including Anomochilidae (related to or nested inside Cylindrophiidae; [Gower et al., 2005](#); [Pyron et al., 2013](#); [Zheng and Wiens, 2016](#)), Xenophiidae (most likely related to Bolyeriidae; [Lawson et al., 2004](#); [Zheng and Wiens, 2016](#)), and Gerrhopilidae and Xenotyphlopidae (related to Typhlopidae; [Vidal et al., 2007](#); [Pyron et al., 2013](#); [Zheng and Wiens, 2016](#)).

supporting a clade including bolyeriids, calabariids, boids, cylindrophiids, uropeltids, xenopeltids, loxocemids, and pythonids (as sister to caenophidians). [Hsiang et al. \(2015\)](#) recently analyzed 21 nuclear loci and 766 morphological characters for a dataset including most snake families. They found strong support for relationships among many snake families in their separate analyses of the molecular data (Fig. 1E), relationships which were largely concordant with those from other recent molecular studies (but with some relationships at odds with previous molecular studies, such as placing bolyeriids as sister to caenophidians). In contrast, they found weak support for most snake relationships from their separate analyses of the phenotypic data. Their analyses of the combined phenotypic and molecular data were generally consistent with the molecular results, but with very weak support (except for placing anomalepidids with leptotyphlopids and typhlopids). Their preferred tree (Fig. 1F) was based on the combined molecular and phenotypic data, but with many relationships constrained to match the phenotype-based tree (despite the weak support for many of these relationships from the phenotypic data). This tree was strongly supported (seemingly because of the constraints)

but very different from other recent analyses of snake relationships (Fig. 1F), including their unconstrained analyses of the same combined dataset. In summary, a strict consensus tree of snake relationships from recent analyses is largely unresolved (Fig. 1A).

In this study, we attempt to resolve higher-level snake relationships using new phylogenomic data and an explicit species-tree approach. Importantly, species-tree methods have not been used in previous studies of snake phylogeny at the deepest phylogenetic scales. We utilize ultra-conserved elements (UCEs) for sequence capture (e.g. [Bejerano et al., 2004](#); [Sandelin et al., 2004](#)), and generate a molecular dataset that is ~100 times larger than that used in previous studies of this phylogenetic question. We utilize an explicit species-tree method (NJst; [Liu and Yu, 2011](#)) to estimate the phylogeny, given that species-tree methods may generally be more accurate than concatenated analyses for multi-locus data (e.g. [Edwards et al., 2007](#); [Leaché and Rannala, 2011](#)). In particular, NJst may be more accurate than concatenated analysis when internal branches are relatively short ([Liu and Yu, 2011](#)), and short branches are known to be problematic for higher-level snake phylogeny, given their association with weak branch support and

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