



Effect of taxon sampling on recovering the phylogeny of squamate reptiles based on complete mitochondrial genome and nuclear gene sequence data

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ABSTRACT

The complete nucleotide sequences of the mitochondrial (mt) genomes of three species of squamate lizards: *Blanus cinereus* (Amphisbaenidae), *Anguis fragilis* (Anguidae), and *Tarentola mauritanica* (Geckkonidae) were determined anew. The deduced amino acid sequences of all 13 mt protein-coding genes were combined into a single data set and phylogenetic relationships among main squamate lineages were analyzed under maximum likelihood (ML) and Bayesian Inference (BI). Within Squamata, the monophyly of Iguanidae, Anguimorpha, Amphisbaenia, Gekkota, Serpentes, and Acrodonta received high statistical support with both methods. It is particularly striking that this is the first molecular analysis that recovers the monophyly of Scincomorpha (including Scincidae, Xantusiidae, Cordylidae, and Lacertidae), although it is only supported in the Bayesian analysis, and it is sensitive to changes in the outgroup (see below). Phylogenetic relationships among the main squamate lineages could not be resolved with ML but received strong support with BI (above 95%). The newly reconstructed phylogeny of squamates does not support the Iguania–Scleroglossa split. Acrodonta and Serpentes form a clade, which is the sister group of the remaining squamate lineages. Within these, Gekkota were the first branching out, followed by Amphisbaenia, and a clade including Anguimorpha as sister group of Scincomorpha + Iguanidae. The recovered topology differed substantially from previously reported hypotheses on squamate relationships, and the relative effect of using different outgroups, genes, and taxon samplings were explored. The sister group relationship of Serpentes + Acrodonta, and their relative basal position within Squamata could be due to a long-branch attraction artifact. Phylogenetic relationships among Scincomorpha, Amphisbaenia, and Anguimorpha were found to be rather unresolved. Future improving of squamate phylogenetic relationships would rely on finding snake and acrodont species with slower mt evolutionary rates, ensuring thorough taxon coverage of squamate diversity, and incorporating more nuclear genes with appropriate evolutionary rates.

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1. Introduction

The molecular phylogeny of land vertebrates is presently among the best documented (Meyer and Zardoya, 2003) owing to newly-compiled large sequence data sets based on mitochondrial (mt) and/or nuclear genes, as well as on rather thorough lineage samplings. This is particularly true for recently reported amphibian (San Mauro et al.,

2005; Frost et al., 2006; Roelants et al., 2007), and mammal (Murphy et al., 2001a,b; Springer et al., 2001) molecular phylogenies, which are relatively robust from a statistical point of view, and will be essential as a framework to any future comparative study pertaining these taxa. In contrast, our understanding of phylogenetic relationships within the third main lineage of tetrapods, i.e. sauropsids (reptiles + birds) is still emerging because thus far accumulated molecular data for this group are limited as compared to mammals and amphibians. The classic hypothesis on sauropsid phylogenetic relationships is based on the absence or presence of two skull temporal fenestrae, and considers a basal split into Anapsida (turtles) and Diapsida (other reptiles + birds), respectively (Meyer and Zardoya, 2003). The latter are further divided into Lepidosauria (squamates + the New Zealand living fossil, the tuatara) and Archosauria (crocodiles + birds). The traditional view of turtles as anapsids (Lee, 2001) has been challenged by several morphological studies suggesting diapsid affinities of turtles (Rieppel and deBraga, 1996; Hill, 2005). Molecular phylogenies (Zardoya and Meyer, 1998; Hedges and Poling, 1999; Kumazawa and Nishida, 1999;

Abbreviations: mt, mitochondrial; ML, maximum likelihood; BI, Bayesian inference; bp, base pairs; AIC, Akaike information criterion; ATP, ATP synthase; AU, Approximately Unbiased test; Cox, Cytochrome *c* oxidase; Cytb, Cytochrome *b*; DHU, dihydrouridine; KH, Kishino–Hasegawa test; MCMC, Markov chains Monte Carlo; Mya, million years ago; Myr, Million years; NADH, NADH dehydrogenase; O_L, origin of mitochondrial light strand replication; PL, Penalized likelihood; RTTM, Root to tip mean; SH, Shimodaira–Hasegawa test; TN, truncated Newton algorithm.

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Hugall et al., 2007) place the turtles as derived diapsids related with Archosauria.

With nearly 8000 living species and a worldwide distribution (Zug et al., 2001; Pianka and Vitt, 2003; Pough et al., 2004), squamate reptiles conform a highly diversified clade that includes lizards, snakes and amphisbaenians (Townsend et al., 2004; Estes et al., 1988). The main lineages of squamates exhibit a great variety of specialized morphological, behavioral and ecological forms (Zug et al., 2001; Pianka and Vitt, 2003; Pough et al., 2004), which have seriously hindered establishing higher-level phylogenetic relationships within the group based on morphology (e.g., Estes et al., 1988; Lee, 1998, 2000; Kearney, 2003). Traditionally, squamates have been divided into two major groupings (Iguania and Scleroglossa) based mostly on osteological and soft anatomy characters (Estes et al., 1988; Lee, 1998; Reynoso, 1998; Lee and Caldwell, 2000). This main cladogenetic split has been linked to major differences in tongue structure and associated feeding behavior (Vitt et al., 2003; Vitt and Pianka, 2005). Iguania, which include iguanids, agamids, and chamaeleonids (the latter two grouped together into Acrodonta), use the tongue for prey prehension (as Tuataras) whereas Scleroglossa, which include the remaining squamates, use teeth and jaw for prey prehension, freeing the tongue for chemosensory reception, and seemingly allowing present-day predominance of scleroglossans over iguanians worldwide (Schwenk, 1993; Vitt et al., 2003; Pough et al., 2004; Townsend et al., 2004; Vidal and Hedges, 2005). Scleroglossa is further divided into three infraorders: Gekkota, Scincomorpha, and

Anguimorpha, with the latter two grouped into a higher rank, the Autarchoglossa. The limbless groups, i.e. Amphisbaenia, Serpentes and Dibamidae are normally left as “incertae sedis” within the Scleroglossa (Estes et al., 1988) (Fig. 1A).

Several recent papers (Townsend et al., 2004; Vidal and Hedges, 2005; Böhme et al., 2007; Douglas et al., 2006; Kumazawa, 2007) have focused on the molecular phylogeny of squamates deriving at very different conclusions (Fig. 1B, C, and D). Thus far, no molecular phylogeny recovers the basal split of squamates into Iguania and Scleroglossa, against morphological evidence (Townsend et al., 2004; Vidal and Hedges, 2005; Kumazawa, 2007) (Fig. 1). Moreover, molecular phylogenies based on either mt (Böhme et al., 2007; Kumazawa, 2007), nuclear (Vidal and Hedges, 2005) or combined (Townsend et al., 2004; Hugall et al., 2007) sequence data fairly agree in supporting Dibamida and Gekkota as the most basal squamate lineages (but see Harris, 2003; Zhou et al., 2006) (Fig. 1). Scincomorpha are recovered generally as paraphyletic with Scincoidea (Scincidae, Xantusiidae, and Cordylidae) placed as a sister group of Lacertoidea (Lacertidae and Teiidae) + Amphisbaenia, and within a larger clade that also includes Anguimorpha and Iguania (Fig. 1). However, phylogenetic relationships within this larger clade remain largely unresolved (Townsend et al., 2004; Vidal and Hedges, 2005; Böhme et al., 2007; Hugall et al., 2007; Kumazawa, 2007), and the monophyly of Scincomorpha cannot be statistically rejected (Kumazawa, 2007). In addition, the relative phylogenetic position of Serpentes varies among studies, and it is particularly volatile in

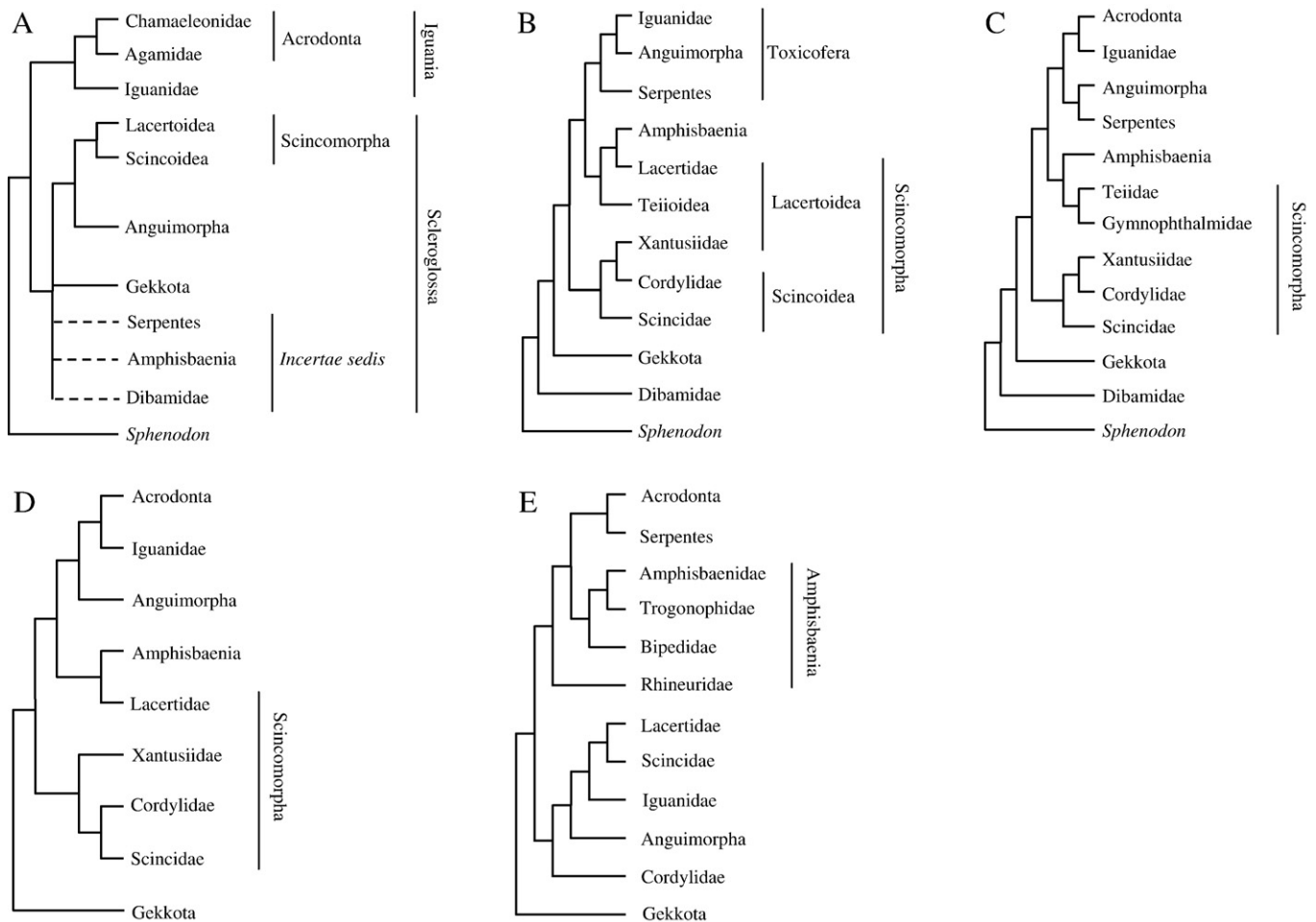


Fig. 1. Alternative hypotheses for squamate phylogenetic relationships. A. Morphology-based hypothesis (Estes et al., 1988); B. Nuclear-based (RAG1, C-mos, RAG2, R35, HOXA13, JUN, alpha-enolase, amelogenin, MAFB genes) hypothesis (Vidal and Hedges, 2005); C. Nuclear-based (RAG1, C-mos genes) hypothesis (Townsend et al., 2004); D. Mt-based (complete mt genomes) hypothesis (Kumazawa, 2007); E. Mt-based (complete mt genomes) hypothesis (Böhme et al., 2007).

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