

MOLECULAR SYSTEMATICS OF THE COFFEE SNAKES, GENUS *Ninia*  
(COLUBRIDAE: DIPSADINAE)

by

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## ABSTRACT

### MOLECULAR SYSTEMATICS OF THE COFFEE SNAKES, GENUS *NINIA* (COLUBRIDAE: DIPSADINAE)

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Although previous studies have addressed issues relating to the systematics and taxonomy in the snake genus *Ninia*, the evolutionary history of the group remains largely unknown. Preliminary morphological studies have been unable to resolve many of the relationships within the genus and have not thoroughly tested the relationship between *Ninia* and other dipsadine snakes. To address these gaps in our knowledge of *Ninia*, I used molecular techniques to infer phylogenetic relationships. I obtained tissue samples for all species of *Ninia* and sequenced two mitochondrial DNA (mtDNA) and one nuclear DNA (nucDNA) locus. In total, this dataset included 2453 base pairs of nucleotide data. Additionally, I obtained tissue samples and sequence data for representatives of other dipsadine genera including *Atractus*, *Chersodromus*, *Cryophis*, *Dipsas*, *Geophis*, and *Sibon*. I reconstructed phylogenetic trees using distance, parsimony, maximum likelihood, and Bayesian inference methods. The mtDNA analyses recovered five well-supported lineages; these include (1) the *N. espinali* lineage, (2) the *N. celata* lineage, (3) the *N. diademata* lineage, (4) the *atrata+maculata+psephota* lineage, and (5) the *N. sebae* lineage. Within the *atrata+maculata+psephota* lineage, *N. atrata* and *N. hudsoni* were recovered as sister taxa, but the monophyly of the closely related species *N. maculata* and *N. pavimentata* could not be

proven. Some of my analyses placed *N. psephota* within the *atrata+hudsoni* lineage, and others placed *N. psephota* within the *maculata+pavimentata* lineage, leaving relationships among these species unresolved. Deep divergences were observed within *N. atrata* that correspond to populations geographically isolated by the Cordillera Occidental and the Cordillera Oriental in Ecuador and Colombia. Within the *maculata+pavimentata* lineage, moderate divergence appears to have occurred between northern and southern populations. Within the *N. diademata* lineage, the optimal topologies suggest a deep divergence between Atlantic and Pacific populations. The molecular data examined herein offered no evidence to suggest that there has been any substantial diversification in *N. sebae* across its large geographic range. Analysis of the nucDNA sequence data did not clearly resolve relationships among species of *Ninia*. The mtDNA analyses support the monophyly of *Ninia*, but inclusion of the nuclear data suggests a sister relationship between *Chersodromus* and *N. espinali*. I hypothesize a Central American origin for the genus, since the most basal split within *Ninia* produced lineages geographically restricted to Central America.

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## CHAPTER 1

### INTRODUCTION

The genus *Ninia* (Colubridae: Dipsidinae) is comprised of a number of small, semi-fossorial neotropical snakes that collectively range from southern Mexico through Central America into South America, reaching the western and northern edges of the Amazon basin in southern Peru, Ecuador, Colombia, Venezuela, and. Although the number of recognized species has changed over time, and may continue to do so as more becomes known about these poorly understood snakes, the current literature suggests that nine species comprise the genus; these include *N. atrata*, *N. celata*, *N. diademata*, *N. espinali*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, *N. psephota*, and *N. sebae*. The type species, *Ninia diademata*, was described more than 150 years ago and the taxonomic arrangement of the genus has remained in a state of flux since then, with numerous descriptions and re-descriptions appearing in the literature as new material became available. In reviewing the many descriptions and taxonomic reviews in the literature, it became obvious to me that the reliance on landmark morphological characters as diagnostic characters for species descriptions and identifications may have inadvertently obscured the true biological identities of these lineages; some of the characters used in classifying *Ninia*, including nuchal collar presence or absence, nuchal collar color and shape and size, dorsal color and pattern, ventral color and pattern, and segmental count, exhibit significant intraspecific variation or little interspecific variation for some or all species. Within the last two decades, several authors have synonymized or described new species of *Ninia* because the apparent plasticity or conservatism of morphological characters had been originally misinterpreted (McCranie and Wilson 1995; Savage and Lahanas 1991). Since the last taxonomic proposal (Smith and Campbell 1996), published more than a decade ago, advances

in molecular techniques and the accumulation of significant amounts of new material make a comprehensive review of the genus *Ninia* timely and appropriate.

Dunn (1935) provided the first review of the genus *Ninia*, recognizing five species at the time: *N. atrata*, *N. diademata*, *N. maculata*, *N. psephota*, and *N. sebae*. Dunn considered *Streptophorus drozii* (Dumeril and Bribon 1854), *Streptophorus lansbergi* (Dumeril and Bribon, 1854), and *Streptophorus spilogaster* (Peters 1881) as synonyms of *Coluber atratus* (Hallowell 1845), while placing *Ninia sebae tessellatus* (Cope 1875) and *Streptophorus subtessellatus* (Werner 1909) in synonymy with *Streptophorus maculatus* (Peters 1861). Dunn was not able to place *Streptophorus maculatus pavimentatus* (Bocourt 1883) in synonymy with *Streptophorus maculatus* because he reported that he had not seen the type specimens. He synonymized *Elapoides fasciatus* (Hallowell 1855) with *Streptophorus sebae* (Dumeril and Bibron 1854) and considered *Streptophorus bifasciatus* (Dumeril and Bibron, 1854) and *Streptophorus labiatus* (Bocourt 1883) as synonyms of *Ninia diademata* (Baird and Girard 1853). Lastly, Dunn recognized *Streptophorus oxynotus* (Werner, 1909) as a synonym of *Catostoma psephota* (Cope 1875). Because Baird and Girard (1853) had described the genus *Ninia* earlier, Dunn placed all the specific names under the generic epithet *Ninia* and changed their gender accordingly.

Nearly twenty years later, Burger and Werler (1954) reviewed the genus, having access to new material and information that accumulated during the interim. During that time, Edward Taylor made collections in Costa Rica and proposed several taxonomic changes based on new material he obtained from his trips (1951, 1954). Taylor resurrected *Streptophorus oxynotus* (Werner 1909) and elevated *Streptophorus sebae tessellatus* (Cope 1875) to *Ninia tessellata*. (1954). In addition, Taylor described one new species, *Ninia cerroensis* (1954). Burger and Werler accepted Dunn's (1935) arrangement for the most part, but followed Taylor's (1951) assessment regarding *Streptophorus oxynotus* (Werner 1909). They did not recognize Taylor's elevation of *Streptophorus sebae tessellata* (Cope 1875) and completely ignored his description

of *Ninia cerroensis* (1954), failing to recognize it or synonymize it. One other species had been described since Dunn's review, *Ninia hudsoni* (Parker 1940), and Burger and Werler accepted that description as valid. Because of taxonomic procedure, Burger and Werler suppressed *Coluber atratus* in place of *Streptophorus lansbergi* (Dumeril and Bibron 1854). Apparently, at the time Hallowell (1845) described *Coluber atratus*, that combination had already been used, so they applied the epithet *Ninia lansbergi*, a change most authors ignored. In addition to recognizing seven nominal species, Burger and Werler also presented subspecific arrangements for *N. diademata*, *N. maculata*, and *N. sebae*. With regards to *N. maculata*, Berger recognized *Streptophorus sebae tessellata* (Cope 1875) as *N. m. tessellata* and followed Stuart's (1948) recognition of *N. m. pavimentata* as distinct from the nominate race. With regards to *N. diademata*, Burger and Werler accepted Smith's (1942) description of *N. d. plorator* as distinct race of the nominate form, recognized *Streptophorus labiatus* (Bocourt 1883) as *N. d. labiosa*, and described a new race, *N. d. nietoi*. Lastly, with regard to *N. sebae*, they accepted the description of *N. s. morleyi* by Schmidt and Andrews (1936). A few years after Burger and Werler published their review of *Ninia*, Schmidt and Rand examined *N. sebae* at length and proposed the addition of two new subspecies (1957). They recognized *Streptophorus sebae* var *punctulata* (Bocourt 1883) as *N. s. punctulata* and described a new subspecies, *N. s. immaculata*.

Savage and Lahanas (1991) provided the next in-depth treatment of the genus through their comprehensive examination *Ninia* species in Costa Rica. The availability of new material and information that had amassed since Burger and Werler examined the genus more than 30 years earlier allowed Savage and Lahanas to examine several species in depth. They concluded that all populations of *N. maculata* in Costa Rica represented a single species, but that the Guatemalan specimens assigned to *N. m. pavimentata* differed enough to warrant recognition as *N. pavimentata*, a conclusion later supported by Smith and Campbell (1996). They also concluded that *N. psephota*, *N. oxynota* (Taylor 1951), and *N. cerroensis* (Taylor

1954) represented different populations of a single, wider ranging species and considered the latter two taxa as synonyms of *N. psephota*.

A few years later, McCranie and Wilson (1995) described two new species: *N. celata* from north-central Costa Rica and western Panama and *N. espinali* from western Honduras and northern El Salvador. Both species superficially resemble *N. atrata* and had remained unrecognized from previous collectors for some time; Taylor had collected and identified the type specimen for *N. celata* 43 years earlier, and he had considered it to be *N. atrata*. Additionally, as a result of their detailed study of *N. atrata*, McCranie and Wilson noted that two specimens from Pallatanga, Ecuador, differed substantially from all other *atrata* in several respects and likely represented a distinct species. They refrained from describing it in the absence of additional material.

Around the same time, Smith (1996) conducted an exhaustive study of morphological variation in *N. sebae* and *N. diademata* using multivariate techniques and analyzed the phylogenetic relationships between the species of the genus using morphological characters. While he was able to detect geographic variation within *N. sebae*, his data generally did not support the conclusions of Schmidt and Rand (1957) with the exception of *N. s. punctulata*. Smith proposed that *N. s. morleyi* and *N. s. immaculata* be synonymized with *N. s. sebae* as they did not represent the true pattern of genetic differentiation as reflected by his multivariate analyses. However, Smith made an argument to retain the subspecific epithet *N. s. punctulata* because of its distinctiveness from other *N. sebae*, and he predicted that molecular data would provide evidence to elevate *N. s. punctulata* to full specific status. Similarly, Smith found geographic variation within *N. diademata* but noted that the differentiation was generally more subtle than compared to *N. sebae*. Even though he found that specimens of *N. diademata* from south of the continental divide along the Pacific versant in Chiapas and Guatemala seemed to be well differentiated from their conspecifics, Smith reported that his analyses provided no strong evidence for recognizing any populations as distinct and concluded that the subspecific

epithets erected by Smith (1942) and Burger and Werler (1954) were not useful in describing variation in *N. diademata*.

To investigate the phylogenetic systematics of the genus *Ninia*, Smith scored 23 morphological characters from two outgroup taxa, *Sibon fischeri* and *Chersodromus liebmanni*, and nine ingroup taxa: *N. atrata*, *N. celata*, *N. diademata*, *N. espinali*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, *N. psephota*, and *N. sebae*. His parsimony analyses recovered *Ninia* as monophyletic with respect to *Chersodromus* but generally did not resolve the relationships within *Ninia*. The analyses suggest that *N. atrata*, *N. celata*, *N. hudsoni*, and *N. espinali* diverged early in the history of the group, but the relationships among these species and the ancestor of the other species of *Ninia* remained unresolved. His analyses also imply that *N. diademata*, *N. maculata*, *N. pavimentata*, *N. psephota*, and *N. sebae* diverged from a common ancestor at some point after the other lineages had diverged, a phenomenon he termed the Central American radiation. However, the relationships among those species remained unresolved except for one case: the analyses indicated *N. diademata* and *N. psephota* as sister species. Ultimately, Smith concluded that two basic groups exist within *Ninia*: a South American group consisting of the dark, uniformly colored species *N. atrata*, *N. celata*, *N. hudsoni*, and *N. espinali* and Central American group consisting of the patterned species *N. diademata*, *N. maculata*, *N. pavimentata*, *N. psephota*, and *N. sebae*. He hypothesized that *Ninia* originated in Central America, and that *N. hudsoni* and *N. atrata* invaded South America in geologically recent time.

Recent works have provided conclusive evidence to include the genus *Ninia* within the Dipsadinae, but the exact phylogenetic position of this genus with respect to other dipsadine genera has not been definitively resolved. Dunn (1935) was one of the first authors to suggest a relationship between *Ninia* and other members of the Dipsadinae. Noting the superficial resemblance of *Chersodromus* to *Ninia*, Dunn considered *Ninia* to be a closer ally of "the least modified members of *Geophis*" and the "least modified members of *Tropidodipsas*", a group he



considered to include *Sibon* and *Sibynomorphus*. Dunn concluded that "*Ninia* occupies a central position between a group of burrowing forms and a group of arboreal forms". In a later paper, Dunn (1951) presented a phylogeny which placed *Ninia* and *Chersodromus* in one clade and *Dipsas*, *Sibon*, and *Sibynomorphus* in another. Cadle (1984) provided the first molecular evidence to classify dipsadine genera. His immunological distance data supported a *Sibon-Geophis* clade which included *Dipsas*, *Geophis*, *Ninia*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*. His data additionally supported a *Geophis-Ninia* clade within the larger *Sibon-Geophis* clade, but the relationship of *Chersodromus* could not be established. Cadle and Greene (1994) revisited Cadle's earlier phylogeny, incorporating ecological information to argue for a *Geophis* clade which included *Adelphicos*, *Atractus*, and *Ninia* and its sister clade which included *Dipsas*, *Sibon*, and *Sibynomorphus*. Fernandes (1995) reevaluated the Dipsadinae, using 58 morphological characters to infer the phylogeny of dipsadine snakes. His analysis indicated *Chersodromus* and *Ninia* as sister taxa. However, he only included two of the nine recognized *Ninia* species in his study, and he concluded that "the monophyly of *Ninia* in relation to *Chersodromus* can not be demonstrated, although there is no compelling evidence of its paraphyly either". Additionally, Fernandes' phylogeny placed *Ninia* and *Chersodromus* within a larger clade that included *Adelphicos*, *Atractus*, and *Geophis*, inferring that *Ninia* had a closer relationship to these genera than those in the clade containing *Dipsas*, *Sibon*, and *Sibynomorphus*. Smith (1996) built upon Fernandes' work by incorporating all of the *Ninia* species in his phylogeny; his data supported the monophyly of *Ninia* with respect to *Chersodromus*. Although his analysis indicated that *Chersodromus* is sister to *Ninia*, that relationship was not fully tested because Smith included only one other outgroup taxon, *Sibon*.

More recent work based on DNA sequence data has provided another glimpse at dipsadid relationships. Daza et al. (2009) investigated the origin and diversification of the genus *Leptodeira*, generating a phylogeny which included several dipsadine genera as outgroups. Their results from both mtDNA and nucDNA sequence data indicate that *Dipsas*, *Sibon*, and

*Ninia* form a clade with respect to *Atractus*, a finding that contradicts Fernandes' morphological analysis. Unfortunately they did not include *Chersodromus* and *Geophis* in their study, so the relationship of those genera to *Ninia* could not be examined. Vidal et al. (2010) provided another look at the placement of *Ninia* within the Dipsadinae. Their inferred phylogeny, using 12s and 16s rRNA sequence data, also suggests that *Ninia* belongs in a clade with *Dipsas*, *Sibon*, and *Sibynomorphus*; however, their analysis lacked support for these relationships and their taxonomic sampling also lacked *Chersodromus* or *Geophis*. Therefore, to date, the relationship of *Ninia*, and its putative sister taxon, *Chersodromus*, to the other dipsadine genera has not been fully explored or resolved.

In this thesis, I present molecular evidence to infer the phylogenetic systematics of *Ninia*. Using DNA sequence data, I reconstruct phylogenetic trees using several methods to test the monophyly of *Ninia*, infer evolutionary relationships within the genus, and assess whether the current taxonomy accurately reflects the genetic diversity of the group. Lastly, I discuss the origin of the genus and hypothesize the biogeographic forces that shaped the distribution of species and patterns of genetic diversity that I observed based on the data.

CHAPTER 2  
PHYLOGENETIC SYSTEMATICS OF THE GENUS *NINIA*

2.1 Materials and Methods

*2.1.1 Data Collection*

I obtained tissue samples consisting of muscle, liver, or skin from 65 *Ninia* specimens, including all species currently recognized in the genus (Appendix A). Localities for each species sampled are depicted in Figures 1-6. Additionally, I obtained tissue from three *Chersodromus* specimens to use for outgroup comparisons. To isolate genomic DNA from the tissue samples, I used a Qiagen DNeasy Blood & Tissue Kit (cat. no. 69506) following the manufacturer's protocol. I amplified three loci (two mtDNA and one nDNA) using Promega GoTaq® Green Master Mix (cat. no. M7122) according to the manufacturer's specifications with modification to the thermal cycling conditions. I set up PCRs in 25 uL volumes, incorporating each at primer a 0.4 uM final concentration and adding 1.0 to 2.0 uL of template DNA. Whenever I performed PCRs, I set up one reaction without template as a negative control. Primers used to amplify the target loci were initially taken from literature, but for many samples these primers did not work. I designed new primers by hand from multiple sequence alignments and tested them for secondary structure formations using OligoAnalyzer (Owczarzy et al. 2008). To amplify the complete coding sequence for the mitochondrial product cytochrome B, I used the primers H14910 and THRSN2 (Burbrink et al. 2000) and S20596F (5' AAC CAC TCT TGT TAA TCA ACT ACA 3') and S21790R (5' ACC CAT GTT TGG TTT ACA AAA ACA ATG CT 3'). For old or degraded templates, I amplified cytochrome B in two fragments using S20596F and S21257R (5' AAT GGG ATT TTG TCG ATG TCT GAG T 3') and S21136F (5' GCA CTA CAC TTT ATC CTC CCA TTC 3') and S21790R. To amplify a fragment of mitochondrial DNA

including partial coding sequence for nicotinamide adenine dinucleotide dehydrogenase subunit 4, complete sequence for tRNA-His, complete sequence for tRNA-Ser, and partial sequence for tRNA-Leu, I used the primers ND4 and LEU (Arevalo et al. 1994) and 621F (5' CCC AAA AGC CCA CGT TGA AGC 3') and L68R (5' TAC CAC TTG GAT TTG CAC CA 3'). For old or degraded templates, I amplified this locus in several smaller fragments using the primers 621F and 990R2 (5' GGT TTT TGT TCG TTC GTA GGT GGT 3'), 910F (5' ATA GCC TTA ATA ATC GCC CAC 3') and 1274R (5' AGG TGT TCT CGT GAG TGT G 3'), 1175F (5' TAA TCA CAG CCT CCT ACT C 3') and H74R (5' TCT ATT GTC AAG GTC ACA GC 3'), and 1256F (5' CAC ACT CAC GAG AAC ACC T 3') and L68R. To amplify a fragment of nuclear DNA containing partial coding sequence for neurotrophin-3, I used the primers NT3-F3 and NT3-R4 (Noonan and Chippindale 2006). Primer information is summarized in Table 1.

I performed PCRs using an Eppendorf Mastercycler Gradient thermocycler and ABI Geneamp PCR System 9700 machines. Typical PCR thermal cycling conditions included an initial denaturation step at 94° C for two minutes followed by 30-40 amplification cycles. Each amplification cycle consisted of a 30 second denaturation step at 94° C followed by a 30 second annealing step at 50° to 55° C followed by a 60 to 90 second extension step at 72° C. A final extension step of seven to ten minutes at 72° C succeeded the amplification cycles before the PCR terminated with a 4° C hold. Depending on the target locus and primers used, I varied the annealing temperature and extension time for optimal amplification. I used touchdown PCR in some instances, successively lowering the annealing temperature every two to three amplification cycles from an initial annealing temperature, usually near one of the primer melting temperatures, to a final annealing temperature 3-8° C below the lowest primer melting temperature. The remainder of the amplification cycles would then be carried out at the final annealing temperature. To verify amplification of the target locus, I visualized 2-3 uL of each PCR product against a 100 bp ladder on a 1% TAE-agarose gel. If successful target amplification occurred in the absence of non-specific amplification, I prepared the PCR product

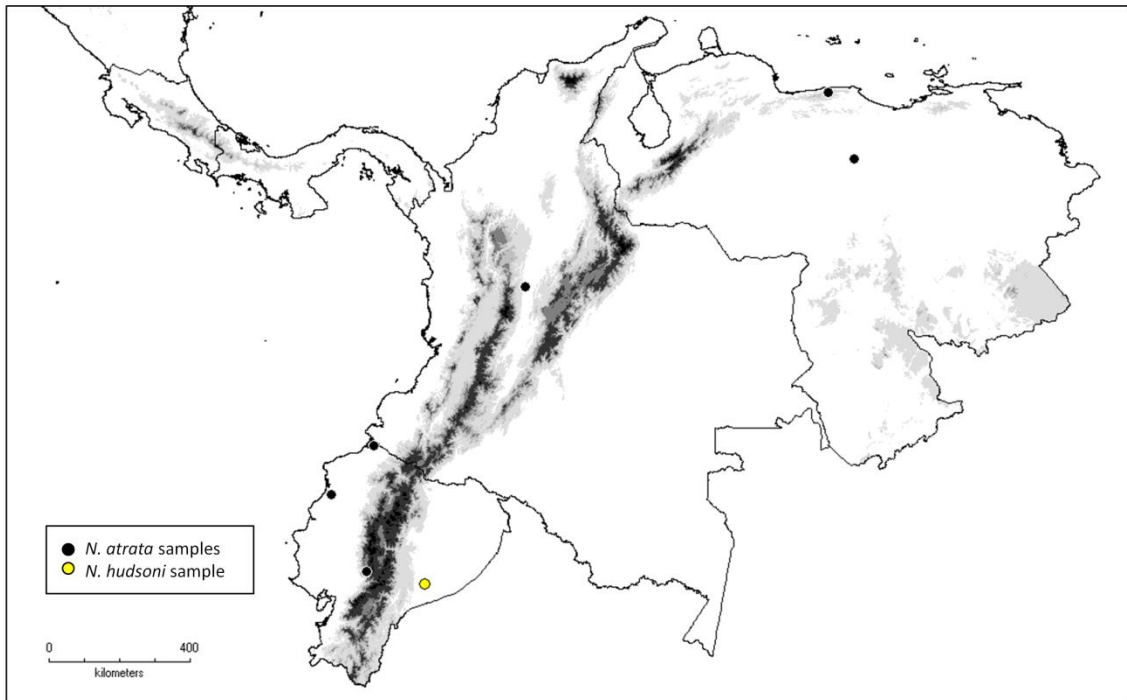


Figure 1. Map of Ecuador, Colombia, and Venezuela depicting localities of *Ninia atrata* and *Ninia hudsoni* sampled in this study. The solid black dots represent *Ninia atrata* localities and the solid yellow dot represents the *Ninia hudsoni* locality

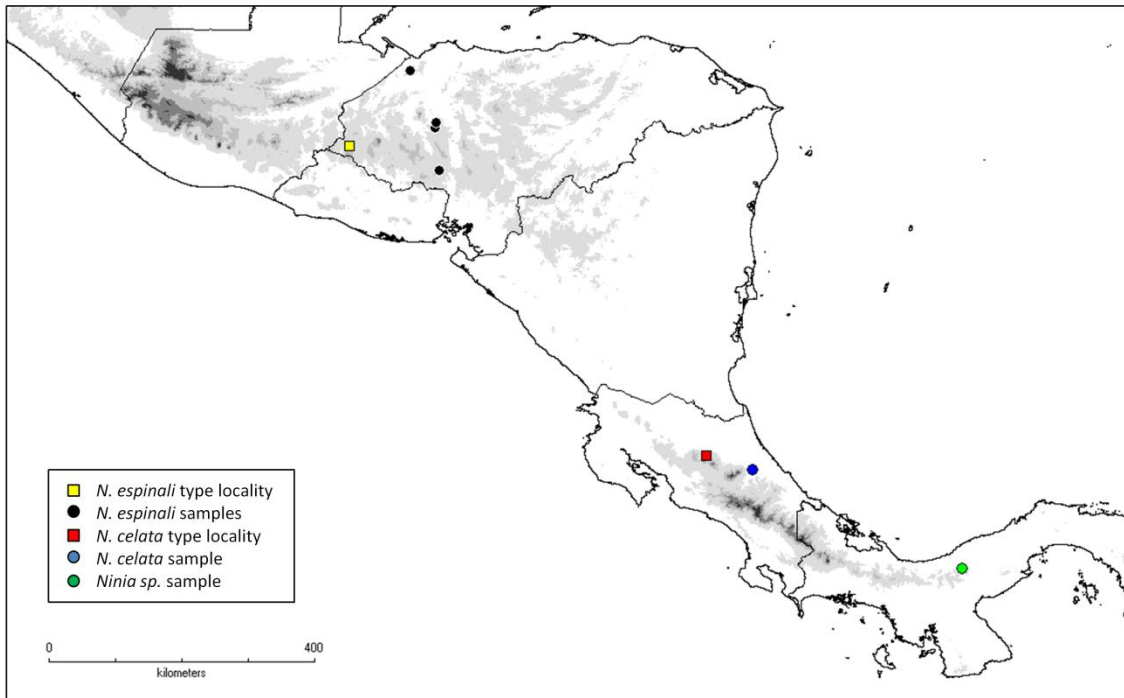


Figure 2. Map of Costa Rica and Panama depicting the type localities of *N. celata* and *N. espinali* and localities sampled in this study. The solid red square represents the type locality for *N. celata*, and the solid blue dot represents the locality sampled in this study. The solid yellow square represents the type locality for *N. espinali*, and the solid black dots represent the localities sampled in this study. The solid green dot represents the locality an unknown *Ninia* sp. sampled in this study

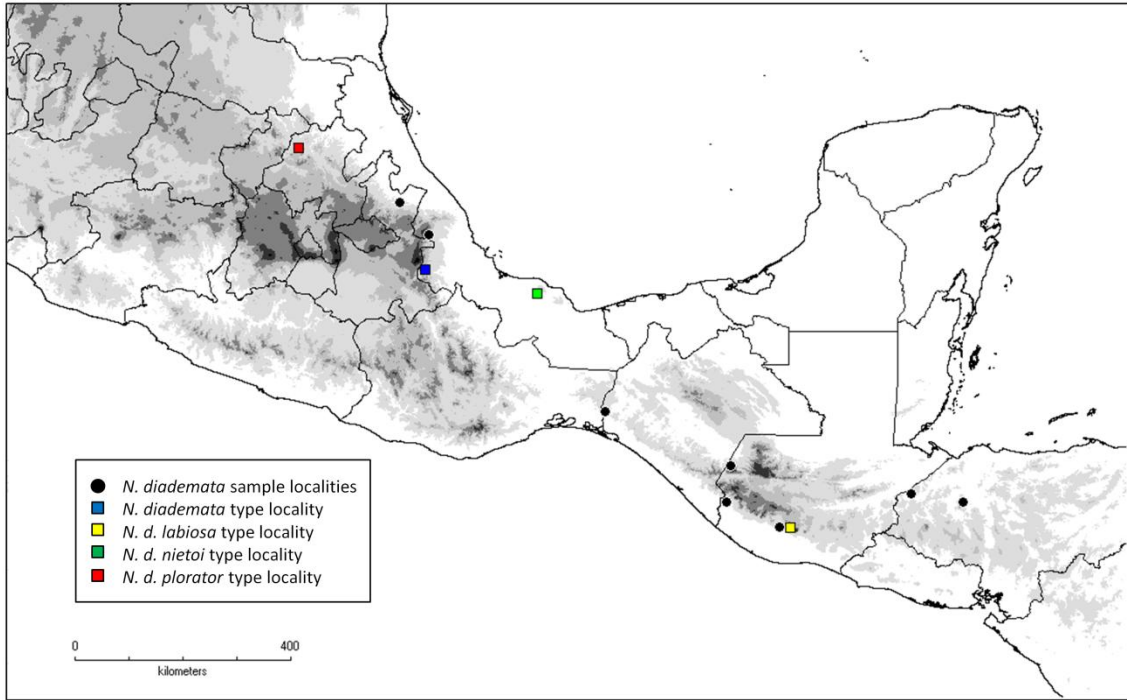


Figure 3. Map of southern Mexico, Guatemala, and Honduras depicting the type localities of *Ninia diademata* and localities sampled in this study. The solid blue square represents the type locality for *N. diademata*, the solid red square represents the type locality for *N. d. plorator*, the solid green square represents the type locality for *N. d. nietoi*, and the solid yellow square indicates the type locality for *N. d. labiosa*. The solid black dots represent localities sampled in this study

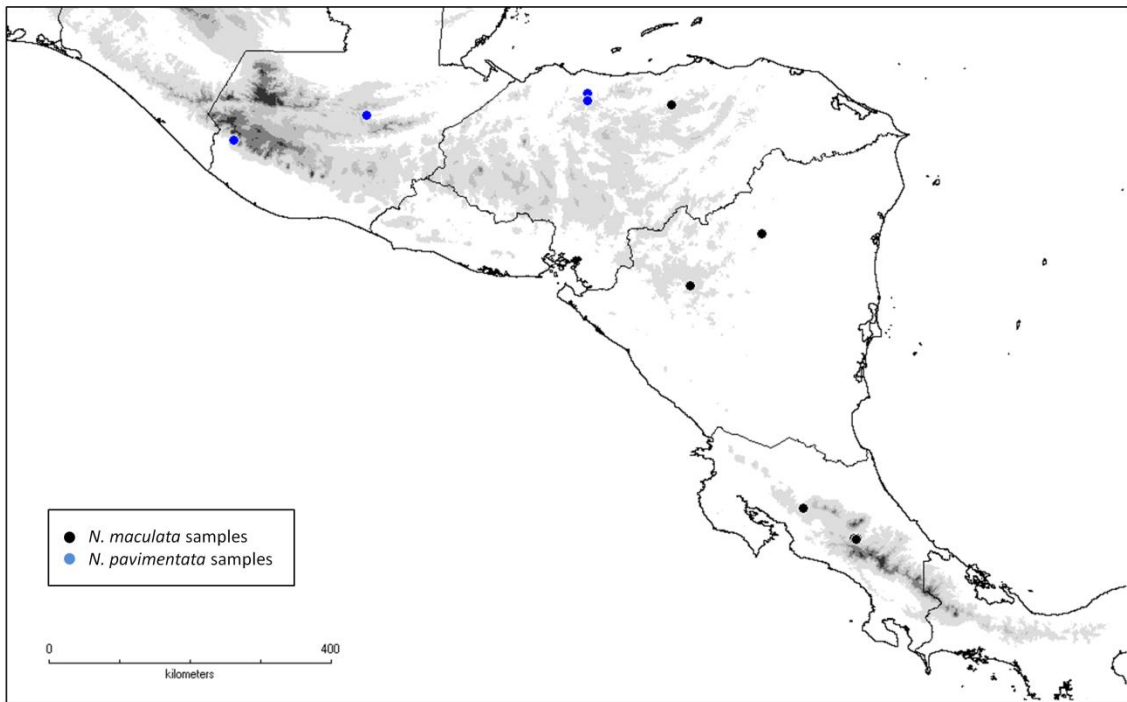


Figure 4. Map of Guatemala, Honduras, Nicaragua, and Costa Rica depicting the localities of *Ninia maculata* and *Ninia pavimentata* sampled in this study. The solid black dots represent localities of *Ninia maculata* and the solid blue dots and represent localities of *Ninia pavimentata*.



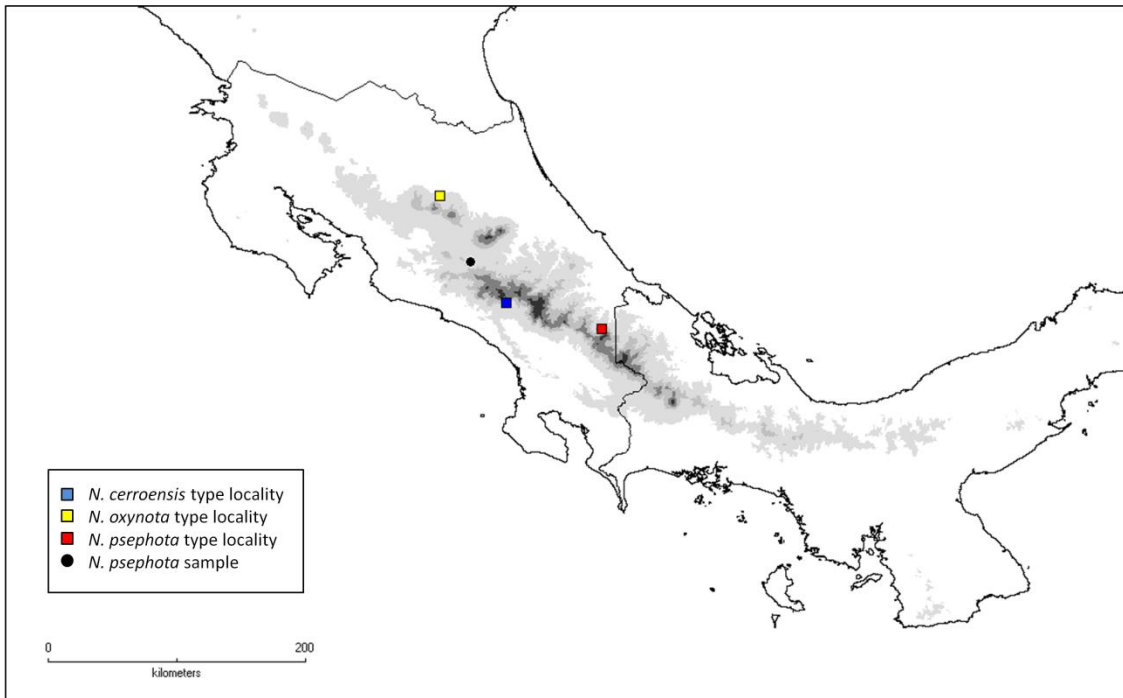


Figure 5. Map of Costa Rica and Panama depicting the type localities of *N. psephota* and the locality sampled in this study. The solid blue square represents the type locality for *N. cerroensis*, the solid yellow square represents the type locality for *N. oxynota*, and the solid red square represents the type locality for *N. psephota*. The solid black dot represents the locality sampled in this study

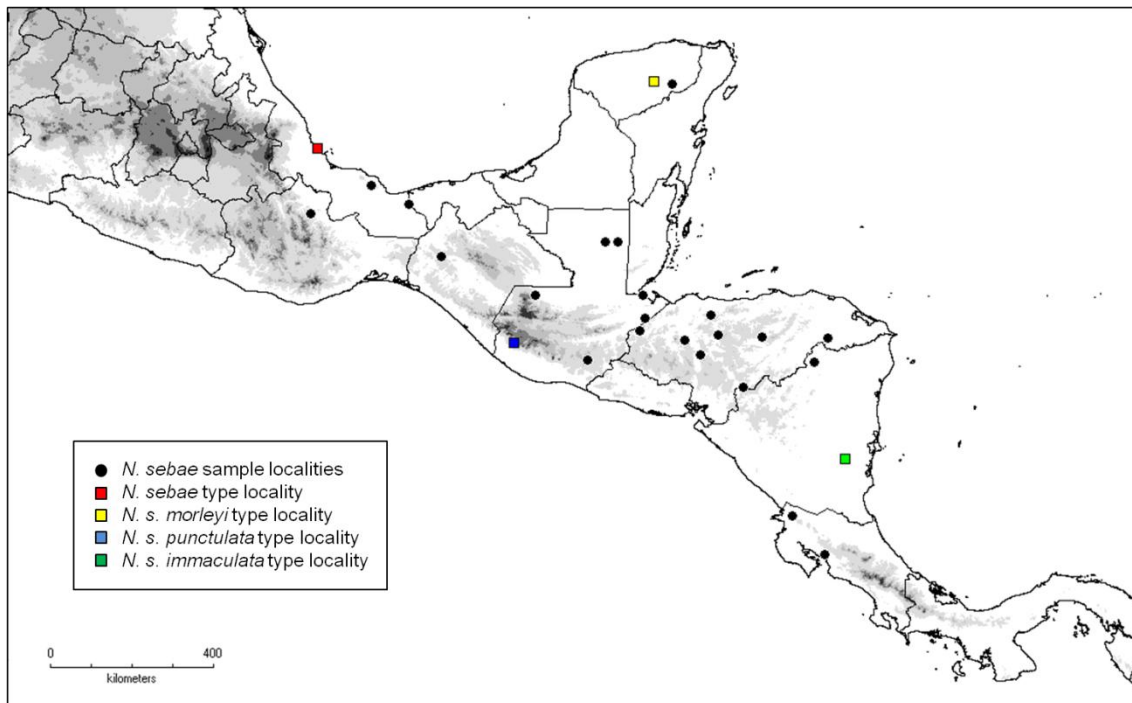


Figure 6. Map of Central America depicting the type localities of *Ninia sebae* and localities sampled in this study. The solid red square represents the type locality for *N. sebae*, the solid yellow square represents the type locality for *N. s. morleyi*, the solid green square represents the type locality for *N. s. immaculata*, and the solid blue square represents the type locality for *N. s. punctulata*. Solid black dots represent localities sampled in this study.

for cycle sequencing by treating every 10 uL of PCR product with 1.0 uL EXOSAP-IT (USB cat. no. 78201) using the manufacturer's incubation and heating protocol to remove excess primers and unincorporated dNTPs. Cycle sequencing reactions using BigDye® Terminator chemistry. were performed by the Genomics Core Facility at the University of Texas at Arlington or by SeqWright, Inc. in Houston, Texas. Sequence data were collected by an Applied Biosystems 3130xl Genetic Analyzer (Genomics Core Facility) or an Applied Biosystems 3730xl DNA Analyzer (Seqwright). In addition to sequence data collected for this study, I obtained outgroup sequence data from Coleman M. Sheehy III and GENBANK (Appendices A, B) for use in the following analyses

### *2.1.2 Data Analysis*

Raw sequence chromatograms were assembled and edited in Sequencher 4.5 (Genecodes 2000). Sequences were aligned in Sequencher and manually adjusted in Sequencher or MacClade 4.08. I performed separate analyses using several methods for each alignment, including concatenated multigene alignments. Maximum parsimony analyses were conducted using PAUP 4.0b10 (Swofford 2000) to run heuristic searches with 10 random addition replicates and TBR branch-swapping in effect. Weighted parsimony analyses were also conducted using PAUP\* 4.0b10, applying a tri-level weighting scheme described by Flores-Villela (2000) to account for different rates of substitution for transitions, transversions, and nonsynonymous substitutions. For parsimony analyses, support for nodes was assessed by non-parametric bootstrapping using 1000 pseudoreplicates. Maximum likelihood analyses were conducting using PAUP\* 4.0b10 (Swofford 2000) to run heuristic searches using the GTR+I+G or HKY models of evolution with TBR branch-swapping in effect. Support for nodes was assessed by non-parametric bootstrapping using 1000 pseudoreplicates. Analyses were also run on MEGA 5.0 (Tamura et al. 2011) using GTR+I+G model of evolution and 1000 bootstap replicates.

Bayesian analyses were performed using MrBayes v3.1 (Ronquist and Huelsenbeck 2003). For the CYTB alignment, I partitioned data by codon position. For the ND4 alignment, I performed the analysis with separate partitions for each codon position and a single partition for the tRNAs. For the NT3 alignment, I performed the analysis without any partitioning. I also performed two combined analyses, using a smaller subset of sequences. For the first analysis, I concatenated both mtDNA loci and partitioned the coding sequence by codon position and included a single partition for the tRNA sequence. For the second, I concatenated all three loci and partitioned the alignment in the same manner as described for the mtDNA with the addition of a single partition for the NT3 sequence. To select a model of evolution for the Bayesian analyses, I used Modeltest v3.7 (Posada and Crandall 1998) or Modelgenerator (Keane et al. 2006) to test each data partition and pick the most appropriate model under the Akaike Information Criterion. Information about the models selected is summarized Table 2. The CYTB Bayesian analysis was set to run for 10 million generations. Two independent runs were initiated, each with one cold chain and three heated chains with temp=0.2, and trees were sampled every 1000 generations. Burn-in was determined after verifying the runs had converged and reached posterior probability stationarity using Tracer (Rambaut and Drummond 2007) and, or, AWTY (Nylander et al. 2008). Bayesian analyses for the ND4, NT3, and combined data sets were carried out in the same manner but set to run for differing numbers of generations. The number of generations and burn-in for each run is described in Table 2. In all phylogenetic analyses except weighted parsimony, gaps were treated as missing data. For weighted parsimony, gaps were treated as a fifth state. To investigate simple genetic distance relationships, UPGMA trees were created using PAUP\* 4.0b10.

Basic summary statistics for each locus, including the number of haplotypes, the number of polymorphic and parsimony informative sites, and nucleotide diversity ( $\pi$ ), were calculated in DnaSP 5 (Librado and Rozas 2009). Basic summary statistics were also calculated for *N. sebae*, after excluding all other taxa, because this species accounted for nearly

Table 1. List of primers used in this study

Primer	Locus	Direction	Sequence	Source
ND4	ND4	Forward	5' CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC 3'	(Arevalo et al. 1994)
LEU	ND4	Reverse	5' CAT TAC TTT TAC TTG GAT TTG CAC CA 3'	(Arevalo et al. 1994)
605F	ND4	Forward	5' GTC TCC ATC TAT GAC TCC CA 3'	This study
621F	ND4	Forward	5' CCC AAA AGC CCA CGT TGA AGC 3'	This study
990R2	ND4	Reverse	5' GGT TTT TGT TCG TTC GTA GGT GGT 3'	This study
910F	ND4	Forward	5' ATA GCC TTA ATA ATC GCC CAC 3'	This study
1274R	ND4	Reverse	5' AGG TGT TCT CGT GAG TGT G 3'	This study
1175F	ND4	Forward	5' TAA TCA CAG CCT CCT ACT C 3'	This study
H47R	ND4	Reverse	5' TCT ATT GTC AAG GTC ACA GC 3'	This study
1256F	ND4	Forward	5' CAC ACT CAC GAG AAC ACC T 3'	This study
L68R	ND4	Reverse	5' TAC CAC TTG GAT TTG CAC CA 3'	This study
H14910	CYTB	Forward	5' GAC CTG TGA TNT GAA AAA CCA YCG TT 3'	(Burbrink et al. 2000)
THRSN2	CYTB	Reverse	5' CTT TGG TTT ACA AGA ACA ATG CTT TA 3'	(Burbrink et al. 2000)
S20563F	CYTB	Forward	5' ATT TTT GCT CTA TCA GAG ACC GGC 3'	This study
S20584F	CYTB	Forward	5' GGC GGC CCG AAA AAC CAC TGT TG 3'	This study
S20596F	CYTB	Forward	5' AAC CAC TCT TGT TAA TCA ACT ACA 3'	This study
S21136F	CYTB	Forward	5' GCA CTA CAC TTT ATC CTC CCA TTC 3'	This study
S21257R	CYTB	Reverse	5' AAT GGG ATT TTG TCG ATG TCT GAG T 3'	This study
S21790R	CYTB	Reverse	5' ACC CAT GTT TGG TTT ACA AAA ACA ATG CT 3'	This study
NT3-F3	NT3	Forward	5' ATA TTT CTG GCT TTT CTC TGT GGC 3'	(Noonan and Chippindale 2006)
NT3-R4	NT3	Reverse	5' GCG TTT CAT AAA AAT ATT GTT TGA CC 3'	(Noonan and Chippindale 2006)

Table 2. Partitions and models used in Bayesian MCMC runs.

Alignment	Number of Taxa	Partition	Partition Length (bp)	AIC Substitution Model	MCMC Generations	Sample Frequency	Burnin (samples)
CYTB	72		1080		>10x10 <sup>6</sup>	1000	1000 (<10%)
		CYTB 1	360	GTR+I+G			
		CYTB 2	360	TVM+I+G			
		CYTB 3	360	GTR+I+G			
ND4	73		873		4x10 <sup>6</sup>	1000	1000 (25%)
		ND4 1	232	HKY+I+G			
		ND4 2	232	HKY+I+G			
		ND4 3	233	GTR+g			
		TRNAs	182	HKY+I+G			
NT3	73		497		2x10 <sup>6</sup>	1000	500 (10%)
		NT3	497	K80+I+G			
CYTB+ND4	29		1780		5x10 <sup>6</sup>	1000	500 (10%)
		CYTB 1	361	TYM+I+G			
		CYTB 2	361	HKY+I+G			
		CYTB 3	361	GTR+G			
		ND4 1	232	TrN+g			
		ND4 2	232	K81uf+I			
		ND4 3	233	TrN			
CYTB+ND4+NT3	25		2453		5x10 <sup>6</sup>	1000	500 (10%)
		CYTB 1	361	TYM+I+G			
		CYTB 2	361	HKY+I+G			
		CYTB 3	361	GTR+G			
		ND4 1	232	TrN+g			
		ND4 2	232	K81uf+I			
		ND4 3	233	TrN			
		tRNAs	177	HKY+I			
		NT3	497	TVM+I			

40% of the sequences in each alignment. Uncorrected p-distances were calculated for pairwise comparisons for both CYTB and ND4 sequences using MEGA 5.0. In addition, mean p-distances were calculated between species. To further investigate the pattern of genetic divergence within *Ninia*, I estimated the mean genetic distance between species according to the Kimura two parameter model using MEGA 5.0. This model was selected because of the high transition to transversion ratio estimated in MEGA 5.0 for the mtDNA data (CYTB R=7.46, ND4 R=6.62).

## 2.2 Results

### 2.2.1 Genetic Diversity

Due to difficulties in amplifying some particularly degraded templates, a few samples were absent from one or more data sets and subsequent analyses. Following alignment, no gaps were found in any protein coding sequence. Alignments for each locus are included in Nexus format in Appendix E for CYTB, Appendix F for ND4, and Appendix G for NT3. Basic summary statistics for each locus are presented in Table 3. The NT3 data set contained both homozygous and heterozygous genotypes. To reconstruct haplotype sequences, the alignment was phased using the PHASE v2.1.1 algorithm (Stephens et al. 2001) implemented in DnaSP before calculating summary statistics. Among the loci sampled, the CYTB sequence yielded the highest amount of nucleotide diversity ( $\pi = 0.1058$ ), and ND4 exhibited a slightly lower level ( $\pi = 0.0833$ ). The amount of nucleotide diversity observed in the NT3 sequence was substantially lower ( $\pi = 0.0240$ ). Values for *N. sebae* followed the same pattern, with estimates of nucleotide diversity approaching approximately 30-35% of those obtained for the total dataset.

Pairwise p-distances are given in Appendix C for CYTB and Appendix D for ND4. Mean p-distances between species of *Ninia* are summarized in Table 4, and mean Kimura 2-parameter distances between species of *Ninia* are summarized in Table 5. Overall, the CYTB data yielded slightly higher estimates of genetic distance. This discrepancy might be explained by the inclusion of tRNA sequence in the ND4 dataset because the tRNA sequence exhibits

less polymorphism than the ND4 coding sequence. The highest distance estimates (Kimura 2-parameter) were found between *N. espinali* and *N. hudsoni* for both CYTB ( $d = 0.188$ ) and ND4 ( $d = 0.158$ ) data sets. Likewise, the lowest estimates were found between *N. maculata* and *N. pavimentata* for both CYTB ( $d = 0.063$ ) and ND4 ( $d = 0.058$ ) data sets. By comparison, estimates of genetic distance between some species of *Ninia* approached or exceeded that obtained for intergeneric comparisons with *Sibon*. Mean genetic distance estimates between *Ninia* and *Sibon* for the CYTB data set ranged from  $d = 0.156$  to  $d = 0.187$ . Similarly, mean genetic distance estimates between *Ninia* and *Sibon* for the ND4 data set ranged from  $d = 0.152$  to  $d = 0.183$ .

### 2.2.2 Phylogenetic analysis of mtDNA data

For phylogenetic analyses, Bayesian posterior probabilities (PP) greater than 95% and bootstrap proportions (BS) greater than 70% were considered strong support for a clade (Felsenstein 2004, Hillis and Bull 1993). Results from the mtDNA Bayesian analyses are depicted in Figures 7, 8, and 10 and described herein. Overall, both single gene and combined analyses of the mtDNA recovered the same major clades, but the analyses differed with respect to deeper relationships among *Ninia* lineages, most notably at short internodes. Usually, where incongruence existed between topologies, one topology lacked support.

Bayesian analyses of the mtDNA supported the monophyly of *Ninia*. The placement of *Chersodromus* as the sister species to *Ninia* was not strongly supported (0.94 posterior probability) by the Bayesian CYTB analysis, and the Bayesian ND4 analyses (0.85 posterior probability) indicated that the sister clade to *Ninia* consisted of members of *Geophis*, *Tropidodipsas*, and *Sibon*. These differing results do not conclusively resolve the relationships between *Ninia* and its closest relatives, but they do support earlier ideas the *Ninia* share a closer connection to these genera than to *Atractus*.

With regard to the South American *N. atrata* group, the analyses of both CYTB and ND4 data sets supported the relationship of *N. hudsoni* and *N. atrata* as sister species.



Table 3. Basic summary statistics for *Ninia* sequence alignments. Values in parentheses indicate the number of sites used in calculations after exclusion of sites with gaps or missing data. Values in brackets indicate standard deviations for  $\pi$ .

Locus	No. of Sequences	No. of Sites (bp)	No. Polymorphic Sites (bp)	No. Parsimony Informative Sites	No. of Haplotypes	Nucleotide Diversity ( $\pi$ )
CYTB	65	1083 (1083)	436	373	49	0.1058 [0.0042]
<i>N. sebae</i>	28	1083 (1083)	87	75	19	0.0210 [0.0011]
ND4	64	874 (803)	284	247	46	0.0833 [0.0035]
<i>N. sebae</i>	26	874 (806)	66	54	18	0.0242 [0.0013]
NT3*	120	497 (497)	75	60	60	0.0240 [0.0009]
<i>N. sebae</i>	46	497 (497)	18	15	24	0.0079 [0.0005]

\*NT3 sequence data contained both homozygous and heterozygous genotypes. To reconstruct haplotype sequences, the alignment was phased using the PHASE v2.1.1 algorithm (Stephens et al. 2001) implemented in DnaSP 5.

Table 4. Uncorrected p-distance averaged over sequence pairs between groups. Values shown for both CYTB (upper right) and ND4 (lower left).

<i>N. atrata</i>		0.131	0.133	0.127	0.138	0.082	0.121	0.116	0.102	0.123	0.129	0.135
<i>N. celata</i>	0.098		0.128	0.126	0.132	0.128	0.128	0.131	0.132	0.125	0.069	0.130
<i>N. diademata</i> (Atlantic)	0.102	0.095		0.108	0.139	0.121	0.132	0.136	0.119	0.133	0.132	0.141
<i>N. diademata</i> (Pacific)	0.094	0.087	0.091		0.138	0.123	0.133	0.130	0.127	0.128	0.125	0.128
<i>N. espinali</i>	0.109	0.110	0.115	0.103		0.144	0.134	0.134	0.126	0.138	0.115	0.124
<i>N. hudsoni</i>	0.073	0.096	0.113	0.101	0.124		0.109	0.103	0.099	0.120	0.122	0.139
<i>N. maculata</i>	0.087	0.100	0.103	0.096	0.108	0.091		0.056	0.103	0.129	0.117	0.139
<i>N. pavimentata</i>	0.088	0.099	0.109	0.099	0.112	0.096	0.052		0.101	0.124	0.123	0.135
<i>N. psephota</i>	0.077	0.095	0.092	0.097	0.114	0.090	0.094	0.090		0.123	0.129	0.138
<i>N. sebae</i>	0.090	0.102	0.110	0.102	0.105	0.102	0.092	0.093	0.090		0.124	0.131
<i>Ninia sp.</i>	0.104	0.059	0.100	0.099	0.123	0.101	0.106	0.107	0.114	0.111		0.135
<i>Sibon nebulatus</i>	0.122	0.129	0.134	0.126	0.128	0.133	0.126	0.128	0.130	0.121	0.141	

Table 5. Estimates of evolutionary distance averaged over sequence pairs between groups. Values shown for both CYTB (upper right) and ND4 (lower left). Analyses were conducted using the Kimura 2-parameter model

<i>N. atrata</i>		0.169	0.172	0.164	0.178	0.096	0.153	0.146	0.124	0.155	0.166	0.176
<i>N. celata</i>	0.118		0.166	0.162	0.170	0.165	0.164	0.170	0.172	0.159	0.079	0.168
<i>N. diademata</i> (Atlantic)	0.124	0.113		0.134	0.183	0.152	0.170	0.178	0.151	0.172	0.172	0.187
<i>N. diademata</i> (Pacific)	0.112	0.100	0.107		0.180	0.157	0.173	0.169	0.164	0.162	0.161	0.165
<i>N. espinali</i>	0.135	0.134	0.143	0.124		0.188	0.171	0.172	0.159	0.178	0.142	0.156
<i>N. hudsoni</i>	0.084	0.115	0.140	0.122	0.158		0.135	0.126	0.119	0.151	0.154	0.181
<i>N. maculata</i>	0.102	0.121	0.125	0.115	0.133	0.108		0.063	0.126	0.165	0.147	0.183
<i>N. pavimentata</i>	0.104	0.119	0.134	0.119	0.139	0.116	0.058		0.122	0.157	0.155	0.176
<i>N. psephota</i>	0.089	0.112	0.109	0.116	0.140	0.106	0.112	0.105		0.156	0.167	0.181
<i>N. sebae</i>	0.107	0.123	0.135	0.124	0.131	0.124	0.109	0.111	0.106		0.155	0.168
<i>Ninia sp.</i>	0.126	0.066	0.120	0.118	0.153	0.121	0.128	0.130	0.139	0.136		0.176
<i>Sibon nebulatus</i>	0.152	0.163	0.172	0.157	0.164	0.170	0.160	0.162	0.165	0.152	0.183	

Additionally, there appears to have been a divergence within *N. atrata*, between the Pacific lowland population in Ecuador and the populations found in the valleys of the Andean Cordilleras in Colombia and eastward into Venezuela. Figure 12 illustrates the locations of the sampled populations and their relationships to each other. There is no strong support for the assignment of the Pallatanga (Chimborazo), Ecuador *N. atrata* to either the Pacific or interior populations, or to *N. hudsoni*. The position of this taxon differed among analyses, but all the mtDNA Bayesian analyses indicated strong support (PP 1.00) for its placement in the *atrata+hudsoni* clade.

The exact phylogenetic position of *N. psephota* remained unresolved. In some analyses, this taxon was indicated as sister to the *maculata+pavimentata* clade; in others it was indicated as sister to the *hudsoni+atrata* clade, but no analysis provided adequate support for either relationship. However, the CYTB analysis supported the node giving rise to all of these taxa (PP 1.00). The ND4 analysis did not indicate this relationship; it instead included *N. psephota* in an *atrata-sebae* clade but this relationship also lacked support. Bayesian analyses of both CYTB and ND4 as well as the combined mtDNA data set supported (PP >0.98) a larger clade containing *N. atrata*, *N. maculata*, *N. psephota*, and *N. sebae* clade. *Ninia psephota* appears to be related to both the *N. maculata* and *N. pavimentata* snakes of Central America and the *N. atrata* and *N. hudsoni* snakes of South America.

All mtDNA analyses recovered *N. maculata* and *N. pavimentata* in the same clade, with high support for the node joining them (PP 1.0). Structure within the clade indicated that some divergence had occurred between the Costa Rican among sampled here and other localities further north. The analyses consistently recovered four groups, a Guatemalan population, a Honduran population, a Nicaraguan population, and a Costa Rican population, but the relationships among the sampled populations varied from one analysis to another. The Bayesian analysis of CYTB data indicated one node (PP 0.69) that included *N. pavimentata* from San Marcos, Guatemala, and *N. maculata* from Nicaragua and Costa Rica but also

produced one supported node (PP .94) that included *pavimentata* from Baja Verapaz, Guatemala, with *N. pavimentata* and *N. maculata* from Honduras. Among mtDNA analyses, *N. pavimentata* from San Marcos were not consistently placed with their conspecifics from Honduras and Baja Verapaz, Guatemala.

Within *Ninia diademata*, all mtDNA Bayesian analyses indicated a deep divergence, resulting in two well supported clades (PP 1.00). Specimens from south of the Continental Divide along Pacific versant of southern Mexico and Guatemala comprised a Pacific clade while those to north and Atlantic side comprised an Atlantic clade. Additionally, the mtDNA analyses indicated divergence within the Pacific clade between specimens from southern Mexico and Huehuetenango, Guatemala, and specimens from San Marcos and Suchitepequez, Guatemala. The node subtending all *N. diademata* was well supported in the analyses (PP 1.00). The relationship of *N. diademata* to other *Ninia* species was not well resolved except in the CYTB Bayesian analysis, which weakly supported (PP >0.90) *N. diademata* as sister to a clade containing *N. espinali* and *N. celata*. The ND4 Bayesian analysis indicated *N. diademata* as sister to *N. celata*, but did not support the the node joining the two (PP<0.70).

*Ninia espinali* was recovered as the sister species to all other *Ninia* in all the mtDNA analyses except for the CYTB Bayesian analysis, in which *N. espinali* was instead recovered as the sister species to *N. celata* with moderate support (PP 0.92). Within the *N. celata* lineage, there appears to be a modest divergence between the Costa Rican specimen included in this study and a unique example from Cocolé, Panama.

The mtDNA analyses all provided strong support for the inclusion of *N. sebae* in a clade with *N. atrata*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, and *N. psephota*. None of the analyses indicated substantial phylogenetic structuring within *N. sebae*. Branch lengths from the terminal nodes to the ancestral *N. sebae* node appear relatively short compared to intraspecific branch lengths recovered for some other *Ninia* species (e.g. *N. atrata*, *N.*

*diademata*, *N. pavimentata*). Analyses repeatedly recovered the same terminal clades, and placement of samples into these clades reflects a pattern of grouping by geographic proximity.

### 2.2.3 Phylogenetic analysis of nucDNA data

Analysis of multiple unlinked loci can provide independent estimates of species trees. To provide an estimate the relationships among the species of *Ninia* independent of the mtDNA, I included one nuclear locus in this study, a portion of one exon of the NT3 gene. I chose this particular locus because it has been widely used in phylogenetic studies, including several dealing with squamates (Noonan and Chippinadle 2006, Townsend et al. 2008, Wiens et al. 2008, Daza et al. 2009). Bayesian analysis of the NT3 data set (Figure 9) produced a different topology all together from the mtDNA analyses, indicating several polytomies and failing to recover both the genus *Ninia* as monophyletic and some of its species as monophyletic. However, many of the inferred relationships lacked adequate support. In this analysis, *Chersodromus* was recovered in polytomy with *N. espinali*, *N. maculata*, *N. pavimentata*, and *N. psephota*, but this clade lacked adequate support. Additionally, *N. maculata* and *N. pavimentata* were not recovered as a monophyletic. Furthermore, the analysis nested *N. celata* within *N. atrata*, but that clade also lacked support. Specimens of *N. diademata* were recovered in two separate lineages, one indicated as the sister lineage to all *Ninia* (PP 0.75), containing only the Honduran specimens, and the other indicated as the sister lineage to *N. sebae* (PP 1.00), containing specimens from both the Atlantic and Pacific localities north of Honduras.

### 2.2.4. Phylogenetic analysis of combined mtDNA and nucDNA data

Bayesian analysis of the combined mtDNA and nucDNA data set suggested similar relationships to those inferred by the mtDNA analyses (Figure 11), but it differed in that it provided strong support for a sister relationship between *Chersodromus* and *N. espinali* (PP 1.00). Like the mtDNA analyses, *N. sebae* was recovered in a well supported clade (PP 1.00) with *N. atrata*, *N. maculata*, *N. pavimentata*, and *N. psephota*. The analysis also indicated *N. psephota* as sister to *N. atrata* (PP 0.90). Likewise, the analysis recovered *N. diademata* in two

well supported clades (1.00), corresponding to an Atlantic clade and a Pacific clade, and it indicated *N. celata* as sister to *N. diademata*, but that relationship was not strongly supported (PP 0.82).

Weighted parsimony analysis using the tri-level weighting scheme has been shown to perform as well as or better than equally weighted parsimony because of its ability to capture additional information in the amino acids (Kjer et al. 2007). Although use of a tri-level weighting scheme violates the assumption of character independence, justification for combining protein and nucleic acid sequences is provided by Agosti et al. (1996) and Flores-Villela et al. (2000). If additional characters support relationships originally supported by the primary sequence, then those characters simply up-weight those relationships. Alternatively, additional characters may not support the original relationships, in which case they do not cause a problem of non-independence because the state of one character is not predictive of the other.

The weighted parsimony analysis based on 5665 total characters (891 parsimony informative characters) derived from combined mtDNA and nucDNA data resulted in three most parsimonious trees, each 3268 steps long. All three trees and the strict-consensus tree indicated a highly similar topology to that of the Bayesian analysis described above. They differed in the placement of a few terminal nodes within species clades, but deeper relationships were congruent with the Bayesian results. Additionally, the weighted parsimony analysis lacked adequate support for the clade containing *N. atrata*, *N. maculata*, *N. pavimentata*, *N. psephota*, and *N. sebae*; this clade was strongly supported by the Bayesian analysis (PP 1.00).

The tree produced by the UPGMA method (Figure 13) also yielded a topology similar to that of the Bayesian analysis. Like the weighted parsimony analysis, it differed in the placement of a few terminal nodes within species clades. Unlike the Bayesian or weighted parsimony analyses, *Chersodromus* was not recovered within the *Ninia* clade.

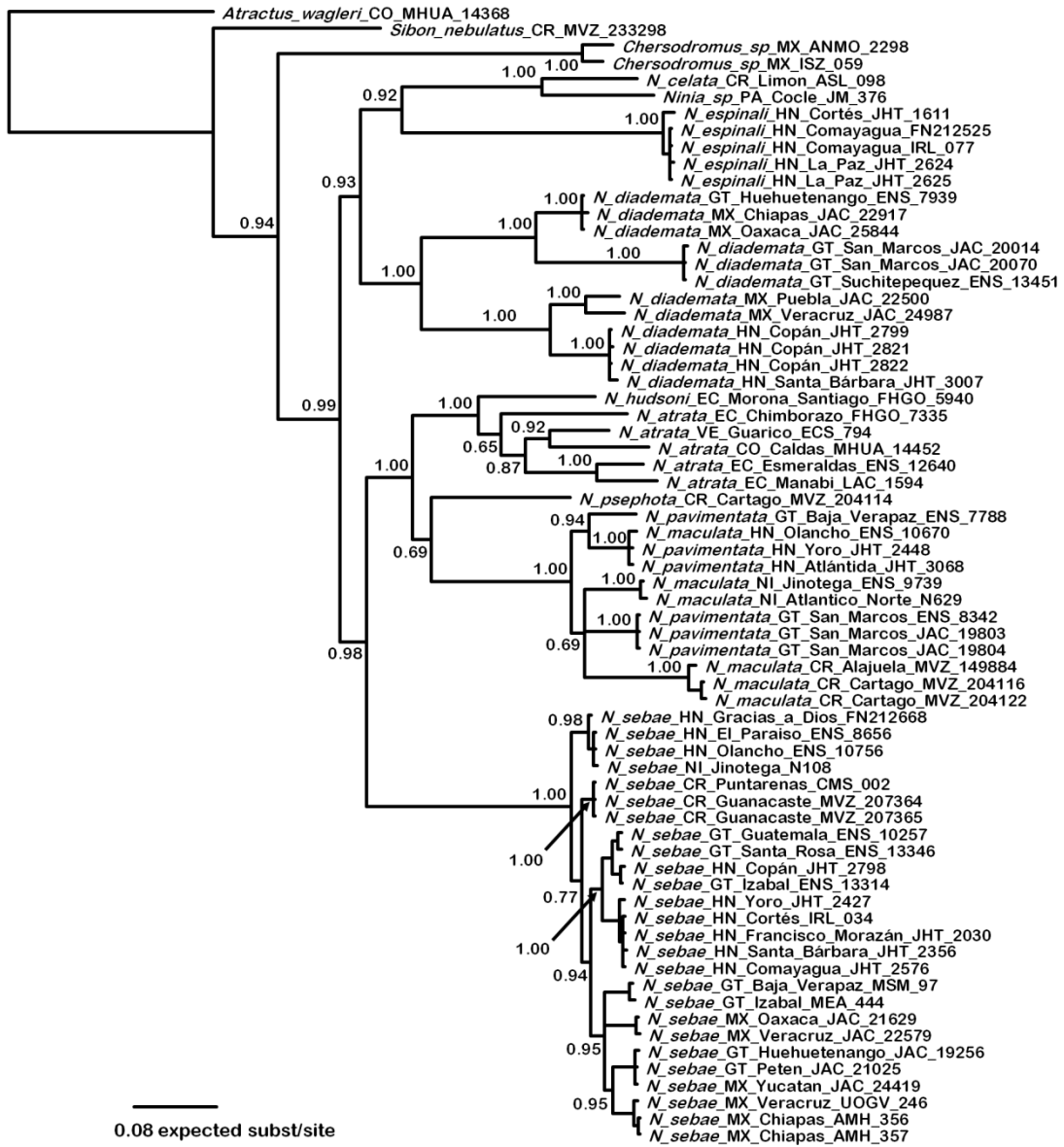


Figure 7. Bayesian phylogram derived from CYTB data. Numbers above or below nodes represent posterior probability values for the indicated clade.





Figure 8. Bayesian phylogram derived from ND4 data. Numbers above or below nodes represent posterior probability values for the indicated clade.



Figure 9. Bayesian phylogram derived from NT3 data. Numbers above or below nodes represent posterior probability values for the indicated clade.

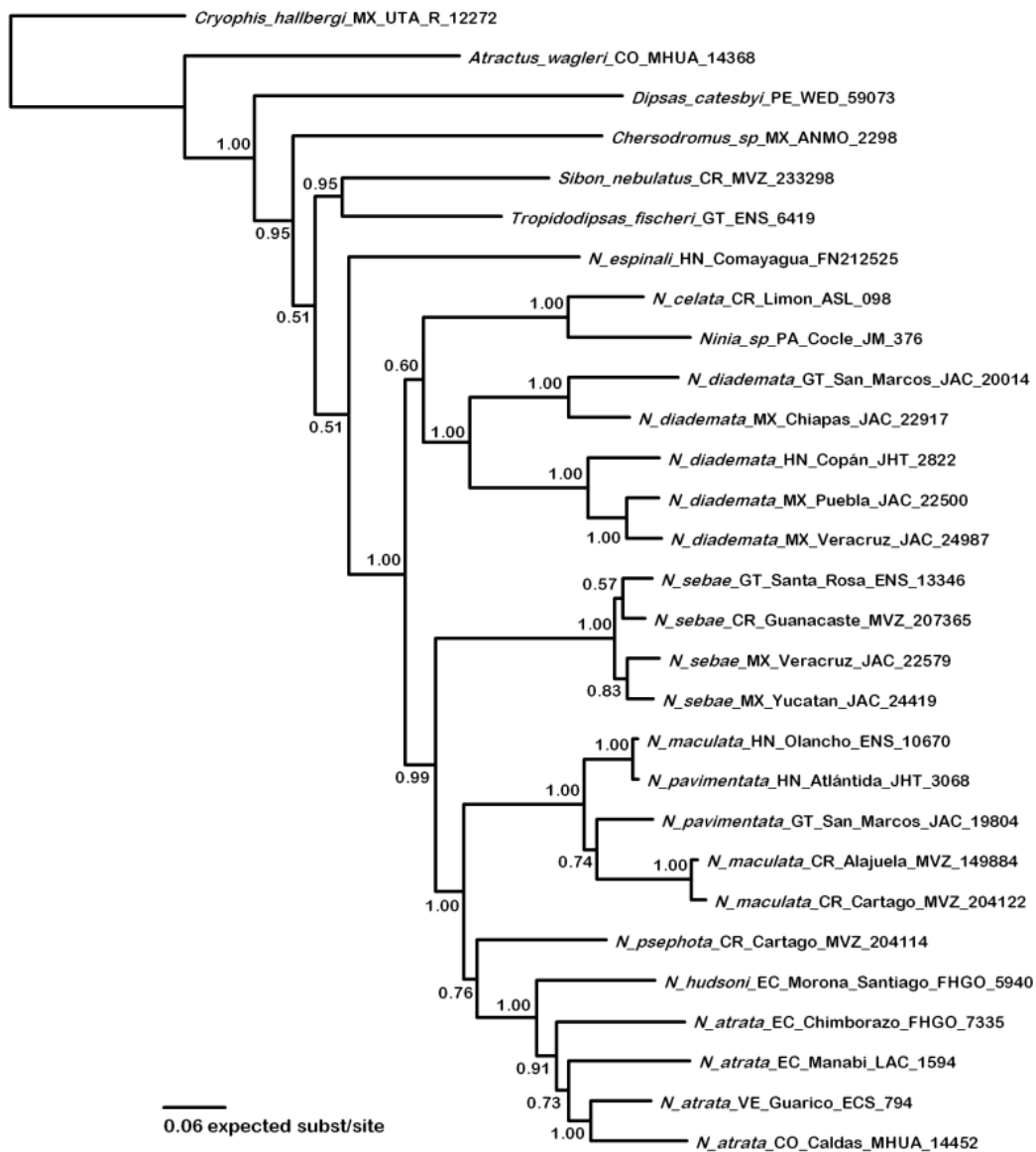


Figure 10. Bayesian phylogram derived from combined mtDNA data (CYTB, ND4). Numbers above or below nodes represent posterior probability values for the indicated clade.

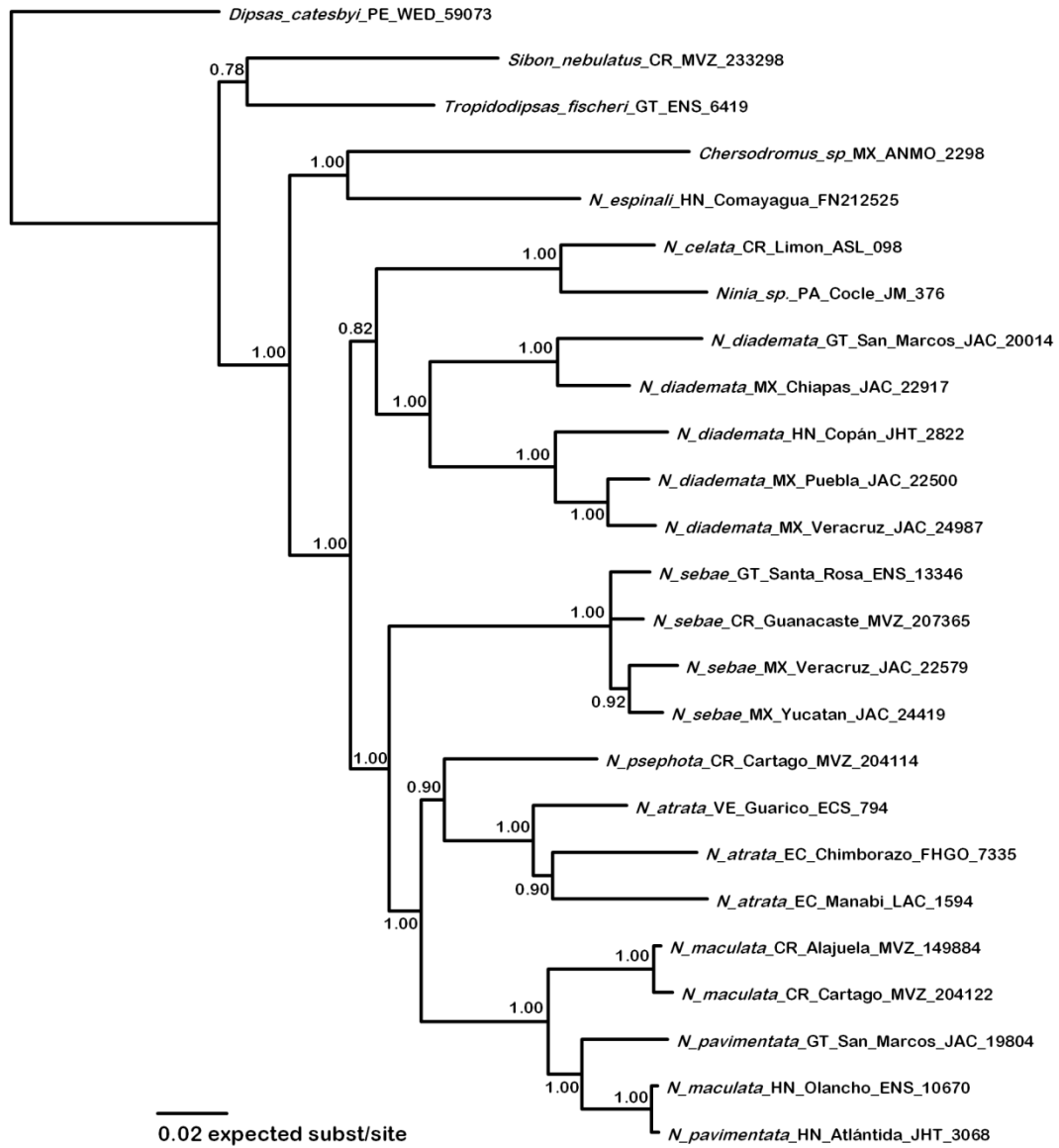


Figure 11. Bayesian phylogram of combined mtDNA and nucDNA data (CYTB, ND4, NT3). Numbers above or below nodes represent posterior probability values for the indicated clade.

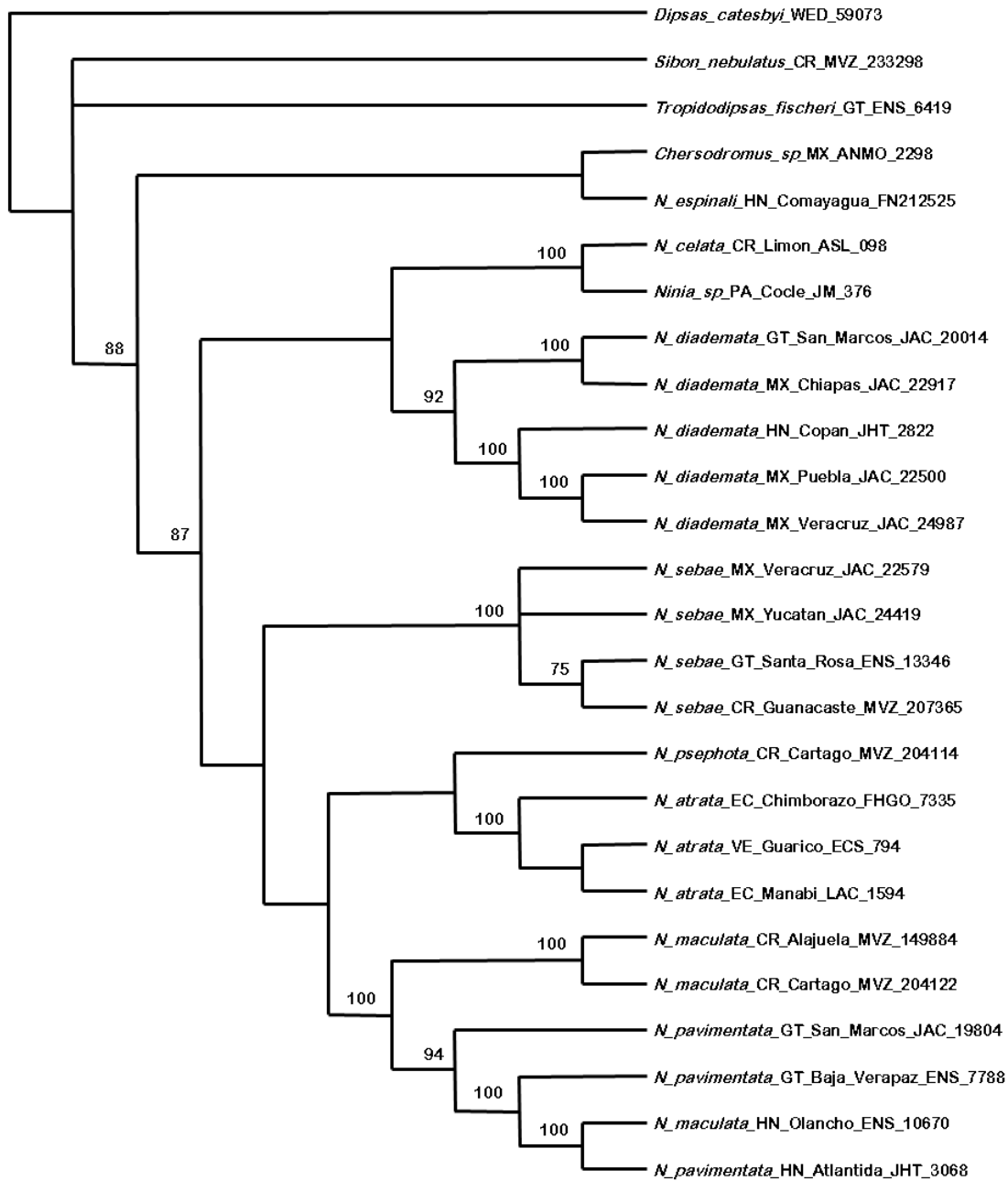


Figure 12. Strict consensus cladogram of the 3 most parsimonious trees recovered from the weighted parsimony analysis of combined mtDNA and nucDNA data (CYTB, ND4, NT3). Numbers above nodes indicate bootstrap proportions; values only shown for branches with  $\geq 70\%$  BS support.

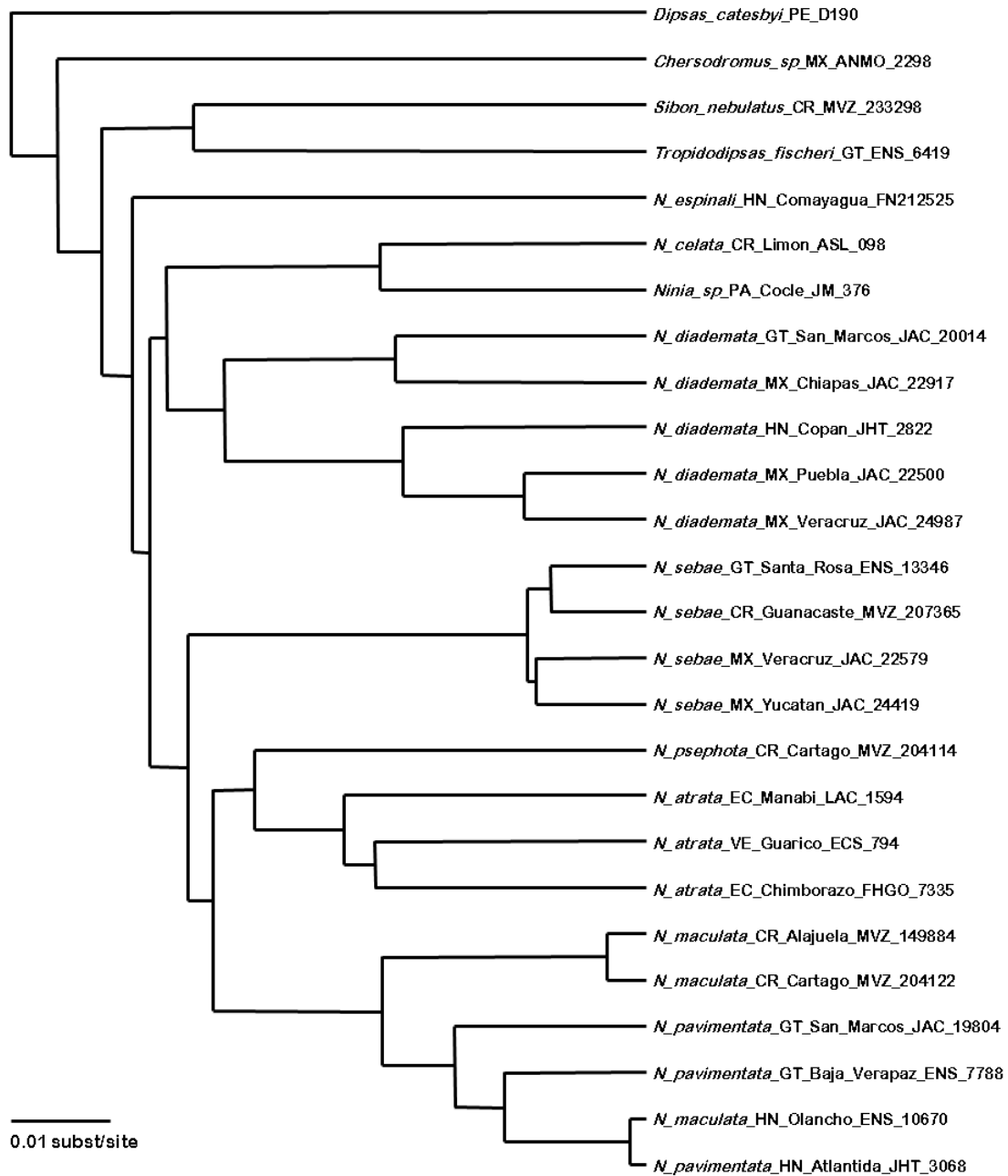


Figure 13. UPGMA phylogram derived from combined mtDNA and nucDNA data (CYTB, ND4, NT3).

## 2.3 Discussion

### *2.3.1 Inference of Phylogenetic Relationships*

Overall, the mtDNA and combined analyses provided the most resolved topologies with the highest support. In addition, they repeatedly recovered several relationships. Notably, all *Ninia* were all included a single clade with or without *Chersodromus*. The analyses strongly supported a *N. diademata* clade containing two strongly supported subclades corresponding to Atlantic and Pacific localities. The analyses all indicated *N. atrata*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, and *N. psephota* as members of another strongly supported clade. Within that larger clade, *Ninia maculata* and *N. pavimentata* were recovered in one strongly supported clade and *N. atrata* and *N. hudsoni* were recovered in another strongly supported clade. All the analyses also strongly supported a sister relationship for *N. celata* from Costa Rica and *Ninia sp.* from Panama.

The molecular data also imply a relationship between *N. celata* and *N. diademata*. Although the analyses lacked support for this relationship, the fact that these two species were recovered as sister lineages by multiple methods hints that a real relationship may exist. Even though the single gene CYTB and NT3 did not recover this relationship, at least for the Bayesian CYTB analysis, both *N. celata* and *N. diademata* were recovered in the same clade with *N. espinali*. Likewise, combined analyses by multiple methods favored the placement of *N. psephota* in a clade with *N. atrata* and *N. hudsoni*. This relationship lacked support, but it is worth noting that distance, parsimony, and likelihood-based methods all converged on this affinity.

All analyses support a strong relationship between *N. celata* and a population labeled *Ninia sp.*(PP 1.00, BS 100%). *Ninia celata* has only been taken from a few localities in Costa Rica and western Panama, but during the course of this study I obtained material from an unidentified specimen collected near Cocle, Panama, outside of the known range and elevation for *N. celata*. Examination of photos of this specimen revealed that the specimen superficially

resembles *N. atrata*, but it exhibits a curious mid-ventral stripe, a feature not shared with either *N. atrata* or *N. celata*. Branch lengths between this species and *N. celata* in the phylograms and the genetic distance estimates (Kimura 2-parameter) between the two species for CYTB ( $d = 0.079$ ) and ND4 ( $d = 0.066$ ) indicate that the two populations have experienced moderate divergence. Given the apparent geographic and altitudinal separation between the two species, examination of additional material may reveal the Panama population to be a distinct species.

Bayesian and weighted parsimony multigene analyses which incorporated NT3 data indicated a sister relationship for *Chersodromus* and *N. espinali*, thus the inclusion of NT3 sequence affects the placement of *Chersodromus* when using these methods. Given the similarity of the *Chersodromus* sequence to *Ninia* as indicated by NT3 Bayesian analysis (Figure 9), it is possible that inclusion of NT3 data simply has an additive effect which increases the overall similarity of *Chersodromus* to *Ninia* relative to other outgroup taxa. However, for the UPGMA method, inclusion of the NT3 sequence did not result in the placement of *Chersodromus* within the *Ninia* clade, suggesting that simple distance measures cannot entirely account for this phenomenon. It should be noted that both parsimony and Bayesian inference methods have been shown to be susceptible to long branch attraction (LBA), especially when considering ingroup LBA to outgroups (Felsenstein 2004, Bergsten 2005, Kolaczkowski and Thornton 2009).

While the inclusion of additional loci and outgroup taxa may further resolve the phylogenetic position of *Chersodromus*, given the present data, a couple alternative hypotheses can be made about the relationship of *Chersodromus* to *Ninia*. It is conceivable that *Chersodromus*, *N. espinali*, and the other species of *Ninia* represent three distinct genera. Analyses indicate *N. espinali* as the earliest diverging *Ninia* species, and this species differs from all others morphologically in several aspects (McCranie and Wilson 1995), most noticeably lacking any indication of a light nuchal collar, even as juveniles. Therefore, a relationship between *Chersodromus* and *N. espinali* (but not any other *Ninia*) would seem to imply the



existence of three monophyletic groups, and the mtDNA data do not reject this hypothesis. Alternatively, *Chersodromus* and *Ninia* may represent a single monophyletic group; however, the mtDNA data fail to support this hypothesis, and the nucDNA on its own does not explicitly support this hypothesis either ( $BP \leq 0.85$  for deep nodes). Thus, if *Chersodromus* and *Ninia* do not represent two separate monophyletic groups, the data are more consistent with the three group hypothesis.

Given the remarkably different results of the nucDNA analysis, lack of congruence between the mtDNA and nucDNA analyses is not surprising when considering the different evolutionary pathways the mitochondrial and nuclear genomes can take. Notably, the two genomes experience different modes of inheritance, have different effective population sizes (upon which stochastic processes such as genetic drift can act), and are subject to different selection pressures. Therefore, it would not seem unlikely to recover different genealogies for mtDNA and nucDNA loci, and there are numerous reports of this occurrence in the literature. More specific explanations have been given for the lack of congruence between mtDNA and nucDNA analyses, and these include homoplasy, incomplete lineage sorting, and poor resolution due to lack of informative variation (Moore 1995, McCracken and Sorenson 2005). Additionally, such incongruence can result from male-biased gene flow between populations, and this asymmetric gene flow has been documented in lizards (Johansson 2008), birds (Gibbs et al. 2000, Helbig et al. 2001), and mammals (Wilmer et al. 1999, Castella et al. 2001, Herreman 2009). Lastly, trees resulting from phylogenetic analysis of paralogous sequences would not be expected to be congruent with other gene-trees because such a tree would not represent true genealogical relationships due to the differing evolutionary history of the paralogues. The lack of resolution of the NT3 tree, combined with low posterior probability support for indicated clades, and the comparatively low number of substitutions (see Table 3) observed in the NT3 sequence data suggest that the relationships indicated from this data set should be considered cautiously because phylogenetic signal may be affected by a lack of

informative variation. Additionally, and the pattern of relationships recovered (e.g. polyphyly and paraphyly) is consistent with what might result from incomplete lineage sorting. In the case of incomplete lineage sorting, because all the alleles present in a species or population do not coalesce into a single ancestral allele, ancestral polymorphism remains and obscures phylogenetic signal. Daza et al. (2009) invoked this phenomenon to explain incongruence between nucDNA data (including that of NT3) with mtDNA data with respect to the dipsadine genus *Leptodeira*.

Estimates of genetic distance between some lineages of *Ninia* approach those between *Ninia* and *Sibon*, suggesting that divergence within *Ninia* occurred relatively early in the evolution of the genus. The difficulty in resolving some of the relationships within *Ninia* and the relationship of the genus to other dipsadine genera may be due to weak phylogenetic signal that could have resulted from multiple diversification events occurring in a narrow window of time. Patterns observed in the data are consistent with this hypothesis (e.g. short internodes). If this is the case, it makes sense that some of the ancestral populations of these species did not persist long enough for complete lineage sorting to occur prior to subsequent speciation events.

### 2.3.2 Divergence and Biogeography

Present day distributions of *Ninia* species point to two main areas of diversity, the highlands of Nuclear Central America and the highlands associated with Talamancan region of Costa Rica and western Panama. Inhabitants of the former include *N. diademata*, *N. espinali*, and *N. pavimentata*, while those of the latter include *N. celata*, *N. maculata*, and *N. psephota*. This pattern of diversity suggests that these areas played a pivotal role in the diversification of *Ninia*. Although altitudinal ranges of *Ninia* vary, as a group, they tend to occupy areas of moist, tropical forest that exist at moderate elevation. Therefore, it seems likely that the ancestor of *Ninia* was not a lowland or montane specialist, and that its generalized habitat requirements allowed dispersal into new areas wherever moist, tropical forests existed.

The complex geological and climatic history of Middle America during the Miocene and Pliocene provides many possible scenarios for the diversification of *Ninia*. Development of the highlands of Nuclear Central America occurred during the Miocene (Savage 2002). Divergence time estimates presented by Daza et al. (2009) put the split between *Ninia* and the ancestor of *Dipsas* and *Sibon* around 10 mya. If that date is realistic, then *Ninia* appear to have arisen during the middle to late Miocene, during or following the formation of the Nuclear Central American highlands, a dynamic period of geological development and climate change.

Application of published mtDNA substitution rates to uncorrected p-distances (CYTB) for *Ninia* can give crude estimates of divergence time. Zamudio and Greene (1997) reported rates 0.47 to 1.32% per million years for reptiles, and Daza et al. (2009) reported a rate of 1.34% per million years for snakes. Based on these values, the split between *Sibon* and *Ninia* occurred 26.4 to 9.3 mya (*Sibon nebulatus*-*N. espinali*). Among *Ninia* lineages, these rates suggest the split between the Atlantic and Pacific *N. diademata* clades occurred 23.1 to 8.1 mya, the split between *N. atrata* and *N. maculata* occurred 25.0 to 9.7 mya, the split between *N. atrata* and *N. psephota* occurred 21.6 to 7.6 mya, and the split between *N. atrata* and *N. hudsoni* occurred 17.4 to 6.1 mya.

Descendants of two early diverging *Ninia* lineages, *N. diademata* and *N. espinali*, collectively occupy areas in southern Mexico, Guatemala, and Honduras, indicating that the ancestor of *Ninia* occurred in Nuclear Central America during that time. The uplift of the Sierra Madres of Mexico in combination with the warming and drying trends of the Miocene led to the formation of a semi-arid barrier in central Mexico (Savage 2002); this barrier likely prevented northward dispersal of *Ninia*. To the south, continued uplift during the Miocene and Pliocene allowed the southward dispersal of Middle American herpetofauna over an emerging landmass (Savage 2002). *Ninia celata*, an endemic of lower Central America, also appears to have diverged relatively early among *Ninia*, indicating that the ancestral *Ninia* populations had successfully dispersed southward to exploit newly emerging lands.

Geographic relationships for *N. diademata* are mapped in Figure 12. Evidence suggests that a highland corridor existed which spanned the Isthmus of Tehuantepec during the Miocene (Barrier et al. 1998). If the Atlantic and Pacific clades of *N. diademata* diverged roughly 23.1 to 8.1 mya, then this interval overlaps with the existence of the highland corridor, and this highland corridor may have isolated populations of *N. diademata* on either side. Within the Pacific clade, the analyses suggest two groups exist, one consisting of specimens from Oaxaca and Chiapas, Mexico, and the other consisting of specimens from the Pacific versant of the Guatemalan highlands. Thus it seems that the highlands of San Marcos and Quezaltenango may have effectively limited gene flow between localities found on the Pacific versant of Guatemala and those found to the north in Chiapas and Oaxaca.

Both *N. sebae* and *N. maculata* have present day distributions that enter both Nuclear Central America and lower Central America. This suggests the ancestor of these lineages, which also gave rise to *N. atrata*, *N. hudsoni*, and *N. psephota*, had a similarly large distribution in Central America. Geologic developments and climatic changes that occurred during the late Miocene and Pliocene appear to have led to a radiation within this *Ninia* lineage. Today, *N. sebae* occupies a more northern distribution in comparison to other descendants from the same ancestral lineage. Therefore, *N. sebae* could have descended from an ancestral population that became isolated from other populations to the south. Evidence suggests that a marine connection existed between the Pacific Ocean and the Caribbean Sea during the Miocene and Pliocene, separating the Nuclear Central American highlands from the Lower Central American highlands (Coates and Obando 1996). This marine barrier could have served to isolate the ancestor of *N. sebae* from populations further south. This barrier has been implicated in speciation events for pit vipers during the middle to late Miocene (Castoe et al 2009), and based on mtDNA rates, *N. sebae* diverged from *N. maculata* during the same time (25.0 to 8.8 mya). Although *N. sebae* can be found as far south as Costa Rica today, it is possible that the species expanded its range southward at a later time, after speciation had occurred and the marine gap

had closed. Geographic relationships for *N. sebae* are illustrated in Figure 15. There do not appear to be any significant geographic barriers for *Ninia sebae*, and the molecular data do not provide evidence for historical divergence events within the species. Thus, the low amount of molecular variation observed over a large geographic area suggests that the species probably experienced a recent population bottleneck followed by a range expansion.

*Ninia maculata* may have originated in Lower Central America as part of the same radiation. Although this species occurs in both Nuclear Central America and Lower Central America, the greater distribution is centered in southern Nicaragua, Costa Rica, and Panama, suggesting the species arose here, then later dispersed north into Honduras and Guatemala after speciation had occurred. The geographic relationships of *N. maculata* and *N. pavimentata* populations are depicted in Figure 13. The high mountainous of areas of San Marcos and Quezaltenango appear to have served as barrier to gene flow between *N. pavimentata* on the Pacific versant and conspecifics to the interior in Baja Verapaz. Also, *Ninia maculata* is largely absent from the central part of Nicaragua and the Miskito coast; these areas may consist of unsuitable habitat that effectively isolate northern populations from the southern ones.

Because of the restriction of *N. psephota* to higher elevations, divergence of this species can be linked to exploitation of novel montane environments that developed from the continued uplift of the Sierra Talamanca during the Miocene. If *N. psephota* diverged 21.6 to 7.6 mya, as estimated from mtDNA substitution rates, then its interval for speciation overlaps that with the uplifting of the Sierra Talamanca during the Miocene.

It seems almost certain that *N. atrata* and *N. hudsoni* arose via a dispersal event into South America. Based on the crude estimate for the divergence between *N. atrata* and *N. hudsoni* (17.4 to 6.1 mya), the ancestor invaded South America prior to the closure of the Panama Isthmus. Lending support to this hypothesis, Daza et al. (2009) cited divergence time estimates for *Leptodeira* that indicated the species had also invaded South America prior to the closure of the Isthmus. The lack of a stable land connection and eustatic sea level fluctuations

during the early Pliocene could have isolated this lineage from *Ninia* in Lower Central America, severing gene flow populations to the north. Geographic relationships for *N. atrata* and *N. hudsoni* populations are depicted in Figure 12. It appears that the ancestor of *N. atrata* and *N. hudsoni* dispersed into South America during or after the final uplift of the Andean cordilleras in eastern Columbia that occurred 25-10 mya (Gregory-Wodzicki 2000), and even though these mountains currently present a geographic barrier, *N. atrata* was initially able to disperse across it, possibly by circumventing the barrier to the north. Ultimately, the Cordilleras have restricted gene flow between populations along the Pacific coast and those to the east of the Andes. *Ninia atrata* from the Pacific lowlands (Esmeraldas, Manabi) occupy areas of moist tropical forest, and it appears that this region is separated from the Pallatanga locality by dry forest. Therefore, even though the Pallatanga valley opens into the coastal plain, intervening areas of dry forest may pose a geographic barrier to *N. atrata*.

### 2.3.3 Comparisons to Previous Works

The results of this study provide evidence supporting many of the conclusions drawn by previous authors regarding the systematics of *Ninia*. Smith (1996), in his analysis of morphological variation in *N. sebae*, found little evidence that suggested the subspecific races assigned to *Ninia* accurately reflected the pattern of genetic differentiation in *N. sebae*. Figure 15 illustrates the genetic relationships among *N. sebae* populations in relationship to their geographic location and subspecific status and demonstrates how the molecular data support his conclusions. Smith also detected a pattern of differentiation within *N. diademata* similar to the pattern of divergence uncovered by the molecular data (Figure 13), namely that the snakes along the Pacific versant of southern Mexico and Guatemala differed from conspecifics found north of the highlands. In consideration of his phylogenetic analysis, this analysis differs in several ways. First, his parsimony analysis of morphological characters suggested that *N. psephota* and *N. diademata* were sister taxa whereas analysis of the molecular data here infers that *Ninia diademata* was the sister taxa to the ancestor of *espinali+celata* and that *N. psephota*

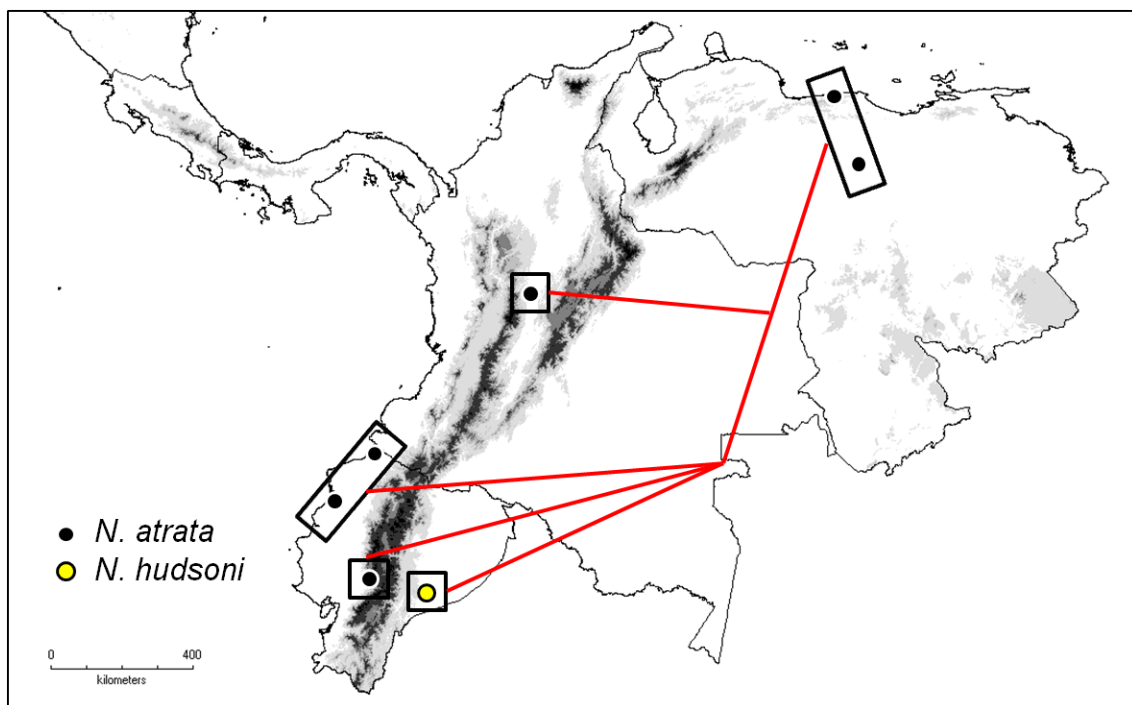


Figure 14. Map depicting relationships among localities of *Ninia atrata* and *Ninia hudsoni* based on mtDNA. Boxes represent terminal clades or terminal nodes. Lines represent branches; the length of lines does not correspond to evolutionary distance.

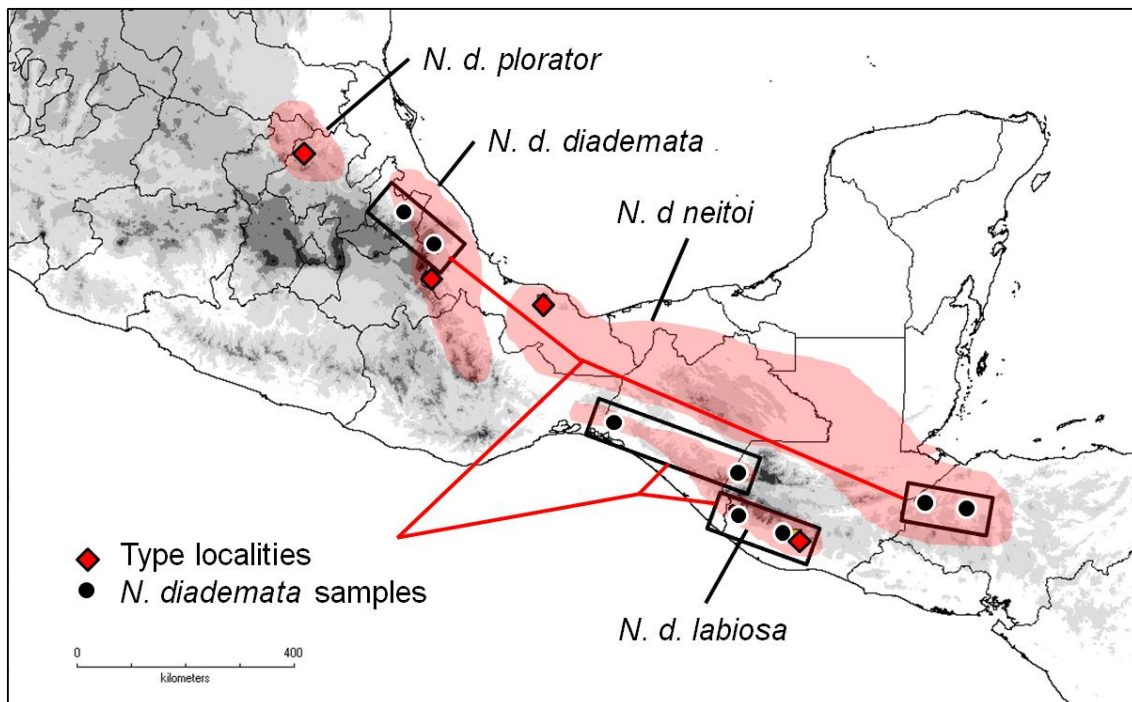


Figure 15. Map depicting relationships among localities of *Ninia diademata* based on mtDNA. Boxes represent terminal clades or terminal nodes. Lines represent branches; the length of lines does not correspond to evolutionary distance. Red shading indicates approximate distributions for *N. diademata* subspecies.



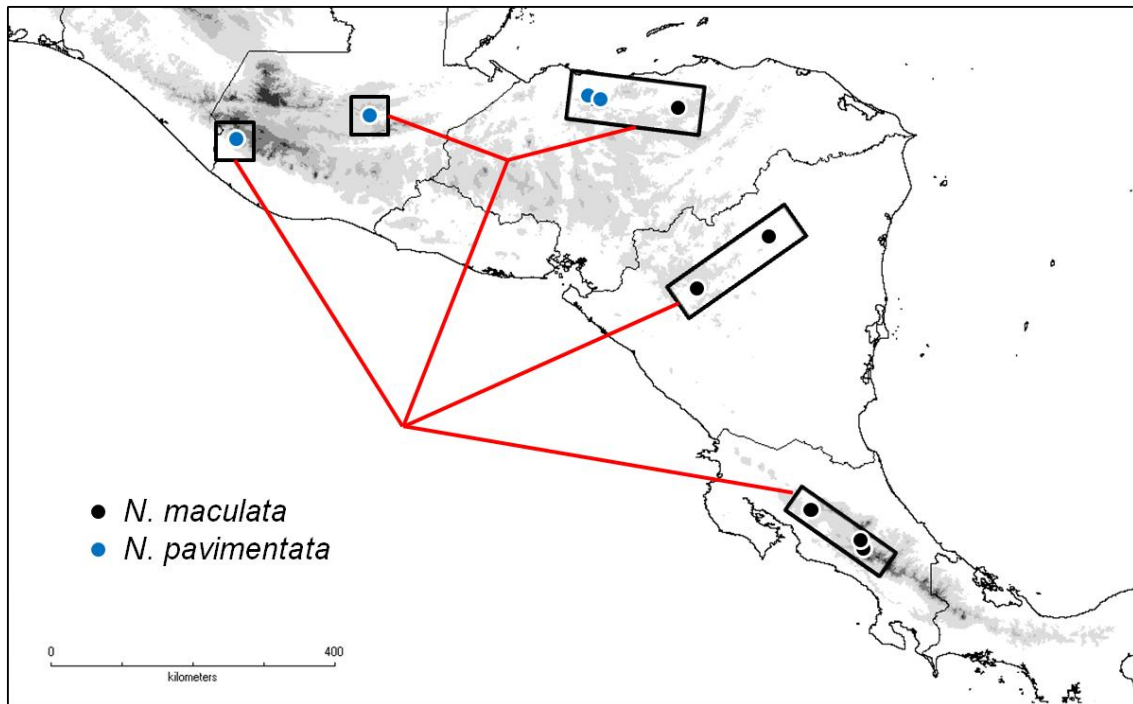


Figure 16. Map depicting relationships among localities of *Ninia maculata* and *Ninia pavimentata* based on mtDNA. Boxes represent terminal clades or terminal nodes. Lines represent branches; the length of lines does not correspond to evolutionary distance.

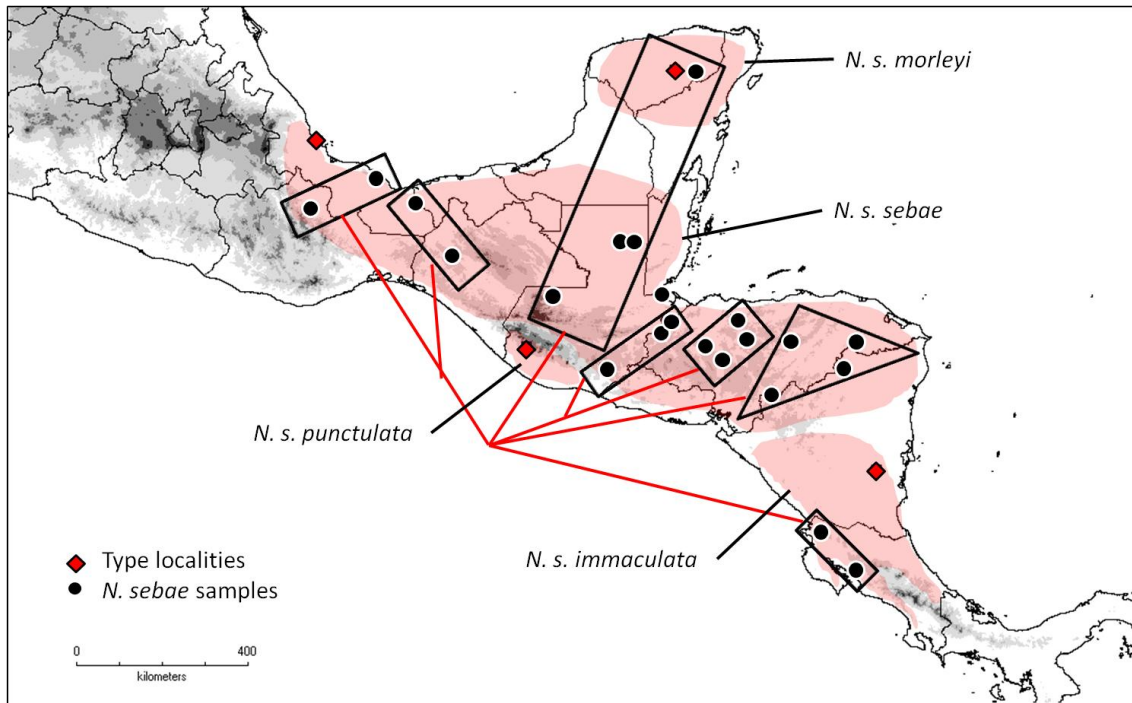


Figure 17. Map depicting relationships among localities of *Ninia sebae* based on mtDNA. Boxes represent terminal clades or terminal nodes. Lines represent branches; the length of lines does not correspond to evolutionary distance. Red shading indicates approximate distributions for *N. sebae* subspecies.

shared a closer connection with the *atrata+maculata* ancestor. Second, his analysis placed *N. sebae* in a clade with *N. diademata*, *N. maculata*, *N. pavimentata*, and *N. psephota*, exclusive of *N. atrata* and *N. hudsoni*. The results here indicate that *N. sebae* shares a more recent common ancestor with the *atrata+maculata* clade than with *N. diademata*. Lastly, his phylogeny infers that *N. atrata*, *N. espinali*, *N. celata*, and *N. hudsoni* diverged earliest among *Ninia*, with *N. celata* indicated as the sister lineage to all other *Ninia*. However, the molecular data suggest that *N. espinali* may have been the earliest to diverge from the *Ninia* ancestor. Smith concluded that two basic groups existed within *Ninia*, a South American and a Central American group. This dichotomy does not seem to reflect the evolutionary history of the group as inferred from the molecular data: *N. atrata* and *N. hudsoni* do not share a more common ancestor with *N. espinali* and *N. celata* exclusive of the other Central American taxa.

In the description of *N. celata* and *N. espinali*, McCranie and Wilson (1995) reported two unusual specimens of *N. atrata* from a valley near Pallatanga (Chimborazo), Ecuador, that they believed represented a unique species. During the course of this study, I received material from that locality to include in the molecular analysis. The resulting data support the conclusions drawn by McCranie and Wilson. It appears that the haplotpye from this specimen this locality is distinctive from both *N. hudsoni* and *N. atrata*, and that the Pallatanga (Chimborazo) population deserves further investigation. Considerating of the geography of that area, it is not difficult to imagine how the Andean Cordilleras have effectively blocked or limited gene flow among populations of *N. atrata*, leading to the pattern of diversification seen in the lineage leading to *N. hudsoni* and *N. atrata*. More extensive sampling of *N. atrata* in the Cordilleras in Ecuador and Colombia is required to clarify the status of *N. atrata* in that region, and such activities may uncover similar situations at other locations. In addition to their conclusion about *N. atrata*, this study validates the recognition of *N. celata* and *N. espinali*. Both species represent lineages clearly distinct from *N. atrata*.

Savage and Lahanas (1991) reported variation in *N. maculata* from Costa Rica and western Panama. They identified three distinctive populations comprised of snakes from the

Pacific lowlands, upland Costa Rica (and western Panama), and the Atlantic lowlands. I obtained material of *N. maculata* from upland Costa Rica, but material from the Pacific lowland and Atlantic lowland populations was not available at the time the molecular analyses were completed. The data indicate that the upland Costa Rican population is distinct from northern populations of *N. pavimentata* and *N. maculata*, but additional molecular data from the Pacific and Atlantic lowland populations is required to fully understand the evolutionary relationships among *N. maculata* populations.

Both Savage and Lahanas (1991) and Smith and Campbell (1996) suggested that northern populations of *N. maculata* from Guatemala represented a distinct species that should be recognized as *N. pavimentata*. It is possible that the Guatemalan populations of *N. maculata* have experienced some recent morphological differentiation, but the molecular data does not support these species as monophyletic groups. If the epithet *pavimentata* only applies to the specimens from the central highlands of Guatemala, then the species may ultimately prove to be polyphyletic. Even if the epithet is broadened to include specimens from Honduras, as suggested by Townsend et al. (2005), *N. maculata* is still rendered paraphyletic.

#### 2.4 Conclusions

In conclusion, this research answers several questions about an enigmatic group of snakes. It presents novel relationships for the species of *Ninia* and the mtDNA data support the monophyly of the genus. Even though the monophyly of the genus cannot be proven conclusively in light of the nucDNA, the analyses indicate all species of *Ninia* as members of the same clade. The assignment of a sister taxon to *Ninia* and the placement of *Chersodromus* remains problematic. The molecular analyses consistently indicate that *N. atrata*, *N. hudsoni*, *N. maculata*, *N. pavimentata*, and *N. psephota* all share a common ancestor, which in turn shared a common ancestor with *N. sebae*. *Ninia hudsoni* and *N. atrata* are inferred as sister taxa, and *N. maculata* and *N. pavimentata* form a monophyletic group, but the monophyly of either species with regard to other is not supported. In addition to recovering interspecific

relationships, this research uncovered interesting relationships within *N. atrata*, *N. diademata*, *N. maculata*, and *N. sebae*.

The research presented here poses several interesting questions about the evolutionary history of *Ninia*, making the group a promising subject for further research. Future efforts should be directed at understanding the population dynamics of the *N. maculata* and *N. pavimentata* complex, examining the relationships of *N. atrata* populations in Colombia and Ecuador, further examining the deep divergence in *N. diademata*, and describing the population of *Ninia* from Panama allied to *N. celata*. This research provides a solid framework from which to base future work on *Ninia* and should aid in making taxonomic evaluations.

APPENDIX A

LIST OF TAXA AND LOCALITIES SAMPLED IN THIS STUDY

Collector No.	Museum	Taxon	Locality	Source of Data
ENS_9039		<i>Adelphicos quadrivirgatus</i>	Guatemala: Huehuetenango	Coleman M. Sheehy
	LSU-H_12441	<i>Atractus trilineatus</i>	Brazil: Roraima	Coleman M. Sheehy
ANMO_2298		<i>Chersodromus sp.</i>	Mexico	This study
ISZ_059		<i>Chersodromus sp.</i>	Mexico	This study
UOGV_062		<i>Chersodromus sp.</i>	Mexico	This study
	UTA_R-12272	<i>Cryophis hallbergi</i>	Mexico: Oaxaca	Coleman M. Sheehy
WED_59073		<i>Dipsas catesbyi</i>	Peru	Coleman M. Sheehy
JAC_30704		<i>Geophis nigrocinctus</i>	Mexico: Jalisco	Coleman M. Sheehy
	FHGO_7335	<i>Ninia atrata</i>	Ecuador: Chimborazo	This study
ENS_12640		<i>Ninia atrata</i>	Ecuador: Esmeraldas	This study
LAC_1594	KU 218424	<i>Ninia atrata</i>	Ecuador: Manabi	This study
N1	No Voucher	<i>Ninia atrata</i>	Venezuela: Caracas	This study
ECS_794		<i>Ninia atrata</i>	Venezuela: Guarico	This study
ASL_098		<i>Ninia celata</i>	Costa Rica: Limon	This study
ENS_7939	UTA R-42291	<i>Ninia diademata</i>	Guatemala: Huehuetenango	This study
JAC_20014	UTA R-46553	<i>Ninia diademata</i>	Guatemala: San Marcos	This study
JAC_20070	UTA R-46554	<i>Ninia diademata</i>	Guatemala: San Marcos	This study
ENS_13451		<i>Ninia diademata</i>	Guatemala: Suchitepequez	This study
JHT_2799		<i>Ninia diademata</i>	Honduras: Copán	This study
JHT_2821		<i>Ninia diademata</i>	Honduras: Copán	This study
JHT_2822		<i>Ninia diademata</i>	Honduras: Copán	This study
JHT_3007		<i>Ninia diademata</i>	Honduras: Santa Bárbara	This study
JAC_22917		<i>Ninia diademata</i>	Mexico: Chiapas	This study
JAC_25844		<i>Ninia diademata</i>	Mexico: Oaxaca	This study
JAC_22500	UTA R-52599	<i>Ninia diademata</i>	Mexico: Puebla	This study
JAC_24987	UTA R-53068	<i>Ninia diademata</i>	Mexico: Veracruz	This study
FN212525	USNM 564116	<i>Ninia espinali</i>	Honduras: Comayagua	This study
IRL_077		<i>Ninia espinali</i>	Honduras: Comayagua	This study
JHT_1611		<i>Ninia espinali</i>	Honduras: Cortés	This study
JHT_2624		<i>Ninia espinali</i>	Honduras: La Paz	This study
JHT_2625		<i>Ninia espinali</i>	Honduras: La Paz	This study
	FHGO_5940	<i>Ninia hudsoni</i>	Ecuador: Morona Santiago	This study
	MVZ_149884	<i>Ninia maculata</i>	Costa Rica: Alajuela	This study
	MVZ_204116	<i>Ninia maculata</i>	Costa Rica: Cartago	This study
	MVZ_204122	<i>Ninia maculata</i>	Costa Rica: Cartago	This study
	MVZ_204124	<i>Ninia maculata</i>	Costa Rica: Cartago	This study
ENS_10670	UTA R-54000	<i>Ninia maculata</i>	Honduras: Olancho	This study
ENS_9739	UTA R-44836	<i>Ninia maculata</i>	Nicaragua: Jinotega	This study
N629		<i>Ninia maculata</i>	Nicaragua: R. A. Atlantico Norte	This study
ENS_7788	UTA R-42427	<i>Ninia pavimentata</i>	Guatemala: Baja Verapaz	This study
ENS_8342	UTA R-42401	<i>Ninia pavimentata</i>	Guatemala: San Marcos	This study
JAC_19803	UTA R-46560	<i>Ninia pavimentata</i>	Guatemala: San Marcos	This study
JAC_19804	UTA R-46561	<i>Ninia pavimentata</i>	Guatemala: San Marcos	This study
JHT_3068		<i>Ninia pavimentata</i>	Honduras: Atlántida	This study
JHT_2448		<i>Ninia pavimentata</i>	Honduras: Yoro	This study
	MVZ_204114	<i>Ninia psephota</i>	Costa Rica: Cartago	This study
	MVZ_207364	<i>Ninia sebae</i>	Costa Rica: Guanacaste	This study
	MVZ_207365	<i>Ninia sebae</i>	Costa Rica: Guanacaste	This study
CMS_002		<i>Ninia sebae</i>	Costa Rica: Puntarenas	This study
MSM_97		<i>Ninia sebae</i>	Guatemala: Baja Verapaz	This study
ENS_10257	UTA R-46879	<i>Ninia sebae</i>	Guatemala: Guatemala	This study
JAC_19256	UTA R-42396	<i>Ninia sebae</i>	Guatemala: Huehuetenango	This study
ENS_13314	UTA R-58901	<i>Ninia sebae</i>	Guatemala: Izabal	This study
MEA_444	UTA R-39539	<i>Ninia sebae</i>	Guatemala: Izabal	This study

Collector No.	Museum	Taxon	Locality	Source of Data
JAC_20998	UTA R-50323	<i>Ninia sebae</i>	Guatemala: Peten	This study
JAC_21025	UTA R-50324	<i>Ninia sebae</i>	Guatemala: Peten	This study
ENS_13346	UTA R-58902	<i>Ninia sebae</i>	Guatemala: Santa Rosa	This study
JHT_2576		<i>Ninia sebae</i>	Honduras: Comayagua	This study
JHT_2798		<i>Ninia sebae</i>	Honduras: Copán	This study
IRL_034		<i>Ninia sebae</i>	Honduras: Cortés	This study
ENS_8656	UTA R-41252	<i>Ninia sebae</i>	Honduras: El Paraiso	This study
JHT_2030		<i>Ninia sebae</i>	Honduras: Francisco Morazán	This study
FN212668	USNM 564122	<i>Ninia sebae</i>	Honduras: Gracias a Dios	This study
ENS_10756	UTA R-53995	<i>Ninia sebae</i>	Honduras: Olancho	This study
JHT_2427		<i>Ninia sebae</i>	Honduras: Yoro	This study
AMH_356		<i>Ninia sebae</i>	Mexico: Chiapas	This study
AMH_357		<i>Ninia sebae</i>	Mexico: Chiapas	This study
JAC_21629	UTA R-51847	<i>Ninia sebae</i>	Mexico: Oaxaca	This study
JAC_22579	UTA R-52616	<i>Ninia sebae</i>	Mexico: Veracruz	This study
UOGV_246		<i>Ninia sebae</i>	Mexico: Veracruz	This study
JAC_24419		<i>Ninia sebae</i>	Mexico: Yucatan	This study
N108		<i>Ninia sebae</i>	Nicaragua: Jinotega	This study
JM_376		<i>Ninia sp.</i>	Panama: Cocle	This study
ENS_6419		<i>Tropidodipsas fischeri</i>	Guatemala	Coleman M. Sheehy
JAC_30401		<i>Tropidodipsas sartorii</i>	Mexico	Coleman M. Sheehy
N625		<i>Tropidodipsas sartorii</i>	Nicaragua	Coleman M. Sheehy

AMH = Alberto Mendoza Hernandez field series

ANMO = Adrian Nieto-Montes de Oca field series

CMS = Coleman M. Sheehy field series

ENS = Eric N. Smith field series

JAC = Jonathan A. Campbell field series

JHT = Josiah H Townsend field series

IRL = Ileana R. Luque-Montes field series

ISZ= Israel Solano Zavaleta field series

LSU-H = Louisiana State University, Museum of Natural Science, Herpetology Collection

MEA = Manuel E. Acevedo field series

MSM = Mahmood Sasa field series

MVZ = Museum of Vertebrate Zoology, University of California, Berkeley

NXXX = Nicaragua field series, Scott Travers and Josiah H Townsend

UOGV = Uri Omar Garcia Vazquez field series

UTA = Amphibian and Reptile Research Diversity Center, University of Texas Arlington

WED = William E. Duellman field series



APPENDIX B

LIST OF ADDITIONAL MATERIALS USED IN THIS STUDY

Museum	Taxon	Locality	Genbank Accession Numbers		
			<u>CYTb</u>	<u>ND4</u>	<u>NT3</u>
MHUA_14368	<i>Atractus wagleri</i>	Colombia: Antioquia	GQ334480		GQ334664
UTA_R-12272	<i>Cryophis hallbergi</i>	Mexico: Oaxaca			GQ334666
MHUA_14452	<i>Ninia atrata</i>	Colombia: Caldas	GQ334553		GQ334683
MHUA_14511	<i>Sibon nebulatus</i>	Colombia: Antioquia	GQ334556		GQ334685
MVZ_233298	<i>Sibon nebulatus</i>	Costa Rica: Limon	EU728583	EU728583	FJ455189

MHUA = Museo Herpetologia de la Universidad the Antioquia, Colombia

MVZ = Museum of Vertebrate Zoology, University of California, Berkeley

UTA = Amphibian and Reptile Research Diversity Center, University of Texas at Arlington

APPENDIX C

TABLE OF PAIRWISE P-DISTANCES FOR CYTB SEQUENCES

Sequence	1	2	3	4	5	6	7	8
N_atrata_CO_Caldas_MHUA_14452	1							
N_atrata_EC_Chimborazo_FHGO_7335	2	0.077						
N_atrata_EC_Esmeraldas_ENS_12640	3	0.072	0.088					
N_atrata_EC_Manabi_LAC_1594	4	0.084	0.092	0.039				
N_atrata_VE_Guarico_ECS_794	5	0.055	0.074	0.066	0.076			
N_celata_CR_Limon_AS_L_098	6	0.135	0.131	0.130	0.139	0.119		
N_diademata_GT_Huehuetenango_ENS_7939	7	0.122	0.120	0.118	0.124	0.115	0.124	
N_diademata_GT_San_Marcos_JAC_20014	8	0.135	0.136	0.132	0.141	0.133	0.128	0.067
N_diademata_GT_San_Marcos_JAC_20070	9	0.134	0.135	0.131	0.140	0.132	0.127	0.066
N_diademata_GT_Suchitepequez_ENS_13451	10	0.134	0.135	0.131	0.140	0.132	0.127	0.066
N_diademata_HN_Copan_JHT_2799	11	0.138	0.132	0.134	0.131	0.128	0.128	0.096
N_diademata_HN_Copan_JHT_2821	12	0.139	0.133	0.135	0.132	0.129	0.129	0.097
N_diademata_HN_Copan_JHT_2822	13	0.138	0.132	0.134	0.131	0.128	0.128	0.096
N_diademata_HN_Santa_Barbara_JHT_3007	14	0.136	0.130	0.132	0.131	0.128	0.129	0.097
N_diademata_MX_Chiapas_JAC_22917	15	0.122	0.120	0.118	0.124	0.115	0.124	0.000
N_diademata_MX_Oaxaca_JAC_25844	16	0.122	0.120	0.118	0.124	0.115	0.124	0.000
N_diademata_MX_Puebla_JAC_22500	17	0.137	0.139	0.138	0.130	0.122	0.130	0.105
N_diademata_MX_Veracruz_JAC_24987	18	0.138	0.138	0.131	0.129	0.127	0.125	0.099
N_espinali_HN_Comayagua_FN212525	19	0.135	0.132	0.143	0.146	0.134	0.132	0.139
N_espinali_HN_Comayagua_IRL_077	20	0.135	0.132	0.143	0.146	0.134	0.132	0.139
N_espinali_HN_Cortes_JHT_1611	21	0.135	0.131	0.145	0.148	0.135	0.133	0.139
N_espinali_HN_La_Paz_JHT_2624	22	0.134	0.131	0.142	0.145	0.133	0.131	0.139
N_espinali_HN_La_Paz_JHT_2625	23	0.135	0.132	0.143	0.146	0.134	0.132	0.139
N_hudsoni_EC_Morona_Santiago_FHGO_5940	24	0.083	0.084	0.084	0.086	0.073	0.128	0.114
N_maculata_CR_Alajuela_MVZ_149884	25	0.125	0.119	0.128	0.129	0.118	0.131	0.124
N_maculata_CR_Cartago_MVZ_204116	26	0.125	0.121	0.128	0.129	0.118	0.131	0.125
N_maculata_CR_Cartago_MVZ_204122	27	0.126	0.122	0.129	0.130	0.119	0.132	0.126
N_maculata_CR_Cartago_MVZ_204124	28	0.125	0.121	0.128	0.129	0.118	0.131	0.125
N_maculata_HN_Olancho_ENS_10670	29	0.115	0.112	0.118	0.123	0.104	0.131	0.121
N_maculata_NI_Atlantico_Norte_N629	30	0.113	0.113	0.119	0.120	0.107	0.121	0.122
N_maculata_NI_Jinotega_ENS_9739	31	0.111	0.111	0.117	0.118	0.105	0.121	0.121
N_pavimentata_GT_Baja_Verapaz_ENS_7788	32	0.114	0.111	0.119	0.122	0.102	0.129	0.117
N_pavimentata_GT_San_Marcos_ENS_8342	33	0.120	0.118	0.127	0.126	0.110	0.134	0.131
N_pavimentata_GT_San_Marcos_JAC_19803	34	0.120	0.118	0.127	0.126	0.110	0.134	0.131
N_pavimentata_GT_San_Marcos_JAC_19804	35	0.120	0.118	0.127	0.126	0.110	0.134	0.131
N_pavimentata_HN_Atlantida_JHT_3068	36	0.114	0.108	0.116	0.121	0.102	0.127	0.118
N_pavimentata_HN_Yoro_JHT_2448	37	0.115	0.110	0.118	0.123	0.104	0.129	0.120
N_psephota_CR_Cartago_MVZ_204114	38	0.105	0.092	0.112	0.109	0.090	0.132	0.116
N_sebae_CR_Guanacaste_MVZ_207364	39	0.125	0.118	0.122	0.130	0.115	0.123	0.124
N_sebae_CR_Guanacaste_MVZ_207365	40	0.125	0.118	0.122	0.130	0.115	0.123	0.124
N_sebae_CR_Puntarenas_CMS_002	41	0.125	0.118	0.122	0.130	0.115	0.123	0.124
N_sebae_GT_Baja_Verapaz_MSM_97	42	0.129	0.120	0.126	0.133	0.122	0.131	0.128
N_sebae_GT_Guatemala_ENS_10257	43	0.128	0.122	0.127	0.134	0.118	0.127	0.127
N_sebae_GT_Huehuetenango_JAC_19256	44	0.126	0.116	0.125	0.133	0.120	0.127	0.124
N_sebae_GT_Izabal_ENS_13314	45	0.129	0.121	0.128	0.133	0.119	0.125	0.127
N_sebae_GT_Izabal_MEA_444	46	0.129	0.120	0.126	0.133	0.122	0.131	0.128
N_sebae_GT_Peten_JAC_21025	47	0.125	0.115	0.124	0.132	0.119	0.127	0.123
N_sebae_GT_Santa_Rosa_ENS_13346	48	0.128	0.122	0.127	0.134	0.118	0.127	0.127
N_sebae_HN_Comayagua_JHT_2576	49	0.127	0.118	0.127	0.133	0.119	0.128	0.126
N_sebae_HN_Copan_JHT_2798	50	0.129	0.121	0.128	0.133	0.119	0.124	0.127
N_sebae_HN_Cortes_IRL_034	51	0.127	0.118	0.127	0.133	0.119	0.128	0.126
N_sebae_HN_El_Paraiso_ENS_8656	52	0.123	0.115	0.126	0.132	0.114	0.124	0.124
N_sebae_HN_Francisco_Morazan_JHT_2030	53	0.127	0.118	0.127	0.133	0.119	0.128	0.126
N_sebae_HN_Gracias_a_Dios_FN212668	54	0.121	0.114	0.124	0.130	0.112	0.122	0.122

Sequence		1	2	3	4	5	6	7	8
N_sebae_HN_Olancho_ENS_10756	55	0.123	0.115	0.126	0.132	0.114	0.124	0.124	0.129
N_sebae_HN_Santa_Barbara_JHT_2356	56	0.128	0.119	0.127	0.134	0.120	0.129	0.127	0.136
N_sebae_HN_Yoro_JHT_2427	57	0.128	0.119	0.127	0.134	0.119	0.129	0.127	0.136
N_sebae_MX_Chiapas_AMH_356	58	0.123	0.114	0.122	0.128	0.117	0.124	0.124	0.131
N_sebae_MX_Chiapas_AMH_357	59	0.123	0.114	0.122	0.128	0.117	0.124	0.124	0.131
N_sebae_MX_Oaxaca_JAC_21629	60	0.119	0.110	0.122	0.130	0.114	0.120	0.121	0.125
N_sebae_MX_Veracruz_JAC_22579	61	0.118	0.109	0.121	0.129	0.113	0.119	0.120	0.124
N_sebae_MX_Veracruz_UOGV_246	62	0.123	0.115	0.122	0.128	0.119	0.124	0.124	0.131
N_sebae_MX_Yucatan_JAC_24419	63	0.125	0.115	0.124	0.132	0.119	0.127	0.123	0.130
N_sebae_NI_Jinotega_N108	64	0.124	0.116	0.127	0.133	0.114	0.125	0.125	0.130
Ninia_sp_PA_Cocle_JM_376	65	0.131	0.127	0.129	0.141	0.115	0.069	0.123	0.128
Sibon_nebulatus_CR_MVZ_233298	66	0.128	0.142	0.139	0.144	0.123	0.130	0.126	0.131

	9	10	11	12	13	14	15	16	17	18	19	20	21
10	0.000												
11	0.119	0.119											
12	0.120	0.120	0.001										
13	0.119	0.119	0.000	0.001									
14	0.120	0.120	0.003	0.004	0.003								
15	0.066	0.066	0.096	0.097	0.096	0.097							
16	0.066	0.066	0.096	0.097	0.096	0.097	0.000						
17	0.117	0.117	0.047	0.048	0.047	0.050	0.105	0.105					
18	0.113	0.113	0.050	0.051	0.050	0.051	0.099	0.099	0.030				
19	0.137	0.137	0.141	0.142	0.141	0.142	0.139	0.139	0.133	0.132			
20	0.137	0.137	0.141	0.142	0.141	0.142	0.139	0.139	0.133	0.132	0.000		
21	0.136	0.136	0.141	0.142	0.141	0.142	0.139	0.139	0.135	0.132	0.006	0.006	
22	0.136	0.136	0.140	0.141	0.140	0.141	0.139	0.139	0.132	0.131	0.001	0.001	0.006
23	0.137	0.137	0.141	0.142	0.141	0.142	0.139	0.139	0.133	0.132	0.000	0.000	0.006
24	0.132	0.132	0.122	0.123	0.122	0.121	0.114	0.114	0.121	0.117	0.144	0.144	0.144
25	0.143	0.143	0.139	0.139	0.139	0.139	0.124	0.124	0.138	0.129	0.135	0.135	0.135
26	0.144	0.144	0.136	0.135	0.136	0.136	0.125	0.125	0.135	0.127	0.135	0.135	0.135
27	0.145	0.145	0.137	0.136	0.137	0.137	0.126	0.126	0.136	0.127	0.136	0.136	0.136
28	0.144	0.144	0.136	0.135	0.136	0.136	0.125	0.125	0.135	0.127	0.135	0.135	0.135
29	0.130	0.130	0.136	0.137	0.136	0.137	0.121	0.121	0.136	0.130	0.130	0.130	0.130
30	0.138	0.138	0.124	0.125	0.124	0.127	0.122	0.122	0.127	0.123	0.130	0.130	0.130
31	0.137	0.137	0.124	0.125	0.124	0.127	0.121	0.121	0.127	0.123	0.130	0.130	0.130
32	0.128	0.128	0.133	0.134	0.133	0.134	0.117	0.117	0.133	0.127	0.128	0.128	0.127
33	0.145	0.145	0.139	0.140	0.139	0.140	0.131	0.131	0.141	0.135	0.140	0.140	0.140
34	0.145	0.145	0.139	0.140	0.139	0.140	0.131	0.131	0.141	0.135	0.140	0.140	0.140
35	0.145	0.145	0.139	0.140	0.139	0.140	0.131	0.131	0.141	0.135	0.140	0.140	0.140
36	0.129	0.129	0.132	0.133	0.132	0.133	0.118	0.118	0.132	0.127	0.128	0.128	0.128
37	0.131	0.131	0.134	0.135	0.134	0.135	0.120	0.120	0.134	0.128	0.130	0.130	0.130
38	0.138	0.138	0.120	0.121	0.120	0.121	0.116	0.116	0.116	0.117	0.126	0.126	0.125
39	0.130	0.130	0.133	0.132	0.133	0.134	0.124	0.124	0.131	0.129	0.139	0.139	0.139
40	0.130	0.130	0.133	0.132	0.133	0.134	0.124	0.124	0.131	0.129	0.139	0.139	0.139
41	0.130	0.130	0.133	0.132	0.133	0.134	0.124	0.124	0.131	0.129	0.139	0.139	0.139
42	0.133	0.133	0.135	0.134	0.135	0.138	0.128	0.128	0.134	0.136	0.143	0.143	0.143
43	0.131	0.131	0.135	0.134	0.135	0.136	0.127	0.127	0.135	0.131	0.139	0.139	0.139
44	0.130	0.130	0.133	0.132	0.133	0.134	0.124	0.124	0.136	0.134	0.139	0.139	0.139
45	0.129	0.129	0.136	0.135	0.136	0.137	0.127	0.127	0.136	0.132	0.139	0.139	0.139
46	0.133	0.133	0.135	0.134	0.135	0.138	0.128	0.128	0.134	0.136	0.143	0.143	0.143
47	0.129	0.129	0.132	0.131	0.132	0.133	0.123	0.123	0.135	0.133	0.139	0.139	0.139
48	0.131	0.131	0.135	0.134	0.135	0.136	0.127	0.127	0.135	0.131	0.139	0.139	0.139
49	0.134	0.134	0.135	0.134	0.135	0.136	0.126	0.126	0.135	0.131	0.139	0.139	0.139
50	0.129	0.129	0.136	0.135	0.136	0.137	0.127	0.127	0.136	0.132	0.139	0.139	0.139

	9	10	11	12	13	14	15	16	17	18	19	20	21
51	0.134	0.134	0.135	0.134	0.135	0.136	0.126	0.126	0.135	0.131	0.139	0.139	0.139
52	0.128	0.128	0.133	0.132	0.133	0.134	0.124	0.124	0.131	0.131	0.138	0.138	0.138
53	0.134	0.134	0.135	0.134	0.135	0.136	0.126	0.126	0.135	0.131	0.139	0.139	0.139
54	0.128	0.128	0.131	0.130	0.131	0.132	0.122	0.122	0.129	0.129	0.138	0.138	0.138
55	0.128	0.128	0.133	0.132	0.133	0.134	0.124	0.124	0.131	0.131	0.138	0.138	0.138
56	0.135	0.135	0.136	0.135	0.136	0.137	0.127	0.127	0.136	0.132	0.140	0.140	0.140
57	0.135	0.135	0.135	0.134	0.135	0.136	0.127	0.127	0.135	0.131	0.139	0.139	0.139
58	0.130	0.130	0.132	0.133	0.132	0.131	0.124	0.124	0.131	0.129	0.138	0.138	0.138
59	0.130	0.130	0.132	0.133	0.132	0.131	0.124	0.124	0.131	0.129	0.138	0.138	0.138
60	0.124	0.124	0.130	0.131	0.130	0.131	0.121	0.121	0.129	0.127	0.130	0.130	0.130
61	0.123	0.123	0.129	0.130	0.129	0.130	0.120	0.120	0.130	0.127	0.129	0.129	0.129
62	0.130	0.130	0.132	0.133	0.132	0.131	0.124	0.124	0.133	0.129	0.136	0.136	0.136
63	0.129	0.129	0.132	0.131	0.132	0.133	0.123	0.123	0.135	0.133	0.139	0.139	0.139
64	0.129	0.129	0.134	0.133	0.134	0.135	0.125	0.125	0.132	0.132	0.139	0.139	0.139
65	0.127	0.127	0.133	0.134	0.133	0.134	0.123	0.123	0.130	0.128	0.115	0.115	0.114
66	0.130	0.130	0.140	0.141	0.140	0.141	0.126	0.126	0.144	0.138	0.124	0.124	0.125

	22	23	24	25	26	27	28	29	30	31	32	33	34
23	0.001												
24	0.143	0.144											
25	0.136	0.135	0.113										
26	0.136	0.135	0.114	0.007									
27	0.137	0.136	0.114	0.008	0.001								
28	0.136	0.135	0.114	0.007	0.000	0.001							
29	0.131	0.130	0.102	0.062	0.064	0.065	0.064						
30	0.131	0.130	0.102	0.060	0.060	0.061	0.060	0.051					
31	0.131	0.130	0.100	0.058	0.058	0.059	0.058	0.049	0.002				
32	0.129	0.128	0.099	0.060	0.062	0.063	0.062	0.037	0.049	0.047			
33	0.141	0.140	0.108	0.059	0.061	0.062	0.061	0.044	0.042	0.041	0.046		
34	0.141	0.140	0.108	0.059	0.061	0.062	0.061	0.044	0.042	0.041	0.046	0.000	
35	0.141	0.140	0.108	0.059	0.061	0.062	0.061	0.044	0.042	0.041	0.046	0.000	0.000
36	0.129	0.128	0.098	0.060	0.062	0.063	0.062	0.004	0.049	0.047	0.033	0.042	0.042
37	0.131	0.130	0.100	0.060	0.062	0.063	0.062	0.004	0.049	0.047	0.035	0.042	0.042
38	0.127	0.126	0.099	0.107	0.107	0.108	0.107	0.100	0.095	0.095	0.098	0.103	0.103
39	0.138	0.139	0.121	0.130	0.130	0.131	0.130	0.121	0.118	0.118	0.125	0.126	0.126
40	0.138	0.139	0.121	0.130	0.130	0.131	0.130	0.121	0.118	0.118	0.125	0.126	0.126
41	0.138	0.139	0.121	0.130	0.130	0.131	0.130	0.121	0.118	0.118	0.125	0.126	0.126
42	0.142	0.143	0.126	0.134	0.134	0.135	0.134	0.127	0.126	0.126	0.128	0.132	0.132
43	0.138	0.139	0.124	0.133	0.133	0.134	0.133	0.121	0.126	0.124	0.127	0.128	0.128
44	0.139	0.139	0.120	0.134	0.132	0.133	0.132	0.121	0.124	0.122	0.123	0.127	0.127
45	0.139	0.139	0.123	0.132	0.132	0.133	0.132	0.122	0.125	0.123	0.126	0.127	0.127
46	0.142	0.143	0.126	0.136	0.136	0.137	0.136	0.127	0.126	0.126	0.128	0.132	0.132
47	0.138	0.139	0.119	0.133	0.133	0.134	0.133	0.122	0.125	0.123	0.124	0.127	0.127
48	0.138	0.139	0.124	0.133	0.133	0.134	0.133	0.121	0.126	0.124	0.127	0.128	0.128
49	0.139	0.139	0.122	0.134	0.134	0.135	0.134	0.124	0.127	0.127	0.127	0.131	0.131
50	0.138	0.139	0.123	0.131	0.131	0.132	0.131	0.122	0.125	0.123	0.126	0.127	0.127
51	0.139	0.139	0.122	0.134	0.134	0.135	0.134	0.124	0.127	0.127	0.127	0.131	0.131
52	0.137	0.138	0.117	0.132	0.132	0.133	0.132	0.119	0.118	0.118	0.123	0.123	0.123
53	0.139	0.139	0.122	0.134	0.134	0.135	0.134	0.124	0.127	0.127	0.127	0.131	0.131
54	0.137	0.138	0.115	0.132	0.132	0.133	0.132	0.119	0.118	0.118	0.123	0.123	0.123
55	0.137	0.138	0.117	0.132	0.132	0.133	0.132	0.119	0.118	0.118	0.123	0.123	0.123
56	0.139	0.140	0.123	0.135	0.135	0.136	0.135	0.125	0.128	0.128	0.128	0.132	0.132
57	0.139	0.139	0.123	0.135	0.135	0.136	0.135	0.125	0.128	0.128	0.128	0.132	0.132
58	0.137	0.138	0.117	0.130	0.132	0.133	0.132	0.124	0.123	0.123	0.126	0.128	0.128
59	0.137	0.138	0.117	0.130	0.132	0.133	0.132	0.124	0.123	0.123	0.126	0.128	0.128

	22	23	24	25	26	27	28	29	30	31	32	33	34
60	0.129	0.130	0.115	0.121	0.123	0.124	0.123	0.116	0.115	0.115	0.118	0.120	0.120
61	0.128	0.129	0.114	0.120	0.122	0.123	0.122	0.115	0.114	0.114	0.117	0.119	0.119
62	0.135	0.136	0.119	0.128	0.130	0.131	0.130	0.122	0.121	0.121	0.124	0.127	0.127
63	0.138	0.139	0.119	0.133	0.133	0.134	0.133	0.122	0.125	0.123	0.124	0.127	0.127
64	0.138	0.139	0.118	0.133	0.133	0.134	0.133	0.120	0.119	0.119	0.124	0.124	0.124
65	0.114	0.115	0.122	0.119	0.118	0.119	0.118	0.121	0.114	0.114	0.123	0.126	0.126
66	0.125	0.124	0.139	0.142	0.141	0.142	0.141	0.131	0.136	0.134	0.132	0.141	0.141

	35	36	37	38	39	40	41	42	43	44	45	46	47
36	0.042												
37	0.042	0.002											
38	0.103	0.098	0.100										
39	0.126	0.117	0.119	0.124									
40	0.126	0.117	0.119	0.124	0.000								
41	0.126	0.117	0.119	0.124	0.000	0.000							
42	0.132	0.123	0.125	0.126	0.024	0.024	0.024						
43	0.128	0.119	0.121	0.122	0.017	0.017	0.017	0.027					
44	0.127	0.117	0.119	0.126	0.026	0.026	0.026	0.024	0.027				
45	0.127	0.118	0.120	0.125	0.017	0.017	0.017	0.027	0.006	0.027			
46	0.132	0.123	0.125	0.126	0.024	0.024	0.024	0.002	0.027	0.024	0.027		
47	0.127	0.118	0.120	0.125	0.025	0.025	0.025	0.023	0.026	0.001	0.026	0.023	
48	0.128	0.119	0.121	0.122	0.017	0.017	0.017	0.027	0.002	0.027	0.006	0.027	0.026
49	0.131	0.122	0.124	0.123	0.017	0.017	0.017	0.027	0.012	0.027	0.014	0.027	0.026
50	0.127	0.118	0.120	0.125	0.017	0.017	0.017	0.026	0.006	0.026	0.001	0.026	0.025
51	0.131	0.122	0.124	0.123	0.017	0.017	0.017	0.027	0.012	0.027	0.014	0.027	0.026
52	0.123	0.115	0.117	0.122	0.016	0.016	0.016	0.027	0.021	0.025	0.021	0.027	0.024
53	0.131	0.122	0.124	0.123	0.017	0.017	0.017	0.027	0.012	0.027	0.014	0.027	0.026
54	0.123	0.115	0.117	0.122	0.014	0.014	0.014	0.029	0.021	0.027	0.021	0.029	0.026
55	0.123	0.115	0.117	0.122	0.016	0.016	0.016	0.027	0.021	0.025	0.021	0.027	0.024
56	0.132	0.123	0.125	0.124	0.018	0.018	0.018	0.028	0.013	0.028	0.015	0.028	0.027
57	0.132	0.123	0.125	0.124	0.018	0.018	0.018	0.028	0.012	0.028	0.014	0.028	0.027
58	0.128	0.120	0.122	0.126	0.022	0.022	0.022	0.024	0.029	0.020	0.029	0.024	0.019
59	0.128	0.120	0.122	0.126	0.022	0.022	0.022	0.024	0.029	0.020	0.029	0.024	0.019
60	0.120	0.113	0.114	0.114	0.026	0.026	0.026	0.026	0.029	0.024	0.029	0.026	0.023
61	0.119	0.112	0.114	0.113	0.027	0.027	0.027	0.027	0.030	0.025	0.030	0.027	0.024
62	0.127	0.118	0.120	0.126	0.022	0.022	0.022	0.024	0.027	0.020	0.027	0.024	0.019
63	0.127	0.118	0.120	0.125	0.025	0.025	0.025	0.023	0.026	0.001	0.026	0.023	0.000
64	0.124	0.116	0.118	0.123	0.017	0.017	0.017	0.028	0.022	0.026	0.022	0.028	0.025
65	0.126	0.119	0.121	0.129	0.121	0.121	0.121	0.129	0.126	0.124	0.127	0.129	0.123
66	0.141	0.129	0.131	0.138	0.125	0.125	0.125	0.139	0.132	0.136	0.133	0.139	0.135

	48	49	50	51	52	53	54	55	56	57	58	59	60
49	0.012												
50	0.006	0.015											
51	0.012	0.000	0.015										
52	0.021	0.019	0.021	0.019									
53	0.012	0.000	0.015	0.000	0.019								
54	0.021	0.019	0.021	0.019	0.002	0.019							
55	0.021	0.019	0.021	0.019	0.000	0.019	0.002						
56	0.013	0.001	0.016	0.001	0.020	0.001	0.020	0.020					
57	0.012	0.002	0.015	0.002	0.020	0.002	0.020	0.020	0.003				
58	0.029	0.027	0.028	0.027	0.028	0.027	0.028	0.028	0.028	0.028			
59	0.029	0.027	0.028	0.027	0.028	0.027	0.028	0.028	0.028	0.028	0.000		
60	0.029	0.029	0.028	0.029	0.029	0.029	0.030	0.029	0.030	0.030	0.022	0.022	
61	0.030	0.030	0.029	0.030	0.030	0.030	0.031	0.030	0.030	0.030	0.023	0.023	0.001

	48	49	50	51	52	53	54	55	56	57	58	59	60
<b>62</b>	0.027	0.027	0.026	0.027	0.028	0.027	0.030	0.028	0.028	0.028	0.002	0.002	0.022
<b>63</b>	0.026	0.026	0.025	0.026	0.024	0.026	0.026	0.024	0.027	0.027	0.019	0.019	0.023
<b>64</b>	0.022	0.020	0.022	0.020	0.001	0.020	0.003	0.001	0.021	0.021	0.029	0.029	0.030
<b>65</b>	0.126	0.125	0.126	0.125	0.122	0.125	0.120	0.122	0.126	0.126	0.124	0.124	0.118
<b>66</b>	0.132	0.133	0.133	0.133	0.127	0.133	0.127	0.127	0.134	0.134	0.136	0.136	0.126

	61	62	63	64	65
<b>62</b>	0.023				
<b>63</b>	0.024	0.019			
<b>64</b>	0.030	0.029	0.025		
<b>65</b>	0.117	0.124	0.123	0.123	
<b>66</b>	0.125	0.134	0.135	0.127	0.135



APPENDIX D

TABLE OF PAIRWISE P-DISTANCES FOR ND4 SEQUENCES

Sequence	1	2	3	4	5	6	7
N_atrata_EC_Chimborazo_FHGO_7335	1						
N_atrata_EC_Esmeraldas_ENS_12640	2	0.060					
N_atrata_EC_Manabi_LAC_1594	3	0.060	0.029				
N_atrata_VE_Caracas_N1	4	0.053	0.058	0.055			
N_atrata_VE_Guarico_ECS_794	5	0.053	0.058	0.055	0.000		
N_celata_CR_Limon_ASL_098	6	0.094	0.103	0.103	0.095	0.095	
N_diademata_GT_Huehuetenango_ENS_7939	7	0.096	0.104	0.100	0.091	0.091	0.089
N_diademata_GT_San_Marcos_JAC_20014	8	0.089	0.096	0.098	0.091	0.091	0.085
N_diademata_GT_San_Marcos_JAC_20070	9	0.086	0.096	0.098	0.089	0.089	0.085
N_diademata_GT_Suchitepequez_ENS_13451	10	0.086	0.096	0.098	0.089	0.089	0.085
N_diademata_HN_Copan_JHT_2799	11	0.096	0.110	0.111	0.096	0.096	0.096
N_diademata_HN_Copan_JHT_2821	12	0.096	0.110	0.111	0.096	0.096	0.096
N_diademata_HN_Copan_JHT_2822	13	0.096	0.110	0.111	0.096	0.096	0.096
N_diademata_HN_Santa_Barbara_JHT_3007	14	0.096	0.110	0.111	0.096	0.096	0.096
N_diademata_MX_Chiapas_JAC_22917	15	0.095	0.103	0.099	0.090	0.090	0.088
N_diademata_MX_Oaxaca_JAC_25844	16	0.095	0.103	0.099	0.090	0.090	0.088
N_diademata_MX_Puebla_JAC_22500	17	0.106	0.108	0.104	0.098	0.098	0.094
N_diademata_MX_Veracruz_JAC_24987	18	0.104	0.104	0.098	0.096	0.096	0.091
N_espinali_HN_Comayagua_FN212525	19	0.104	0.115	0.110	0.105	0.105	0.109
N_espinali_HN_Comayagua_IRL_077	20	0.104	0.115	0.110	0.105	0.105	0.109
N_espinali_HN_Cortes_JHT_1611	21	0.109	0.118	0.113	0.110	0.110	0.111
N_espinali_HN_La_Paz_JHT_2624	22	0.105	0.116	0.111	0.106	0.106	0.108
N_espinali_HN_La_Paz_JHT_2625	23	0.103	0.114	0.109	0.104	0.104	0.108
N_hudsoni_EC_Morona_Santiago_FHGO_5940	24	0.070	0.075	0.068	0.076	0.076	0.096
N_maculata_CR_Alajuela_MVZ_149884	25	0.085	0.094	0.096	0.081	0.081	0.103
N_maculata_CR_Cartago_MVZ_204116	26	0.083	0.096	0.096	0.086	0.086	0.100
N_maculata_CR_Cartago_MVZ_204122	27	0.085	0.099	0.099	0.086	0.086	0.103
N_maculata_CR_Cartago_MVZ_204124	28	0.083	0.096	0.096	0.086	0.086	0.100
N_maculata_HN_Olancho_ENS_10670	29	0.093	0.095	0.093	0.085	0.085	0.104
N_maculata_NI_Atlantico_Norte_N629	30	0.079	0.085	0.083	0.080	0.080	0.098
N_maculata_NI_Jinotega_ENS_9739	31	0.079	0.085	0.083	0.080	0.080	0.098
N_pavimentata_GT_Baja_Verapaz_ENS_7788	32	0.098	0.094	0.091	0.086	0.086	0.104
N_pavimentata_GT_San_Marcos_ENS_8342	33	0.083	0.086	0.088	0.081	0.081	0.094
N_pavimentata_GT_San_Marcos_JAC_19803	34	0.083	0.086	0.088	0.081	0.081	0.094
N_pavimentata_GT_San_Marcos_JAC_19804	35	0.083	0.086	0.088	0.081	0.081	0.094
N_pavimentata_HN_Atlantida_JHT_3068	36	0.096	0.096	0.094	0.086	0.086	0.103
N_pavimentata_HN_Yoro_JHT_2448	37	0.095	0.098	0.095	0.088	0.088	0.101
N_psephota_CR_Cartago_MVZ_204114	38	0.081	0.080	0.081	0.071	0.071	0.095
N_sebae_CR_Guanacaste_MVZ_207364	39	0.090	0.084	0.086	0.086	0.086	0.099
N_sebae_CR_Guanacaste_MVZ_207365	40	0.089	0.083	0.085	0.085	0.085	0.098
N_sebae_CR_Puntarenas_CMS_002	41	0.090	0.084	0.084	0.086	0.086	0.099
N_sebae_GT_Baja_Verapaz_MSM_97	42	0.099	0.096	0.091	0.094	0.094	0.101
N_sebae_GT_Guatemala_ENS_10257	43	0.093	0.089	0.089	0.095	0.095	0.108
N_sebae_GT_Huehuetenango_JAC_19256	44	0.086	0.084	0.086	0.081	0.081	0.096
N_sebae_GT_Izabal_ENS_13314	45	0.093	0.089	0.089	0.095	0.095	0.105
N_sebae_GT_Izabal_MEA_444	46	0.099	0.094	0.094	0.094	0.094	0.101
N_sebae_GT_Peten_JAC_21025	47	0.089	0.086	0.086	0.081	0.081	0.098
N_sebae_GT_Santa_Rosa_ENS_13346	48	0.091	0.088	0.088	0.094	0.094	0.106
N_sebae_HN_Comayagua_JHT_2576	49	0.090	0.085	0.085	0.093	0.093	0.101
N_sebae_HN_Copan_JHT_2798	50	0.093	0.089	0.089	0.095	0.095	0.105
N_sebae_HN_Cortes_IRL_034	51	0.090	0.085	0.085	0.093	0.093	0.101
N_sebae_HN_El_Paraiso_ENS_8656	52	0.090	0.088	0.083	0.085	0.085	0.103
N_sebae_HN_Francisco_Morazan_JHT_2030	53	0.090	0.085	0.085	0.093	0.093	0.101

Sequence		1	2	3	4	5	6	7
N_sebae_HN_Gracias_a_Dios_FN212668	54	0.089	0.086	0.084	0.084	0.084	0.101	0.100
N_sebae_HN_Olancho_ENS_10756	55	0.089	0.086	0.084	0.084	0.084	0.101	0.100
N_sebae_HN_Santa_Barbara_JHT_2356	56	0.090	0.085	0.085	0.093	0.093	0.101	0.104
N_sebae_HN_Yoro_JHT_2427	57	0.090	0.085	0.085	0.093	0.093	0.101	0.104
N_sebae_MX_Chiapas_AMH_356	58	0.093	0.093	0.093	0.085	0.085	0.099	0.104
N_sebae_MX_Chiapas_AMH_357	59	0.094	0.094	0.094	0.086	0.086	0.100	0.103
N_sebae_MX_Oaxaca_JAC_21629	60	0.094	0.094	0.091	0.086	0.086	0.105	0.110
N_sebae_MX_Veracruz_JAC_22579	61	0.093	0.093	0.090	0.085	0.085	0.103	0.109
N_sebae_MX_Veracruz_UOGV_246	62	0.093	0.093	0.093	0.085	0.085	0.099	0.104
N_sebae_MX_Yucatan_JAC_24419	63	0.088	0.085	0.085	0.080	0.080	0.096	0.096
N_sebae_NI_Jinotega_N108	64	0.089	0.086	0.084	0.084	0.084	0.101	0.100
Ninia_sp_PA_Cocle_JM_376	65	0.101	0.104	0.109	0.104	0.104	0.059	0.100
Sibon_nebulatus_CR_MVZ_233298	66	0.115	0.128	0.120	0.123	0.123	0.129	0.124

	8	9	10	11	12	13	14	15	16	17	18	19	20
9	0.003												
10	0.003	0.000											
11	0.083	0.084	0.084										
12	0.083	0.084	0.084	0.000									
13	0.083	0.084	0.084	0.000	0.000								
14	0.083	0.084	0.084	0.000	0.000	0.000							
15	0.046	0.046	0.046	0.093	0.093	0.093	0.093						
16	0.046	0.046	0.046	0.093	0.093	0.093	0.093	0.000					
17	0.091	0.093	0.093	0.056	0.056	0.056	0.056	0.094	0.094				
18	0.093	0.094	0.094	0.058	0.058	0.058	0.058	0.100	0.100	0.024			
19	0.099	0.098	0.098	0.115	0.115	0.115	0.115	0.108	0.108	0.118	0.113		
20	0.099	0.098	0.098	0.115	0.115	0.115	0.115	0.108	0.108	0.118	0.113	0.000	
21	0.099	0.098	0.098	0.113	0.113	0.113	0.113	0.108	0.108	0.118	0.113	0.005	0.005
22	0.098	0.096	0.096	0.114	0.114	0.114	0.114	0.106	0.106	0.116	0.111	0.001	0.001
23	0.098	0.096	0.096	0.114	0.114	0.114	0.114	0.106	0.106	0.116	0.111	0.001	0.001
24	0.101	0.101	0.101	0.114	0.114	0.114	0.114	0.100	0.100	0.111	0.110	0.124	0.124
25	0.103	0.103	0.103	0.101	0.101	0.101	0.101	0.096	0.096	0.111	0.111	0.110	0.110
26	0.100	0.100	0.100	0.099	0.099	0.099	0.099	0.096	0.096	0.111	0.111	0.108	0.108
27	0.103	0.103	0.103	0.099	0.099	0.099	0.099	0.096	0.096	0.114	0.114	0.110	0.110
28	0.100	0.100	0.100	0.099	0.099	0.099	0.099	0.096	0.096	0.111	0.111	0.108	0.108
29	0.105	0.105	0.105	0.116	0.116	0.116	0.116	0.100	0.100	0.109	0.109	0.119	0.119
30	0.091	0.091	0.091	0.100	0.100	0.100	0.100	0.088	0.088	0.103	0.101	0.106	0.106
31	0.091	0.091	0.091	0.100	0.100	0.100	0.100	0.088	0.088	0.103	0.101	0.106	0.106
32	0.109	0.109	0.109	0.119	0.119	0.119	0.119	0.103	0.103	0.110	0.115	0.116	0.116
33	0.095	0.093	0.093	0.101	0.101	0.101	0.101	0.095	0.095	0.100	0.100	0.106	0.106
34	0.095	0.093	0.093	0.101	0.101	0.101	0.101	0.095	0.095	0.100	0.100	0.106	0.106
35	0.095	0.093	0.093	0.101	0.101	0.101	0.101	0.095	0.095	0.100	0.100	0.106	0.106
36	0.101	0.101	0.101	0.115	0.115	0.115	0.115	0.099	0.099	0.108	0.108	0.115	0.115
37	0.103	0.103	0.103	0.116	0.116	0.116	0.116	0.100	0.100	0.109	0.109	0.116	0.116
38	0.098	0.098	0.098	0.091	0.091	0.091	0.091	0.096	0.096	0.093	0.094	0.114	0.114
39	0.095	0.095	0.095	0.113	0.113	0.113	0.113	0.096	0.096	0.108	0.110	0.118	0.118
40	0.096	0.096	0.096	0.111	0.111	0.111	0.111	0.095	0.095	0.106	0.109	0.116	0.116
41	0.098	0.098	0.098	0.113	0.113	0.113	0.113	0.096	0.096	0.108	0.110	0.118	0.118
42	0.104	0.104	0.104	0.110	0.110	0.110	0.110	0.104	0.104	0.108	0.105	0.119	0.119
43	0.106	0.106	0.106	0.110	0.110	0.110	0.110	0.106	0.106	0.108	0.110	0.109	0.109
44	0.096	0.096	0.096	0.103	0.103	0.103	0.103	0.096	0.096	0.105	0.105	0.106	0.106
45	0.106	0.106	0.106	0.113	0.113	0.113	0.113	0.106	0.106	0.108	0.110	0.113	0.113
46	0.105	0.105	0.105	0.114	0.114	0.114	0.114	0.105	0.105	0.111	0.109	0.124	0.124
47	0.096	0.096	0.096	0.105	0.105	0.105	0.105	0.094	0.094	0.105	0.105	0.109	0.109

	8	9	10	11	12	13	14	15	16	17	18	19	20
48	0.108	0.108	0.108	0.109	0.109	0.109	0.109	0.108	0.108	0.106	0.109	0.110	0.110
49	0.105	0.105	0.105	0.106	0.106	0.106	0.106	0.103	0.103	0.106	0.109	0.109	0.109
50	0.106	0.106	0.106	0.113	0.113	0.113	0.113	0.106	0.106	0.108	0.110	0.113	0.113
51	0.105	0.105	0.105	0.106	0.106	0.106	0.106	0.103	0.103	0.106	0.109	0.109	0.109
52	0.101	0.101	0.101	0.114	0.114	0.114	0.114	0.100	0.100	0.109	0.109	0.118	0.118
53	0.105	0.105	0.105	0.106	0.106	0.106	0.106	0.103	0.103	0.106	0.109	0.109	0.109
54	0.100	0.100	0.100	0.113	0.113	0.113	0.113	0.099	0.099	0.108	0.108	0.116	0.116
55	0.100	0.100	0.100	0.113	0.113	0.113	0.113	0.099	0.099	0.108	0.108	0.116	0.116
56	0.105	0.105	0.105	0.106	0.106	0.106	0.106	0.103	0.103	0.106	0.109	0.109	0.109
57	0.105	0.105	0.105	0.106	0.106	0.106	0.106	0.103	0.103	0.106	0.109	0.109	0.109
58	0.103	0.103	0.103	0.106	0.106	0.106	0.106	0.103	0.103	0.109	0.109	0.115	0.115
59	0.104	0.104	0.104	0.108	0.108	0.108	0.108	0.101	0.101	0.110	0.110	0.116	0.116
60	0.111	0.111	0.111	0.119	0.119	0.119	0.119	0.109	0.109	0.111	0.111	0.115	0.115
61	0.110	0.110	0.110	0.116	0.116	0.116	0.116	0.108	0.108	0.111	0.109	0.113	0.113
62	0.103	0.103	0.103	0.106	0.106	0.106	0.106	0.103	0.103	0.109	0.109	0.115	0.115
63	0.098	0.098	0.098	0.104	0.104	0.104	0.104	0.095	0.095	0.104	0.104	0.108	0.108
64	0.100	0.100	0.100	0.113	0.113	0.113	0.113	0.099	0.099	0.108	0.108	0.116	0.116
65	0.100	0.099	0.099	0.100	0.100	0.100	0.100	0.099	0.099	0.100	0.101	0.123	0.123
66	0.128	0.126	0.126	0.134	0.134	0.134	0.134	0.125	0.125	0.134	0.133	0.129	0.129

	21	22	23	24	25	26	27	28	29	30	31	32	33
22	0.004												
23	0.006	0.003											
24	0.124	0.123	0.123										
25	0.110	0.109	0.109	0.089									
26	0.108	0.106	0.106	0.091	0.008								
27	0.110	0.109	0.109	0.091	0.008	0.003							
28	0.108	0.106	0.106	0.091	0.008	0.000	0.003						
29	0.119	0.118	0.118	0.098	0.059	0.059	0.061	0.059					
30	0.106	0.105	0.105	0.090	0.051	0.051	0.054	0.051	0.043				
31	0.106	0.105	0.105	0.090	0.051	0.051	0.054	0.051	0.043	0.000			
32	0.116	0.115	0.115	0.101	0.063	0.063	0.065	0.063	0.021	0.044	0.044		
33	0.104	0.105	0.105	0.091	0.053	0.053	0.055	0.053	0.039	0.036	0.036	0.038	
34	0.104	0.105	0.105	0.091	0.053	0.053	0.055	0.053	0.039	0.036	0.036	0.038	0.000
35	0.104	0.105	0.105	0.091	0.053	0.053	0.055	0.053	0.039	0.036	0.036	0.038	0.000
36	0.115	0.114	0.114	0.101	0.063	0.063	0.065	0.063	0.004	0.046	0.046	0.023	0.043
37	0.116	0.115	0.115	0.100	0.061	0.061	0.064	0.061	0.003	0.045	0.045	0.021	0.041
38	0.114	0.113	0.113	0.090	0.098	0.098	0.100	0.098	0.091	0.086	0.086	0.095	0.086
39	0.115	0.116	0.116	0.098	0.093	0.093	0.095	0.093	0.095	0.083	0.083	0.091	0.084
40	0.114	0.115	0.115	0.096	0.093	0.093	0.095	0.093	0.094	0.081	0.081	0.090	0.083
41	0.115	0.116	0.116	0.095	0.094	0.094	0.096	0.094	0.095	0.083	0.083	0.091	0.084
42	0.116	0.118	0.118	0.108	0.101	0.101	0.104	0.101	0.096	0.086	0.086	0.098	0.090
43	0.106	0.108	0.108	0.100	0.090	0.090	0.093	0.090	0.099	0.084	0.084	0.098	0.085
44	0.104	0.105	0.105	0.100	0.093	0.093	0.095	0.093	0.089	0.076	0.076	0.090	0.080
45	0.110	0.111	0.111	0.103	0.095	0.095	0.098	0.095	0.099	0.084	0.084	0.098	0.085
46	0.121	0.123	0.123	0.108	0.101	0.101	0.104	0.101	0.096	0.091	0.091	0.098	0.090
47	0.106	0.108	0.108	0.103	0.095	0.095	0.098	0.095	0.091	0.079	0.079	0.090	0.083
48	0.108	0.109	0.109	0.101	0.091	0.091	0.094	0.091	0.098	0.083	0.083	0.096	0.084
49	0.106	0.108	0.108	0.098	0.094	0.094	0.096	0.094	0.098	0.083	0.083	0.096	0.084
50	0.110	0.111	0.111	0.103	0.095	0.095	0.098	0.095	0.099	0.084	0.084	0.098	0.085
51	0.106	0.108	0.108	0.098	0.094	0.094	0.096	0.094	0.098	0.083	0.083	0.096	0.084
52	0.115	0.116	0.116	0.099	0.093	0.093	0.095	0.093	0.094	0.081	0.081	0.093	0.085
53	0.106	0.108	0.108	0.098	0.094	0.094	0.096	0.094	0.098	0.083	0.083	0.096	0.084
54	0.114	0.115	0.115	0.098	0.091	0.091	0.094	0.091	0.093	0.083	0.083	0.091	0.084

	21	22	23	24	25	26	27	28	29	30	31	32	33
55	0.114	0.115	0.115	0.098	0.091	0.091	0.094	0.091	0.093	0.083	0.083	0.091	0.084
56	0.106	0.108	0.108	0.098	0.094	0.094	0.096	0.094	0.098	0.083	0.083	0.096	0.084
57	0.106	0.108	0.108	0.098	0.094	0.094	0.096	0.094	0.098	0.083	0.083	0.096	0.084
58	0.113	0.114	0.114	0.104	0.091	0.091	0.094	0.091	0.095	0.083	0.083	0.096	0.086
59	0.114	0.115	0.115	0.103	0.090	0.090	0.093	0.090	0.094	0.084	0.084	0.095	0.088
60	0.115	0.114	0.114	0.103	0.096	0.096	0.099	0.096	0.098	0.084	0.084	0.099	0.091
61	0.113	0.111	0.111	0.101	0.094	0.094	0.096	0.094	0.095	0.083	0.083	0.096	0.089
62	0.113	0.114	0.114	0.104	0.091	0.091	0.094	0.091	0.095	0.083	0.083	0.096	0.086
63	0.105	0.106	0.106	0.101	0.094	0.094	0.096	0.094	0.090	0.078	0.078	0.089	0.081
64	0.114	0.115	0.115	0.098	0.091	0.091	0.094	0.091	0.093	0.083	0.083	0.091	0.084
65	0.123	0.121	0.121	0.101	0.108	0.108	0.110	0.108	0.111	0.101	0.101	0.109	0.103
66	0.126	0.128	0.128	0.133	0.129	0.125	0.128	0.125	0.128	0.125	0.125	0.133	0.126
	34	35	36	37	38	39	40	41	42	43	44	45	46
35	0.000												
36	0.043	0.043											
37	0.041	0.041	0.001										
38	0.086	0.086	0.090	0.091									
39	0.084	0.084	0.096	0.098	0.085								
40	0.083	0.083	0.095	0.096	0.084	0.001							
41	0.084	0.084	0.096	0.098	0.085	0.003	0.001						
42	0.090	0.090	0.098	0.099	0.094	0.024	0.025	0.026					
43	0.085	0.085	0.100	0.101	0.090	0.030	0.029	0.030	0.036				
44	0.080	0.080	0.090	0.091	0.080	0.021	0.020	0.021	0.023	0.029			
45	0.085	0.085	0.100	0.101	0.093	0.028	0.026	0.028	0.034	0.006	0.029		
46	0.090	0.090	0.098	0.099	0.093	0.024	0.025	0.026	0.008	0.039	0.023	0.036	
47	0.083	0.083	0.093	0.094	0.083	0.021	0.020	0.021	0.023	0.031	0.003	0.031	0.023
48	0.084	0.084	0.099	0.100	0.091	0.029	0.028	0.029	0.035	0.001	0.028	0.005	0.038
49	0.084	0.084	0.099	0.100	0.086	0.024	0.023	0.024	0.030	0.010	0.025	0.009	0.033
50	0.085	0.085	0.100	0.101	0.093	0.028	0.026	0.028	0.034	0.006	0.029	0.000	0.036
51	0.084	0.084	0.099	0.100	0.086	0.024	0.023	0.024	0.030	0.010	0.025	0.009	0.033
52	0.085	0.085	0.095	0.096	0.089	0.009	0.008	0.009	0.025	0.029	0.023	0.026	0.028
53	0.084	0.084	0.099	0.100	0.086	0.024	0.023	0.024	0.030	0.010	0.025	0.009	0.033
54	0.084	0.084	0.094	0.095	0.088	0.008	0.006	0.008	0.024	0.028	0.021	0.025	0.026
55	0.084	0.084	0.094	0.095	0.088	0.008	0.006	0.008	0.024	0.028	0.021	0.025	0.026
56	0.084	0.084	0.099	0.100	0.086	0.024	0.023	0.024	0.030	0.010	0.025	0.009	0.033
57	0.084	0.084	0.099	0.100	0.086	0.024	0.023	0.024	0.030	0.010	0.025	0.009	0.033
58	0.086	0.086	0.096	0.098	0.089	0.024	0.023	0.024	0.025	0.029	0.013	0.029	0.028
59	0.088	0.088	0.095	0.096	0.090	0.025	0.024	0.025	0.026	0.030	0.014	0.030	0.029
60	0.091	0.091	0.101	0.100	0.091	0.035	0.034	0.035	0.034	0.035	0.026	0.033	0.036
61	0.089	0.089	0.099	0.098	0.090	0.033	0.031	0.033	0.031	0.033	0.024	0.030	0.034
62	0.086	0.086	0.096	0.098	0.089	0.024	0.023	0.024	0.025	0.029	0.013	0.029	0.028
63	0.081	0.081	0.091	0.093	0.081	0.020	0.019	0.020	0.021	0.030	0.001	0.030	0.021
64	0.084	0.084	0.094	0.095	0.088	0.008	0.006	0.008	0.024	0.028	0.021	0.025	0.026
65	0.103	0.103	0.111	0.111	0.114	0.111	0.110	0.111	0.111	0.110	0.105	0.110	0.116
66	0.126	0.126	0.126	0.128	0.130	0.125	0.124	0.123	0.124	0.115	0.119	0.118	0.124

	47	48	49	50	51	52	53	54	55	56	57	58	59
48	0.030												
49	0.028	0.009											
50	0.031	0.005	0.009										
51	0.028	0.009	0.000	0.009									
52	0.023	0.028	0.023	0.026	0.023								
53	0.028	0.009	0.000	0.009	0.000	0.023							
54	0.021	0.026	0.021	0.025	0.021	0.001	0.021						
55	0.021	0.026	0.021	0.025	0.021	0.001	0.021	0.000					
56	0.028	0.009	0.000	0.009	0.000	0.023	0.000	0.021	0.021				
57	0.028	0.009	0.000	0.009	0.000	0.023	0.000	0.021	0.021	0.000			
58	0.015	0.028	0.025	0.029	0.025	0.020	0.025	0.019	0.019	0.025	0.025		
59	0.016	0.029	0.026	0.030	0.026	0.021	0.026	0.020	0.020	0.026	0.026	0.001	
60	0.029	0.034	0.029	0.033	0.029	0.031	0.029	0.030	0.030	0.029	0.029	0.031	0.033
61	0.026	0.031	0.026	0.030	0.026	0.029	0.026	0.028	0.028	0.026	0.026	0.029	0.030
62	0.015	0.028	0.025	0.029	0.025	0.020	0.025	0.019	0.019	0.025	0.025	0.000	0.001
63	0.001	0.029	0.026	0.030	0.026	0.021	0.026	0.020	0.020	0.026	0.026	0.014	0.015
64	0.021	0.026	0.021	0.025	0.021	0.001	0.021	0.000	0.000	0.021	0.021	0.019	0.020
65	0.106	0.109	0.110	0.110	0.110	0.113	0.110	0.111	0.111	0.110	0.110	0.109	0.108
66	0.121	0.116	0.116	0.118	0.116	0.125	0.116	0.124	0.124	0.116	0.116	0.120	0.119

	60	61	62	63	64	65
61	0.003					
62	0.031	0.029				
63	0.028	0.025	0.014			
64	0.030	0.028	0.019	0.020		
65	0.115	0.113	0.109	0.105	0.111	
66	0.123	0.123	0.120	0.120	0.124	0.141

APPENDIX E

NEXUS FILE FOR CYTB SEQUENCE ALIGNMENT

```

#NEXUS
Begin data;
  dimensions ntax=73 nchar=1083;
  format datatype=dna missing=? gap=-;
  matrix
  Adelphicos_quadrivirgatus_GT_ENS_9039
    CTATATTTTAACTACTACCAGTAGTTTAAACATTCTACCTGATGAAACTTCGGCTCAATACTACTAGCCTGTTCAGC
    ACTACAAATTTAACC GGATTCTTCTTAGCAATCCACTATACTGCTAACATTAATCTGGCCTTCTCATCTGTTGTTTCATATCACACGA
    GACGTCCCATGCGGATGAATCATACAAAATATTCACGCAACCGGGCATCTATATTTTTTCAATTTGTATCTACATCCACATCGCACGG
    GACTATATTACGGCTCCTATTTAAATAAAGAAGTCTGACTATCGGGGTAGCCCTCCTTACTATCTAATAGCAACTGCCTTTTTTGG
    TTATGTCTTACCATGAGGACAAATATCATTCTGAGCCGCAACAGTAATTACTAATCTACTAACTGCCGTCCCATACTAGGAACCACT
    CTGACAACCTGACTCTGGGGGGATTCTCTATTAACGATCCAACCTTACACGGTCTTTGCATTACACTTTATCTACCATTGCCA
    TTATTTCAATTATCCTCCATCCATATTATACTTCTTCATAATGAAGGTCTAGCAATCCACTTGGAAACCACTCAGACATTGATAAAAT
    CCCATTCCACCATAACCCTCCTACAAGACGCCTTAATACTAACCATTTCTTATTACCCTCCTATTCCCATCATATCATTGCCCC
    AACATATTTAATGACCCGAAAACCTTCTCTAAAGCCAACCCCATAGTAACACCCCAACACATTAAGCCAGAGTGATCTTTTTATTG
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    ACCCTCTACTCGGATGATCAGAAAATAAAAATTATG
  Atractus_wagleri_CO_MHUA_14368
    CTCCTATTTAACTCCTCCCGTAGGACTAAACATCTCCACCTGGTGAAACTTTGGCTCAATACTATTAGCCTGCTCAGC
    ACTACAAATTTAACC GGATTCTTTTTAGCAATCCACTACACGCCAACGTTAACTTGGCTTCTCATCCGTTATTTCATATCACACGA
    GACGTCCCATGCGGATGAATCATACAAAATATACATGCAACCGGGCATCTATATTTTTTCAATTTGTATCTACATCCACATCGCACGG
    GACTTTTATTACGGCTCTTATCTAAACAAAGAGTTTGATTATCAGGAGTAACCTTCTCGCCGTCTAATGGCAACAGCCTTCTTCGG
    CTACGCTTACCATGAGGACAAATATCATTCTGAGCCGCAACAGTAATTACCAATCTCCTAACCGCTATTCCATACCTAGGACTATT
    CTAACAACCTGGTTGTGGGGGGGTTCTCCATCAACGCCAACCTTAACACGATTTTTTCGCATTACACTTCATTCTCCCATTTGCCA
    TCATCTCTTATCCGATCCACATCATACTTCTTTCACAACAAGGGTCCAGCAACCCACTCGGAACCACTCAGATATTGATAAAAT
    CCCATTCCACCATAATCATTCTACAAGACACCCTAATACTAACCCCTCATCACCTACTATTTCATCATATATTTTACCCCA
    AACATTTTCAATGACCCGAAAATTTCTCTAAAGCCAATCCCATAGTACACCCGCAACACATCAAACCCGATGATATTTCTATTG
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    CTCCTATTTAACTCCTTCTGTAGGACTAAACATCTCCACTTGTGAAACTTCGGTCTATGTTACTAGCCTGCTCAGC
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    TTATGTCTTACCATGAGGACAAATATCATTCTGAGCCGCAACAGTAATTACTAATCTTCTAACCGCTAATGGCAACAGCCTTTCTTTGG
    CTAACAACCTGGTTGTGAGGGGGGTTTCTATCAGCGATCCAACCTCACACGATTTCTTGCACACTACACTTCATTCTTCCATTTACTA
    TCATCTCACTATCTTCCATCCATATCATACTTCTTTCACAACGAAGGCTCCAGCAACCCACTTGGAAACAAATTCAGACATTGACAAAAT
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*Tropidodipsas\_fischeri*\_GT\_ENS\_6419

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End;

APPENDIX F

NEXUS FILE FOR ND4 SEQUENCE ALIGNMENT



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Geophis nigrocinctus\_MX\_JAC\_30704

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N\_atrata\_EC\_Chimborazo\_FHGO\_7335

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N\_atrata\_EC\_Esmeraldas\_ENS\_12640

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N\_atrata\_EC\_Manabi\_LAC\_1594

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N\_atrata\_VE\_Caracas\_N1

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N\_atrata\_VE\_Guarico\_ECS\_794

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N\_celata\_CR\_Limon\_AS\_L\_098

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N\_diademata\_GT\_Huehuetenango\_ENS\_7939

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N\_diademata\_GT\_San\_Marcos\_JAC\_20014

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N\_diademata\_GT\_San\_Marcos\_JAC\_20070

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N\_diademata\_GT\_Suchitepequez\_ENS\_13451

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N diademata HN Copan JHT 2799  
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N diademata HN Copan JHT 2821  
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N diademata HN Copan JHT 2822  
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N diademata HN Santa Barbara JHT 3007 ----  
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N diademata MX Chiapas JAC 22917  
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N diademata MX Oaxaca JAC 25844  
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N\_diademata\_MX\_Puebla\_JAC\_22500

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N\_diademata\_MX\_Veracruz\_JAC\_24987

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N\_espinali\_HN\_Comayagua\_FN212525

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N\_espinali\_HN\_Comayagua\_IRL\_077

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N\_espinali\_HN\_Cortes\_JHT\_1611

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N\_espinali\_HN\_La\_Paz\_JHT\_2624

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N\_espinali\_HN\_La\_Paz\_JHT\_2625

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N\_hudsoni\_EC\_Morona\_Santiago\_FHGO\_5940

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N\_maculata\_CR\_Alajuela\_MVZ\_149884

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N\_maculata\_CR\_Cartago\_MVZ\_204116

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N\_maculata\_CR\_Cartago\_MVZ\_204122

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N\_maculata\_CR\_Cartago\_MVZ\_204124

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N\_maculata\_HN\_Olancho\_ENS\_10670

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N\_maculata\_NI\_Atlantico\_Norte\_N629

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N\_maculata\_NI\_Jinotega\_ENS\_9739

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N\_pavimentata\_GT\_Baja\_Verapaz\_ENS\_7788

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N\_pavimentata\_GT\_San\_Marcos\_ENS\_8342

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N\_pavimentata\_GT\_San\_Marcos\_JAC\_19803

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CGAACACCCCCACCATAAACTTTCACAGGAGAACATTAATTGATCATCCCTATTCAACTGATGTCCAACAACAATCATATCTTC  
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CGAGGGTGTATAAGACCTGCTAACTCTTTAATCTGAAATTAACACTCAGCCCCCTCTACTAAAGGATAGTAGT-  
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N\_pavimentata\_GT\_San\_Marcos\_JAC\_19804

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N\_pavimentata\_HN\_Atlantida\_JHT\_3068

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N\_pavimentata\_HN\_Yoro\_JHT\_2448

TCCTATTGCAGGTTCAATAGTACTAGCCGCCATTCTCTTAAATTAGGAGGGTACGGAATTATCCGAATAATACAAATCC  
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N\_psephota\_CR\_Cartago\_MVZ\_204114

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CGAGGGGGTTATAAGACCTGCTAACTCTTTAACTGAGATTAACACTCAGCCCCCTCTACTGAAGGATAATAGT-  
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N\_sebae\_CR\_Guanacaste\_MVZ\_207364

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N\_sebae\_CR\_Guanacaste\_MVZ\_207365

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N\_sebae\_CR\_Puntarenas\_CMS\_002

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N\_sebae\_GT\_Baja\_Verapaz\_MSM\_97

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N\_sebae\_GT\_Guatemala\_ENS\_10257 ---

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N\_sebae\_GT\_Huehuetenango\_JAC\_19256

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N\_sebae\_GT\_Izabal\_ENS\_13314

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ATTCCACTGGTCTTAGGCACCAAAATCT

N\_sebae\_GT\_Izabal\_MEA\_444

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N\_sebae\_GT\_Peten\_JAC\_21025

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N\_sebae\_GT\_Santa\_Rosa\_ENS\_13346

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N\_sebae\_HN\_Comayagua\_JHT\_2576

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N\_sebae\_HN\_Copan\_JHT\_2798

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ATTCCACTGGTCTTAGGCACCAAAATTTCT

N\_sebae\_HN\_Cortes\_IRL\_034

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ATTCCACTGGTCTTAGGCACCAAAATTTCT

N\_sebae\_HN\_El\_Paraiso\_ENS\_8656

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AGGTTCAATAGTACTAGCCGCCATCCTCCTTAAATTAGGAGGATATGGAATTATCCGAATAACACAAATCCTTCCCTCCAACAAAAACA
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N\_sebae\_HN\_Francisco\_Morazan\_JHT\_2030

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N\_sebae\_HN\_Gracias\_a\_Dios\_FN212668

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N\_sebae\_HN\_Olancho\_ENS\_10756

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N\_sebae\_HN\_Santa\_Barbara\_JHT\_2356

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N\_sebae\_HN\_Yoro\_JHT\_2427

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N\_sebae\_MX\_Chiapas\_AMH\_356

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N\_sebae\_MX\_Oaxaca\_JAC\_21629

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N\_sebae\_MX\_Veracruz\_JAC\_22579

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N\_sebae\_MX\_Yucatan\_JAC\_24419

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Sibon\_nebulatus\_CR\_MVZ\_233298

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Tropidodipsas\_sartorii\_JAC\_30401

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APPENDIX G

NEXUS FILE FOR NT3 SEQUENCE ALIGNMENT

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N\_sebae\_NI\_Jinotega\_N108

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Ninia\_sp\_PA\_Cocle\_JM\_376

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Sibon\_nebulatus\_CO\_MHUA\_14511

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Sibon\_nebulatus\_CR\_MVZ\_233298 -----

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Tropidodipsas\_fischeri\_GT\_ENS\_6419

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Tropidodipsas\_sartorii\_NI\_N625

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;  
end;

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## BIOGRAPHICAL INFORMATION

Illinoisan by birth, Matthew John Ingrassi grew up in the suburbs of Chicago. He attended high school at Nazareth Academy, and after graduating, continued his education at Saint Louis University where he earned a B.S. in Biology with Honors. After graduation, Matt held several jobs before returning to school to complete his Masters degree. His passion for herpetology, which began at a very early age, led him to pursue a career in the field of Biology. Matt plans to use his talents any way he can to make a living and continue research in herpetology as time and resources permit.