PHYLOGENETIC RELATIONSHIPS AND FEEDING BEHAVIOR OF NEOTROPICAL SNAIL-EATING SNAKES (DIPSADINAE, DIPSADINI)

by

COLEMAN MATTHEW SHEEHY III

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ABSTRACT

PHYLOGENETIC RELATIONSHIPS AND FEEDING BEHAVIOR

OF NEOTROPICAL SNAIL-EATING SNAKES

(DIPSADINAE, DIPSADINI)

Coleman Matthew Sheehy III, PhD

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Supervising Professor: Eric Nelson Smith

The snake subfamily Dipsadinae contains more than 350 ecologically diverse species in about 32 genera. Members of the tribe Dipsadini are gastropod specialists, and many possess a suite of adaptations for eating snails. I tested chemosensory prey preference in *Dipsas*, *Sibon* and *Tropidodipsas* species. Additionally, I described the feeding behavior of *Tropidodipsas annuliferus*, *T. philippii* and *Sibon nebulatus*. All snakes preferred gastropod prey. *Tropidodipsas philippii* also showed strong interest in the earthworm scent and subsequently consumed earthworms. Snakes snagged or wedged snail shells on surface irregularities and extracted snails using muscular contractions of the body, representing an undescribed feeding behavior in vertebrates. I used two mitochondrial (cyt-b and ND4) and two nuclear (NT3 and DNAH3) genes totaling 3241 bp to test relationships among the Dipsadini and among dipsadine genera. *Geophis* is deeply nested within the Dipsadini. I synonymize *Sibynomorphus* with *Dipsas* and three *Sibon* species with *S. dimidiatus*. I identify five new genera and 11 dipsadine tribes: Diaphorolepini, Dipsadini, Leptodeirini, Nothopsini, Tribe nov. 1 (*Adelphicos* + *Cryophis*), Tribe nov. 2 (*Atractus*), Tribe nov. 3 ((*Amastridium* + *Chapinophis*) + (*Trimetopon* (*Coniophanes* (*Rhadinaea* + *Urotheca*)))), Tribe nov. 4 (*Chersodromus* + *Ninia*), Tribe nov. 5 (*Enuliophis* + *Enulius*), Tribe nov. 6 (*Hydromorphus* + *Tretanorhinus*), Tribe nov. 7 (*Rhadinophanes* + *Tantalophis*). The tree topology supports the hypothesis that dipsadine snakes experienced a dietary shift and adaptive radiation.

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CHAPTER 1

CHEMOSENSORY PREY PREFERENCE AND FEEDING BEHAVIOR IN NEOTROPICAL GASTROPOD-EATING SNAKES (COLUBRIDAE: DIPSADINAE: DIPSADINI)

1.1 Introduction

Subsequent to their mid-Cretaceous origins approximately 100 million years ago (Caldwell, 2007), snakes have radiated into all the major biomes on the planet except the polar and deep sea regions to become an ecologically diverse group of vertebrates (Savitzky, 1983). It is widely proposed that their unique and highly kinetic skulls helped drive this diversity by enabling snakes to adapt to a wide variety of diets ranging from ants to antelope (Greene, 1997). Therefore, knowledge of diet and feeding habits in snakes is likely useful for understanding patterns of diversification within this extremely successful group of vertebrates (Greene, 1983; Savitzky, 1983; Schwenk, 2000). This information is particularly important given that dietary specialization is relatively common among the roughly 3,378 extant snake species. Thus, identification of interspecific variation in feeding behavior, whether subtle or dramatic, is useful for better understanding the origin and maintenance of dietary specialization.

At least six snake groups are known to contain species that feed on terrestrial gastropods (Dipsadinae, Smith, 1943; Dunn, 1951; Sazima, 1989; *Duberria*, Branch, 1975; Pareatinae, Pope, 1935; Götz, 2002; *Storeria*, Brown, 1979; Rossman and Myer, 1990; *Thamnophis*, Fox, 1952; Britt et al., 2006; and *Tomodon*, Bizerra, 1998; Bizerra et al., 2005). Although all these groups contain species that consume slugs to varying degrees, only the Dipsadinae, Pareatidae, and the genera *Duberria* and *Storeria* contain species known to also consume land snails. Extreme snail specialization — the consumption of gastropod prey to the

exclusion of all other available prey using a suite of specialized behavioral and morphological adaptations to extract snails from their shells — has evolved independently in the Old World Pareatidae and the New World Dipsadinae. This convergence is evidenced by the large phylogenetic separation between the Pareatidae and the Dipsadinae (Lawson et al., 2005; Zaher et al. 2009; Pyron et al. 2011).

Current phylogenetic hypotheses suggest that, within the snake subfamily Dipsadinae, the tribe Dipsadini forms a monophyletic group comprising the genera *Dipsas*, *Sibon*, *Sibynomorphus*, *Tropidodipsas* and the monotypic genus *Plesiodipsas* (Fernandes, 1995; Wallach, 1995; Harvey et al., 2008). These snakes are gastropod specialists, and the most specialized genera (*i.e.*, *Dipsas* and *Sibynomorphus*) possess a suite of morphological and behavioral characteristics generally accepted as adaptations for extracting land snails from their shells (Dunn, 1951; Peters, 1960). Within the Dipsadini, detailed feeding behavior studies have only included species in the genera *Dipsas* (Peters, 1960; Gans, 1972, 1975; Sazima, 1989) and *Sibynomorphus* (Laporta-Ferreira, et al., 1988). *Dipsas* and *Sibynomorphus* species extract snails from their shells using alternating insertions of the mandibles, and this behavior is likely aided by several morphological adaptations including the inward inflection of the maxilla and maxillary teeth, the freeing of the pterygoid bone from the quadrate-articular articulation, the reduction or loss of teeth on the pterygoid, the presence of a hingelike intramandibular joint, the loss of the mental groove, and various changes in mandibular musculature (Peters, 1960; Gans, 1975; Kofron, 1985). Furthermore, some *Dipsas* and *Sibynomorphus* species produce weak venom that may help relax snails making them easier to extract from their shells (Oliveira et al., 2008). The genera *Sibon* and *Tropidodipsas* possess some of the morphological features present in *Dipsas* and *Sibynomorphus* but lack some of the changes in mandibular shape and musculature (Scott, 1967). Furthermore, as with most other alethinophidian (or “advanced”) snakes, they possess a mental groove making it unlikely that these genera extract snails from their shells using the same method as described in *Dipsas* and *Sibynomorphus*. Thus, *Sibon*

and *Tropidodipsas* likely differ from *Dipsas* and *Sibynomorphus* in feeding behavior, and any variation in feeding behavior may provide insight into how dietary specialization evolved in this group of snakes.

Carl Gans (1983:459) briefly described anecdotally the behavior of one captive *Sibon nebulatus* feeding on a snail as "crawling backwards through the cage, scraping its prey against the walls and bottom, apparently trying to dislodge it". Gans continued to note how the *S. nebulatus* extracted the snail using muscular contractions of the body (rather than mandibular movements alone as in *Dipsas* and *Sibynomorphus*) after wedging the shell against the substrate. However, Gans' observations have not been substantiated and, aside from his single anecdotal observation, no description of feeding behavior exists for any other *Sibon* or *Tropidodipsas* species. Furthermore, the assumption that members of the Dipsadini prefer gastropod prey to other potential prey options has never been explicitly tested in any species within the tribe. The goals of this study are two-fold. First, I test the assumption that *Dipsas*, *Sibon* and *Tropidodipsas* species prefer gastropod prey to other potentially encountered prey items. Second, I describe for the first time the feeding behavior in two of the six species of *Tropidodipsas* (*T. annuliferus* and *T. philippii*) and elaborate on the feeding behavior of *Sibon nebulatus*.

1.2 Materials and Methods

1.2.1 Animal Collection and Maintenance

The Dipsadini as a group ranges from northeastern Mexico to southern South America, although no single species spans that entire range. I collected three *Dipsas gaigeae* (one juvenile and two adults), two adult *Sibon nebulatus*, six *Tropidodipsas philippii* (one juvenile and five adults) and two adult *Tropidodipsas annuliferus* from the states of Colima and Oaxaca, Mexico during the rainy season between June and July 2009 (Fig. 1.1; see Appendix A for specimen numbers). These snakes were found crossing roads at night. Additionally, I collected an adult *S. nebulatus* from Puerto Ayacucho, Venezuela in 2007, which was found active along

a stream at night. Two adult *Leptodeira septentrionalis* were previously collected from northern Mexico (Fig. 1.1). All snakes were returned to the laboratory at the University of Texas, Arlington (UTA), where chemosensory tests and feeding observations were conducted.

Snakes were housed individually in transparent plastic terraria (29 x 17.5 x 17 cm) with locking ventilated lids and maintained in a designated animal room at UTA. Each terrarium contained pine-bark substrate, a water bowl, a large mass of *Sphagnum* spp. moss for hiding and to retain moisture, and a large curved piece of bark for hiding, climbing and shedding. Water was available *ad libitum* and snakes were misted each night or every other night soon after dark, which often stimulated activity and feeding. I maintained all snakes on a 12:12 h day:night photoperiod at a temperature between 26–27ºC, which is the average temperature in Colima, Mexico during the active season. In captivity, the snakes were offered and readily ate two species of snails collected locally in Arlington, Texas, USA (see below). I fed snakes 6–8 snails per week at night. All snakes were maintained in captivity for about four months before beginning the study except the *S. nebulatus* from Venezuela, which was maintained for about three years prior to the study.

1.2.2 Prey Species

I observed several unidentified snails crossing the roads in areas of Colima where the snakes were collected. These snails all had dextral shells that were long, conical, and lacked opercula. However, it is not known whether the snakes consume these particular snails in the wild. Because it was not possible to bring live snails or slugs from Colima for conducting the feeding trials, I offered the snakes two locally-collected dextral snail species lacking opercula and with differing shell morphologies (long and conical, *Rabdotus dealbatus*, and round and flat, *Bradybaena similaris*; Fig. 1.2). I used *Rabdotus dealbatus* to offer snails with shell morphologies as similar as possible to those I observed in their natural habitat. However, I used *B. similaris* in case these snakes consume snails with this shell morphology. Old World snail-eating snakes possess functional adaptations for feeding on dextral snails with round and

flat shell morphologies (Hoso et al., 2007). The occurrence of similar adaptations has not been tested in New World snail-eating snakes. Thus, offering snails with these two differing shell morphologies allows me to potentially identify performance biases between the two shell morphologies. Lastly, I also fed snakes locally collected garden slugs (*Limax flavus*) for the study (Fig. 1.2).

1.2.3 Chemosensory Prey Preference

Chemosensory prey preference has been quantified in numerous squamates by presenting scents and comparing tongue-flick rates under the assumption that increased tongue-flick rates represent stronger interest in a particular scent (Burghardt, 1967; Cooper and Burghardt, 1990; Cooper and Secor, 2007). To test the assumption that members of the Dipsadini prefer gastropod prey to other potentially available prey items, I offered to three *Dipsas gaigeae*, six *Tropidodipsas philippii*, two *T. annuliferus* and three *Sibon nebulatus* the scents of four prey items plus both a positive and negative control. I also offered the same prey and control scents to two *Leptodeira septentrionalis* as a control species for comparison. *Leptodeira* are closely related to the Dipsadini but have a more generalized diet consisting of vertebrate prey and their eggs (Mulcahy, 2007). Thus, *Leptodeira* should show stronger interest in the vertebrate scents if their tongue-flick rates accurately represent prey preference. The prey scents used were from an introduced Asian tramp snail (*Bradybaena similaris*), a Rio Grande chirping frog (*Eleutherodactylus cystignathoides*), a common earthworm (*Lumbricus terrestris*) and a domestic cricket (*Acheta domestica*). Earthworms (advertised as Canadian nightcrawlers) and crickets were purchased from a local bait shop and pet store, respectively. The *E. cystignathoides* were collected locally in Arlington, Texas and were used because the genus is present and common in many parts of Mexico, including Colima, making it ecologically relevant. For the positive control I used crushed leaves of the plant herb cilantro (*Coriandrum sativum*), which has a strong odor but should not be recognized as food by these snakes.

Deionized water (dH_2O) was used as the negative control to test for a reaction to the presence of the swab and water without a scent.

Scents were offered via a 15 cm wooden cotton-tipped swab after first dipping the tip into dH_2O and then thoroughly rubbing the cotton tip on the prey or control for 5–10 s (Cooper and Secor, 2007). Under a red light, the tip was then held approximately 1.0 cm in front of the snake's face for 60 s, during which time I counted the number of tongue flicks as the response variable. The 60 s trial began with the first tongue flick directed toward the swab. Scent trials were repeated three times per individual snake in random order. Three trials were performed per day and with 1 hour intervals between trials to allow the snakes to return to their original resting behavior. This minimized the possibility of a trial influencing the results of a subsequent trial (*i.e.*, circularity or sphericity). During each 1 hour interval, all snakes appeared to return to their typical resting state, which usually involved hiding under the bark. I gently misted all snakes with room-temperature tap water in the evening just before dark and feeding trials began shortly after dark. The misting in general appeared to stimulate the snakes to become alert without becoming defensive.

1.2.4 Feeding Behavior Trials

I included six *Tropidodipsas philippii*, two *T. annuliferus* and three *Sibon nebulatus* in the feeding behavior trials (Fig. 1.1). All individuals were fed three different prey types: round snails, conical snails and slugs (identified above). Feeding trials were conducted three times per snake for each prey type in random order. As with the chemosensory study, I gently misted all snakes in the evening just before dark and feeding trials began shortly after dark. Under a red light, I placed a single prey item into a snake terrarium and allowed it to crawl around freely. I recorded the following data for each snail feeding trial: initial method of prey location (sight or chemoreception), time watching prey prior to strike, number of tongue flicks between prey location and strike, approximate strike distance from prey, location of strike on prey (head or tail), time holding snail still before first extraction attempt, method of successful extraction (using

mandibles, wedging between objects or snagging shell aperture), whether mandibular movements were used to facilitate extraction, whether pushing and twisting using the head was used to facilitate extraction, whether muscular contractions of the body were used to drag the snail along the substrate, total number of extraction attempts, and total extraction time (time from strike to successful extraction). These same data were recorded for slug feeding trials, except those that pertained to snail extraction.

1.2.5 Statistical analyses

Comparing maximum tongue flick rates is more biologically meaningful than a comparison of mean tongue flick rates because it represents the maximum excitement level exhibited by each snake in response to each scent. Therefore, I calculated the mean maximum tongue flick responses for all individuals. Each individual snake was presented with scents in random order, and scent trials were repeated three times per individual. For each scent, the single maximum tongue flick rate recorded among all three trials for each individual was the value used to represent each individual's interest level. This resulted in a single value (maximum) per individual, which avoided pseudoreplication and allowed the use of one-way analysis of variance (ANOVA) to test for differences between responses to scents (Sokal and Rohlf, 1995). Furthermore, any error created by autocorrelation would likely be evenly spread across all trials due to the random order of the trials. Evenly spread autocorrelation would tend to reduce the statistical power and increase the likelihood of type II error, which would render significant results conservative (Sokal and Rohlf, 1995). I also performed a repeated-measures analysis of variance (rmANOVA) to test for autocorrelation among means of multiple trials from the repeated use of the same individuals (Sokal and Rohlf, 1995). This would help identify, for example, if snakes consistently showed an increased interest or aversion to a scent after smelling a particular scent. All data were $\log_{10}$ transformed prior to analyses. Statistical analyses were performed using SYSTAT 12 (Systat Software, Inc., Chicago, IL, USA).

1.2.6 Taxonomy

The tribe Dipsadini has historically included various species recognized by different authors (see Wallach, 1995 and Harvey, 2008 for taxonomic summaries). I follow the usage as defined by Cadle (2007) and Harvey et al. (2008) to include within the tribe only the genera *Dipsas*, *Sibon*, *Sibynomorphus*, *Tropidodipsas* and *Plesiodipsas*. Although Kofron (1985) synonymized *Tropidodipsas* with *Sibon* based on hemipenal morphology, cranial osteology and diet, Wallach (1995) revalidated the genus *Tropidodipsas* and noted that its members share the absence of a tracheal lung as a synapomorphy. I use his revised definition of the genus *Tropidodipsas* here. Smith (1982) argued that the genus *Sibon* is a masculine noun and that, according to the rules of the International Code of Zoological Nomenclature (ICZN), the specific epithet also needs to be masculine. I agree and use the masculine noun form of the specific epithet (*e.g.*, *Sibon nebulatus*, not *S. nebulata*) regardless of the feminine usage by many previous authors.

1.3 Results

1.3.1 Chemosensory Prey Preference

Because the results of the feeding behavior study suggested there was no apparent preference for either type of snail, the snails with round, flat shells (*Bradybaena similaris*) were used for chemosensory prey preference trials.

Results of the one-way ANOVA revealed a significant difference in mean maximum tongue flick rates between different scents for *D. gaigeae* ($F_{5,12} = 10.53$, $p < 0.001$; Fig. 1.3), *S. nebulatus* ($F_{5,12} = 7.10$, $p = 0.003$; Fig. 1.4), *T. annuliferus* ($F_{5,6} = 7.21$, $p = 0.016$; Fig. 1.5), and *T. philippii* ($F_{5,30} = 0.96$, $p < 0.001$; Fig. 1.6), but not for *L. septentrionalis* ($F_{5,12} = 1.2$, $p > 0.05$; Fig. 1.7). The *Dipsas*, *Sibon* and *Tropidodipsas* species tested showed higher maximum tongue flick rates for gastropod prey than for the control scents. Both *Leptodeira* individuals showed higher mean and maximum tongue flicks towards the frog scent than to the control scents (Fig. 1.7); however, the results of the $\log_{10}$-transformed data were not significant for this species. The rmANOVA suggests that there were not significant differences between repeated

trials of the same individuals for *D. gaigeae* ($F_{10,30}$ = 2.144, p = 0.052), *S. nebulatus* ($F_{10,30}$ = 0.401, p = 0.936), *T. annuliferus* ($F_{5,30}$ = 0.500, p = 0.774), and *L. septentrionalis* ($F_{5,30}$ = 1.43, p = 0.243). However, there were differences between trials of *T. philippii* (rmANOVA, $F_{25,70}$ = 1.840, p = 0.024). The number of tongue flicks varied between species (Table 1.1). *Tropidodipsas philippii* showed the strongest interest in the snail scent relative to other scents, but it also showed a heightened interest in the earthworm scent (Fig. 1.6). One *T. philippii* bit the swab when presented with the earthworm scent. No other snake species bit the swabs except the two *Leptodeira*, which both bit the swabs when presented with the frog scent. Subsequent to feeding trials, all snakes were offered live earthworms. However, *T. philippii* was the only species that showed interest. Three of the six individuals immediately bit and consumed earthworms, whereas the other three individuals showed prolonged interest but did not bite the prey.

1.3.2 Feeding Behavior

The feeding behavior associated with prey location, tracking and biting was similar among *Tropidodipsas philippii*, *T. annuliferus* and *Sibon nebulatus*. Mean tongue flicks and ranges for each prey type are listed in Table 1.1. In all trials, the snakes were initially attracted to prey (snail or slug) by seeing its movement. This was evident by a noticeable change in behavior once the prey moved into the field of vision of a resting snake and by the approach behavior. Snakes were initially resting and still, but when the prey moved into the field of vision, the snakes quickly turned to face the prey directly and advanced toward the prey in a straight line with their heads elevated and with relatively few tongue flicks. This occurred even when the snails and snakes were at opposite ends of the terrarium or when the snails were in adjacent terraria. If the prey stopped moving, the snakes would often also pause their approach until the prey began moving again. On one occasion, a snail moved out of the field of vision as the snake began following it. The snake then lowered its head and began rapidly tongue flicking

the substrate as it followed the scent trail of the snail until it could see the snail moving again, at which time tongue flicking slowed and the approach resumed using vision as described above.

Behavior of all three species as they reached the snail or slug was similar to that described for *Dipsas indica* (Sazima, 1989) and *Pareas carinatus* (Götz, 2002) in that the snakes closely and intensely watched the movements of the prey with infrequent tongue flicks and often with their necks strongly bent (Table 1.1 and Fig. 1.8a). Frequently I observed the eyes moving as they visually followed the prey movements. As with *Dipsas indica* (Sazima, 1989), the snakes followed the prey until they identified its anterior end based presumably on the prey's forward movement. All (100%) predatory strikes by the three snake species were directed at the head of the snail or slug from a distance of approximately between 0.5–2.0 cm. After grabbing the prey by the head, the feeding behavior differed between snails and slugs.

1.3.2.1 Snails

All three snake species always grasped both snail species on the head and the grip was secured by chewing as the snail retracted resulting in the mandible being pulled partially inside the shell aperture (Fig. 1.8b). Once a grip was secured, a holding period of variable time followed where the snakes remained still (Table 1.1). Following the holding period, the snakes proceeded to lift the snail partially into the air as they carried the snail forward over the substrate. While carrying the snail, the snakes tapped the snail on the substrate frequently and then pulled back in an apparent effort to locate irregularities in the substrate on which to wedge or snag the shell. Usually this involved using the rough edges of the bark strips or the narrow space between the water container and the side of the terrarium. Once the snakes sensed the resistance of a potentially wedged shell, they relaxed their heads momentarily and moved their tails and posterior body around the terrarium in an effort to firmly anchor the tail on the substrate. Then, with the tail anchored for resistance, the snakes used muscular contractions of the body to pull the shell against the substrate, often while simultaneously twisting its head (Fig. 1.8c). The snakes pulled firmly and steadily until the snail was pulled slightly out of the shell,

after which the snake quickly advanced its jaws over the exposed section of snail by chewing and resumed pulling. This alternate pulling and advancing was repeated until the snail was fully extracted from the shell and swallowed several minutes later (Fig. 1.8d; Table 1.1). If the shell slipped out of its hold, the snakes immediately moved forward and repositioned the shell in the same spot and tried again, repeating up to five times if necessary before successfully extracting the snail or moving to retry at a different location. The number of tongue flicks when approaching snails was similar among all three snake species towards both round and conical snails (Table 1.1). However, *Tropidodipsas annuliferus* and *Sibon nebulatus* exhibited much longer holding times for round snails than for conical snails (Table 1.1). The total extraction time was greater for round snails than for conical snails in all three snake species; however, the difference in time was relatively small for *T. philippii* and *S. nebulatus* (Table 1.1).

1.3.2.2 *Slugs*

All three snake species located slugs visually and grasped them on the head or anterior region in the same manner as described above for snails. After grasping the slug, however, the snakes typically lifted the slugs above the substrate and proceeded to ingest the slugs immediately without a holding period (Table 1.1). A large amount of thick mucus remained in the mouth after the slug was swallowed, which the snakes attempted to remove by rubbing the sides of the mouth against the substrate. The swallowing time for slugs was similar for all three snake species (Table 1.1).

1.4 Discussion

Members of the genera *Dipsas*, *Sibon* and *Tropidodipsas* that were tested preferred gastropod prey to other potentially available prey. Both *Leptodeira* individuals clearly demonstrated a stronger response to the frog scent than to all other scents, but the low sample size likely resulted in this difference not being significant. *Tropidodipsas philippii* showed strong interest in earthworms and ate them when offered, suggesting that this species likely eats them in the wild in addition to gastropods. Feeding on earthworms is shared with *T. fischeri* (pers.

obs.) and could represent an ancestral diet of the genus and possibly of the Dipsadini. These results are overall consistent with the hypothesis that evolutionary changes in diet should occur in tandem with changes in chemosensory responses to preference for the new diet in snakes (Cooper, 2008).

The "snag and drag" feeding behavior observed in *Sibon nebulatus*, *Tropidodipsas philippii* and *T. annuliferus* is a novel feeding behavior in snakes that represents an undescribed feeding strategy allowing gape-limited predators to consume relatively large prey. This highly derived feeding behavior is likely a synapomorphy among the genera *Sibon* and *Tropidodipsas*. Thus, these results support a *Sibon* + *Tropidodipsas* clade and a *Dipsas* + *Sibynomorphus* clade. These intergeneric relationships have been suggested based on some morphological (Wallach, 1995; Harvey et al., 2008) and molecular (Mulcahy et al., 2011; Grazziotin et al., 2012) studies. However, it remains unclear whether these two groups are each monophyletic or whether they are sister to each other (*e.g.*, Pyron et al., 2011).

The Dipsadini are a relatively young group compared to the Old World snail eating Pareatidae (Lawson et al., 2005; Zaher et al., 2009; Pyron et al., 2011). Pareatine snakes do not possess the diversity of feeding behavior present in the Dipsadini; all members that feed on snails extract them in a manner similar to *Dipsas* (Götz, 2002). However, they have become morphologically and behaviorally asymmetric resulting in the efficient extraction of only snails with dextral shells (Hoso, 2007). This type of specialization has not been observed within the Dipsadini (pers. obs.; Hoso, pers. comm.). Thus, some of the variation in feeding behavior in the Dipsadini may reflect intermediate stages that have been lost in the Pareatidae.

This study did not use snakes that were naive to feeding on snails. Future studies should use hatchlings that are naive to determine if gastropod prey preference is learned or if any of these species exhibit ontogenetic dietary shifts. Studies on naive *Pareas iwasakii* from Japan show that gastropod prey preference in this species is present immediately after hatching

(Hoso, 2007). This is consistent with studies on other snake species that are dietary specialists (Cooper and Secor, 2007).

Another consideration is that this study was conducted using gastropods that do not occur in the snakes' native habitat, which could have affected responses and feeding behavior. However, their enthusiasm towards eating the non-native snails and slugs suggests that dipsadini snakes may not be selective in what species of gastropods to consume. This raises the question of what chemoattractants snakes are using to identify gastropods from other available prey items since this cue is likely common to gastropods in general. A similar study on Queen snakes (*Regina septemvittata*), which are dietary specialists, identified the specific chemoattractant used by the snakes to identify their freshly-molted crayfish prey (Jackrel and Reinert, 2011). However, because vision is also used extensively to identify gastropod prey, experiments should be conducted to quantify the individual roles of both vision and chemoattractants these snakes use to identify gastropod prey.

In summary, information regarding diet and feeding habits may aid in understanding morphological and behavioral diversification patterns within snakes (Schwenk, 2000), particularly among groups containing dietary specialists. *Sibon* and *Tropidodipsas* share a novel feeding behavior that has not been previously described in vertebrates in which the snakes extract snails by dragging them against the substrate in an effort to snag the shell on surface irregularities. This feeding behavior differs substantially from that shared by *Dipsas* and *Sibynomorphus*, which both extract snails from their shells using alternating movements of their highly modified mandibles. These different feeding behaviors agree with morphological studies that suggest *Sibon* + *Tropidodipsas* form a clade (Kofron, 1985b) and that *Dipsas* + *Sibynomorphus* form another clade (Peters, 1960). However, it remains unclear whether these are sister clades. Potentially fruitful directions for future studies might include investigating the cranial anatomy for morphological asymmetry in the Dipsadini similar to that which has been demonstrated in Old World snail-eating snakes of the family Pareatidae (Hoso et al., 2007).

Dipsadine snakes clearly use visual and chemosensory cues to locate gastropod prey. However, it would be interesting to test the relative importance of these cues independently. Finally, using the feeding behaviors identified in this study to better understand the evolution of gastropod specialization in the Dipsadini would be aided by a detailed phylogeny of the tribe and subfamily.

Table 1.1 Feeding behavior data for *Tropidodipsas philippii*, *T. annuliferus* and *Sibon nebulatus* as discussed in the text. Prey consists of snails with either round or conical shells, and slugs. Sample sizes (*n*) for each species represent the same individuals repeated for different prey types, and data are presented as mean ± SE (range). Times are in seconds. Extraction time for slugs is the swallowing time.

	n	Prey	Tongue flicks	Time watching	Holding time	Extraction time	Total time
T. philippii	6	Conical	11.06 ± 1.66 (2–26)	60.11 ± 13.74 (19–271)	1348.78 ± 218.57 (0–2739)	2766.56 ± 370.15 (292–6597)	4115.33 ± 467.42 (292–7940)
T. philippii	6	Round	11.0 ± 1.97 (4–32)	52.06 ± 11.95 (16–198)	1101.67 ± 186.20 (28–2990)	3517.78 ± 416.65 (988–8047)	4619.44 ± 406.45 (2023–8481)
T. philippii	6	Slug	6.72 ± 0.98 (2–17)	17.0 ± 2.12 (5–39)	0	87.28 ± 6.97 (32–163)	87.28 ± 6.97 (32–163)
T. annuliferus	2	Conical	10.50 ± 2.77 (2–20)	195.83 ± 164.09 (15–1015)	75.83 ± 43.85 (0–273)	1119.0 ± 273.72 (115–1980)	1194.83 ± 262.60 (234–1980)
T. annuliferus	2	Round	12.67 ± 3.45 (6–28)	52.67 ± 15.08 (24–124)	763.83 ± 259.80 (36–1641)	2687.83 ± 594.99 (985–5082)	3451.67 ± 710.86 (1053–6333)
T. annuliferus	2	Slug	8.0 ± 1.59 (3–13)	22.83 ± 4.47 (7–41)	0	72.33 ± 12.44 (48–132)	72.33 ± 12.44 (48–132)
S. nebulatus	3	Conical	17.56 ± 2.04 (7–24)	51.0 ± 19.17 (9–196)	907.22 ± 237.50 (113–2292)	3683.67 ± 306.22 (2524–4907)	4590.89 ± 355.91 (2848–5996)
S. nebulatus	3	Round	15.22 ± 2.32 (7–27)	31.22 ± 3.37 (19–54)	1834. 44 ± 158.59 (1161–2489)	3532.78 ± 181.20 (2564–4414)	5367.22 ± 215.04 (4117–6094)
S. nebulatus	3	Slug	7.11 ± 1.39 (3–17)	21.22 ± 2.74 (10–35)	0	79.33 ± 8.21 (40–120)	79.33 ± 8.21 (40–120)

Figure 1.1 Dipsadine snakes used in the chemosensory prey preference study included (a) *Dipsas gaigeae*, (b) *Sibon nebulatus*, (c) *Tropidodipsas philippii*, (d) *Tropidodipsas annuliferus*, and an outgroup (e) *Leptodeira septentrionalis*.

Figure 1.2 Pulmonate gastropod prey items used for chemosensory and feeding behavior studies in *Sibon* and *Tropidodipsas* included two snail species (a) *Bradybaena similaris*, (b) *Rabdotus dealbatus*, and one slug species (c) *Limax flavus*.

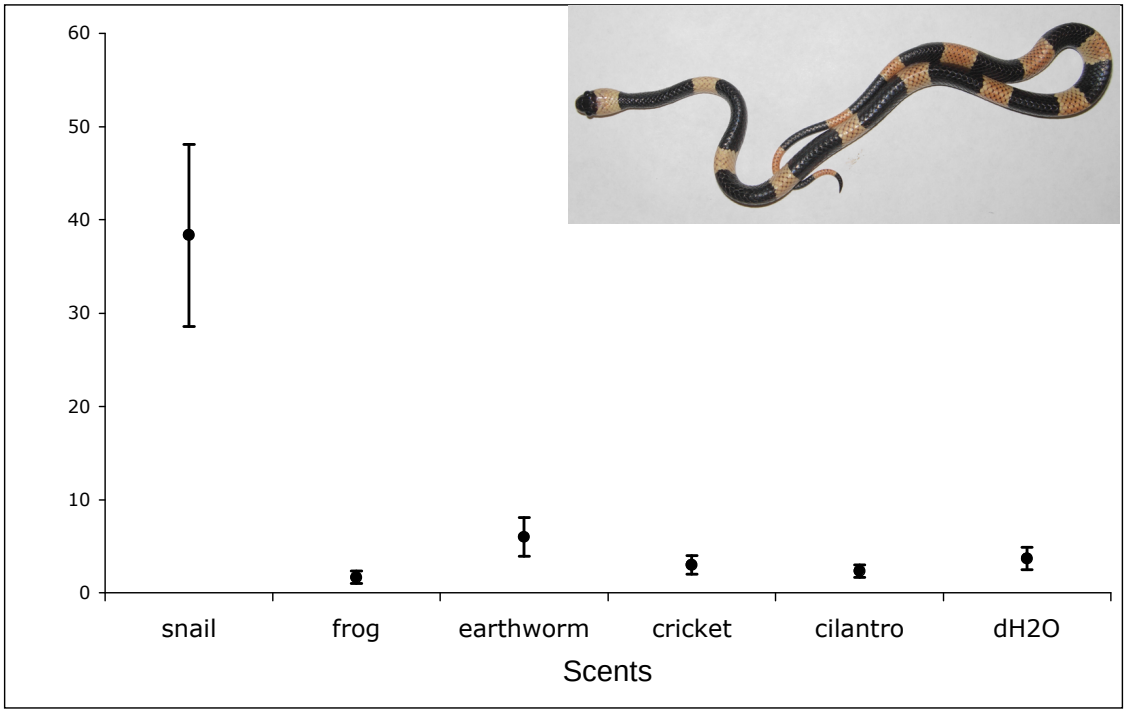

Figure 1.3 Results of ANOVA on mean maximum tongue flick rates (± SE) for *Dipsas gaigeae* (n = 3) in response to various prey scents ($p < 0.001$). Data shown are untransformed to clearly show patterns; however, data were log transformed prior to all analyses.

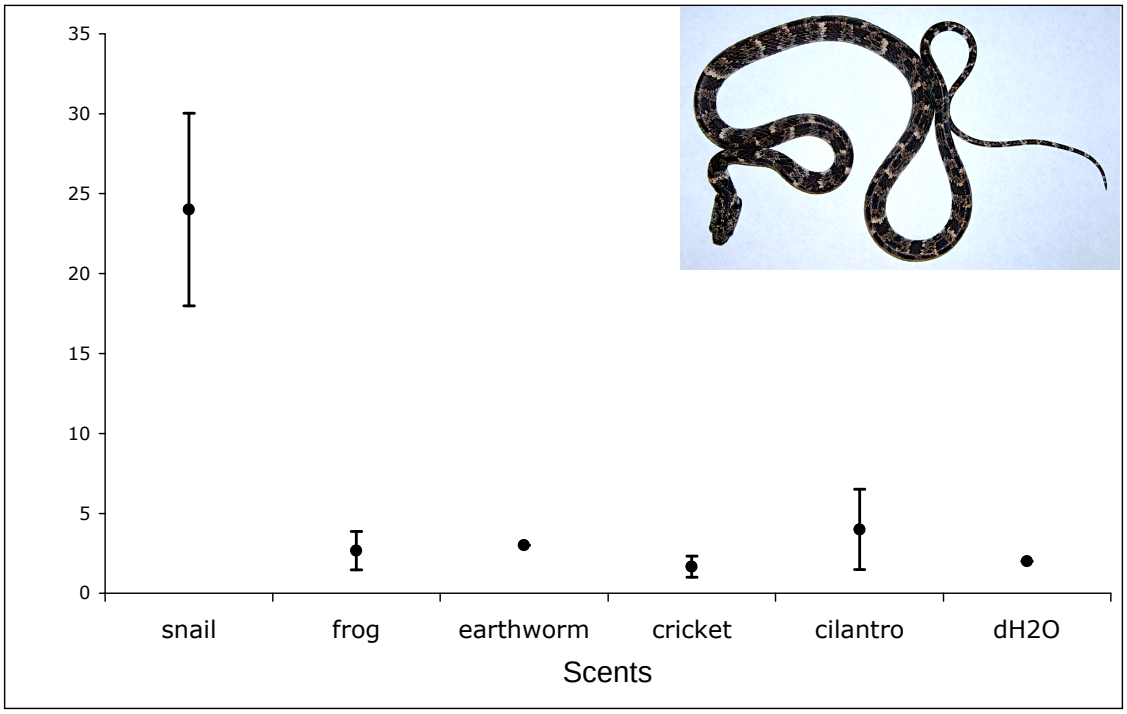

Figure 1.4 Results of ANOVA on mean maximum tongue flick rates (± SE) for *Sibon nebulatus* (n = 3) in response to various prey scents (p = 0.003). Data shown are untransformed to clearly show patterns; however, data were log transformed prior to all analyses.

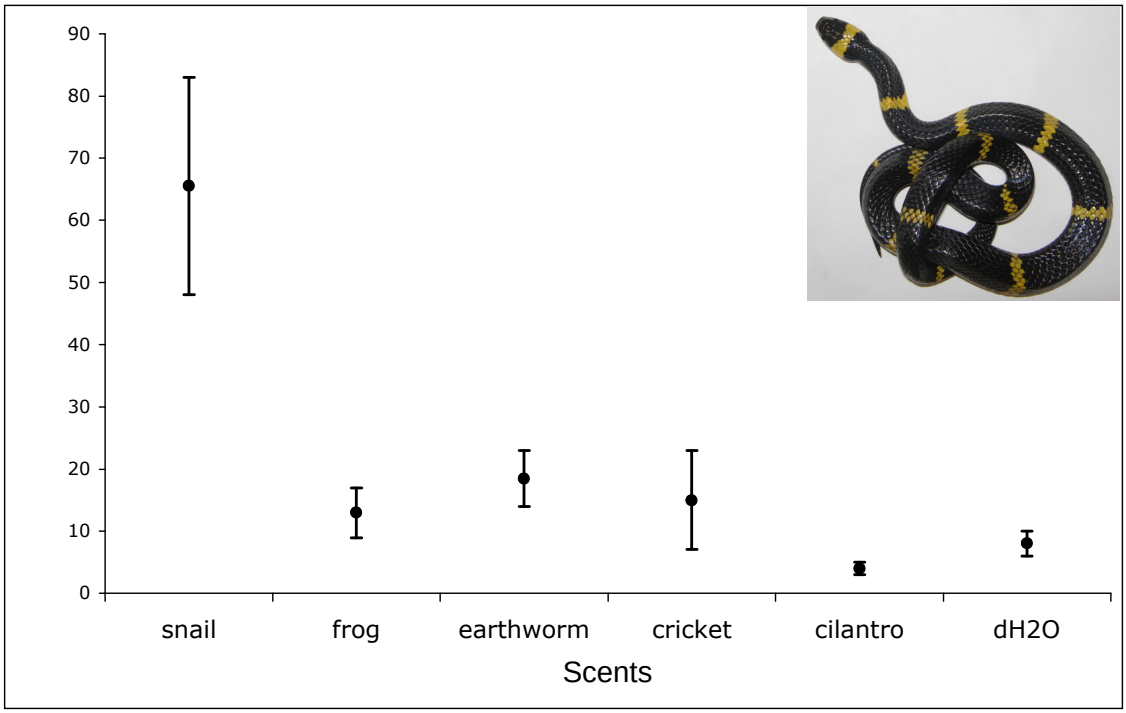

Figure 1.5 Results of ANOVA on mean maximum tongue flick rates (± SE) for *Tropidodipsas annuliferus* (n = 2) in response to various prey scents (p = 0.016). Data shown are untransformed to clearly show patterns; however, data were log transformed prior to all analyses.

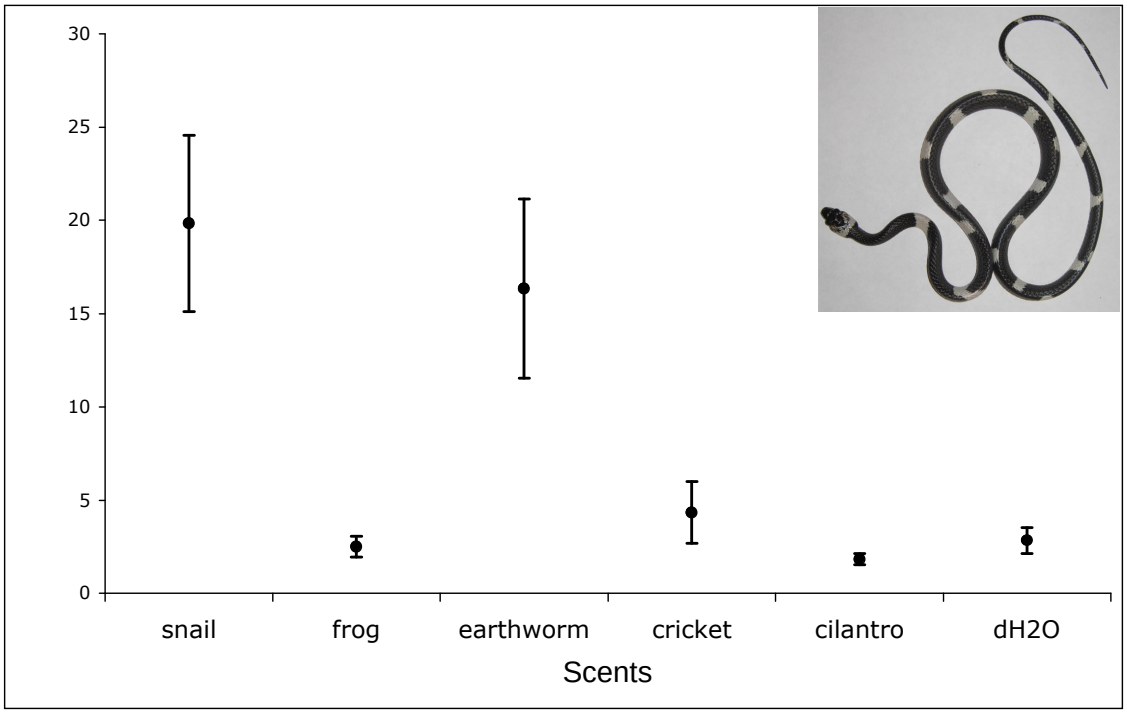

Figure 1.6 Results of ANOVA on mean maximum tongue flick rates (± SE) for *Tropidodipsas philippii* (n = 6) in response to various prey scents ($p < 0.001$). Data shown are untransformed to clearly show patterns; however, data were log transformed prior to all analyses.

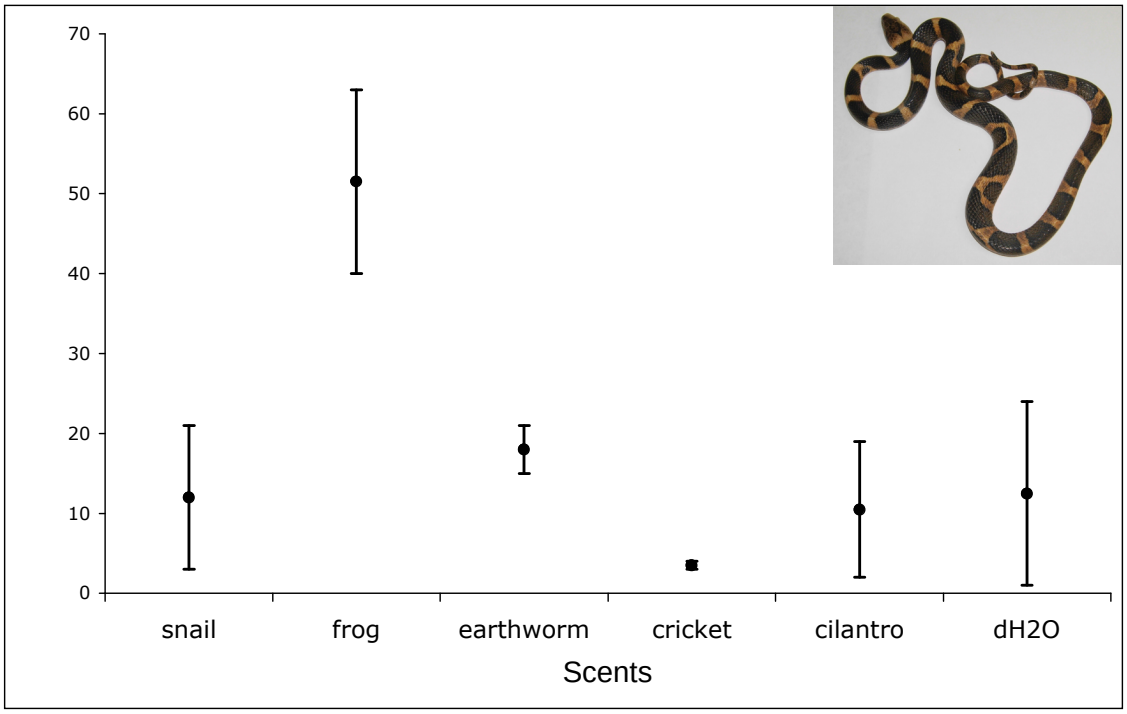

Figure 1.7 Results of ANOVA on mean maximum tongue flick rates (± SE) for *Leptodeira septentrionalis* (n = 2) in response to various prey scents ($p > 0.05$). Data shown are untransformed to clearly show patterns; however, data were log transformed prior to all analyses.

Figure 1.8 Sequence of feeding behavior by *Tropidodipsas philippii* (shown), *T. annuliferus* and *Sibon nebulatus*. Sequence involved (a) gazing at prey to identify the anterior end, (b) biting the anterior end and dragging the shell along the subtrate, (c) wedging shell or snagging shell aperture on substrate, and (d) pulling until snail is extracted. Step (c) is repeated if the shell slips from its hold.

CHAPTER 2

PHYLOGENETIC RELATIONSHIPS AMONG THE NEOTROPICAL GASTROPOD-EATING SNAKES (COLUBRIDAE: DIPSADINI)

2.1 Introduction

The superfamily Colubroidea, or "advanced snakes", is a monophyletic assemblage of diverse families and subfamilies that includes the vast majority (~2801 species, or ~83%) of all 3395 extant snake species (Lawson et al., 2005; Pyron et al., 2011; Uetz, 2012). This large clade includes seven well-supported families: Colubridae (1763 species), Elapidae (351 species), Viperidae (308 species), Lamprophiidae (303 species), Homalopsidae (44 species), Xenodermatidae (17 species), and Pareatidae (15 species) (Wiens et al., 2008; Pyron et al., 2011). Within the Colubridae, the snake subfamlies Dipsadinae (Bonaparte, 1840) and Xenodontinae (Bonaparte, 1845) appear to form a monophyletic group and together represent the largest group of colubrid snakes with ~733 species in ~92 genera (Vidal et al., 2010).

The subfamily Dipsadinae contains ~350 species in ~33 genera, and forms a large and ecologically diverse group of snakes that are distributed primarily throughout Mexico and Central America (Cadle, 1984b; Cadle and Greene, 1993). Several genera are primarily arboreal (*e.g.*, *Dipsas, Imantodes*, and *Sibon*), whereas other genera are primarily either terrestrial (*e.g.*, *Hypsiglena*, *Rhadinaea*, and *Sibynomorphus*), fossorial (*e.g.*, *Atractus* and *Geophis*), or highly aquatic (*e.g.*, *Hydromorphus* and *Tretanorhinus*). Many genera are rear-fanged and feed on vertebrates (*e.g.*, *Coniophanes*, *Leptodeira*, and *Nothopsis*), whereas many other genera lack rear fangs and feed on invertebrates (*e.g.*, *Atractus*, *Dipsas*, and *Ninia*). Although some genera are relative dietary generalists (*e.g.*, *Coniophanes* and *Leptodeira*), dietary specialization has evolved in many genera, particularly within the tribe Dipsadini (*i.e.*, *Dipsas*, *Plesiodipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*). Members of the Dipsadini, or "goo-eaters" (Cadle and Greene, 1993), feed primarily or entirely on gastropods, and many

species possess a suite of behavioral and morphological characteristics generally accepted as adaptations for extracting snails from their shells (Peters, 1960; Savitzky, 1983; see chapter 1 for a discussion of these adaptations).

The tribe Dipsadini has experienced an inconsistent nomenclatural history over the 130+ years since Cope's (1886) early attempt to organize colubrid relationships and taxonomy (see Peters [1960] and Fernandes [1995] for excellent historical reviews of dipsadine nomenclature). Dunn (1935) was one of the first authors to group members of the Dipsadini together when he recognized three clades of xenodontines: 1) *Atractus* and *Geophis*, 2) *Ninia* and *Chersodromus*, and 3) *Dipsas*, *Sibon*, and *Sibynomorphus*. Although Dunn (1935) excluded the genus *Tropidodipsas* from the third clade, he suspected that it was closely related but that it exhibited many ancestral characteristics. Romer (1958), Brongersma (1958), and Peters (1960) removed the Asiatic snail-eating snake genera from the Dipsadinae, which restricted the subfamily to include only the Neotropical genera *Dipsas*, *Sibon*, and *Sibynomorphus*. Underwood (1967) moved the subfamily Dipsadinae from the family Colubridae to the family Dipsadidae, which still contained only the genera *Dipsas*, *Sibon*, and *Sibynomorphus.* Dowling and Duellman (1978) placed the genera *Dipsas*, *Sibon*, and *Sibynomorphus* into the tribe Dipsadini, but placed *Tropidodipsas* in the tribe Alsophiini. Following the allocation of *Dipsas*, *Sibon*, and *Sibynomorphus* to the tribe Dipsadini, the definition of the subfamily Dipsadinae was subsequently expanded, and many authors now consider it to be synonymous with the "Central American xenodontines" later described by Cadle (1984a,b,c) and Cadle and Greene (1993). Several authors (*e.g.*, Jenner and Dowling, 1985; Ferrarezzi, 1994; Fernandes, 1995; Wallach, 1995; Zaher, 1999) subsequently referred to the tribe Dipsadini, although its definition has varied. Kofron (1985) synonymized *Tropidodipsas* with *Sibon* based on morphological synapomorphies. Wallach (1995) revalidated the genus *Tropidodipsas* based on characteristics of soft anatomy, and defined the Dipsadini to include *Dipsas*, *Sibon*, and *Sibynomorphus* to the exclusion of *Tropidodipsas*, although he suggested

that *Tropidodipsas* was sister to the Dipsadini due to their numerous morphological and ecological similarities. Zaher (1999) later defined the Dipsadini to include *Dipsas*, *Sibon*, *Sibynomorphus* and *Tropidodipsas*, and Cadle (2007) agreed with this definition. Most recently, Harvey et al. (2008) expanded the Dipsadini to include the newly described genus *Plesiodipsas*, which was rescued from synonymy with *Dipsas*. Thus, most researchers currently recognize the tribe Dipsadini to include five genera (*Dipsas*, *Plesiodipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*), which in turn is nested within the subfamily Dipsadinae.

Despite long-term interest in the group, relationships within the Dipsadini are largely unresolved among genera and among species within genera. In his seminal monograph on the group, Peters (1960) first revised the taxonomy of *Dipsas*, *Sibon*, and *Sibynomorphus* by assigning members of *Dipsas* and *Sibon* to species groups and by describing new species and subspecies based primarily on external morphology (*i.e.*, scalation and length) and color pattern variation. Peters (1960) divided *Dipsas* into seven species groups: the *D. articulata* group (*D. articulata*, *D. bicolor*, *D. brevifacies*, *D. gaigeae*, *D. gracilis*, *D. maxillaris*, *D. temporalis*, *D. tenuissima*, and *D. viguieri*), the *D. catesbyi* group (*D. catesbyi*, *D. copei*, *D. pavonina*, and *D. vermiculata*), the *D. indica* group (*D. indica indica*, *D. indica bucephala*, *D. indica cisticeps*, *D. indica ecuadorensis*, and *D. neivai*), the *D. oreas* group (*D. elegans*, *D. ellipsifera*, and *D. oreas*), the *D. polylepis* group (*D. longicaudata*, *D. poecilolepis*, *D. polylepis*, and *D. leucomelas*), the *D. pratti* group (*D. boettgeri*, *D. latifasciata*, *D. latifrontalis*, *D. peruana*, *D. pratti*, *D. sanctijoannis*, and *D. schunkei*), and the *D. variegata* group (*D. albifrons*, *D. incerta*, *D. variegata variegata*, *D. variegata nicholsi,* and *D. variegata trinitatis*). However, he did not divide *Sibynomorphus* into species groups, and he did not include the genus *Tropidodipsas* in his work. Harvey (2008) later revised Peters' (1960) *Dipsas* species groups based on comparisons of hemipenes, scalation, body color pattern, and soft anatomy (*i.e.*, lung morphology and inter-organ distances), and he recognized eight *Dipsas* species groups: the *D. articulata* group (*D. articulata, D. brevifacies*, D. gracilis, *D. tenuissima*, and *D. viguieri*), the *D.*

catesbyi group (*D. catesbyi*, *D. copei*, and *D. pavonina*), the *D. indica* group (*D. indica*, *D. bucephala bucephala*, *D. bucephala cisticeps*, *D. indica ecuadorensis*, *D. indica indica*, and *D. indica petersi*), the *D. incerta* group (*D. alternans*, *D. incerta*, and *D. praeornata*), the *D. oreas* group (*D. elegans*, *D. ellipsifera*, and *D. oreas*), the *D. pratti* group (*D. baliomelas*, *D. chaparensis*, *D. peruana*, *D. pratti*, *D. sanctijoannis*, and *D. schunkei*), the *D. temporalis* group (*D. pakaraima*, *D. temporalis*, and *D. vermiculata*), and the *D. variegata* group (*D. albifrons*, *D. andiana*, *D. nicholsi*, *D. trinitatis*, and *D. variegata*). Furthermore, he described a new species from Colombia, and presented a new key to South American *Dipsas*. Although Peters (1960) placed *D. gaigeae* in his *D. articulata* group, Harvey (2008) removed this species from his redefined *D. articulata* group due to numerous differences he and other authors noted between *D. gaigeae* and other members of the group (Kofron, 1982; Wallach, 1995) and considered its relationship to other *Dipsas* species unresolved. Harvey and Embert (2008) further revised the taxonomy of many South American *Dipsas*. Based on analysis of 58 morphological characters, Fernandes (1995) concluded the genus *Dipsas* to be paraphyletic with respect to *Sibynomorphus* and recommended that *Sibynomorphus* be synonymized with *Dipsas*. Similarly, Cadle (2007) concluded that the monophyly of the genus *Sibynomorphus* could not be confirmed with respect to *Dipsas*, and he noted that better taxon and character sampling is needed to test these relationships.

Smith (1982) argued that the genus *Sibon* is a masculine noun and that, according to the rules of the International Code of Zoological Nomenclature (ICZN), the specific epithet also needs to be masculine. I agree and use the masculine noun form of the specific epithet (*e.g.*, *Sibon nebulatus*, not *S. nebulata*) regardless of the feminine usage by many previous authors. Peters (1960) divided the genus *Sibon* into three species groups: the *annulatus* group (S. *annulatus*, *S. anthracops*, *S. dimidiatus dimidiatus*, *S. dimidiatus grandoculis*, and *S. sanniolus*), the *argus* group (*S. argus* and *S. longifrenis*), and the *nebulatus* group (*S. carri*, *S. dunni*, *S. nebulatus nebulatus*, *S. nebulatus hartwegi*, *S. nebulatus leucomelas*, and *S. nebulatus*

popayanensis). Kofron (1985) synonymized *Tropidodipsas* with *Sibon* based on hemipenal morphology, cranial osteology and diet, and, in a series of subsequent papers, revised several species groups of the genus *Sibon*. Kofron (1987) created the *S. fasciata* group to include *S. fasciata*, *S. philippii*, and *S. anthracops* based on external morphology, tooth counts, and scalation. The *S. sartorii* group of Kofron (1988) included *S. sartorii*, *S. annulifera*, and *S. zweifeli* based on external morphology, body pattern coloration, and tooth counts. Based on external morphology, tooth counts, and scalation, Kofron (1990) created the *S. dimidiatus* group to include *S. dimidiatus* and *S. sanniolus*, and he synonymized *S. annulatus*, *S. argus*, and *S. longifrenis* with *S. dimidiatus*. Kofron (1990) also redefined the *S. nebulatus* group to include only *S. nebulatus* and *S. dunni*. Wallach (1995) later revalidated the genus *Tropidodipsas* and noted that its members share the absence of a tracheal lung as a synapomorphy, thus assigning five species to the genus *Tropidodipsas*: *T. annulifera*, *T. fasciata*, *T. fischeri*, *T. philippii*, and *T. sartorii*. Furthermore, Wallach (1995) criticized the presumed synapomorphies Kofron (1985a) used to synonymize *Tropidodipsas* with *Sibon*, noting that they were in fact not reliable synapomorphies. Kofron (1985a) and Fernandes (1995) both recognized the uniqueness of *Tropidodipsas fischeri* and both suggested that it be placed in a new genus. Wallach (1995) considered the position *T. fischeri* to be undetermined.

Several species of *Sibon* have been described since Peters (1960) formed his three species groups. *Sibon miskitus* (McCranie, 2006) and *S. manzanaresi* (McCranie, 2007) were both described from Honduras and placed in the *S. annulatus* group as most closely related to *S. dimidiatus*. *Sibon lamari* (Solórzano, 2001) was described from Costa Rica and placed in the *S. annulatus* group. Köhler et al. (2010) described *Sibon perissostichon* from western Panama, but did not assign it to a species group presumably because of its unique dorsal scale counts. Most recently, Rovito et al. (2012) described *Sibon merendonensis* from Guatemala and placed it in the *S. annulatus* group.

The placement of the Dipsadini within the larger subfamily Dipsadinae is also unclear. Numerous authors have suggested a close relationship between the Dipsadini and the genera *Adelphicos*, *Atractus*, *Chersodromus*, *Geophis*, and *Ninia* based on morphological studies (*e.g.*, Dunn, 1935; Downs, 1967; Jenner and Dowling, 1985; Cadle and Greene, 1993; Ferrarezzi, 1994; Zaher, 1999). Several molecular studies have also suggested close relationships among these genera (*e.g.*, Cadle, 1984b; Mulcahy, 2007, Daza et al., 2009; Vidal et al., 2010; Pyron et al., 2011). However, no stable consensus has been reached. Difficulties in establishing relationships among the Dipsadini arise at least in part due to the fact that no single molecular studie has included all of these genera, and because taxon sample sizes have been very small, resulting in consistently low nodal support for relationships. These same issues have hindered progress with inferring intergeneric relationships within the Dipsadini using molecular data. Of the Dipsadini genera, Daza et al. (2009) included two *Dipsas* and one *Sibon* species, and their results supported (>95% Bayesian PP and ML bootstrap) a *Dipsas* + *Sibon* + *Ninia* clade, which was sister to *Atractus*. Vidal et al. (2010) included five *Dipsas*, two *Sibynomorphus*, and one *Sibon* species, but none of their intergeneric relationships among the Dipsadini had significant nodal support. Pyron et al. (2011) included only two *Dipsas*, one *Sibon*, and one *Tropidodipsas* species, and their results supported (75% bootstrap) only a *Dipsas* + *Sibon* + *Tropidodipsas* + *Ninia* clade. Most recently, Grazziotin et al. (2012) included six *Dipsas*, five *Sibynomorphus* and one *Sibon* species in an analysis using 246 terminal taxa and eight genes. Their results suggested that *Sibynomorphus* was paraphyletic with respect to *Dipsas* and that the Dipsadini was paraphyletic with respect to *Ninia*, but none of those intergeneric relationships had any significant nodal support.

The goals of this study are four-fold. First, I test the monophyly of the tribe Dipsadini. Second, I test whether each of the Dipsadini genera *Dipsas*, *Sibon*, *Sibynomorphus* and *Tropidodipsas* is monophyletic. Third, I test whether the *Dipsas* and *Sibon* species groups proposed by Peters (1960), and the *Dipsas* groups proposed by Harvey (2008), are supported.

Fourth, I assess whether *Tropidodipsas fischeri* should be moved into a new genus as suggested by Kofron (1985b) and Fernandes (1995).

2.2 Materials and Methods

2.2.1 Taxon Sampling

This study includes the most extensive and complete taxon sampling to date for the Dipsadini. Previous molecular studies contained three of the five genera (*Sibon*, *Dipsas* and *Sibynomorphus*), and about 16% of their species (Grazziotin et al., 2012). This study includes four of the five Dipsadini genera (*Sibon*, *Dipsas*, *Sibynomorphus* and *Tropidodipsas*) and 55% of their species (Table 2.1). More specifically, this study includes 14 of the 15 species (87%) of *Sibon*, five of the seven species (71%) of *Tropidodipsas*, 15 of the 33 species (46%) of *Dipsas*, and four of the 12 species (33%) of *Sibynomorphus*. Tissues from the recently described genus *Plesiodipsas* were not available. This study also includes multiple sequences for many species from different localities (Fig. 2.1). Two of the four *Sibynomorphus* species (*S. petersi* and *S. oligozonatus*) included represent the trans-Andian or "northern" species of Cadle (2007), whereas *S. mikanii* and *S. turgidus* represent the cis-Andian or "southern" species of Cadle (2007).

In addition to the Dipsadini, this study contains the most extensive sampling of genera in the subfamily Dipsadinae for use as outgroups, and four genera are sequenced here for the first time (*Chersodromus*, *Enuliophis*, *Rhadinophanes*, and *Synophis*). Including the five Dipsadini genera, this study contains 27 of the 33 dipsadine genera (82%) that are either assigned to the subfamily Dipsadinae or are considered Dipsadinae *incertae sedis* (Table 2.1). This study also includes multiple species for some genera (Fig. 2.1). Besides *Plesiodipsas*, the only six dipsadine genera not included in this study are *Diaphorolepis*, *Emmochliophis*, *Omoadiphas*, *Psomophis* and *Taeniophallus*.

To test the monophyly of the subfamily Dipsadinae, representatives of the subfamily Carphophiinae as defined by Zaher et al., (2009) (*Carphophis*, *Contia*, *Diadophis*, *Farancia*, and

Heterodon) were included, along with representatives of the subfamilies Colubrinae (*Coluber* and *Drymobius*), Elapinae (*Micrurus*), Natricinae (*Natrix* and *Thamnophis*), and Xenodontinae (*Alsophis*, *Arrhyton*, *Conophis*, *Helicops*, *Hydrops*, *Oxyrhopus*, *Phalotris*, *Xenodon*, and *Xenoxybelis*). The tree was rooted with a crotaline (*Crotalus tigris*).

2.2.2 Gene Sampling

The data matrix generated in this study includes up to two mitochondrial (ND4 + tRNAs and cyt-b) and two nuclear (NT3 and DNAH3) genes for 194 taxa and up to 3241 base pairs. Five loci were used: (1) a 714 base pair fragment of the mitochondrial NADH dehydrogenase subunit 4 (ND4), (2) a 199 base pair fragment of tRNAs His, Ser and Leu, (3) a 1071 base pair fragment of the mitochondrial cytochrome-b gene (cyt-b), (4) a 525 base pair fragment of the nuclear protein-coding neurotrophin-3 (NT3) gene, and (5) a 732 base pair fragment of the nuclear protein-coding dynein, axonemal, heavy chain 3 (DNAH3) gene (see Table 2.2 for primers used). Sequencing coverage was more complete for the mitochondrial markers than for the nuclear markers. An effort was made to, at a minimum, sequence all individuals for the two mitochondrial genes, each species from different localities for NT3, and each different species from one locality for DNAH3 (Table 2.1). The resulting matrix had 32% missing characters, many of which were associated with the second and third tRNAs Ser and Leu as the ND4 primers tapered off. The genes NT3 and DNAH3 were used because they were each previously screened and represent potentially informative, single-copy, unlinked loci that are likely evolving at different rates (NT3 faster than DNAH3) (Townsend et al., 2008).

2.2.3 Molecular Data

Genomic DNA was isolated from tissues using a Qiagen DNeasy kit (Qiagen, Valencia, California, USA). All amplification reactions used GoTaq® Green Master Mix, 2X (Promega Corporation, Madison, Wisconsin, USA). Thermal cycling was performed on a GeneAmp® PCR System 9700 machine (Applied BioSciences, Foster City, California, USA). The ND4 + tRNA fragments were amplified using an initial 5 min denaturation cycle at 95℃, followed by 30s

denaturing at 94℃, 45s annealing at 52℃ and 1 min extension at 72℃ for 38 cycles, and a final 5 min extension at 72℃. The cyt-b fragments were amplified using an initial 2 min denaturation cycle at 95℃, followed by 30s denaturing at 94℃, 30s annealing at 53℃ and 1 min 15s extension at 72℃ for 2 cycles, followed by 30s denaturing at 94℃, 30s annealing at 52℃ and 1 min 15s extension at 72℃ for 3 cycles, followed by 30s denaturing at 94℃, 30s annealing at 51℃ and 1 min 15s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 50℃ and 1 min 15s extension at 72℃ for 30 cycles, followed by a 7 min extension at 72℃. The NT3 and DNAH3 fragments were amplified using an initial 1 min 30s denaturation cycle at 94℃, followed by 30s denaturing at 94℃, 30s annealing at 51℃ and 1 min 30s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 50℃ and 1 min 30s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 49℃ and 1 min 30s extension at 72℃ for 10 cycles, followed by 30s denaturing at 94℃, 30s annealing at 48℃ and 1 min 30s extension at 72℃ for 30 cycles, followed by a 7 min extension at 72℃. PCR product was quantified by visualization on 1% agarose gel stained with ethidium bromide. Successfully amplified PCR products were prepared for sequencing by using the ExoSAP-IT kit (United States Biochemical). A BigDye Terminator Cycle Sequencing Kit (Applied Biosystems Inc.) was used for sequencing following the manufacturer's protocol and using PCR primers. The sequenced products were precipitated using an ethanol/sodium acetate method and rehydrated in HPLC purified formamide (HIDI). The sample was then analyzed on an ABI PRISM 3100xl Genetic Analyzer in the Genomics Core Facility at the University of Texas at Arlington, USA.

Alignments were constructed using the program Sequencher 4.8 (Gene Codes, Ann Arbor, Michigan, USA), and edited by eye using the program MacClade 4.08 (Maddison and Maddison, 2005). The tRNAs were aligned using an annotated mitochondrial genome for *Sibon nebulatus* (GenBank EU728583) as a template sequence. Uncorrected percent pairwise distances were generated in MEGA 5 (Tamura et al., 2011).

2.2.4 Phylogenetic Analyses

Phylogenetic analyses were conducted using Maximum Likelihood (ML), Parsimony, Bayesian, and distance (Neighbor Joining, or NJ) methods on the data matrix consisting of 194 taxa and up to 3241 base pairs. Various models of molecular evolution were tested using the software package MEGA 5 (Tamura et al., 2011) on the complete alignment partitioned by gene fragment (seven partitions: ND4, cytb, tRNA His, tRNA Ser, tRNA Leu, NT3, and DNAH3). The model test results identified GTR+I+G and GTR+G as among the best-fit models of nucleotide substitution for each gene fragment based on corrected Akaike Information Criterion (AICc), although they did not always receive the best scores. The ML analyses employing the rapid bootstrapping algorithm were conducted using the program RAxML 7.3.0 (Stamatakis, 2006) on the CIPRIS Science Gateway server v3.2 (Miller et al., 2010) using the model GTR+G instead of GTR+I+G because the 25 discrete rate categories appear to better estimate invariant sites (Stamatakis, 2006). The multiple alignment was partitioned by gene region (five partitions: ND4, cytb, tRNAs, NT3, DNAH3), which allowed RAxML to calculate and apply the most appropriate gamma distribution parameter to each partition separately. Nodal support for ML was provided by rapid bootstrapping (1000 pseudoreplicates), with bootstrap values ≥0.70 considered strong support (Hillis and Bull, 1993).

Bayesian analyses were conducted with the computer program MrBayes (Huelsenbeck and Ronquist, 2001) on a partitioned alignment using the reversible-jump Markov chain Monte Carlo algorithm (mixed model), which avoids the risk of acquiring misleadingly high posterior probabilities at the nodes of hard or nearly hard polytomies due to their arbitrary resolution (Lewis et al., 2005). Each of the four protein coding genes in the alignment was partitioned by codon position with one partition including the first and second positions and another including the third position for a total of nine partition schemes (the three tRNAs were not partitioned). Two independent runs were conducted simultaneously with four Markov chains (three heated and one cold) per run, and average standard deviation of the split frequencies below 0.01 was

considered acceptable. Stationarity was determined to be reached visually using Tracer v1.5 (Rambaut and Drummond, 2009). The analysis ran for 17,000,000 generations while sampling trees every 1000 generations. Stationarity was reached after approximately 11,500,000 generations, after which the stanard deviation of the split frequencies dropped to 0.008. Therefore, I sampled the resulting 5000 trees from from the last 5 million generations (12–17 million generations), which should be a good representation of the posterior distribution of trees. The initial 12 million generations were discarded as burn-in, and a 50% majority rule consensus tree with estimates of Bayesian support was constructed using the remaining sampled trees. Posterior probabilities (PP) provided nodal support for Bayesian analyses, with PP values ≥0.95 considered strong support (Alfaro et al., 2003; Huelsenbeck and Rannala, 2004; Mulcahy et al., 2011).

I conducted a weighted parsimony (WP) analysis using a tri-level weighting scheme that incorporated three different levels of information on the structure and inferred function of nucleotide substitutions (Benabib et al., 1997; Flores-Villela et al., 2000; Jadin et al., 2011). Transitions were given a weight of 1, transversions were given a weight of 2, and any nucleotide substitution that caused an amino-acid substitution was weighted +1 more (Kjer et al., 2007; Jadin et al., 2011).

Parsimony (UP and WP) analyses were conducted in the program TNT (Goloboff et al., 2008). Distance (NJ) analyses were performed in PAUP* (Swofford, 2002). Nodal support for UP and WP was provided by bootstrap ratcheting using the New Technology algorithm (2000 pseudoreplicates). Because all four analyses produced similar tree topologies, only the ML tree is shown with support values for ML, WP, and Bayesian analyses (Fig. 2.2).

2.3 Results

The ML analysis resulted in a best likelihood score of -63458.181332. The unweighted parsimony analysis resulted in five equally parsimonious trees with a length of 14,527. The weighted parsimony analysis resulted in five equally parsimonious trees with a length of 20,615.

Bayesian posterior probability support values ≥95 almost always corresponded to ML bootstrap support values ≥70. Parsimony and distance methods did not strongly support any relationships not strongly supported on the Bayesian tree. However, the WP tree contained more strongly-supported clades than the UP tree, and both parsimony trees contained more strongly-supported clades than the NJ tree. Figure 2.2 shows the best ML tree for the Dipsadini.

2.3.1 Phylogenetic Relationships and Nodal Support

2.3.1.1 Monophyly of the Tribe Dipsadini

Nodal support is presented as posterior probabilities/ML bootstrap/weighted parsimony bootstrap/unweighted parsimony bootstrap/NJ bootstrap for nodes with posterior probabilities ≥ 80% and for bootstrap support ≥ 50%. A dash (-) denotes support below the cutoff value. The paraphyly of the tribe dipsadini with respect to the genus *Geophis* was strongly supported by Bayesian and ML analyses, but not by Parsimony or NJ analyses (94/86/58/-/-) (Fig. 2.2). A clade consisting of *Ninia* + *Chersodromus* as sister to the Dipsadini + *Geophis* clade was strongly supported (95/99/97/78/-). Sister to the *Ninia* + *Chersodromus* + Dipsadini + *Geophis* clade was the genus *Atractus* (95/87/68/-/-). Sister to all of these taxa, but with medium support (89/64/60/-/-), was a well-supported clade consisting of *Adelphicos* and *Cryophis* (100/86/70/-/74).

2.3.1.2 Monophyly of the Dipsadini Genera

The monophyly of the genus *Sibon* was strongly supported by the Bayesian analysis (100/-/-/-/-). However, the placement of *S. sanniolus* was not supported by any analyses and remains unresolved (Fig. 2.2). To the exclusion of *D. gaigeae*, a paraphyletic *Dipsas* clade with respect to *Sibynomorphus* was strongly supported (95/99/94/60/-). *Dipsas gaigeae* was monophyletic but did not group with other *Dipsas* in any analyses and its placement remains unresolved. The genus *Sibynomorphus* was paraphyletic with respect to *Dipsas,* but with low support. *Sibynomorphus mikanii* was always sister to *S. turgidus* (100/100/100/96/-), and *S.*

petersi was always sister to *S. oligozonatus* (100/100/100/94/72); however, the two *Sibynomorphus* clades were never sister to each other. The genus *Tropidodipsas* was paraphyletic and formed three clades: 1) a *T. philippii* + *T. fasciata* clade (100/96/87/67/-), 2) a *T. sartorii* + *T. annuliferus* + *Geophis* clade (97/68/58/-/-), and 3) a monophyletic *T. fischeri* clade (100/100/99/99/100). *Tropidodipsas sartorii* (100/100/99/98/84), *T. annuliferus* (100/100/99/99/100), and the genus *Geophis* (100/64/-/-/89) were each monophyletic. However, relationships among *Tropidodipsas sartorii*, *T. annuliferus*, and *Geophis* were not supported and remain unresolved. A clade sister to the *T. philippii* + *T. fasciatus* represent an undescribed species (100/95/93/94/-) (Fig. 2.2).

2.3.1.3 Relationships Among the Dipsadini

Sibon nebulatus forms a strongly-supported monophyletic group (100/100/100/87/-). Within the *S. nebulatus* clade, two distinct clades are well supported: 1) a South American clade from Colombia, Ecuador, Panama and Trinidad (100/100/99/99/-), and 2) a Central American clade from Guatemala, Honduras, Mexico, and Nicaragua (100/100/100/99/-). Sister to *S. nebulatus* is *S. anthracops* (100/93/79/-/-). Sister to *S. nebulatus* + *S. anthracops* is a clade containing *S. dimidiatus*, *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* (100/96/97/57/-). The *S. dimidiatus*, *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* clade is a strongly-supported monophyletic group, with *S. dimidiatus* basal to the clade and paraphyletic with respect to *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* (100/100/100/99/100). *Sibon annulatus*, *S. lamari*, and *S. perissostichon* form a monophyletic group (100/100/100/99/53). However, *S. annulatus* is paraphyletic with respect to *S. lamari* (100/98/93/67/-), and *S. perissostichon* (100/97/95/73/-). A clade with *S. carri* sister to the *S. annulatus* + *S. lamari* + *S. perissostichon* clade was only supported by the Bayesian analysis (99/-/-/-/-). *Sibon argus* and *S. longifrenis* form a well-supported clade (100/100/100/99/99). Although Bayesian and ML analyses placed the *S. argus* + *S. longifrenis* clade sister to the *S. carri* + *S. annulatus* + *S. lamari* + *S. perissostichon* clade, neither had significant nodal support (73/22, respectively).

Both Bayesian and ML analyses place *Tropidodipsas* as sister to *Sibon*, but without support. However, the genus *Tropidodipsas* was not monophyletic. The *T. philippi* + *T. fasciata* clade was ladderized and generally correlated with a south to north trend, with the most basal members being from Oaxaca followed next by Guerrero, Nayarit, Sinaloa, Michoacan and Colima.

The genus *Dipsas* was sister to the rest of the Dipsadini with strong support in the Bayesian and ML analyses (94/86/-/-/-). However, *Dipsas* was paraphyletic with respect to *Sibynomorphus*. *Dipsas nicholsi* and *D. andiana* were sister taxa (100/100/100/99/-), and were sister to a clade containing *D. temporalis*, and a *Sibynomorphus oligozonatus* + *S. petersi* clade (98/51/-/-/-). *Dipsas variegata* from Venezuela and Suriname were sister to *D. trinititis* (98/100/100/100/-), which were sister to *D. vermiculata* (94/57/-/-/100). *Dipsas bicolor* and *D. articulata* form sister taxa (100/100/100/99/64), which were sister to *D. gracilis* (100/99/100/96/50). *Dipsas catesbyi* was paraphyletic with respect to *D. pavonina* (100/100/100/100/100), and this clade was sister to *D. peruana* in Bayesian, ML and WP analyses but without support. *Dipsas pratti* from Colombia and Venezuela formed sister taxa, but it formed a polytomy with other *Dipsas* clades rendering its placement unresolved. The placement of the *Sibynomorphus mikanii* + *S. turgidus* clade remains unresolved within *Dipsas* due to poor support. However, this clade never formed a clade with the other *Sibynomorphus*, with or without support.

2.4 Discussion

These results strongly support a paraphyletic Dipsadini with respect to *Geophis*, suggesting that the genus *Geophis* should be added to the tribe Dipsadini. With *Geophis* included, the Dipsadini is a strongly-supported monophyletic group. Given that *Tropidodipsas fasciata* is the type species for the genus, the generic name stays with that clade, which includes *T. philippii*. *Tropidodipsas sartorii* and *T. annuliferus* form a monophyletic group with *Geophis*. The *Geophis* species included in this study belong to the *G. omiltemanus* and *G.*

chalybeus groups and thus include true *Geophis* given that *G. chalybeus* is the type species (Downs, 1967). Therefore, *T. sartorii* and *T. annuliferus* need to be assigned to new genera given the relatively old age of the divergences among these three species. The *Tropidodipsas fischeri* appears to be distinct from other *Sibon* and *Tropidodipsas* species and likely needs to be placed into a new genus. Additional characters and faster-evolving molecular markers (*e.g.*, microsatellites) might help resolve the extremely shallow internal branches of this taxon to aid in identifying its sister taxa.

Bayesian analyses supported a monophyletic *Sibon*, and most species appear to be valid. However, several taxonomic issues need to be resolved within this genus. *Sibon annulatus*, *S. argus*, and *S. longifrenis* are all well-supported and valid species and should not be synonymized with *S. dimidiatus* as proposed by Kofron (1990). A well-supported clade containing *S. dimidiatus*, *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* renders *S. dimidiatus*, *S. manzanaresi* and *S. miskitus* paraphyletic. Additionally, there are extremely shallow divergences among all four species (<1.0% mtDNA), suggesting that these represent a single species. Therefore, because *Sibon dimidiatus* is basal to the group and the first of the four to be described, I recommend that *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* be synonymized with *S. dimidiatus*. The authors who described *S. manzanaresi*, *S. merendonensis*, and *S. miskitus* all recognized many similarities these species share with *S. dimidiatus*. Although their synonymy will decrease the number of species in the genus *Sibon*, it will increase our understanding of the phenotypic and ecological variation in S. *dimidiatus*. This species appears to have recently undergone, or is currently undergoing, an adaptive radiation. Further phylogenetic and ecological studies of this recent radiation might help shed new light on the processes that lead to other older speciation events within the Dipsadini.

Sibon annulatus is rendered paraphyletic due to *S. lamari* and *S. perissostichon*. The type locality of *S. annulatus* is in Costa Rica near Catago (Günther, 1872), which would reserve the name for the Costa Rican *S. annulatus* clade sister to *S. perissostichon*. The Panamanian

S. annulatus clade sister to *S. lamari* might therefore need to be described as a new species. Although this might be appropriate, further morphological and molecular data on these three species from throughout their ranges are needed to support making this taxonomic change instead of synonymyzing *S. lamari* and *S. perissostichon* with *S. annulatus*. *Sibon annulatus* ranges from Honduras (McCranie, 2011) south to Colombia (Moreno-Arias, 2010) and likely Ecuador (Paul S. Hamilton, Pers. Comm.). Therefore, a more thorough analysis of the variation within this species from throughout more of its range is needed before the implementation of taxonomic changes can be justified.

The two *Sibon nebulatus* clades (South American and Central American) appear to be separated somewhere in Costa Rica or northern Panama. Tissues from these regions are needed to identify the boundaries to the two clades, which may be two different species.

Using 58 morphological, glandular, and myological characters, Fernandes (1995) suggested that the genus *Dipsas* is paraphyletic with respect to *Sibynomorphus*. My results also suggest that the genus *Sibynomorphus* is deeply nested within *Dipsas* rendering *Dipsas* paraphyletic, and a *Dipsas* + *Sibynomorphus* clade is strongly-supported. The two *Sibynomorphus* clades are more closely related to various *Dipsas* species than they are to each other, suggesting that *Sibynomorphus* is also paraphyletic. The two well-supported *Sibynomorphus* clades in this study correspond with the "northern" (*S. oligozonatus* and *S. petersi*) and "southern" (*S. mikanii* and *S. turgidus*) clades identified by Cadle (2007), with *S. oligozonatus* and *S. petersi* (both from Ecuador) consistently grouping separately from *S. mikanii* (from Brazil) and *S. turgidus* (from Bolivia). Therefore, in order to maintain a monophyletic *Dipsas*, I recommend that the genus *Sibynomorphus* be synonymized with the genus *Dipsas*. The two *Sibynomorphus* clades recovered are consistent with the widely disjunct (~1500 km minimum straight line distance) *cis*- and *trans*-Andean distribution of *Sibynomorphus* (Cadle, 2007), which suggests that members of its two disjunct clades may

have evolved terrestrial ecologies convergently from arboreal *Dipsas* ancestors. Ancestral state reconstruction analyses could be useful in testing this hypothesis.

2.4.1 Species Groups in the Dipsadini

2.4.1.1 *Sibon*

Peters (1960) proposed three species groups for members of the genus *Sibon*. Based on the results of this study, I propose three well-supported *Sibon* species (*S. anthracops*, *S. carri* and *S. dimidiatus* [*sensu stricto*]) and three well-defined species groups: a *S. nebulatus* group (*S. nebulatus* composed of two distinct South American and Central American clades), a *S. annulatus* group (*S. annulatus*, *S. lamari*, and *S. perissostichon*), and a *S. argus* group (*S. argus* and *S. longifrenis*). *Sibon sanniolus* is a well-supported species, but groupings with other *Sibon* species were not supported in any analyses. Therefore, I consider the placement of this seemingly highly-diverged species to be unresolved and unassigned to any group. I was unable to acquire tissues from *S. dunni*; thus, the placement of this rare South American species is currently unknown.

Numerous authors have posited close relationships between *S. dimidiatus* and *S. annulatus* based on similar lepidosis, morphology, and coloration. Peters (1960) placed *S. dimidiatus* in his *S. annulatus* group, and Kofron (1990) later synonymized *S. annulatus* with *S. dimidiatus*. Furthermore, several recently-described species have been assigned to the *S. annulatus* group of Peters (1960) with proposed close relationships to *S. dimidiatus* (*e.g.*, McCranie, 2006, 2007; Rovito et al., 2012). However, analysis of molecular data does not support a close relationship between these two species. *Sibon annulatus* and *S. dimidiatus* typically share a single postmental scale (but not always), and a similar body shape and color pattern, which are likely responsible for their proposed close relationships. However, molecular data strongly suggest that these characters are not synapomorphies but rather the result of convergence.

Sibon argus, *S. lamari*, and *S. longifrenis* all have a similar body coloration consisting of dark-reddish blotches on a mossy-green background, and it has been proposed that this pattern mimics that of the green-phased arboreal eyelash pitviper, *Bothriechis schlegelii* (Solórzano, 2001). However, the molecular data suggest that this color pattern has evolved at least twice independently, once in *S. lamari* and once in the *S. argus* + *S. longifrenis* clade. This convergence supports the hypothesis that this color pattern is likely adaptive, and that it could be involved in mimicry.

2.4.1.1 *Dipsas*

This study contains representatives of all seven of Peters' (1960) species groups except his *D. polylepis* group. Of the eight species groups proposed by Harvey (2008), this study contains all but the *D. incerta* and *D. oreas* groups. Peters (1960:92) synonymized *D. andiana* with *D. oreas*. However, *D. andiana* was revalidated by Cadle and Myers (2003).

The molecular data in this study suggest that *Dipsas catesbyi* and *D. pavonina* are closely related, but a larger sample size is necessary to ascertain whether *D. pavonina* is a valid species or whether it should be synonymized with *D. catesbyi*. These two species were previously grouped based on similar body pattern (Peters, 1960), by similar head pattern, and by having a snout-heart interval greater than 40% (Harvey, 2008). Peters (1960) also included *D. vermiculatus* in his *D. catesbyi* group; however, molecular data place this species as sister to the *D. variegata* + *D. trinitatis* and not sister to *D. catesbyi* + *D. pavonina*. I was not able to obtain tissues of *D. copei*, which both Peters (1960) and Harvey (2008) also place within their *D. catesbyi* groups.

A *Dipsas articulata* + *D. bicolor* clade was sister to *D. gracilis*, suggesting that these three closely related species form a group more similar to the revised *D. articulata* group proposed by Harvey (2008) than by Peters' (1960) original definition. Peters (1960) also included *D. gaigeae* and *D. brevifacies* within his *D. articulata* group; however, Harvey (2008) excluded *D. gaigeae* from his revised *D. articulata* group to "emphasize its distinctiveness". The

results of the molecular data corroborate the distinctiveness of *D. gaigeae* and support the exclusion of this species from the *D. articulata* group. Although *D. gaigeae* and *D. brevifacies* represent the two northernmost members of the genus, Kofron (1982) noted many differences between these two species. However, I was not able to obtain tissues from *D. brevifacies* in order to test this hypothesis.

The molecular analyses identified *Dipsas variegata* and *D. trinitatis* as sister taxa, which were sister to *D. vermiculata*. *Dipsas andiana* and *D. nicholsi* also formed a strongly-supported clade. However, this clade was not sister to the *D. variegata* + *D. trinitatis* clade, which is surprising given that *D. andiana* and *D. nicholsi* were previously considered subspecies of *D. variegata* (Peters, 1960). Although *D. andiana* and *D. nicholsi* have widely disjunct distributions (Ecuador and central Panama, respectively), similarities in morphology and head pattern led Cadle and Myers (2003) to consider these species to be sister taxa. My results corroborate the conclusion that these two species are sister taxa. *Dipsas trinitatis* was also considered to be a subspecies of *D. variegata* before Harvey and Embert (2008) elevated it to full species based on morphological distinctiveness and allopatry. The molecular data support the conclusion that *D. trinitatis* deserves full species status and that it is sister to *D. variegata*.

Peters (1960) placed *D. vermiculata* in his *D. catesbyi* group, and Harvey (2008) placed *D. vermiculata* in his *D. temporalis* group. However, the results of the molecular analyses placed *D. vermiculata* as sister to the *D. variegata* + *D. trinitatis* clade. *Dipsas temporalis* from Panama and Colombia formed sister taxa, which were sister to a *Sibynomorphus oligozonatus* + *S. petersi* clade but with low support. However, a clade containing *D. temporalis* + (*D. andiana* + *D. nicholsi*) + (*Sibynomorphus oligozonatus* + *S. petersi*) is strongly supported.

The molecular data suggest that *Dipsas indica*, *D. peruana*, and *D. pratti* are all distinct species within the well-supported *Dipsas* (*sensu stricto*) clade. However, the nodal support was too low to identify any group affinities among these three species with any confidence. In addition, I was unable to acquire tissues from members of the *D. oreas* and *D. incerta* groups

proposed by Harvey (2008), thus I was not able to test these groupings. Nonetheless, the results of the molecular data suggest that the species of *Dipsas* included in this study can be organized into roughly eight species groups: a *D. catesbyi* group (*D. catesbyi* and *D. pavonina*), a *D. variegata* group (*D. variegata*, and *D. trinitatis*), a *D. vermiculata* group (*D. vermiculata*), a *D. indica* group (*D. indica*), *D. temporalis* group (*D. temporalis*), a *D. nicholsi* group (*D. andiana* and *D. nicholsi*), a *D. articulata* group (*D. articulata*, *D. bicolor*, and *D. gracilis*), and a *D. pratti* group (*D. pratti*). However, more complete taxon sampling is needed for more accurate assessment of species groups within the genus *Dipsas*. Although the placement of *D. gaigeae* received nodal support below my cutoff values, this distinct species never grouped with other *Dipsas* in any of the molecular analyses and therefore should be placed into a new genus.

Although numerous authors have suggested a close relationship between the Dipsadini and the genera *Adelphicos*, *Atractus*, *Chersodromus*, *Geophis*, and *Ninia* (*e.g.*, Dunn, 1935; Downs, 1967; Cadle, 1984b; Jenner and Dowling, 1985; Cadle and Greene, 1993; Ferrarezzi, 1994; Zaher, 1999; Mulcahy, 2007, Daza et al., 2009; Vidal et al., 2010; Pyron et al., 2011), no stable consensus regarding their intergeneric relationships has been reached. However, the molecular data in this study provide well-supported intergeneric relationships among these genera. The genera *Ninia* and *Chersodromus* form a clade that is sister to the Dipsadini. Sister to the Dipsadini + (*Ninia* + *Chersodromus*) clade is *Atractus*, and sister to that entire clade is a *Cryophis* + *Adelphicos* clade.

The results of this study highlight how misleading aspects of lepidosis and color pattern alone have been in establishing stable taxonomic relationships among the Dipsadini, especially in the genus *Sibon*. Extensive variation in some species (*e.g.*, *Sibon dimidiatus*) has been interpreted as representing multiple full species, whereas similarities in these characteristics have been interpreted as representing common ancestry between some species (*e.g.*, *Sibon annulatus* and *S. dimidiatus*). Studies incorporating morphology (*e.g.*, teeth counts, hemipenial morphology, and skull morphology) provided an improvement (*e.g.*, Kofron, 1982, 1985a,

1985b). However, the results of the molecular data most closely agreed with studies including additional morphological characters such as internal viscera (*e.g.*, Wallach, 1995; Harvey, 2008), corroborating that these characters are taxonomically informative with the Dipsadini.

Table 2.1 Specimen information and GenBank accession numbers for 194 OTUs used in this study. Sequences added specifically in this study are indicated in bold.

Taxa	Locality	Voucher[a]	Latitude	Longitude	ND4	cyt-b	NT3	DNAH3
Adelphicos quadrivirgatus	Guatemala: Huehuetenango	UTA R-44724	15.8863333	-91.2455	**JX398446**	**JX398598**	**JX398728**	**JX293836**
Alsophis portoricensis	USA: Puerto Rico	No voucher	18.187408	-66.565711	U49308	AF471085		
Amastridium veliferum	Guatemala: Izabal	UTA R-46905	15.765504	-89.376523	GQ334580	GQ334479	GQ334663	GQ334557
Arrhyton exiguum	USA: Puerto Rico	CAS 200732	18.187408	-66.565711		AF471071		
Atractus elaps	Peru: Madre de Dios	KU 214837	-12.583333	-69.083333	EF078584	EF078536		
Atractus trilineatus	Brazil: Roraima	LSUMZ-H 12441	2.737597	-62.0751	**JX398447**	**JX398599**	**JX398731**	**JX293837**
Atractus trilineatus	Tobago: Cambleton	UWIZM.2011.19.11	11.312453	-60.547636	**JX398448**	**JX398600**		
Atractus wagleri	Colombia: Antioquia	MHUA 14368	6.26425	-75.56944	GQ334581	GQ334480	GQ334664	GQ334558
Carphophis amoenus	USA: Illinois	CAS 160710	40.277403	-89.044225		AF471067		
Carphophis vermis	USA: North Carolina	MVZ 137554	35.7474	-78.5793	**JX398449**	**JX398602**	**JX398729**	**JX293838**
Chapinophis xanthochilus	Guatemala: Baja Verapaz	UTA R-37591	15.07875	-90.412517	**JX398450**	**JX398603**	**JX398730**	**JX293838**
Chersodromus liebmanni	Mexico: Oaxaca: Totontepec	ANMO 2298	17.242972	-96.029586	**JX398451**	**JX398604**	**JX398732**	**JX293840**
Coluber constrictor	USA: California	CAS 212760; SDSU 3929	36.778261	-119.417931	AY487041	EU180467	EU390914	EU402743
Coniophanes fissidens	Guatemala: San Marcos	UTA R-46544	14.940833	-92.031667	**JX398452**	**JX398605**	**JX398733**	**JX293841**
Conophis lineatus	Guatemala: Zacapa	UTA R-46849	14.88383333	-89.7755		**JX398606**	**JX398739**	**JX293842**
Contia tenuis	USA: California	CAS 224886	36.083833	-118.602917	DQ364664	GU112398		
Crotalus tigris	USA: Arizona: Pima Co.	CLP 169	32.837161	-109.831578	AF156574	AY223606		
Cryophis hallbergi	Mexico: Oaxaca	UTA R-12272	17.604025	-96.377994	GQ334582	GQ334481	GQ334666	GQ334559
Diadophis punctatus	USA: Oklahoma	UTA R-55882	34.01117	-97.04543	**JX398484**	**JX398633**	**JX398755**	**JX293860**
Dipsas andiana	Ecuador: Los Ríos	JM[a] 79	-1.8	-79.53	**JX398453**	**JX398607**	**JX398744**	**JX293843**
Dipsas articulata	Costa Rica: Limon-Uatsi	D161	9.614186	-82.887603	**JX398454**		**JX398740**	
Dipsas bicolor	Costa Rica: Guayacan de Siquirres	ASL 277	10.064456	-83.543319	**JX398455**		**JX398741**	**JX293844**
Dipsas catesbyi	Ecuador: Napo	ENS 13477	-1.046868	-77.776923	**JX398456**	**JX398608**		
Dipsas catesbyi	Ecuador: Tungurahua: El Topo	UTA R-55949	-1.41436	-78.20743	**JX398457**	**JX398609**	**JX398742**	**JX293845**
Dipsas catesbyi	Ecuador: Tungurahua: El Topo	UTA R-55974	-1.38622	-78.19625	**JX398458**	**JX398610**	**JX398743**	**JX293846**
Dipsas catesbyi	Peru: Madre de Dios	KU 214851	-12.583333	-69.083333	EF078537	EF078585		
Dipsas catesbyi	Peru: Madre de Dios	WED 59073	-12.583333	-69.083333	**JX398459**	**JX398611**	**JX398745**	**JX293847**
Dipsas gaigeae	Mexico: Colima	JAC 28000	19.284	-104.15847	**JX398460**			**JX293848**
Dipsas gaigeae	Mexico: Colima	JAC 28327	19.04969	-103.78654	**JX398461**	**JX398612**		**JX293849**
Dipsas gaigeae	Mexico: Colima	JAC 28587	19.07346	-103.77519	**JX398462**	**JX398613**	**JX398735**	**JX293850**
Dipsas gaigeae	Mexico: Colima	JAC 30511	19.01993	-103.76609	**JX398463**			
Dipsas gaigeae	Mexico: Guerrero	JRV 30	17.7583	-101.529	**JX398464**	**JX398614**	**JX398738**	**JX293851**
Dipsas gracilis	Colombia: Cesar	ICN 12019	7.950556	-73.349444	**JX398465**	**JX398615**	**JX398746**	**JX293852**

Table 2.1 *Continued*

Dipsas gracilis	Ecuador: Esmeraldas	UTA R-55943	1.18333	-78.75349	**JX398466**	**JX398616**	**JX398747**	**JX293853**
Dipsas gracilis	Ecuador: Esmeraldas	UTA R-55944	1.18333	-78.75349	**JX398467**	**JX398617**	**JX398748**	
Dipsas indica	Peru: Madre de Dios	KU 204908	-12.583333	-69.083333	**JX398468**	**JX398618**	**JX398734**	**JX293854**
Dipsas nicholsi	Panama: Parque Nacional General Omar Torrijos	JM[b] 812	8.6667	-80.6167	**JX398469**	**JX398619**		
Dipsas pavonina	Brazil: Amazonas	LSUMZ-H 13989	-2.578633	-64.115486	**JX398470**	**JX398620**	**JX398749**	**JX293855**
Dipsas peruana	Ecuador: Tungurahua: Banos	ENS 12421	-1.3884	-78.418272	**JX398471**	**JX398621**		
Dipsas peruana	Peru: Pasco	LSUMZ-H 1532	-10.447575	-75.154539	**JX398472**	**JX398622**	**JX398750**	**JX293856**
Dipsas pratti	Venezuela: Zulia	MBUCV 6837	10.3425	-72.562222	**JX398473**	**JX398624**	**JX398751**	
Dipsas pratti	Colombia: Antioquia	MHUA 14638	6.9003	-75.1533	**JX398474**	**JX398623**		
Dipsas temporalis	Colombia: Antioquia	MHUA 14278	7.201775	-76.43411944	GQ334583	GQ334482	GQ334667	GQ334560
Dipsas temporalis	Panama: Parque Nacional General Omar Torrijos	JM[b] 663	8.6667	-80.6167	**JX398475**	**JX398625**		
Dipsas temporalis	Panama: Parque Nacional General Omar Torrijos	JM[b] 664	8.6667	-80.6167	**JX398476**	**JX398626**		
Dipsas temporalis	Panama: Parque Nacional General Omar Torrijos	JM[b] 758	8.6667	-80.6167	**JX398477**	**JX398627**	**JX398752**	
Dipsas temporalis	Panama: Parque Nacional General Omar Torrijos	JM[b] 795	8.6667	-80.6167	**JX398478**	**JX398628**	**JX398753**	
Dipsas trinitatis	Trinidad: Arima Valley	UWIZM.2011.20.25	10.672922	-61.289828	**JX398479**	**JX398629**		
Dipsas variegata	French Guiana, Cayenne	D99	5.11692	-52.951221	**JX398480**	**JX398630**	**JX398737**	**JX293857**
Dipsas variegata	Venezuela: Bolivar	ENS 11187	4.58578	-61.10523	**JX398481**	**JX398631**		
Dipsas variegata	Suriname: Marowijne: Tepoe	UTA R-15772	5.5661	-54.412906	**JX398482**	**JX398601**	**JX398736**	**JX293858**
Dipsas vermiculata	Ecuador: Morona-Santiago	UTA R-55939	-2.95133	-78.35187	**JX398483**	**JX398632**	**JX398754**	**JX293859**
Drymobius margaritiferus	Guatemala: San Marcos	UTA R-46708	14.9408333	-92.0316667		**JX398634**	**JX398756**	**JX293861**
Enuliophis sclateri	Nicaragua	N316	11.321939	-84.739314	**JX398485**	**JX398635**	**JX398757**	**JX293863**
Enulius flavitorques	Mexico: Oaxaca	JAC 22914	16.553988	-94.182778	**JX398486**	**JX398636**	**JX398758**	
Farancia abacura	USA: Florida	CAS 184359	29.606036	-82.2996	DQ902302	U69832		
Geophis bicolor	Mexico: Michoacan	JAC 24684	19.44787	-102.41592	**JX398487**	**JX398637**	**JX398759**	**JX293862**
Geophis nigrocinctus	Mexico: Jalisco	JAC 30704	20.35511	-105.01158	**JX398488**	**JX398638**		
Geophis omiltemanus	Mexico: Guerrero	ENS 11496	17.55793	-99.67225		**JX398639**	**JX398760**	
Geophis tarascae	Mexico: Michoacan	JAC 24692	19.35383	-102.05696	**JX398489**	**JX398640**	**JX398761**	**JX293870**
Helicops angulatus	Trinidad	LSUMZ-H 3346	10.806792	-61.029831	U49310	AF471037		
Heterodon platirhinos	USA: North Carolina	MVZ 175928; DCC 2858; YPM 13421	35.225	-79.3913	AF402659	GU112412	EU390921	EU402749
Heterodon simus	USA: Florida	CAS 195598	29.606036	-82.2996	DQ902310	AF217840		
Hydromorphus concolor	Guatemala: Izabal	UTA R-46678	15.38117	-88.6905	**JX398490**	**JX398641**	**JX398762**	**JX293871**
Hydrops triangularis	Peru: Loreto	LSUMZ-H 3105	-4.258622	-74.223564		AF471039		
Hypsiglena slevini	Mexico: Baja California Sur	MVZ 234613	23.8110864	-110.0687733	EF078547	EF078499	FJ455191	FJ455223
Imantodes cenchoa	Costa Rica: Cahuita	MVZ 149878	9.73333	-82.85	EF078505	EF078553	FJ455187	FJ455219

Table 2.1 *Continued*

Leptodeira annulata	Honduras: El Paraiso	UTA R-41255	14.0784	-86.417117	GQ334611	GQ334509	GQ334672	GQ334565
Leptodeira septentrionalis	Mexico: Sinaloa	UTA R-51978	24.407852	-106.704003	EF078525	EF078573		
Leptodeira uribei	Mexico: Colima	JAC 30139	19.31764	-104.1267	**JX398491**	**JX398642**		
Leptodeira uribei	Mexico: Guerrero	LSUMZ 39524	17.196475	-99.600256	EF078579	EF078531	FJ810243	FJ810229
Micrurus fulvius	USA: Texas	ENS 10807	27.247549	-98.823136	**JX398492**	**JX398643**	**JX398763**	
Natrix natrix	Spain: Catalonia	MVZ 200534	41.591158	1.520861	AY487800	AY487756	EU390931	EU402762
Ninia atrata	Colombia: Caldas	MHUA 14452	5.32	-74.9153	GQ334659	GQ334553	GQ334683	GQ334577
Ninia atrata	Trinidad: Maracas Waterfall	UWIZM.2011.20.20	10.69715	-61.379953	**JX398493**	**JX398644**		
Ninia diademata	Guatemala: Huehuetenango	UTA R-42291	15.557924	-91.96236		**JX398645**	**JX398764**	**JX293864**
Nothopsis rugosus	Costa Rica: Cartago	UTA R-40098	9.753639	-83.678689	**JX398494**	**JX398646**	**JX398765**	**JX293865**
Oxyrhopus petola	Guatemala: Izabal	UTA R-46698	15.36	-88.723	GQ334660	GQ334554	GQ334684	GQ334578
Phalotris nasutus	Brazil	CHUNB 34844	0.719808	-57.395036		GQ895880		
Pliocercus elapoides	Mexico: Oaxaca	UTA R-52571	18.257	-96.767	**JX398495**	**JX398647**	**JX398766**	**JX293866**
Pseudoleptodeira latifasciata	Mexico: Colima	JAC 30119	19.02501	-103.78044	**JX398496**	**JX398648**	**JX398767**	**JX293867**
Rhadinaea pulveriventris	Costa Rica: Tapanti	MVZ 204129	9.73565	-83.78368	**JX398497**	**JX398649**	**JX398768**	**JX293868**
Rhadinophanes monticola	Mexico: Guerrero	JAC 29554	17.466447	-100.164869	**JX398498**	**JX398650**	**JX398769**	
Sibon annulatus	Costa Rica: Guayacan	B45-57	10.064456	-83.543319	**JX398499**		**JX398770**	
Sibon annulatus	Costa Rica: Guayacan	D167	10.064456	-83.543319	**JX398501**	**JX398652**	**JX398772**	**JX293869**
Sibon annulatus	Costa Rica: Limon	B45-75	10.064456	-83.543319	**JX398500**	**JX398651**	**JX398771**	
Sibon annulatus	Nicaragua	N740	11.321939	-84.739314	**JX398505**		**JX398777**	
Sibon annulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 407	8.6667	-80.6167	**JX398502**	**JX398653**	**JX398773**	
Sibon annulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 705	8.6667	-80.6167	**JX398503**	**JX398654**	**JX398774**	
Sibon annulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 759	8.6667	-80.6167		**JX398655**	**JX398775**	
Sibon annulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 794	8.6667	-80.6167	**JX398504**	**JX398656**	**JX398776**	
Sibon anthracops	Costa Rica: Santa Rosa	ASL 198	10.844411	-85.563731	**JX398506**	**JX398657**	**JX398778**	**JX293872**
Sibon anthracops	Guatemala: Jalapa	UTA R-39185	14.780697	-90.179944		**JX398658**	**JX398779**	**JX293873**
Sibon argus	Costa Rica	D137	10.064456	-83.543319	**JX398509**			
Sibon argus	Costa Rica: Guayacan de Siquirres	ASL 004	10.064456	-83.543319	**JX398507**	**JX398659**	**JX398780**	**JX293874**
Sibon argus	Costa Rica: Guayacan de Siquirres	ASL 283	10.064456	-83.543319	**JX398508**	**JX398660**	**JX398781**	**JX293878**
Sibon argus	Panama: Parque Nacional General Omar Torrijos	JM[b] 745	8.6667	-80.6167	**JX398510**	**JX398661**	**JX398782**	
Sibon argus	Panama: Parque Nacional General Omar Torrijos	JM[b] 751	8.6667	-80.6167	**JX398511**	**JX398662**	**JX398783**	

Table 2.1 *Continued*

Sibon argus	Panama: Parque Nacional General Omar Torrijos	JM[b] 755	8.6667	-80.6167	**JX398512**	**JX398663**	**JX398784**	
Sibon carri	Guatemala: Zacapa	UTA R-44750	15.23225278	-89.24375278	**JX398513**	**JX398664**	**JX398785**	**JX293875**
Sibon carri	Guatemala: Zacapa	UTA R-45493	15.240109	-89.176796	**JX398514**	**JX398665**	**JX398786**	**JX293876**
Sibon dimidiatus	Costa Rica: Limon	B45-62	10.064456	-83.543319	**JX398515**	**JX398666**	**JX398787**	**JX293877**
Sibon dimidiatus	Guatemala: Peten	UTA R-46123	16.912093	-90.932021	**JX398518**	**JX398669**	**JX398790**	
Sibon dimidiatus	Honduras: Olancho	USNM 565823	14.928831	-85.804922	**JX398516**	**JX398667**	**JX398788**	
Sibon dimidiatus	Honduras: Olancho	USNM 565824	14.928831	-85.804922	**JX398517**	**JX398668**	**JX398789**	
Sibon lamari	Costa Rica: Guayacan de Siquirres	ASL 362	10.064456	-83.543319	**JX398519**	**JX398670**		
Sibon lamari	Costa Rica: Guayacan de Siquirres	no number	10.064456	-83.543319	**JX398520**	**JX398671**	**JX398791**	**JX293879**
Sibon longifrenis	Costa Rica: Guayacan de Siquirres	ASL 220	10.064456	-83.543319	**JX398521**	**JX398672**	**JX398792**	**JX293880**
Sibon longifrenis	Costa Rica: Guayacan de Siquirres	ASL 282	10.064456	-83.543319	**JX398522**	**JX398673**	**JX398793**	**JX293881**
Sibon longifrenis	Nicaragua	N095	11.321939	-84.739314	**JX398523**	**JX398674**	**JX398794**	**JX293882**
Sibon manzanaresi	Honduras: Gracias a Dios	USNM 570455	15.341806	-84.606044	**JX398524**	**JX398685**	**JX398795**	**JX293883**
Sibon manzanaresi	Honduras: Gracias a Dios	USNM 578381	15.341806	-84.606044	**JX398525**	**JX398686**	**JX398796**	
Sibon merendonensis	Guatemala: Zacapa	MVZ 263880	14.93042	-89.4167	**JX398526**	**JX398675**	**JX398797**	**JX293884**
Sibon miskitus	Honduras: Gracias a Dios	USNM 565598	15.341806	-84.606044	**JX398527**	**JX398676**	**JX398798**	
Sibon miskitus	Honduras: Gracias a Dios	USNM 570454	15.341806	-84.606044	**JX398528**	**JX398677**	**JX398799**	**JX293885**
Sibon nebulatus	Colombia: Antioquia	MHUA 14511	5.95257	-74.8504	GQ334662	GQ334556	GQ334685	GQ334579
Sibon nebulatus	Colombia: Cesar: Rio de Oro	ICN 11463	8.272556	-73.406389	**JX398532**			
Sibon nebulatus	Colombia: Santander	ICN 11510	6.549605	-73.126413	**JX398533**		**JX398803**	
Sibon nebulatus	Colombia: Tolima	SN 0001	4.218525	-74.681378	**JX398544**	**JX398684**	**JX398809**	**JX293892**
Sibon nebulatus	Colombia: Tolima	SN 02	4.218525	-74.681378	**JX398545**			
Sibon nebulatus	Ecuador: cf. Guayas	JM[a] 73	-2	-80	**JX398543**	**JX398683**	**JX398808**	**JX293890**
Sibon nebulatus	Ecuador: Esmeraldas	ENS 12459	1.18333	-78.75349	**JX398530**		**JX398801**	
Sibon nebulatus	Ecuador: Esmeraldas	ENS 12500	1.18333	-78.75349	**JX398531**		**JX398802**	
Sibon nebulatus	Guatemala: Huehuetenango	UTA R-42429	15.87	-91.225833	**JX398534**			**JX293887**
Sibon nebulatus	Guatemala: Izabal	UTA R-42431	15.36	-88.723	**JX398549**	**JX398690**	**JX398812**	**JX293891**
Sibon nebulatus	Honduras: Gracias a Dios	USNM 564142	15.341806	-84.606044	**JX398547**		**JX398810**	
Sibon nebulatus	Honduras: Gracias a Dios	USNM 564143	15.341806	-84.606044	**JX398548**		**JX398811**	
Sibon nebulatus	Mexico: Chiapas	UOGV 332	16.344247	-91.611528	**JX398546**			
Sibon nebulatus	Mexico: Colima	JAC 28055	19.40784	-104.05303	**JX398535**	**JX398678**		**JX293889**
Sibon nebulatus	Mexico: Colima	JAC 28140	19.2284	-104.20312	**JX398536**			**JX293893**
Sibon nebulatus	Mexico: Colima	JAC 28589	19.01834	-103.77038	**JX398537**			**JX293894**
Sibon nebulatus	Mexico: Colima	JAC 30102	19.37525	-103.94473	**JX398538**			
Sibon nebulatus	Mexico: Guerrero	UTA R-51854	17.493333	-100.201389	**JX398550**		**JX398813**	

Table 2.1 *Continued*

Sibon nebulatus	Mexico: Guerrero	UTA R-57502	17.35477	-99.4582	**JX398529**		**JX398800**	**JX293886**
Sibon nebulatus	Nicaragua	N068	11.321939	-84.739314	**JX398542**	**JX398682**	**JX398807**	
Sibon nebulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 703	8.6667	-80.6167	**JX398539**	**JX398679**	**JX398804**	
Sibon nebulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 722	8.6667	-80.6167	**JX398540**	**JX398680**	**JX398805**	
Sibon nebulatus	Panama: Parque Nacional General Omar Torrijos	JM[b] 793	8.6667	-80.6167	**JX398541**	**JX398681**	**JX398806**	
Sibon nebulatus	Trinidad: Lopinot Valley	UWIZM.2011.20.26	10.684636	-61.326333	**JX398551**	**JX398687**		
Sibon perissostichon	Panama: Chiriqui	SMF 88716	8.67465	-82.216167	**JX398552**	**JX398688**	**JX398814**	**JX293888**
Sibon sanniolus	Mexico	MX21-35	20.59323	-88.81725		**JX398691**		
Sibon sanniolus	Mexico: Yucatan	JAC 24427	20.59323	-88.81725		**JX398689**		
Sibon sanniolus	Mexico: Yucatan	MX21-36	20.59323	-88.81725	**JX398553**	**JX398692**	**JX398815**	**JX293895**
Sibynomorphus mikanii	Brazil: Sao Paulo	CTMZ 495	-23.940319	-47.037808		**JX398693**	**JX398816**	**JX293896**
Sibynomorphus oligozonatus	Ecuador: Manabi	ENS 12817	-1.002089	-80.313342	**JX398554**	**JX398694**	**JX398817**	**JX293897**
Sibynomorphus petersi	Ecuador: Azuay	JM[a] 72	-2.929503	-79.054205	**JX398555**	**JX398695**	**JX398818**	**JX293898**
Sibynomorphus turgidus	Bolivia	LSUMZ-H 6458	-17.850696	-63.153744	**JX398556**	**JX398696**	**JX398819**	**JX293899**
Synophis bicolor	Ecuador: Esmeraldas	UTA R-55956	1.03212	-78.61378	**JX398557**	**JX398697**	**JX398820**	**JX293900**
Tantalophis discolor	Mexico: Oaxaca	EBUAP 1853	15.956622	-96.451528	EF078541	EF078589	**JX398835**	**JX293915**
Thamnophis fulvus	Guatemala: Quiche	UTA R-42315	15.456552	-90.806769	**JX398591**	**JX398721**	**JX398836**	**JX293916**
Tretanorhinus variabilis	Cuba: Pinar de Rio	USNM 335893	22.407561	-83.8473	**JX398592**	**JX398722**	**JX398837**	**JX293917**
Trimetopon gracile	Costa Rica: Tapanti	MVZ 204249	9.79484	-83.85216	**JX398593**	**JX398723**	**JX398838**	**JX293918**
Tropidodipsas annuliferus	Mexico: Colima	JAC 30142	19.32706	-103.93855	**JX398560**	**JX398700**		
Tropidodipsas annuliferus	Mexico: Colima	JAC 30143	19.31912	-103.92693	**JX398561**	**JX398701**		
Tropidodipsas annuliferus	Mexico: Guerrero	IDF-89	16.976506	-99.763336	**JX398558**	**JX398698**	**JX398824**	**JX293902**
Tropidodipsas annuliferus	Mexico: Guerrero	JAC 27792	17.80859	-101.4381	**JX398559**	**JX398699**		**JX293914**
Tropidodipsas fasciatus	Mexico: Guerrero	JRV 31	17.782	-101.478	**JX398562**			
Tropidodipsas fasciatus	Mexico: Oaxaca	JAC 21117	16.9625	-96.196233		**JX398703**	**JX398821**	**JX293901**
Tropidodipsas fasciatus	Mexico: Oaxaca	JAC 22545	16.5734	-94.8614			**JX398828**	
Tropidodipsas fasciatus	Mexico: Oaxaca	JAC 22920	16.553988	-94.182778		**JX398702**		
Tropidodipsas fasciatus	Mexico: Oaxaca	UTA R-52645	16.553988	-94.182778		**JX398704**		
Tropidodipsas fischeri	Guatemala: Guatemala	ENS 11779	14.61625	-90.6284	**JX398563**	**JX398705**	**JX398822**	
Tropidodipsas fischeri	Guatemala: Guatemala	ENS 11780	14.61625	-90.6284	**JX398564**	**JX398706**		**JX293904**
Tropidodipsas fischeri	Guatemala: Quetzaltenango	UTA R-38119	14.76667	-91.66667	**JX398565**			
Tropidodipsas fischeri	Guatemala: San Marcos	UTA R-38932	14.931	-91.868	**JX398566**	**JX398707**	**JX398823**	**JX293903**
Tropidodipsas fischeri	Guatemala: San Marcos	UTA R-39204	14.931	-91.868	**JX398567**	**JX398708**		**JX293905**
Tropidodipsas fischeri	Guatemala: San Marcos	UTA R-39205	14.931	-91.868	**JX398568**	**JX398709**	**JX398827**	**JX293906**
Tropidodipsas philippii	Mexico: Colima	JAC 28262	19.37663	-104.07398	**JX398573**			**JX293910**
Tropidodipsas philippii	Mexico: Colima	JAC 28325	19.03289	-103.78745	**JX398574**			**JX293911**

Table 2.1 *Continued*

Tropidodipsas philippii	Mexico: Colima	JAC 30135	19.41027	-104.01166	**JX398575**		**JX398825**	
Tropidodipsas philippii	Mexico: Colima	JAC 30136	19.37675	-104.07481	**JX398576**			
Tropidodipsas philippii	Mexico: Colima	JAC 30737	19.03300	-103.78814	**JX398578**			
Tropidodipsas philippii	Mexico: Colima	JAC 30738	19.05100	-103.78688	**JX398579**			
Tropidodipsas philippii	Mexico: Guerrero hwy 134	JAC 27750	17.9568	-101.27126	**JX398571**	**JX398711**		**JX293908**
Tropidodipsas philippii	Mexico: Jalisco	ENS 11639	20.3867	-105.31201	**JX398569**			**JX293907**
Tropidodipsas philippii	Mexico: Michoacan	JAC 27923	18.48627	-103.54229	**JX398572**	**JX398712**		**JX293909**
Tropidodipsas philippii	Mexico: Nayarit	JAC 24811	21.751383	-104.845461	**JX398570**	**JX398710**	**JX398826**	
Tropidodipsas philippii	Mexico: Oaxaca	JAC 30740	16.76485	-95.03998	**JX398580**	**JX398713**		
Tropidodipsas philippii	Mexico: Oaxaca	JAC 30800	16.77036	-95.01822	**JX398581**	**JX398714**		
Tropidodipsas philippii	Mexico: Sinaloa	JAC 30601	23.32376	-105.98733	**JX398577**			
Tropidodipsas sartorii	Costa Rica: Guanacaste	CMS 125	10.9	-85.6	**JX398582**	**JX398715**	**JX398829**	
Tropidodipsas sartorii	El Salvador: La Libertad	KU 289806	13.682867	-89.356661	EF078588	EF078540		
Tropidodipsas sartorii	Guatemala: San Marcos	UTA R-45915	14.929667	-91.8815	**JX398589**	**JX398719**		
Tropidodipsas sartorii	Honduras: Gracias a Dios	USNM 564144	15.341806	-84.606044	**JX398585**	**JX398717**	**JX398831**	**JX293912**
Tropidodipsas sartorii	Honduras: Gracias a Dios	USNM 564145	15.341806	-84.606044	**JX398586**		**JX398832**	
Tropidodipsas sartorii	Honduras: Gracias a Dios	USNM 564146	15.341806	-84.606044	**JX398587**	**JX398718**	**JX398833**	
Tropidodipsas sartorii	Honduras: Santa Barbara	USNM 578078	15.119628	-88.426764	**JX398588**		**JX398834**	**JX293913**
Tropidodipsas sartorii	Mexico: Jalisco	JAC 30401	20.364213	-105.315216	**JX398583**	**JX398716**		
Tropidodipsas sartorii	Nicaragua	N625	11.321939	-84.739314	**JX398584**			
Tropidodipsas sp.	Mexico: Oaxaca	JAC 24267	15.8562	-96.46508	**JX398594**	**JX398724**	**JX398839**	**JX293919**
Urotheca decipiens	Costa Rica: Tapanti	MVZ 204126	9.71506	-83.80367	**JX398595**	**JX398725**	**JX398840**	**JX293920**
Urotheca guentheri	Costa Rica: Volcan Cacao	MVZ 207366	10.93333	-85.45	**JX398596**	**JX398726**	**JX398841**	**JX293921**
Xenodon rhabdocephalus	Guatemala: Izabal	UTA R-42297	15.415871	-89.094615	**JX398597**	**JX398727**	**JX398842**	**JX293922**
Xenoxybelis boulengeri	Peru: Madre de Dios	KU 214888	-12.583333	-69.083333		GQ895898		

[a] Voucher information: ANMO = Adrián Nieto-Montes de Oca (field number, UNAM); ASL = Alejandro Solórzano (private collection, Serpentario Nacional, Costa Rica); CAS = California Academy of Sciences, Herpetological Collection, USA; CHUNB = Coleção Herpetológica da Universidade de Brasília, Brazil; CLP = Christopher L. Parkinson (field number, UCF); CMS = Coleman M. Sheehy (field number, UTA); CTMZ = Coleção de Tecidos do Museu de Zoologia, Universidade de São Paulo, Brazil; EBUAP = Escuela de Biología de la Universidad Autónoma de Puebla, Mexico; ENS = Eric N. Smith (field number, UTA); ICN = Instituto de Ciencias Naturales, Universidad Nacional de Bogotá, Colombia; IDF = Itzel Durán Fuentes (field number); JAC = Jonathan A. Campbell (field number, UTA); JM[a] = Juan Daza (field number); JM[b] = Julie Ray (field number, private collection); JRV = Jacobo Reyes Velasco (field number); KU = University of Kansas, Museum of Natural History, Division of Herpetology, USA; LSUMZ = Louisiana State University, Museum of Zoology, USA; MBUCV = Museo de Biología, Universidad Central de Venezuela, Venezuela; MHUA = Museo de Herpetología, Universidad de Antioquia, Colombia; MVZ = Museum of Vertebrate Zoology, University of California, USA; UOGV = Uri Omar Garcia Vazquez (field number); USNM = Smithsonian Instution National Museum of Natural History, USA; UTA = University of Texas at Arlington, Amphibian and Reptile Diversity Research Center, USA; UWIZM = University of the West Indies Zoology Museum, Trinidad and Tobago; WED = William E. Duellman (field number, KU).

Table 2.2 Names and sequences of primers used in this study.

Region	Name	Sequence: 5'–3'	Source
cyt-b	S20596F (F)	AACCACTCTTGTTAATCAACTACA	Ingrasci, 2011
cyt-b	S21790R (R)	ACCCATGTTTGGTTTACAAAAACAATGCT	Ingrasci, 2011
cyt-b	GLUDG (F)	TGACTTGAARAACCAYCGTTG	Parkinson et al., 2002
cyt-b	AtrCB3 (R)	TGAGAAGTTTTCYGGGTGRTT	Parkinson et al., 2002
ND4	ND4 (F)	CACCTATGACTACCAAAAGCTCATGTAGAAGC	Arévalo et al., 1994
ND4	LEU (R)	CATTACTTTTACTTGGATTTGCACCA	Arévalo et al., 1994
ND4	605F (F)	GTCTCCATCTATGACTCCCA	Ingrasci, 2011
ND4	L68R (R)	TACCACTTGGATTTGCACCA	Ingrasci, 2011
NT3	NT3-F3 (F)	ATATTTCTGGCTTTTCTCTGTGGC	Noonan and Chippindale, 2006
NT3	NT3-R4 (R)	GCGTTTCATAAAAATATTGTTTGACCGG	Noonan and Chippindale, 2006
DNAH3	DNAH3-f1 (F)	GGTAAAATGATAGAAGAYTACTG	Townsend et al., 2008
DNAH3	DNAH3-r6 (R)	CTKGAGTTRGAHACAATKATGCCAT	Townsend et al., 2008

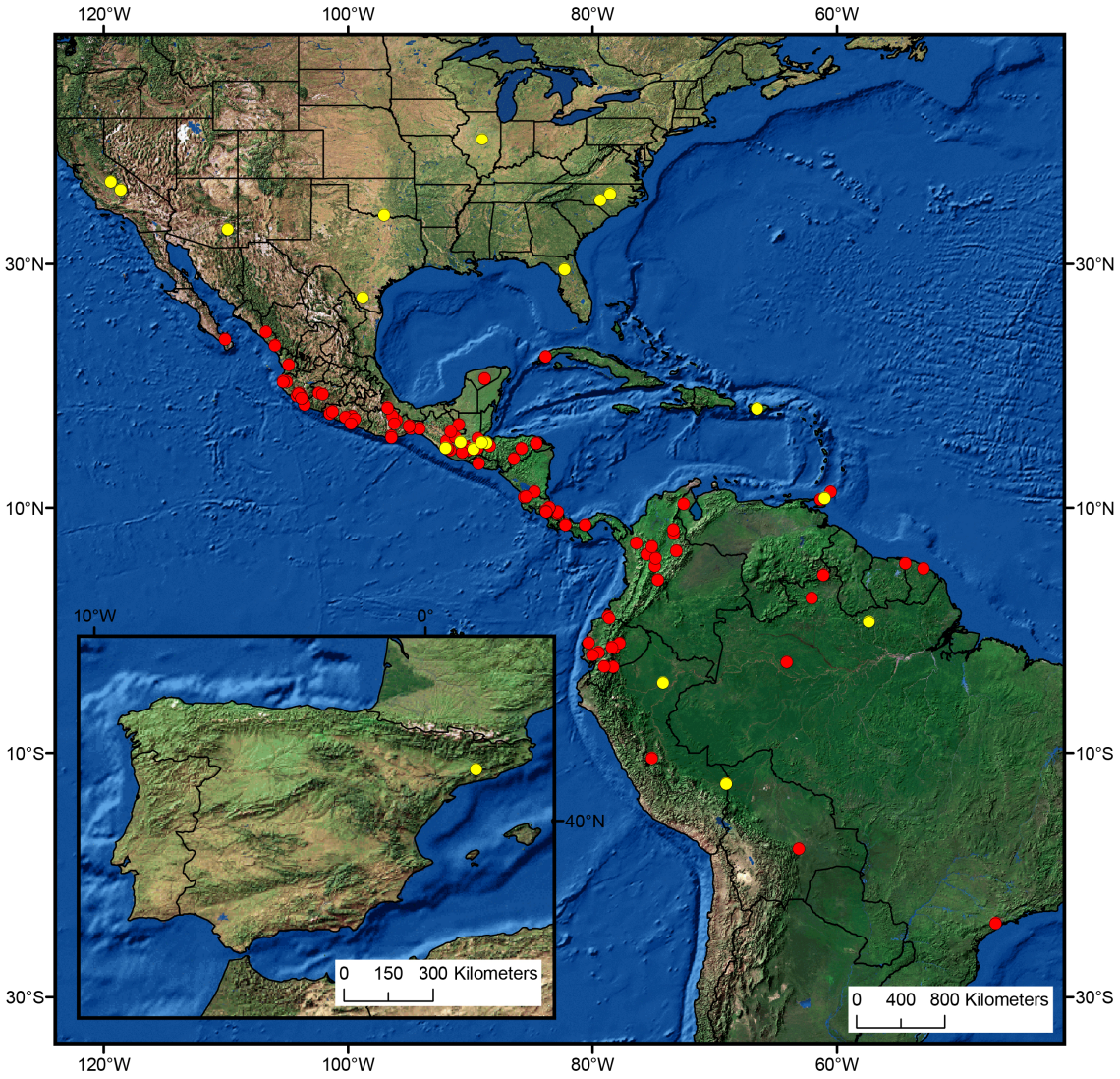

Figure 2.1 Localities of 194 tissue samples for dipsadine snakes (red) and outgroup taxa (yellow) used in this study. Map inset shows a tissue locality in Spain.

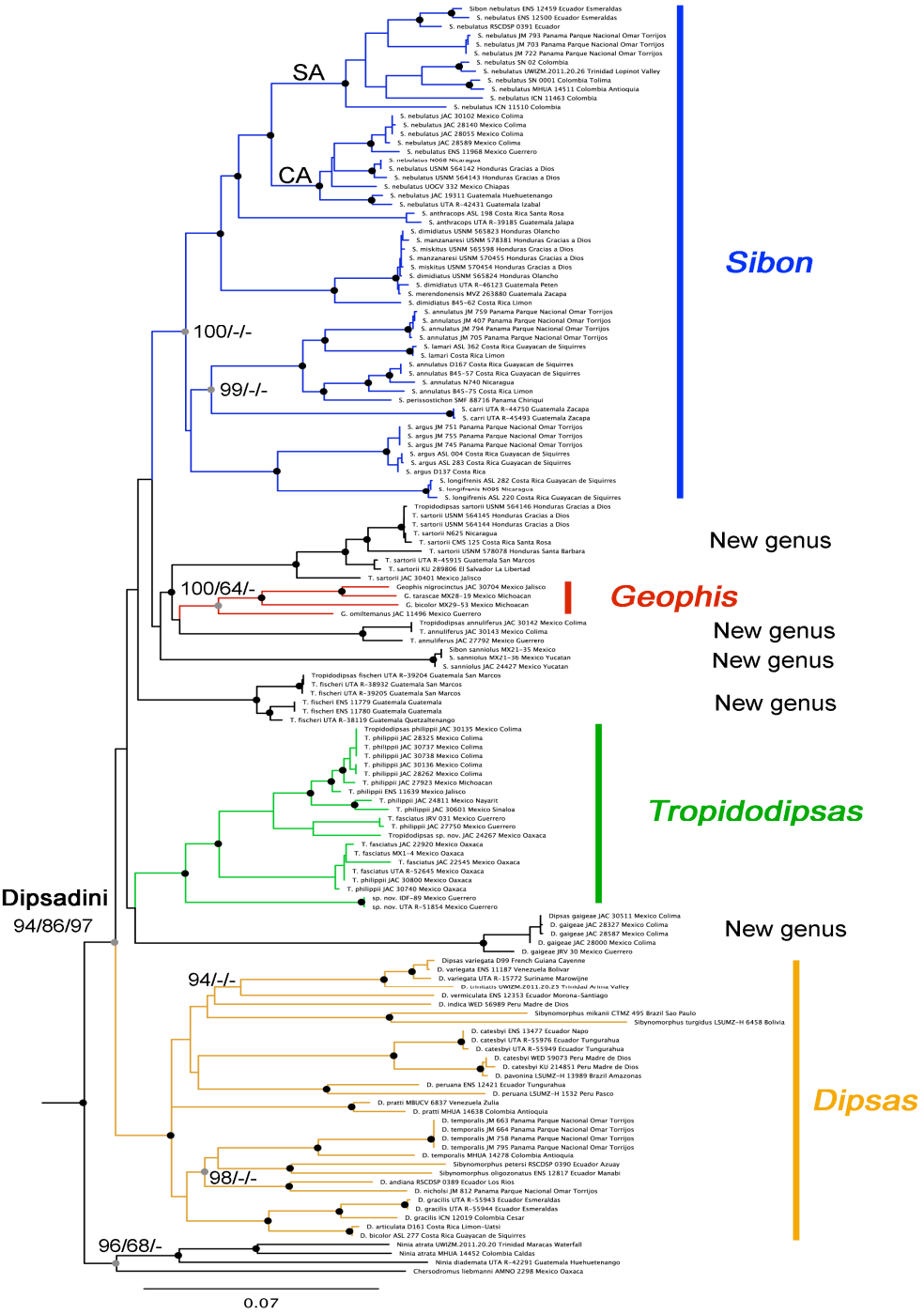

Figure 2.2 Phylogeny of the Dipsadini using the best ML tree. Black circles denote strong nodal support (≥0.95 PP and ≥0.70 ML and WP bootstrap). Gray circles indicate strong support by some but not all methods (PP/ML/WP). A dash (-) indicates support below the cutoff value. *Sibon nebulatus* contains a South American (SA) and a Central American (CA) clade.

CHAPTER 3

INTERGENERIC RELATIONSHIPS AMONG THE DIPSADINE SNAKES (COLUBRIDAE: DIPSADINAE)

3.1 Introduction

The superfamily Colubroidea, or “advanced snakes”, is a monophyletic assemblage of diverse families and subfamilies that includes the vast majority (~2801 species, or ~83%) of all 3395 extant snake species (Lawson et al., 2005; Pyron et al., 2011; Uetz, 2012). This large clade includes seven well-supported families: Colubridae (1763 species), Elapidae (351 species), Viperidae (308 species), Lamprophiidae (303 species), Homalopsidae (44 species), Xenodermatidae (17 species), and Pareatidae (15 species) (Wiens et al., 2008; Pyron et al., 2011). Within the Colubridae, the snake subfamlies Dipsadinae (Bonaparte, 1840) and Xenodontinae (Bonaparte, 1845) appear to form a monophyletic group and together represent the largest group of colubrid snakes with ~733 species in ~92 genera (Vidal et al., 2010).

The majority of molecular phylogenetic studies conducted on these sister subfamilies has focused on the Xenodontinae, with smaller numbers of dipsadine species being used as outgroups (*e.g.*, Vidal et al., 2000, 2010; Zaher et al., 2009; Grazziotin et al., 2012). However, several recent studies have addressed relationships among dipsadine subgroups *Hypsiglena* (Mulcahy, 2006), Leptodeirini (Mulcahy, 2007; Daza et al., 2009; Mulcahy et al., 2011), and *Pseudoleptodeira* (Reyes-Velasco and Mulcahy, 2010; Mulcahy et al., 2011). Nonetheless, the subfamily Dipsadinae has been poorly sampled resulting in many unresolved intergeneric relationships and many taxa (i.e., *Chersodromus*, *Enuliophis*, *Rhadinophanes* and *Synophis*) considered *incertae sedis* (Zaher et al., 2009; Grazziotin et al., 2012).

The subfamily Dipsadinae contains ~350 species in ~32 genera, and forms a large and ecologically diverse group of snakes that are distributed primarily throughout Mexico and Central America (Cadle, 1984b; Cadle and Greene, 1993). Several genera are primarily arboreal (*e.g.*, *Dipsas, Imantodes*, and *Sibon*), whereas other genera are primarily either terrestrial (*e.g.*, *Hypsiglena*, *Rhadinaea*, and *Sibynomorphus*), fossorial (*e.g.*, *Atractus* and *Geophis*), or highly aquatic (*e.g*., *Hydromorphus* and *Tretanorhinus*). Many genera are rear-fanged and feed on vertebrates (*e.g.*, *Coniophanes*, *Leptodeira*, and *Nothopsis*), whereas many other genera lack rear fangs and feed on invertebrates (*e.g.*, *Atractus*, *Dipsas*, and *Ninia*). Although some genera are relative dietary generalists (*e.g.*, *Coniophanes* and *Leptodeira*), many genera are dietary specialists (*i.e.*, *Dipsas*, *Enulius*, *Plesiodipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*).

Although members of the subfamily Dipsadinae exhibit wide range of diets, a strong pattern appears to exist within the lineage. Unlike the xenodontines, dipsadine snakes appear to have undergone a major dietary shift from opisthoglyphous species that feed on vertebrates to aglyphous species that feed on invertebrates (Mulcahy, 2007). This dietary shift appears to be coorelated with a loss of rear fangs and a more than three-fold increase in the number of species (80+ vs. 270+ spp.) subsequent to the shift, suggesting that invertebrate feeders may have experienced an adaptive radiation (Mulcahy, 2007; Mulcahy, 2011). However, a robust phylogeny of the subfamily is needed to test the hypotheses of dietary shift and adaptive radiation within this lineage.

The subfamily Dipsadinae has had a long and inconsistent taxonomic history, particularly regarding its relationship to xenodontine snakes. Bonaparte (1840, 1845) recognized a Central American clade (Dipsadinae) and a South American clade (Xenodontinae), whereas Cadle (1984a,b,c) Cadle (1985), Cadle and Greene (1993), and Vidal et al. (2000) grouped both clades into the subfamily Xenodontinae. Vidal et al. (2007, 2010) and Grazziotin et al. (2012) recognized both subfamilies Dipsadinae and Xenodontinae, which

they placed into the family Dipsadidae. Pyron (2011) and Zaher et al. (2009) both grouped the Xenodontinae into the subfamily Dipsadinae; however, Pyron et al. (2011) placed the subfamily Dipsadinae within the family Colubridae, whereas Zaher et al. (2009) placed it within the family Dipsadidae. I follow here the original usage of Bonaparte (1840, 1845) and refer to two sister subfamilies Dipsadinae and Xenodontinae, which are primarily Middle American and South American, respectively.

Morphological studies using various characters have proposed several relationships, including four tribes (Diaphorolepini; Dipsadini, Leptodeirini, and Nothopsini) within the Dipsadinae (Peters, 1960; Myers, 1974; Dowling and Duellman, 1978; Jenner, 1981; Jenner and Dowling, 1985; Myers and Cadle, 1994; Zaher, 1999). Peters (1960) suggested close relationships among the genera *Dipsas*, *Sibon*, and *Sibynomorphus* (see Chapter 2). Myers (1974) proposed several species groups of *Rhadinaea* and suggested a close relationship among the genera *Rhadinaea*, *Coniophanes*, *Pliocercus*, *Trimetopon* and *Urotheca*. Savage and Crother (1989) synonymized *Pliocercus* with *Urotheca*. However, *Pliocercus* was later removed from synonymy with *Urotheca* by Myers and Cadle (1994). Dowling and Duellman (1978) included the dipsadine genera *Atractus*, *Hydromorphus*, and *Tropidodipsas* into the tribe Alsophiini, and they placed the dipsadine genera *Amastridium*, *Chersodromus*, and *Ninia* into the tribe Nothopsini. Zaher (1999) proposed close relationships among *Ninia*, *Chersodromus*, *Enulius*, *Enuliophis*, and *Geophis* based on the presence and position of a highly developed Harderian gland in these genera. Myers and Campbell (1981) described the genus *Rhadinophanes* and proposed this genus to be closely related to *Tantalophis* based on similar hemipenial morphology, even though these genera are apparently allopatric and appear very dissimilar in most other ways. Although *Rhadinophanes* and *Tantalophis* exhibit hemipenial morphologies similar to various alsophiine colubrids, Myers and Campbell (1981) suggested both genera could have close affinities to either a *Rhadinaea-Coniophanes* group or to a *Leptodeira-Cryophis* group. Campbell and Smith (1998) described the genus *Chapinophis* and

proposed close affinities of this species to *Adelphicos*, *Atractus*, *Geophis*, *Ninia* and *Chersodromus* based on similar features of the maxilla. However, they also noted that *Chapinophis* exhibits similarities in hemipenial morphology with the genera *Rhadinophanes* and *Tantalophis*, suggesting a possible close relationship with these genera.

Although most of these intergeneric dipsadine relationships have not been adequately tested with molecular data, some groups have been investigated. Mulcahy (2007) and Daza et al. (2009) found support for a paraphyletic Leptodeirini containing *Leptodeira* and *Imantodes*. Vidal et al. (2010) added *Nothopsis* to the Leptodeirini tribe, although this relationship was not supported. Mulcahy (2007) identified a clade containing *Hypsiglena* and *Pseudoleptodeira*, which was sister to a clade containing *Cryophis* and the Dipsadini. Mulcahy et al. (2011) and Pyron et al. (2011) found support for a monophyletic Leptodeirini, but only the former author recovered support for a clade containing *Coniophanes* and *Rhadinaea*. Mulcahy et al. (2011) and Pyron et al. (2011) also recovered *Tantalophis* as sister (basal) to the Dipsadinae. Some studies support the tribe Dipsadini as monophyletic (e.g., Cadle, 1984b), which contains at least the genera *Dipsas*, *Plesiodipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas* (but see Chapter 2 of this dissertation). However, some studies suggest that the Dipsadini is paraphyletic (Zaher et al., 2009; Grazziotin et al., 2012; Chapter 2 of this dissertation). Zaher et al. (2009) refrained from assigning dipsadine tribes due to their scant sampling within the subfamily, but they recognized a closely related group of snakes containing the genera *Carphophis*, *Contia*, *Diadophis*, *Farancia*, and *Heterodon* that they considered the subfamily Carphophiinae. Vidal et al. (2010) found this group to be paraphyletic, however. As a result of continued poor sampling of dipsadines in molecular studies, Zaher et al. (2009) placed the genera *Diaphorolepis*, *Emmochliophis*, *Enuliophis*, *Enulius*, *Hydromorphus*, *Nothopsis*, *Rhadinophanes*, *Synophis*, and *Tantalophis* within the Dipsadinae as *incertae sedis*.

The goals of the present study are five-fold. First, I test the monophyly of the subfamily Dipsadinae and attempt to reconstruct the intergeneric relationships. Second, I test whether the

subfamily Carphophiinae (Zaher et al., 2009) is supported for the genera *Carphophis*, *Contia*, *Diadophis*, *Farancia*, and *Heterodon*. Third, I identify the relationships of *Chersodromus* and other currently *incertae sedis* genera. Fourth, I identify what taxa are sister to the Dipsadini. Fifth, I comment on dietary shift and adaptive radiation in the subfamily and propose an evolutionary/ecological scenario for the origin of gastropod specialization within the Dipsadini based on the tree topology.

3.2 Materials and Methods

3.2.1 Taxon Sampling

This study contains the most extensive sampling to date of genera in the subfamily Dipsadinae, and four genera are sequenced here for the first time (*Chersodromus*, *Enuliophis*, *Rhadinophanes*, and *Synophis*). Furthermore, this study includes 27 of the 33 dipsadine genera (82%) that are either assigned to the subfamily Dipsadinae or are considered Dipsadinae *incertae sedis* (Table 2.1). Multiple species for some genera are also included. The only six dipsadine genera not included in this study are *Diaphorolepis*, *Emmochliophis*, *Omoadiphas*, *Plesiodipsas*, *Psomophis* and *Taeniophallus*.

In addition to the subfamily Dipsadinae, this study includes the most extensive and complete taxon sampling to date for the tribe Dipsadini. Previous molecular studies contained three of the five genera (*Sibon*, *Dipsas* and *Sibynomorphus*), and about 16% of their species (Grazziotin et al., 2012). This study includes four of the five Dipsadini genera (*Sibon*, *Dipsas*, *Sibynomorphus* and *Tropidodipsas*) and 55% of their species (Table 2.1). More specifically, this study includes 14 of the 15 species (87%) of *Sibon*, five of the seven species (71%) of *Tropidodipsas*, 15 of the 33 species (46%) of *Dipsas*, and four of the 12 species (33%) of *Sibynomorphus*. Tissues from the recently described genus *Plesiodipsas* were not available. This study also includes multiple sequences for many species from different localities. Two of the four *Sibynomorphus* species (*S. petersi* and *S. oligozonatus*) included represent the trans-

Andian or “northern” species of Cadle (2007), whereas *S. mikanii* and *S. turgidus* represent the cis-Andian or “southern” species of Cadle (2007).

To test the monophyly of the subfamily Dipsadinae, representatives of the subfamily Carphophiinae as defined by Zaher et al., (2009) (*Carphophis*, *Contia*, *Diadophis*, *Farancia*, and *Heterodon*) were included, along with representatives of the subfamilies Colubrinae (*Coluber* and *Drymobius*), Elapinae (*Micrurus*), Natricinae (*Natrix* and *Thamnophis*), and Xenodontinae (*Alsophis*, *Arrhyton*, *Conophis*, *Helicops*, *Hydrops*, *Oxyrhopus*, *Phalotris*, *Xenodon*, and *Xenoxybelis*). The tree was rooted with a crotaline (*Crotalus tigris*).

3.2.2 Gene Sampling

The data matrix generated in this study includes two mitochondrial (ND4 + tRNAs and cyt-b) and two nuclear (NT3 and DNAH3) genes for 194 taxa and up to 3241 base pairs. Five loci were used: (1) a 714 base pair fragment of the mitochondrial NADH dehydrogenase subunit 4 (ND4), (2) a 199 base pair fragment of tRNAs His, Ser and Leu, (3) a 1071 base pair fragment of the mitochondrial cytochrome-b gene (cyt-b), (4) a 525 base pair fragment of the nuclear protein-coding neurotrophin-3 (NT3) gene, and (5) a 732 base pair fragment of the nuclear protein-coding dynein, axonemal, heavy chain 3 (DNAH3) gene (see Table 2.2 for primers used). Sequencing coverage was more complete for the mitochondrial markers than for the nuclear markers. An effort was made to, at a minimum, sequence all individuals for the two mitochondrial genes, each species from different localities for NT3, and each different species from one locality for DNAH3 (Table 2.1). The resulting matrix had 32% missing characters, many of which were associated with the second and third tRNAs Ser and Leu as the ND4 primers tapered off. The genes NT3 and DNAH3 were used because they were each previously screened and represent potentially informative, single-copy, unlinked loci that are likely evolving at different rates (NT3 > DNAH3) (Townsend et al., 2008).

3.2.3 Molecular Data

Where possible, tissues (e.g., blood, liver, muscle, or shed skin) were obtained from the type species in each genus and from as close as possible to the type locality. Tissues were collected from throughout the distributional range of dipsadine snakes (Fig. 2.1). Genomic DNA was isolated from tissues using a Qiagen DNeasy kit (Qiagen, Valencia, California, USA). All amplification reactions used GoTaq® Green Master Mix, 2X (Promega Corporation, Madison, Wisconsin, USA). Thermal cycling was performed on a GeneAmp® PCR System 9700 machine (Applied BioSciences, Foster City, California, USA). The ND4 + tRNA fragments were amplified using an initial 5 min denaturation cycle at 95℃, followed by 30s denaturing at 94℃, 45s annealing at 52℃ and 1 min extension at 72℃ for 38 cycles, and a final 5 min extension at 72℃. The cyt-b fragments were amplified using an initial 2 min denaturation cycle at 95℃, followed by 30s denaturing at 94℃, 30s annealing at 53℃ and 1 min 15s extension at 72℃ for 2 cycles, followed by 30s denaturing at 94℃, 30s annealing at 52℃ and 1 min 15s extension at 72℃ for 3 cycles, followed by 30s denaturing at 94℃, 30s annealing at 51℃ and 1 min 15s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 50℃ and 1 min 15s extension at 72℃ for 30 cycles, followed by a 7 min extension at 72℃. The NT3 and DNAH3 fragments were amplified using an initial 1 min 30s denaturation cycle at 94℃, followed by 30s denaturing at 94℃, 30s annealing at 51℃ and 1 min 30s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 50℃ and 1 min 30s extension at 72℃ for 5 cycles, followed by 30s denaturing at 94℃, 30s annealing at 49℃ and 1 min 30s extension at 72℃ for 10 cycles, followed by 30s denaturing at 94℃, 30s annealing at 48℃ and 1 min 30s extension at 72℃ for 30 cycles, followed by a 7 min extension at 72℃. PCR product was quantified by visualization on 1% agarose gel stained with ethidium bromide. Successfully amplified PCR products were prepared for sequencing by using the ExoSAP-IT kit (United States Biochemical). A BigDye Terminator Cycle Sequencing Kit (Applied Biosystems Inc.) was used for sequencing following the manufacturer's protocol and using PCR primers. The sequenced products were precipitated using an ethanol/sodium acetate method and rehydrated

in HPLC purified formamide (HIDI). The sample was then analyzed on an ABI PRISM 3100xl Genetic Analyzer in the Genomics Core Facility at the University of Texas at Arlington, USA.

Alignments were constructed using the program Sequencher 4.8 (Gene Codes, Ann Arbor, Michigan, USA), and edited by eye using the program MacClade 4.08 (Maddison and Maddison, 2005). The tRNAs were aligned using an annotated mitochondrial genome for *Sibon nebulatus* (GenBank EU728583) as a template sequence. Uncorrected percent pairwise distances were generated in MEGA 5 (Tamura et al., 2011).

3.2.4 Phylogenetic Analyses

Phylogenetic analyses were conducted using Maximum Likelihood (ML), Parsimony, Bayesian, and distance (Neighbor Joining, or NJ) methods on the data matrix consisting of 194 taxa and up to 3241 base pairs. Various models of molecular evolution were tested using the software package MEGA 5 (Tamura et al., 2011) on the complete alignment partitioned by gene fragment (seven partitions: ND4, cytb, tRNA His, tRNA Ser, tRNA Leu, NT3, and DNAH3). The model test results identified GTR+I+G as among the best-fit models of nucleotide substitution for each gene fragment based on corrected Akaike Information Criterion (AICc), although it did not always receive the best score. The ML analyses employing the rapid bootstrapping algorithm were conducted using the program RAxML 7.3.0 (Stamatakis, 2006) on the CIPRIS Science Gateway server v3.2 (Miller et al., 2010) using the model GTR+G instead of GTR+I+G because the 25 discrete rate categories appear to better estimate invariant sites (Stamatakis, 2006). The multiple alignment was partitioned by gene region (five partitions: ND4, cytb, tRNAs, NT3, DNAH3), which allowed RAxML to calculate and apply the most appropriate gamma distribution parameter to each partition separately. Nodal support for ML was provided by rapid bootstrapping (1000 pseudoreplicates), and bootstrap values ≥0.70 were considered strongly supported (Hillis and Bull, 1993).

Bayesian analyses were conducted with the computer program MrBayes (Huelsenbeck and Ronquist, 2001) on a partitioned alignment using the reversible-jump Markov chain Monte

Carlo algorithm (mixed model), which avoids the risk of acquiring misleadingly high posterior probabilities at the nodes of hard or nearly hard polytomies due to their arbitrary resolution (Lewis et al., 2005). Each of the four protein coding genes in the alignment was partitioned by codon position with one partition including the first and second positions and another including the third position for a total of nine partition schemes (the three tRNAs were not partitioned). Two independent runs were conducted simultaneously with four Markov chains (three heated and one cold) per run, and average standard deviation of the split frequencies below 0.01 were considered acceptable. Stationarity was determined to be reached visually using Tracer v1.5 (Rambaut and Drummond, 2009). The analysis ran for 17,000,000 generations while sampling trees every 1000 generations. Stationarity was reached after approximately 11,500,000 generations, after which the stanard deviation of the split frequencies dropped to 0.008. Therefore, I sampled the resulting 5000 trees from from the last 5 million generations (12–17 million generations), which should be a good representation of the posterior distribution of trees. The initial 12 million generations were discarded as burn-in, and a 50% majority rule consensus tree with estimates of Bayesian support was constructed using the remaining sampled trees. Posterior probabilities (PP) provided nodal support for Bayesian analyses, with PP values ≥0.95 considered strong support (Alfaro et al., 2003; Huelsenbeck and Rannala, 2004; Mulcahy et al., 2011).

I conducted a weighted parsimony (WP) analysis using a tri-level weighting scheme that incorporated three different levels of information on the structure and inferred function of nucleotide substitutions (Benabib et al., 1997; Flores-Villela et al., 2000; Jadin et al., 2011). Transitions were given a weight of 1, transversions were given a weight of 2, and any nucleotide substitution that caused an amino-acid substitution was weighted +1 more (Kjer et al., 2007; Jadin et al., 2011).

Parsimony (UP and WP) analyses were conducted in the program TNT (Goloboff et al., 2008). Distance (NJ) analyses were performed in PAUP* (Swofford, 2002). Nodal support for

UP and WP was provided by bootstrap ratcheting using the New Technology algorithm (2000 pseudoreplicates). Because all four analyses produced similar tree topologies, only the ML tree is shown with support values for ML, WP, and Bayesian analyses (Fig. 3.1).

3.3 Results

The ML analysis resulted in a best likelihood score of -63458.181332. The unweighted parsimony analysis resulted in five equally parsimonious trees with a length of 14,527. The weighted parsimony analysis resulted in five equally parsimonious trees with a length of 20,615. Bayesian posterior probability support values ≥95 almost always corresponded to ML bootstrap support values ≥70. Parsimony and distance methods did not strongly support any relationships not strongly supported on the Bayesian tree. However, the WP tree contained more strongly-supported clades than the UP tree, and both parsimony trees contained more strongly-supported clades than the NJ tree. Figure 3.1 shows the best ML tree for the Dipsadini.

3.3.1 Monophyly of the Subfamily Dipsadinae

Nodal support is presented as posterior probabilities/ML bootstrap/weighted parsimony bootstrap/unweighted parsimony bootstrap/NJ bootstrap for nodes with posterior probabilities ≥ 80% and for bootstrap support ≥ 50%. A dash (-) denotes support below the cutoff value. The monophyly of the subfamily Dipsadinae was strongly supported (97/79/-/-/-), with *Synophis* as the most basal genus.

3.3.2 Intergeneric Relationships among the Dipsadinae

The paraphyly of the tribe Dipsadini with respect to the genus *Geophis* was strongly supported by Bayesian and ML analyses, but not by Parsimony or NJ analyses (94/86/58/-/-). A clade consisting of *Ninia* + *Chersodromus* as sister to the Dipsadini + *Geophis* clade was strongly supported (95/99/-/78/-). Sister to the *Ninia* + *Chersodromus* + Dipsadini + *Geophis* clade was the genus *Atractus* (95/87/68/-/-). Sister to all of these taxa, but with weak support (89/64/60/-/-), was a well-supported clade consisting of *Adelphicos* and *Cryophis* (100/86/70/-

/74). Sister to all of these taxa with strong support (95/88/91/-/-) was a well-supported clade consisting of *Hydromorphus* and *Tretanorhinus* (100/100/100/99/100). A *Leptodeira* + *Imantodes* clade was well supported (98/96/99/73/87), as was a *Hypsiglena* + *Pseudoleptodeira* clade (100/99/90/-/82). The placement of *Nothopsis* as sister to the *Hypsiglena* + *Pseudoleptodeira* clade was weakly supported by the Bayesian analysis (91/51/-/-/-). The *Leptodeira* + *Imantodes* clade formed a polytomy with the ((*Hypsiglena* + *Pseudoleptodeira*) + *Nothopsis*) clade. However, a large clade containing the Dipsadini + *Geophis*, *Ninia* + *Chersodromus*, *Atractus*, *Adelphicos* + *Cryophis*, *Hydromorphus* + *Tretanorhinus*, *Leptodeira* + *Imantodes*, *Hypsiglena* + *Pseudoleptodeira*, and *Nothopsis* was well-supported (97/69/70/-/-). Sister to this entire clade (97/35/-/-/-) was a large clade (100/-/-/-/-) containing seven genera of which *Urotheca* was sister to *Pliocercus* (100/100/100/100/100), *Rhadinaea* was sister to the *Urotheca* + *Pliocercus* clade (99/66/-/-/64), *Coniophanes* was sister to the *Rhadinaea* + *Urotheca* + *Pliocercus* clade (100/96/-/-/78), *Trimetopon* was sister to the *Coniophanes* + *Rhadinaea* + *Urotheca* + *Pliocercus* clade (98/-/-/-/-), which was sister to *Amastridium* + *Chapinophis* (99/-/-/-/-). However, a *Trimetopon* + *Chapinophis* clade was weakly supported by NJ the analysis (-/-/-/-/60). Furthermore, the genus *Pliocercus* appears to render the genus *Urotheca* paraphyletic (100/100/100/99/100). Sister to this entire clade (97/76/-/-/-) is a clade (98/75/-/-/-) containing two pairs of sister taxa: a *Rhadinophanes* + *Tantalophis* clade (100/100/100/99/100), and an *Enulius* + *Enuliophis* clade (100/100/97/-/62). The genus *Synophis* was sister to this entire clade and basal to the subfamily (97/79/-/-/-).

The results recovered strong support for a monophyletic subfamily Xenodontinae (100/82/63/-/-), but the subfamilies Dipsadinae and Xenodontinae as sister clades were not supported with posterior probabilities or bootstrap support. However, several relationships within the Xenodontinae were supported, including a *Helicops* + *Hydrops* clade (100/98/96/50/-), an *Oxyrhopus* + *Xenoxybelis* clade (96/78/63/-/-), and an *Alsophis* + *Arrhyton* clade (100/98/86/67/99). The Bayesian tree placed the genus *Xenodon* as sister to the *Alsophis* +

Arrhyton clade, but with weak support (87/-/-/-/-). The subfamily Carphophiinae was recovered in all analyses except the neighbor joining analysis, but it never received nodal support above the cutoff values. Within the Carphophiinae, however, the results supported a *Carphophis* + *Farancia* clade (100/95/86/-/-).

3.4 Discussion

3.4.1. Monophyly of the subfamily Dipsadinae and intergeneric relationships

The results of this study support the monophyly of the subfamilies Dipsadinae and Xenodontinae. However, support for these subfamilies as a monophyletic group was very low. This could be due to the low sampling of the Xenodontinae relative to the Dipsadinae. Because the focus of this study was on relationships among the Dipadinae, my taxon sampling was strongly biased towards this subfamily. However, several other studies with sampling biased toward xenodontines provide support for the sister relationship between these two large subfamilies (*e.g.*, Vidal et al., 2010; Grazziotin et al., 2012).

Given that the relationships among the Dipsadini are discussed in detail in Chapter 2 of this dissertation, I will discuss only the intergeneric relationships here. These results strongly support a paraphyletic Dipsadini with respect to *Geophis*, suggesting that the genus *Geophis* should be added to the tribe Dipsadini. With *Geophis* included, the Dipsadini is a strongly-supported monophyletic group. *Geophis* forms a well-supported clade with *Tropidodipsas sartorii* and *T. annuliferus*. Given that *Tropidodipsas fasciata* is the type species for the genus, the generic name stays with that clade, which includes *T. philippii*. Because the genus name *Geophis* (Wagler, 1830) precedes the genus *Tropidodipsas* (Günther, 1858), *T. sartorii* and *T. annuliferus* could be synonymized with *Geophis* to become *Geophis sartorii* and *G. annuliferus*. Alternatively, *T. sartorii* and *T. annuliferus* could each be assigned to new genera, which may be a more appropriate solution given the relatively old age of the divergences among these three species. *Tropidodipsas fischeri*, *Dipsas gaigeae*, and *Sibon sanniolus* appear to be distinct from other *Tropidodipsas*, *Dipsas*, and *Sibon* species and may need to be placed into

new genera. However, the analyses failed to place these taxa with any support, likely due to extremely shallow internal nodes. The results suggest that the genus *Sibynomorphus* is deeply nested within *Dipsas* rendering *Dipsas* paraphyletic, and a *Dipsas* + *Sibynomorphus* clade is strongly-supported. The two *Sibynomorphus* clades are more closely related to various *Dipsas* species than they are to each other, suggesting that *Sibynomorphus* is also paraphyletic. The two well-supported *Sibynomorphus* clades in this study correspond with the "northern" (*S. oligozonatus* and *S. petersi*) and "southern" (*S. mikanii* and *S. turgidus*) clades identified by Cadle (2007), with *S. oligozonatus* and *S. petersi* (both from Ecuador) consistently grouping separately from *S. mikanii* (from Brazil) and *S. turgidus* (from Bolivia). Therefore, in order to maintain a monophyletic *Dipsas*, I recommend that the genus *Sibynomorphus* be synonymized with the genus *Dipsas*. The *Dipsas* clade (*sensu stricto*) is sister to the Dipsadini, suggesting that these snakes diverged very early from all other Dipsadines. This agrees with variation in feeding behaviors of the Dipsadini in that *Dipsas* and *Sibynomorphus* extract snails using alternating movements of their mandibles, whereas *Sibon* and *Tropidodipsas* extract snails by dragging and snagging or wedging the shell on surface irregularities (Chapter 1 of this dissertation).

Sister to the Dipsadini is a clade containing the genera *Ninia* and *Chersodromus*. A close relationship between these genera was proposed by Zaher (1999) based on characteristics of the Harderian and infralabial glands. Ingrasci (2011) also suggested close affinities between *Ninia* and *Chersodromus* based on mitochondrial and nuclear data. The results placed *Atractus* as sister to the *Ninia* + *Chersodromus* + Dipsadini (including *Geophis*) clade. Zaher (1999) considered *Atractus* and *Adelphicos* closely related due to the presence of a highly-developed cervicomandibularis muscle in both genera. The results of this study, however, suggest that *Adelphicos* is sister to *Cryophis*, and that this clade is perhaps sister to the *Atractus* + *Ninia* + *Chersodromus* + Dipsadini (including *Geophis*) clade. However, this placement of the *Adelphicos* + *Cryophis* clade was not strongly supported (PP = 89). Thus, it is

not clear whether *Atractus* and *Adelphicos* have a similar cervicomandibularis muscle arrangenment due to shared ancestry or because of convergent adaptation to fossoriality. A close relationship between *Cryophis* and *Adelphicos* is surprising given that *Adelphicos* is fossorial, aglyphous, and feeds on invertebrates (Cadle and Greene, 1993), whereas *Cryophis* is semiarboreal, opisthoglyphous, and feeds on vertebrates (Bogert and Duellman, 1963; Mulcahy, 2007). Bogert and Duellman (1963) proposed that this species was most closely related to either *Leptodeira* or *Tantalophis*. Given that taxa higher in the dipsadine tree all feed on invertebrates and taxa lower in the tree all feed primarily on vertebrates, it appears that the divergence of *Cryophis* and *Adelphicos* may be involved with this major dietary transition.

The results placed *Hydromorphus* and *Tretanorhinus* as sister taxa with strong support. This is not surprising given that, in general, both genera have similar distributions throughout Central America and both are semiaquatic inhabitants of slow-moving bodies of freshwater (Campbell, 1998; Lee, 2000).

The genera *Leptodeira* and *Imantodes* formed well-supported sister taxa. However, I did not include in this study *Imantodes inornatus*, which has prevented the genus *Imantodes* from being monophyletic in previous studies (Mulcahy, 2007; Daza et al., 2009). The genera *Pseudoleptodeira* and *Hypsiglena* also formed sister taxa, and *Nothopsis* was placed as sister to this *Pseudoleptodeira* + *Hypsiglena* clade. The ML analyses provided weak support (ML bootstrap = 51) that these two groups formed a clade. However, these two clades collapsed into a polytomy with the Bayesian analysis. Nonetheless, these results support the inclusion of *Nothopsis* in the "nightsnake" clade (*Pseudoleptodeira* + *Hypsiglena*) of Mulcahy et al. (2011), and not in the Leptodeirini clade proposed by Vidal et al. (2010).

Although I only included two *Urotheca* and one *Pliocercus* species in this study, the genus *Urotheca* was paraphyletic with respect to the genus *Pliocercus* with strong support. Savage and Crother (1989) synonymized *Pliocercus* with *Urotheca*. However, Myers and Cadle (1994) later removed *Pliocercus* from synonymy with *Urotheca*. The results of this study

suggest that *Pliocercus* may need to be synonymized with *Urotheca*, and that *Rhadinaea* is sister to *Urotheca*. However, more complete taxon sampling of *Pliocercus* and *Urotheca* is needed to verify this conclusion. The genus *Coniophanes* formed the sister taxon to the *Rhadinaea* + *Pliocercus* + *Urotheca* clade with strong support, and the genus *Trimetopon* formed the sister taxon to the *Coniophanes* + *Rhadinaea* + *Pliocercus* + *Urotheca* clade with strong support. A close relationship among these similar-looking genera is not surprising and has previously been suggested by Myers (1974), who suggested a close relationship among *Rhadinaea*, *Coniophanes*, *Pliocercus*, and *Trimetopon*.

Sister to the *Trimetopon* + *Coniophanes* + *Rhadinaea* + *Pliocercus* + *Urotheca* clade is a strongly-supported clade containing the genera *Amastridium* and *Chapinophis*. This strong sister relationship is somewhat surprising given the numerous differences between the two genera. *Amastridium* inhabits tropical wet forest habitat between 150–650 m elevation and has a distinct canthal ridge, whereas *Chapinophis* inhabits cloud forest habitat between 1829–2300 m elevation and has a rounded canthus (Campbell, 1998; Campbell and Smith, 1998). Furthermore, *Amastridium* has enlarged posterior maxillary teeth with a diastema and a noncapitate hemipenis (Wilson and Myers, 1969; Savage, 2002), whereas *Chapinophis* has reduced posterior maxillary teeth with no diastema and a bicapitate hemipenis (Campbell and Smith, 1998). However, both genera are found in Guatemala, both are relatively small (generally <75.0 cm total length), and both have a dark body color with an unusual pattern consisting of a linear series of small light dorsolateral spots or dashes (Campbell, 1998; Campbell and Smith, 1998; Savage, 2002). *Chapinophis* has dentition that is more similar to the tooth condition found in *Adelphicos*, *Atractus*, *Geophis* and *Sibon* than in *Amastridium*, *Trimetopon*, *Tantalophis*, and *Rhadinophanes*; however, *Chapinophis* shares several distinct hemipenial characteristics with *Rhadinophanes* and *Tantalophis* (Campbell and Smith, 1998). *Chapinophis* is the only member of the clade including *Amastridium*, *Trimetopon*, *Coniophanes*, *Rhadinaea, Pliocercus*, and *Urotheca* that lacks enlarged posterior maxillary teeth with a

diastema. Givent the tree topology, the most parsimonius explanation for this is that the common ancestor of this clade had enlarged posterior maxillary teeth with a diastema, but that this condition was lost in *Chapinophis* resulting in dentition convergently similar to members of the goo eaters. This convergence is likely why Campbell and Smith (1998) had difficulty identifying the phylogenetic affinities of this genus. Information regarding the diet of *Chapinophis* may provide additional insight into the selective pressures maintaining its unusual dentition.

The genera *Tantalophis* and *Rhadinophanes* form well-supported sister taxa to a clade containing *Enulius* and *Enuliophis*. Myers and Campbell (1981) proposed a close relationship between *Tantalophis* and *Rhadinophanes* based on similar unusual hemipenial morphology, even though these genera are apparently allopatric and appear very dissimilar in many other ways including color pattern, pupil shape, body size, and cranial osteology. McCranie and Villa (1993) placed *Enulius sclateri* into the new genus *Enuliophis* based on differences in the structure of the maxilla, total body length, and hemipenial morphology. Some authors (*e.g.*, Savage, 2002) question the validity of this decision and argue that Zaher (1999) demonstrated similar levels of hemipenial variation within individual species. However, the results of this study provide strong support that these two genera are valid and sister taxa. Furthermore, the long branches of each taxon suggest that these genera are highly divergent from one another.

Although several dipsadine genera are missing from this study, I can still propose some hypotheses regarding their phylogenetic placements based on the relationships of purportedly related species. Jenner (1981) placed *Diaphorolepis* and *Synophis* into the tribes Diaphorolepini and Phylodryadini, respectively. Jenner did not, however, include *Emmochliophis* in her study. Hillis (1990) noticed that the genera *Emmochliophis*, *Diaphorolepis* and *Synophis* all share similar hemipenial morphology, and suggested that *Emmochliophis* and *Synophis* are sister taxa that in turn are sister to *Diaphorolepis*. Given the basal placement of *Synophis*, it seems likely that *Emmochliophis* and *Diaphorolepis* would

share similar basal positions relative to other dipsadines. Harvey et al. (2008) revived *Plesiodipsas* from synonymy with *Dipsas* and hypothesized the placement of this species within the Dipsadini as either sister to *Dipsas* or sister to the Dipsadini. Köhler et al. (2001) described the genus *Omoadiphas* from Honduras and proposed affinities of the new genus to members of the "goo-eaters" group of Cadle and Greene (1993). Although differences between *Omoadiphas* and other "goo-eaters" appear to be small, Köhler et al. (2001) suspected this genus to be most closely related to the genera *Atractus*, *Adelphicos*, *Chapinophis*, *Chersodromus*, *Geophis*, and *Ninia*. Tissues will likely be needed to reliably place this species relative to other dipsadines. Myers and Cadle (1994) rescued *Psomophis* from synonymy with *Rhadinaea*, but they were unsure of its close phylogenetic affinities. Myers (1974) suggested that *Taeniophallus* had close affinities to *Rhadinaea*. However, Grazziotin et al. (2012) demonstrated that *Psomophis* and *Taeniophallus* are nested in the subfamily Xenodontinae.

3.4.2. Dietary shift and adaptive radiation

The results of this study support the hypothesis that a dietary shift occurred in the Dipdadinae lineage from relatively ancestral species feeding primarily on vertebrates to derived species feeding on invertebrates (Fig. 3.2). This dietary shift appears to have occurred during the Miocene between about 10–20 million years ago (Daza et al., 2009) and may have occurred between common ancestors of *Cryophis* and *Adelphicos*. This suggests that the dietary shift may have occurred in northern Middle America and southern Mexico, and may have occurred among taxa living in cool, wet, cloud forest habitat between 1100 and 2000 meters. In this habitat, vertebrate prey are likely more difficult to find than invertebrate prey. Although *Adelphicos* feeds on earthworms (Cadle and Greene, 1993), little is known of the diet of *Cryophis*. However, the fact that it is arboreal and has enlarged postmaxillary teeth that are separated from anterior teeth by a diastema (Bogert and Duellman, 1963) suggests that *Cryophis* feeds at least in part on vertebrates. More detailed information on the breadth of prey types consumed by *Cryophis* could help better understand the ecology of the dietary shift.

The tree topology of dipsadine snakes is consistent with the idea that invertebrate feeders experienced an adaptive radiation subsequent to the dietary shift (Fig. 3.2). Rapid speciation events are often represented topologically as relatively short branches (or even polytomies) at internal nodes (Schluter, 2000), and this pattern occurs in the tree only after the dietary shift (Fig. 3.2). Furthermore, the number of species more than tripled after the dietary shift. However, the radiation does not appear to be due simply to an invertebrate diet, but rather also to dietary specialization. The shortest internal branches are associated with the gastropod specialists and not for the earthworm-eating species that are sister to them (Fig. 3.2). Thus, an adaptive radiation in this lineage appears to be driven at least in part by dietary specialization. As the most speciose genus of dipsadine snakes, *Atractus* may have also experienced an adaptive radiation. This radiation may also be due to the dietary shift, but not necessarily dietary specialization. *Atractus* feeds on earthworms (Cadle and Greene, 1993), which may not require morphological specialization to consume. The dietary shift likely offered these snakes a significant ecological opportunity to exploit a wealth of resources with little to no competition from other snakes. Bogert and Duellman (1963) noted that the snakes *Pliocercus elapoides*, *Coniophanes imperialis*, *Drymobius chloroticus*, and *Tantilla schistosa* were observed at or near the locality where they collected *Cryophis*. Of these, only *Tantilla* feeds on invertebrates, and it feeds primarily or exclusively on centipedes (Campbell, 1998). Similarly, feeding predominantly on gastropods would have offered species the opportunity to exploit an additional wealth of resources with even less competition. In addition to snakes, gastropods have many predators including birds and mammals (Allen, 2004), beetles (Symondson, 2004), dipteran flies (Coupland and Barnes, 2004), planarians (Winsor et al., 2004), gastropods (Barker and Efford, 2004), myriopods (Barker, 2004), spiders (Pollard and Jackson, 2004) and mites (Fain, 2004). However, it is not known to what extent these predators are competing with Neotropical gastropod-eating snakes for this resource. Presumably, consuming gastropods benefited from the evolution of many morphological modifications, which drove morphological

divergence between the Dipsadini and its sister taxa. These hypotheses need further testing using rigorous quantitative and statistical methods such as ancestral state reconstruction and Bayesian analyses of temporal variation in divergence rates.

Using tree topology and information on the feeding behavior and diet of dipsadine taxa, I propose a scenario of how gastropod specialization might have evolved in the Dipsadini.

3.4.3. Evolutionary scenario for dietary specialization in the Dipsadini

The ancestral diet for the Dipsadini was likely earthworms, given that they appear to comprise the majority of the diet in all other invertebrate-feeding dipsadines (*i.e.*, *Adelphicos*, *Atractus*, *Chersodromus*, and *Ninia*) (Cadle and Greene, 1993). Furthermore, some members of the Dipsadini likely also include earthworms in their diet in part (*e.g.*, *Tropidodipsas philippii*), whereas some eat exclusively earthworms (*e.g.*, *Tropidodipsas fischeri* and *Geophis*) (see Chapter 1). A dietary transition likely occurred from feeding predominantly on earthworms to incorporating slugs and occasionally small snails that were swallowed whole. Species of *Ninia* feed on earthworms and slugs, and they are known to consume small snails whole (Cadle and Greene, 1993; Smith, 1994; Lee, 2000). Furthermore, *Ninia* is sister to the Dipsadini. This transition is consistent with the Correlated Occurrence hypothesis, in which a novel prey item is more likely to be encountered if its density is correlated with that of some typical food of the animal (de Queiroz and Rodriguez-Robles, 2006). Slugs, snails and earthworms can be found in similar habitats, and they may have shared surface chemistries (Arnold, 1980, 1981). Furthermore, similarities in cranial osteology between *Ninia* and members of the Dipsadini (Scott, 1967) suggest that the tooth and jaw morphology needed for feeding on earthworms likely initially served as exaptations for feeding on gastropods. Snakes foraging for earthworms likely often encounter slugs and snails, and over time some snake populations may have began to incorporate a larger proportion of gastropods into their diet. This may have occurred in karst limestone habitats, which often support large gastropod population densities and species diversity (Schilthuizen et al., 2003). In Mexico, areas with large amounts of karst limestone

(*e.g.*, the Yucatán Peninnsula) currently support relatively large species diversities of snail-eating snakes, with some species being endemic to those areas (Lee, 2000).

Locating earthworms likely requires active foraging using primarily or entirely chemosensory cues, and snake genera that feed primarily on earthworms (*e.g.*, *Adelphicos*, *Atractus*, and *Geophis*) typically exhibit adaptations for fossoriality including flattened heads, smooth scales, and relatively small eyes. However, gastropods are typically more mobile above ground than earthworms and often crawl on the ground as well as in trees where they can be located visually. Thus, it may be energetically less costly to rely on vision to locate the movements of gastropods than to actively forage for earthworms. In some wet, high-elevation habitats, *Ninia* and *Tropidodipsas fischeri* can be found in trees where they are presumeably feeding on earthworms that also live in trees (e.g., in bromeliads). As the Dipsadini evolved gastropod specialization, the teeth and jaw morphology became modified for more efficient feeding. In addition, these snakes retained the plesiomorphic characteristic of having relatively large eyes from their vertebrate-feeding ancestors, and vision remained involved in prey location. Thus, gastropod-eating snakes could become sit-and-wait predators rather than active foragers (Sheehy et al., 2011; see Chapter 1). Once gastropods became the principle prey type, specialization on snails resulted in reduced competition with earthworm eaters and allowed some snail-eaters to adopt arboreal lifestyles with very little competition. Arboreality would have likely excluded earthworms from the diet leading to a strong dependence on gastropod prey, which could have provided intense selective pressure for efficiently locating and extracting snails. The most arboreal genus (*Dipsas*) extracts snails using solely mandibular movements and evolved a suite of morphological adaptations for efficient snail extraction (Peters, 1960), whereas *Sibon* and *Tropidodipsas* snag and pull snail shells against substrate irregularities to extract the snails (see Chapter 1). The latter method may be easier on the ground than in trees. Reduced competition with other earthworm-eating dipsadine snakes was perhaps a tradeoff for consuming a food with a lower nutrient value that is only seasonally

available in some regions (*e.g.*, the Pacific versant of central Mexico). This selective pressure may have driven gastropod specialization to further increase feeding efficiency, and may have selected for additional adaptations pertaining to digestive physiology and metabolic rate that would allow gastropod feeders to maximize nutrient absorption and to survive extended periods without food (Britt, et al., 2006). *Dipsas catesbyi* is arboreal and the second most abundant snake species found within a Neotropical snake assemblage in Cusco Amazónico, Peru (Duellman, 2005), suggesting that the combination of arboreality and gastropod monophagy is an extremely successful life history strategy in some regions. Cis- and trans-Andian members of the genus *Dipsas* secondarily, and likely independently, became more terrestrial and were previously grouped into the genus *Sibynomorphus*.

3.4.4. Secondary structure of tRNA

Although it is beyond the scope of this study, I noticed several interesting patterns in the tRNA histidine (His) sequence that appear to be phylogenetically informative and, as such, warrant mention. The stop codon sequence for the gene ND4 is TAG for all species of *Dipsas* (except *D. gaigeae*), for all *Sibynomorphus*, and for *Sibon nebulatus* from South America and Panama. However, in these species the terminal G of the stop codon is also the beginning of the tRNA His. In all other Dipsadine taxa, and in *S. nebulatus* from Central America north of Panama, the stop codon sequence is TAA and the tRNA His begins with a G afterwards with no overlapping. In all *Tropidodipsas*, there is an additional A between the TAA stop codon and the G at the beginning of His, and in *D. gaigeae* there is an additional G between the stop codon and the G in His. Seemingly in all other dipsadine taxa, the tRNA His begins with a G immediately following the stop codon sequence TAA. These sequence changes are interesting given that histidine is an essential amino acid. Because these differences are at the beginning of the His sequence, they should be part of a stem region and should be conserved relative to the loop regions. Thus, these sequence differences potentially confer some advantage in terms of secondary structure of the tRNA molecule.

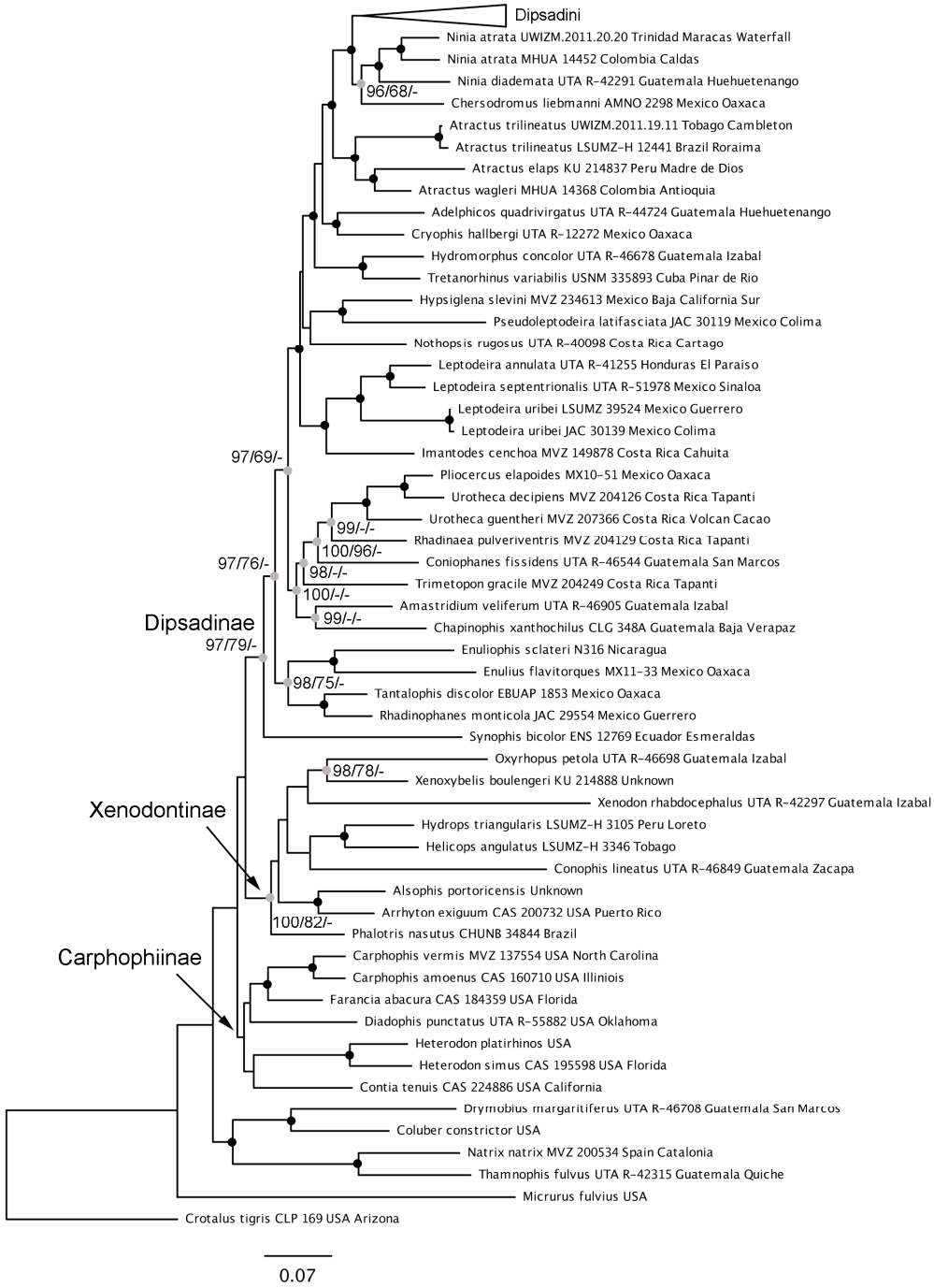

Figure 3.1 Phylogeny of the Dipsadinae using the best ML tree. Black circles denote strong nodal support (≥0.95 PP and ≥0.70 ML and WP bootstrap). Gray circles indicate strong support by some but not all methods (PP/ML/WP). A dash (-) indicates support below the cutoff value.

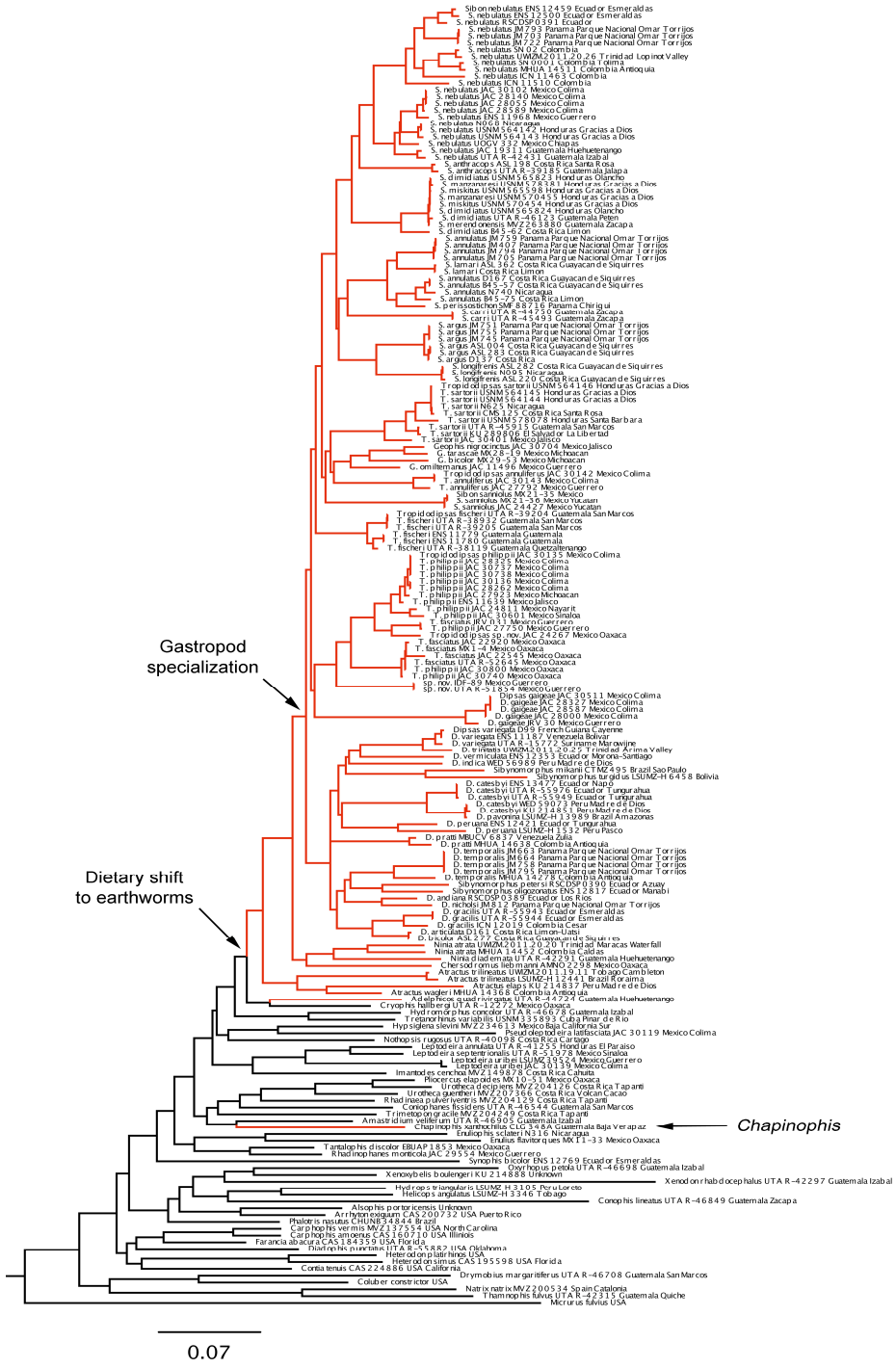

Figure 3.2 Phylogeny of the Dipsadinae showing the transition from feeding on vertebrates (black) to feeding on invertebrates (red). *Chapinophis* may have evolved a diet of invertebrates independently.

APPENDIX A

SPECIMEN DATA FOR SNAKES USED IN FEEDING BEHAVIOR STUDIES

Dipsas gaigeae MEXICO**: Colima**: road from Comala to Minatitlán, 496 m, JAC 30083; road from HWY 54 to Ixtlahuacan, 352 m, JAC 30511; road from HWY 54 to Ixtlahuacan, JAC 30673.

Sibon nebulatus MEXICO**: Colima**: road from Comala to Minatitlán, 739 m, JAC 30102; road from Ixltahuacan to La Salada, 301 m, JAC 30124; VENEZUELA**: Amazonas**: Puerto Ayacucho, UTA R-60230.

Tropidodipsas annuliferus MEXICO**: Colima**: road from Comala to Minatitlán, 589 m, JAC 30142; road from Comala to Minatitlán, 552 m, JAC 30143.

Tropidodipsas philippii MEXICO**: Colima**: road from Comala to Minatitlán, 410 m, JAC 30141; road from Villa de Alvarez to Minatitlán, JAC 30539; road from HWY 54 to Ixtlahuacan, 281 m, JAC 30737; road from HWY 54 to Ixtlahuacan, 321 m, JAC 30738; **Oaxaca:** road between Lagunas and Ajal, 201 m, JAC 30740; road between Lagunas and Ajal, 182 m, JAC 30800.

Leptodeira septentrionalis MEXICO**: Colima**: road from Comala to Minatitlán, 701 m, JAC 30436; **Veracruz**: Coetzala, road to Coexapotitla, 10 min by car from the Municipal capital, JAC 30886.

APPENDIX B

PROPOSED SYNONOMY AND TAXONOMY FOR DIPSADINE SNAKE GENERA AND DIPSADINI SPECIES

Family **Colubridae** Cope

Colubridae Cope, 1886. Proc. Amer. Philos. Soc. 23:479.

Type genus: *Coluber* Linnaeus.

Subfamily **Dipsadinae** Bonaparte

Dipsadinae Bonaparte, 1840. Memorie della Reale Accademia della Scienze di Torino 2:385–456. Contents (35 genera): *Adelphicos*, *Amastridium*, *Atractus*, *Chapinophis*, *Chersodromus*, *Coniophanes*, *Cryophis*, *Diaphorolepis*, *Dipsas*, *Emmochliophis*, *Enuliophis*, *Enulius*, *Geophis*, *Hydromorphus*, *Hypsiglena*, *Imantodes*, *Leptodeira*, *Ninia*, *Nothopsis*, *Omoadiphas*, *Plesiodipsas*, *Pseudoleptodeira*, *Rhadinaea*, *Rhadinophanes*, *Sibon*, *Tantalophis*, *Tretanorhinus*, *Trimetopon*, *Tropidodipsas*, *Urotheca*, Gen. nov. 1, Gen. nov. 2, Gen. nov. 3, Gen. nov. 4., Gen. nov. 5.

Tribe **Diaphorolepini**

Contents: *Diaphorolepis*, *Emmochliophis* and *Synophis*. Hillis (1990) concluded that the genera *Emmochliophis*, *Diaphorolepis* and *Synophis* all share similar hemipenial morphology, and suggested that *Emmochliophis* and *Synophis* are sister taxa that in turn are sister to *Diaphorolepis*. Thus, *Diaphorolepis*, *Emmochliophis* and *Synophis* form a tribe that is sister to other dipsadines in the subfamily.

Genus ***Diaphorolepis*** Jan

Diaphorolepis Jan, 1863. Elenco Sistema Ofidi:94.

Type species: *Diaphorolepis wagneri* Jan, 1863.

Diaphorolepis (2 species):

Diaphorolepis laevis Werner, 1923

Diaphorolepis wagneri Jan, 1863

Genus ***Emmochliophis*** Fritts and Smith

Synophis Peracca, 1896. Boll. Mus. Zool. Anat. Comp. Torino 11(266):1.

Type species: *Synophis bicolor* Peracca, 1896.

Emmochliophis Fritts and Smith, 1969. Trans. Kansas Acad. Sci. 72:60–66.

Type species: *Emmochliophis fugleri* Fritts and Smith, 1969.

Emmochliophis (2 species):

Emmochliophis fugleri Fritts and Smith, 1969

Emmochliophis miops (Boulenger, 1898)

Genus ***Synophis*** Peracca

Synophis Peracca, 1896. Boll. Mus. Zool. Anat. Comp. Torino 11(266):1.

Type species: *Synophis bicolor* Peracca, 1896.

Synophis (4 species):

Synophis bicolor Peracca, 1896

Synophis calamitus Hillis, 1990

Synophis lasallei (Maria, 1950)

Synophis plectovertebralis Sheil and Grant, 2001

Tribe **Dipsadini** Dowling and Duellman, 1978

Contents: *Dipsas*, *Geophis*, *Plesiodipsas*, *Sibon*, *Tropidodipsas*, Gen. nov. 1, Gen. nov. 2, Gen. nov. 3, Gen. nov. 4, Gen. nov. 5. Large percent pairwise differences among cytb sequences of

some *Geophis* species groups suggest that the genus may be paraphyletic, which would potentially result in some *Geophis* species being removed from this tribe.

Genus ***Dipsas*** Laurenti

Dipsas Laurenti, 1768. Synops. Rept.:89.

Type species: *Dipsas indica* Laurenti, 1768.

Bungarus Oppel (partim; non *Bungarus* Daudin, 1803), 1810. Ann. Mus. Hist. Nat. Paris 13:391.

Type species: none designated.

Sibynomorphus Fitzinger, 1843. Syst. Rept.:27.

Type species: *Dipsas mikanii* Schlegel, 1837.

Pholidolaemus Fitzinger, 1843. Syst. Rept. 1:27.

Type species: *Coluber bucephala* Shaw, 1802.

Dipsadomorus Duméril, 1853. Mém. Acad. Sci., Paris 23:467.

Type species: *Dipsas indica* Laurenti, 1768.

Leptognathus Duméril (non *Leptognathus* Swainson, 1839), 1853. Mém. Acad. Sci., Paris 23:467.

Type species: none designated.

Stremmatognathus Duméril, 1853. Mém. Acad. Sci., Paris 23:468.

Type species: *Coluber catesbeii* Sentzen, 1796.

Anholodon Duméril, Bibron and Duméril, 1854. Erp. Gén. 7:1165.

Type species: *Sibynomorphus mikanii* Schlegel, 1837.

Cochliophagus Duméril, Bibron and Duméril, 1854. Erp. Gén. 7:478.

Type species: *Sibynomorphus inaequifasciatus* Duméril and Bibron, 1854.

Neopareas Günther, 1895. Biol. Centr. Amer. Rept. 178.

Type species: *Neopareas bicolor* Günther, 1895.

Pseudopareas Boulenger, 1896. Cat. Snakes Brit. Mus. 3:462.

Type species: *Sibynomorphus vagus* Jan, 1863.

Heterorhachis Amaral, 1923. Proc. New Engl. Zool. Club 8:94.

Type species: *Heterorhachis poecilolepis* Amaral, 1923.

Dipsas (49 species):

Dipsas albifrons (Sauvage, 1884). Bull. Soc. Philomath., Paris (7)8:145.

Dipsas alternans (Fischer, 1885). V. Herpetol. Bemerkungen. Jahrb. Hamburg. Wiss. Anst. 2:105.

Dipsas andiana (Boulenger, 1896). Cat. Snakes Brit. Mus. 3:452.

Dipsas articulata (Cope, 1868). Proc. Acad. Nat. Sci. Philad. 20:135.

Dipsas baliomelas (Harvey, 2008). Herpetologica 64(4):423.

Dipsas bicolor (Günther, 1895). Biol. Cent. Am. Rept. Batr.: 178.

Dipsas boettgeri (Werner, 1901). Abh. Ber. K. Zool. Anthro. Ethno. Mus. Dresden 9:11.

Dipsas brevifacies (Cope, 1866). Proc. Acad. Nat. Sci. Philad. 1866:127.

Dipsas bucephala (Shaw, 1802). Syst. Nat. Hist. 3(2):422.

Dipsas catesbyi (Sentzen, 1796). Meyer's Zool. Arch. 2:66.

Dipsas chaparensis Reynolds and Foster, 1992. Herp. Monog. 6:101.

Dipsas copei (Günther, 1872). Ann. Mag. Nat. Hist. (4)9:30.

Dipsas elegans (Boulenger, 1896). Cat. Snakes Brit. Mus. 3:452.

Dipsas ellipsifera (Boulenger, 1898). Proc. Zool. Soc. London 1898:117.

Dipsas gracilis (Boulenger, 1902). Ann. Mag. Nat. Hist. (7)9:57.

Dipsas inaequifasciata (Duméril, Bibron and Duméril, 1854). Erp. Gén. 7:480.

Dipsas incerta (Jan, 1863). Elenco Sist. Ofid.:101.

Dipsas indica Laurenti, 1768. Synops. Rept.:90.

Dipsas infrenalis Rosen, 1905. Ann. Mag. nat. Hist. (7)15:181.

Dipsas latifasciata (Boulenger, 1913). Ann. Mag. Nat. Hist. (8)12:72.

Dipsas latifrontalis (Boulenger, 1905). Ann. Mag. Nat. Hist. (7)15:561.

Dipsas lavillai (Scrocchi, Porto and Rey). Rev. Brasil. Biol. 53:200.

Dipsas maxillaris (Werner, 1909). Zool. Jb. Abt. Syst. Okol. Geogr. 28(1909):279.

Dipsas mikanii Schlegel, 1837. Essai Physion. Serpens 2:277.

Dipsas neivai Amaral, 1926. Arch. Mus. Nac. Rio de Janeiro 26:108.

Dipsas neuwiedi (Ihering, 1910). Rev. Mus. Paulista 8:333.

Dipsas nicholsi (Dunn, 1933). Copeia 1933:193.

Dipsas oligozonata (Orcés and Almendáriz, 1989). Politecnica 14:63.

Dipsas oneilli (Rossman and Thomas, 1979). Occas. Pap. Mus. Zool. Luis St. Univ. 54:1.

Dipsas oreas (Cope, 1868). Proc. Acad. Nat. Sci. Philad. 20:109.

Dipsas pakaraima MacCulloch and Lathrop, 2004. Rev. Biol. Trop. 52(1):240.

Dipsas pavonina Schlegel, 1837. Essai Physion. Serpens 2:280.

Dipsas peruana (Boettger, 1898). Kat. Rept. Samml. Mus. Senckenb. Naturforsch. Ges. 2:128.

Dipsas petersi (Orcés and Almendáriz, 1989). Politecnica 14:58.

Dipsas polylepis (Boulenger, 1912). Ann. Mag. Nat. Hist. (8)10:422.

Dipsas pratti (Boulenger, 1897). Ann. Mag. Nat. Hist. (6)20:523.

Dipsas sanctijoannis (Boulenger, 1911). Ann. Mag. Nat. Hist. (8)7:24.

Dipsas sazimai Fernandes, Marquez and Argôlo, 2010. Zootaxa 2691:57–66.

Dipsas schunkii (Boulenger, 1908). Ann. Mag. Nat. Hist. (8)1:115.

Dipsas temporalis (Werner, 1909). Mitt. Naturhist. Mus. Hamburg 26:241.

Dipsas tenuissima Taylor, 1954. Univ. Kansas Sci. Bull. 26:771.

Dipsas turgidus (Cope, 1868). Proc. Acad. Nat. Sci. Philad. 1868:136.

Dipsas vagrans (Dunn, 1923). Proc. Biol. Soc. Wash. 36:187.

Dipsas vaga (Jan, 1863). Elenco Sist. Ofidi: 100.

Dipsas variegata (Duméril, Bibron and Duméril, 1854). Erp. Gén. 7:477.

Dipsas ventrimaculata (Boulenger, 1885). Ann. Mag. Nat. Hist. (5)16:87.

Dipsas vermiculata Peters, 1960. Misc. Publ. Mus. Zool. Univ. Mich. 114:65.

Dipsas viguieri (Bocourt, 1884). Bull. Soc. Philomath., Paris (7)8:136.

Dipsas williamsi (Carrillo de Espinoza, 1974). Publ. Mus. Hist. Nat. Javier Prado, Ser. A. (Zool) 24:1–16.

Genus ***Geophis*** Wagler

Catostoma Wagler, 1830. Nat. Syst. Amphib.:194.

Type species: *Catostoma chalybeum* Wagler, 1830.

Geophis Wagler, 1830. Nat. Syst. Amphib.: 342 (This was a substitute name for *Catostoma* Wagler [1830] to prevent confusion with the fish genus *Catostomus* Lesueur, 1817).

Type species: *Catostoma chalybeum*

Rhabdosoma Duméril, Mem. Acad. Sci. 23:440.

Type species: *Rhabdosoma semidoliatum* Duméril, Bibron and Duméril, 1854.

Colobognathus Peters, 1859. Monats. Akad. Wiss. Berlin 1859:275.

Type species: *Colobognathus hoffmanni* Peters, 1859.

Geophidium Peters, 1861. Monats. Akad. Wiss. Berlin 1861:923.

Type species: *Geophidium dubium* Peters, 1861.

Colophrys Cope, 1868. Proc. Acad. Nat. Sci. Phila. 1868:130.

Type species: *Colophrys rhodogastor* Cope, 1868.

Parageophis Bocourt, 1883. Miss. Sci. Mex., Rept.: 534.

Type species: *Rabdosoma semidoliatum* Duméril, Bibron and Duméril, 1854.

Dirosema Boulenger, 1894. Cat. Snakes Brit. Mus. 2:298.

Type species: *Geophis bicolor* Günther, 1868.

Geophis (48 species):

Geophis anocularis Dunn, 1920

Geophis bellus Myers, 2003

Geophis betaniensis Restrepo and Wright, 1987

Geophis bicolor Günther, 1868

Geophis blanchardi Taylor and Smith, 1939

Geophis brachycephalus (Cope, 1871)

Geophis cancellatus Smith, 1941

Geophis carinosus Stuart, 1941

Geophis chalybeus (Wagler, 1830)

Geophis championi Boulenger, 1894

Geophis damiani Wilson, McCranie and Williams, 1998

Geophis downsi Savage, 1981

Geophis dubius (Peters, 1861)

Geophis duellmani Smith and Holland, 1969

Geophis dugesii Bocourt, 1883

Geophis dunni Schmidt, 1932

Geophis fulvoguttatus Mertens, 1952

Geophis godmani Boulenger, 1894

Geophis hoffmanni (Peters, 1859)

Geophis immaculatus Downs, 1967

Geophis incomptus Duellman, 1959

Geophis isthmicus (Boulenger, 1894)

Geophis juarezi Nieto-Montes De Oca, 2003

Geophis juliai Pérez-Higareda, Smith and López-Luna, 2001

Geophis laticinctus Smith and Williams, 1963

Geophis laticollaris Smith, Lynch and Altig, 1965

Geophis latifrontalis Garman, 1883

Geophis maculiferus Taylor, 1941

Geophis mutitorques (Cope, 1885)

Geophis nasalis (Cope, 1868)

Geophis nephodrymus Townsend and Wilson, 2006

Geophis nigroalbus Boulenger, 1908

Geophis nigrocinctus Duellman, 1959

Geophis occabus Pavón-Vázquez, García-Vázquez, Blancas-Hernández and Nieto-Montes De Oca, 2011

Geophis omiltemanus Günther, 1893

Geophis petersii Boulenger, 1894

Geophis pyburni Campbell and Murphy, 1977

Geophis rhodogaster (Cope, 1868)

Geophis rostralis (Jan, 1865)

Geophis russatus Smith and Williams, 1966

Geophis ruthveni Werner, 1925

Geophis sallaei Boulenger, 1894

Geophis semidoliatus (Duméril, Bibron and Duméril, 1854)

Geophis sieboldi (Jan, 1862)

Geophis talamancae Lips and Savage, 1994

Geophis tarascae Hartweg, 1959

Geophis tectus Savage and Watling, 2008

Geophis zeledoni Taylor, 1954

Gen. nov. 1

Type species: *Dipsas gaigeae* (Oliver, 1937). Occas. Pap. Mus. Zool. Univ. Mich. 360:22. No generic names available through synonymy.

Gen. nov. 2

Type species: *Tropidodipsas fischeri* Fischer, 1885. Jahrb. Hamburg. Wiss. Anst. 2:95. No generic names available through synonymy.

Gen. nov. 3

Type species: *Tropidodipsas annuliferus* Boulenger, 1894. Cat. Snakes Brit. Mus. 2:297. No generic names available through synonymy.

Gen. nov. 4

Type species: *Tropidodipsas sartorii* Cope, 1863. Proc. Acad. Nat. Sci. Philad. 1863:100. No generic names available through synonymy.

Gen. nov. 5

Type species: *Sibon sanniolus* Cope, 1866. No generic names available through synonymy.

Genus ***Plesiodipsas*** Harvey, Rivas Fuenmayor, Caicedo Portilla, and Rueda-Alm

Plesiodipsas Harvey, Rivas Fuenmayor, Caicedo Portilla, and Rueda-Alm, 2008. Herpetol. Monogr. 22(1):109.

Type species: *Tropidodipsas perijanensis* Alemán, 1953, by monotypy.

Plesiodipsas (1 species):

Plesiodipsas perijanensis Alemán, 1953 (1952). Mem. Soc. Cien. Nat. La Salle 12(31):11-30.

Genus ***Sibon*** Fitzinger

Sibon Fitzinger, 1826. Neue Classification der Rept.:31.

Type species: *Coluber nebulatus* Linnaeus, 1758.

Sibynon Fitzinger, 1843. Syst. Rept.:27.

Type species: *Coluber nebulatus* Linnaeus, 1758.

Petalognathus Duméril, 1853. Mem. Acad. Sci., Paris 23:466.

Type species: *Coluber nebulatus* Linnaeus, 1758.

Mesopeltis Cope, 1866. Proc. Acad. Nat. Sci. Phila. 18:318.

Type species: *Mesopeltis sanniolus* Cope, 1866.

Asthenognathus Bocourt, 1884. Bull. Soc. Philom. Paris (7)8:141.

Type species: *Petalognathus multifasciatus* Jan.

Sibon (11 species):

Sibon annulatus (Günther, 1872). Ann. Mag. Nat. Hist. (4)9:30.

Sibon anthracops (Cope, 1868). Proc. Acad. Nat. Sci. Philad. 20:136.

Sibon argus (Cope, 1876). J. Acad. Nat. Sci. Philad. 8(2):130.

Sibon carri (Shreve, 1951). Copeia 1951:52.

Sibon dimidiatus (Günther, 1872). Ann. Mag. Nat. Hist. (4)9:31.

Sibon dimidiatus dimidiatus Günther, 1872.

Sibon dimidiatus grandoculis Müller, 1878.

Sibon dunni Peters, 1957. Copeia 1957:110.

Sibon lamari Solórzano, 2001. Rev. Biol. Trop. 49(3-4):1112.

Sibon linearis Pérez-Higareda, López-Luna, and Smith, 2002. Bull. Maryland Herp. Soc. 38(2):62.

Sibon longifrenis (Stejneger, 1909). Proc. U.S. Natl. Mus. 36:457.

Sibon nebulatus (Linnaeus, 1758). Syst. Nat. 10th ed.:222.

Sibon nebulatus nebulatus Linnaeus, 1758. Central American clade

Sibon nebulatus leucomelas Boulenger, 1896. South American clade.

Sibon perissostichon Köhler, Lotzkat, and Hertz, 2010. Herpetologica 66(1):81.

Genus ***Tropidodipsas*** Günther

Tropidodipsas Günther, 1858. Cat. Snakes Brit. Mus.:180.

Type species: *Tropidodipsas fasciata* Günther, 1858.

Galedon Jan, 1863. Elenco Sist. Ofidi:95.

Type species: *Galedon annularis* Jan, 1863.

Tropidogeophis Müller, 1878. Verh. Naturforsch. Ges. Basel 6:411.

Type species: *Geophis annulatus* Peters.

Dipeltophis Cope, 1887. Bull. U.S. Nat. Mus. 32:91.

Type species: *Leptognathus albocinctus* Fischer.

Geatractus Dugès, 1898. Naturaleza, Mexico (2)3:52.

Type species: *Geophis tecpanecus* Dugès, 1898.

Exelencophis Smith, 1942. Zoologica 27:33.

Type species: *Exelencophis nelsoni* Smith, 1942.

Tropidodipsas (7 species):

Tropidodipsas fasciata Günther, 1858. Cat. Colubrine Snakes Coll. Brit. Mus.:181.

Tropidodipsas philippii (Jan, 1863). Elen. Sist. Ofidi:101.

Tropidodipsas repleta Smith, Lemos-Espinal, Hartman, and Chiszar, 2005. Bull. Maryland Herp. Soc. 41:39.

Tropidodipsas zweifeli (Liner and Wilson, 1970). Copeia 1970:787.

Tropidodipsas sp. nov. 1

Tropidodipsas sp. nov. 2

Tropidodipsas sp. nov. 3

Tribe **Leptodeirini**

Contents: *Imantodes* and *Leptodeira*. This tribe has been supported by Mulcahy (2007) and Daza et al. (2009).

Genus ***Imantodes*** Duméril

Imantodes Duméril, 1853. Mém. Acad. Sci., Paris 23:507.

Type species: *Coluber cenchoa* Linnaeus, 1758.

Himantodes Cope (emendation of *Imantodes* Duméril), 1860. Proc. Acad. Nat. Sci. Phila. 1860:264.

Imantodes (6 species):

Imantodes cenchoa (Linnaeus, 1758)

Imantodes gemmistratus (Cope, 1861)

Imantodes inornatus (Boulenger, 1896)

Imantodes lentiferus (Cope, 1894)

Imantodes phantasma Myers, 1982

Imantodes tenuissimus (Cope, 1867)

Genus ***Leptodeira*** Fitzinger

Leptodeira Fitzinger, 1843. Syst. Rept. 27

Type species: *Coluber annulatus* Linnaeus, 1758.

Leptodeira Agassiz, 1847. Nomencl. Zool. 12:206. (Unjustified emendation of *Leptodeira* Fitzinger).

Megalops Hallowell, 1861 (dated 1860). Proc. Acad. Nat. Sci. Phila. 1860:488.

Type species: *Megalops maculatus* Hallowell, 1861.

Anoplophallus Cope, 1893. Amer. Natur. 27:480. (Substitute for *Megalops* Hallowell, 1861).

Type species: *Megalops maculatus* Hallowell, 1861.

Leptodeira (10 species):

Leptodeira annulata (Linnaeus, 1758)

Leptodeira bakeri Ruthven, 1936

Leptodeira frenata (Cope, 1886)

Leptodeira maculata (Hallowell, 1861)

Leptodeira nigrofasciata Günther, 1868

Leptodeira punctata (Peters, 1866)

Leptodeira rubricata (Cope, 1893)

Leptodeira septentrionalis Kennicott, 1859

Leptodeira splendida Günther, 1895

Leptodeira uribei (Bautista and Smith, 1992)

Tribe **Nothopsini** Dowling and Duellman, 1978

Contents: *Hypsiglena*, *Pseudoleptodeira* and *Nothopsis*. *Hypsiglena* and *Pseudoleptodeira* are sister taxa and sister to *Nothopsis*. Although the placement of *Nothopsis* received nodal support below my cutoff values, it consistently grouped as sister to *Hypsiglena* and *Pseudoleptodeira*. Thus, these three genera form a tribe that is sister to a clade including

Adelphicos, *Atractus*, *Chersodromus*, *Cryophis*, *Hydromorphus*, *Ninia*, *Tretanorhinus* and the Dipsadini.

Genus ***Hypsiglena*** Cope

Hypsiglena Cope, 1860. Proc. Acad. Nat. Sci. Phila. 1860:246.

Type species: *Hypsiglena ochrorhynchus* Cope, 1860.

Comastes Jan, 1863. Elenco. Sist. Ofidi:102.

Type species: *Comastes quincunciatus* Jan, 1871 (=*Hypsiglena torquata*, Günther).

Eridiphas Leviton and Tanner, 1960. Occas. Pap. California Acad. Sci. 27:2.

Type species: *Eridiphas slevini* Tanner, 1943.

Hypsiglena (7 species):

Hypsiglena affinis Boulenger, 1894

Hypsiglena chlorophaea Cope, 1860

Hypsiglena jani (Dugès, 1865)

Hypsiglena ochrorhyncha Cope, 1860

Hypsiglena slevini Tanner, 1943

Hypsiglena tanzeri Dixon and Lieb, 1972

Hypsiglena torquata (Günther, 1860)

Genus ***Nothopsis*** Cope

Nothopsis Cope, 1871. Proc. Acad. Nat. Sci. Phila. 1871:201.

Type species: *Nothopsis rugosus* Cope, 1871.

Nothopsis (1 species):

Nothopsis rugosus Cope, 1871

Genus ***Pseudoleptodeira*** Taylor

Pseudoleptodeira Taylor, 1939 (dated 1938). Univ. Kansas Sci. Bull. 25:343.

Type species: *Hypsiglena latifasciata* Günther, 1894.

Pseudoleptodeira (1 species):

Pseudoleptodeira latifasciata (Günther, 1894)

Tribe Nov. 1

Contents: *Adelphicos* and *Cryophis*. This tribe is sister to a clade consisting of *Atractus*, *Chersodromus*, *Ninia*, and the Dipsadini.

Genus ***Adelphicos*** Jan

Adelphicos Jan, 1862. Arch. Zool. Anat. Fis. 2:18.

Type species: *Adelphicos quadrivirgatus* Jan, 1862.

Rhegnops Cope, 1866. Proc. Acad. Nat. Sci. Philadelphia 18:128–129.

Type species: *Rhegnops visoninus* Cope, 1866.

Adelphicos (6 species):

Adelphicos daryi Campbell and Ford, 1982

Adelphicos ibarrorum Campbell and Brodie, 1988

Adelphicos latifasciatus Lynch and Smith, 1966

Adelphicos nigrilatum Smith, 1942

Adelphicos quadrivirgatus Jan, 1862

Adelphicos veraepacis Stuart, 1941

Genus ***Cryophis*** Bogert and Duellman

Cryophis Bogert and Duellman, 1963. Am. Mus. Novitat. 2162:2.

Type species: *Cryophis hallbergi* Bogert and Duellman, 1963.

Cryophis (1 species):

Cryophis hallbergi Bogert and Duellman, 1963

Tribe Nov. 2

Contents: *Atractus*. This tribe contains the most speciose dipsadine genus and is sister to the clade containing *Ninia*, *Chersodromus*, and the Dipsadini.

Genus ***Atractus*** Wagler

Atractus Wagler, 1828. Isis von Oken 21:741.

Type species: *Atractus trilineatus* Wagler, 1828.

Urobrachys Fitzinger, 1843. Syst. Rept.:24.

Type species: *Brachyorrhos flammigerus* Boie, 1827.

Isoscelis Günther, 1858. Cat. Snakes Brit. Mus.:204.

Type species: *Isoscelis maculata* Günther, 1858.

Atractopsis Despax, 1910. Bull. Mus. Hist. Nat. Paris 16:372.

Type species: *Atractus* (*Atractopsis*) *paucidens* Despax, 1910.

Atractus (138 species):

Atractus acheronius Passos, Rivas and Barrio-Amorós, 2009

Atractus albuquerquei Da Cunha and Do Nascimento, 1983

Atractus alphonsehogei Da Cunha and Do Nascimento, 1983

Atractus altagratiae Passos and Fernandes, 2008

Atractus andinus Prado, 1944

Atractus apophis Passos and Lynch, 2010

Atractus arangoi Prado, 1939

Atractus atratus Passos and Lynch, 2010

Atractus attenuates Myers and Schargel, 2006

Atractus avernus Passos, Chiesse, Torres-Carvajal and Savage, 2009

Atractus badius (Boie, 1827)

Atractus balzani Boulenger, 1898

Atractus biseriatus Prado, 1941

Atractus bocki Werner, 1909

Atractus bocourti Boulenger, 1894

Atractus boettgeri Boulenger, 1896

Atractus boulengerii Peracca, 1896

Atractus caete Passos, Fernandes, Bérnils and Moura-Leite, 2010

Atractus carrioni Parker, 1930

Atractus caxiuana Da Costa Prudente and Santos-Costa, 2006

Atractus charitoae Silva Haad, 2004

Atractus chthonius Passos and Lynch, 2010

Atractus clarki Dunn and Bailey, 1939

Atractus collaris Peracca, 1897

Atractus crassicaudatus (Duméril, Bibron and Duméril, 1854)

Atractus darienensis Myers, 2003

Atractus davidhardi Silva Haad, 2004

Atractus depressiocellus Myers, 2003

Atractus duboisi (Boulenger, 1880)

Atractus duidensis Roze, 1961

Atractus dunni Savage, 1955

Atractus echidna Passos, Mueses-Cisneros, Lynch and Fernandes, 2009

Atractus ecuadorensis Savage, 1955

Atractus edioi Da Silva, Rodrigues Silva, Ribeiro, Souza and Do Amaral Souza, 2005

Atractus elaps (Günther, 1858)

Atractus emersoni Silva Haad, 2004

Atractus emigdioi Gonzales-Sponga, 1971

Atractus emmeli (Boettger, 1888)

Atractus eriki Esqueda, La Marca and Bazó, 2007

Atractus erythromelas Boulenger, 1903

Atractus favae (Filippi, 1840)

Atractus flammigerus (Boie, 1827)

Atractus franciscopaivai Silva Haad, 2004

Atractus francoi Passos, Fernandes, Bérnils and Moura-Leite, 2010

Atractus fuliginosus (Hallowell, 1845)

Atractus gaigeae Savage, 1955

Atractus gigas Myers and Schargel, 2006

Atractus guentheri (Wucherer, 1861)

Atractus guerreroi Myers and Donnelly, 2008

Atractus heliobelluomini Silva Haad, 2004

Atractus hoogmoedi Prudente and Passos, 2010

Atractus hostilitractus Myers, 2003

Atractus imperfectus Myers, 2003

Atractus indistinctus Prado, 1940

Atractus insipidus Roze, 1961

Atractus iridescens Peracca, 1896

Atractus janethae Silva Haad, 2004

Atractus kangueryensis Cacciali, Villalba and Yanosky, 2007

Atractus lancinii Roze, 1961

Atractus lasallei Amaral, 1931

Atractus latifrons (Günther, 1868)

Atractus lehmanni Boettger, 1898

Atractus limitaneus (Amaral, 1935)

Atractus loveridgei Amaral, 1930

Atractus lucilae Silva Haad, 2004

Atractus macondo Passos, Lynch and Fernandes, 2009

Atractus maculatus (Günther, 1858)

Atractus major Boulenger, 1894

Atractus manizalesensis Prado, 1940

Atractus mariselae Lancini, 1969

Atractus matthewi Markezich and Barrio-Amorós, 2004

Atractus medusa Passos, Mueses-Cisneros, Lynch and Fernandes, 2009

Atractus melanogaster Werner, 1916

Atractus melas Boulenger, 1908

Atractus meridensis Esqueda and La Marca, 2005

Atractus micheleae Esqueda and La Marca, 2005

Atractus microrhynchus (Cope, 1868)

Atractus mijaresi Esqueda and La Marca, 2005

Atractus modestus Boulenger, 1894

Atractus multicinctus (Jan, 1865)

Atractus multidentatus Passos, Rivas and Barrio-Amorós, 2009

Atractus nasutus Passos, Fernandes and Lynch, 2009

Atractus natans Hoogmoed and Prudente, 2003

Atractus nicefori Amaral, 1930

Atractus nigricaudus Schmidt and Walker, 1943

Atractus nigriventris Amaral, 1933

Atractus obesus Marx, 1960

Atractus obtusirostris Werner, 1916

Atractus occidentalis Savage, 1955

Atractus occipitoalbus (Jan, 1862)

Atractus ochrosetrus Esqueda and La Marca, 2005

Atractus oculotemporalis Amaral, 1932

Atractus orcesi Savage, 1955

Atractus paisa Passos, Fernandes and Lynch, 2009

Atractus pamplonensis Amaral, 1937

Atractus pantostictus Fernandes and Puorto, 1993

Atractus paraguayensis Werner, 1924

Atractus paravertebralis Henle and Ehrl, 1991

Atractus paucidens Despax, 1910

Atractus pauciscutatus Schmidt and Walker, 1943

Atractus peruvianus (Jan, 1862)

Atractus poeppigi (Jan, 1862)

Atractus potschi Fernandes, 1995

Atractus punctiventris Amaral, 1933

Atractus resplendens Werner, 1901

Atractus reticulatus (Boulenger, 1885)

Atractus riveroi Roze, 1961

Atractus ronnie Passos, Fernandes and Borges-Nojosa, 2007

Atractus roulei Despax, 1910

Atractus sanctaemartae Dunn, 1946

Atractus sanguineus Prado, 1944

Atractus schach (Boie, 1827)

Atractus serranus Amaral, 1930

Atractus snethlageae Da Cunha and Do Nascimento, 1983

Atractus steyermarki Roze, 1958

Atractus surucucu Prudente, 2008

Atractus taeniatus Griffin, 1916

Atractus tamaensis Esqueda and La Marca, 2005

Atractus tamessari Kok, 2006

Atractus taphorni Schargel and García-Pérez, 2002

Atractus thalesdelemai Passos, Fernandes and Zanella, 2005

Atractus titanicus Passos, Fernandes and Lynch, 2009

Atractus torquatus (Duméril, Bibron and Duméril, 1854)

Atractus trihedrurus Amaral, 1926

Atractus trilineatus Wagler, 1828

Atractus trivittatus Amaral, 1933

Atractus turikensis Barros, 2000

Atractus typhon Passos, Mueses-Cisneros, Lynch and Fernandes, 2009

Atractus univittatus (Jan, 1862)

Atractus variegatus Prado, 1942

Atractus ventrimaculatus Boulenger, 1905

Atractus vertebralis Boulenger, 1904

Atractus vertebrolineatus Prado, 1941

Atractus vittatus Boulenger, 1894

Atractus wagleri Prado, 1945

Atractus werneri Peracca, 1912

Atractus zebrinus (Jan, 1862)

Atractus zidoki Gasc and Rodrigues, 1979

Tribe Nov. 3

Contents: *Amastridium*, *Chapinophis*, *Coniophanes*, *Rhadinaea*, *Trimetopon* and *Urotheca*. This diverse tribe is sister to a clade containing *Adelphicos*, *Atractus*, *Chersodromus*, *Cryophis*, *Ninia*, *Hydromorphus*, *Hypsiglena*, *Imantodes*, *Leptodeira*, *Nothopsis*, and the Dipsadini.

Genus ***Amastridium*** Cope

Amastridium Cope, 1861 (dated 1860). Proc. Acad. Nat. Sci. Philadelphia 1860:370.

Type species: *Amastridium veliferum* Cope, 1861.

Fleischmannia Boettger, 1898. Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main 2:69.

Type species: *Fleischmannia obscura* Boettger, 1898.

Mimometopon Werner, 1903. Abhandl. Königl. Bayer. Akad. Wissensch. 22(2):343–384.

Type species: *Mimometopon sapperi* Werner, 1903.

Phrydops Boulenger, 1905. Ann. Mag. Nat. Hist. (7) 15 (89):453–456.

Type species: *Phrydops melas* Boulenger, 1905.

Amastridium (1 species):

Amastridium veliferum Cope, 1860

Genus ***Chapinophis*** Campbell and Smith

Chapinophis Campbell and Smith, 1998. Herpetologica 54(2):207–220.

Type species: *Chapinophis xanthocheilus* Campbell and Smith, 1998.

Chapinophis (1 species):

Chapinophis xanthocheilus Campbell and Smith, 1998

Genus ***Coniophanes*** Hallowell

Coniophanes Hallowell, 1860. In Cope, 1860. Proc. Acad. Nat. Sci. Philadelphia 1860:248.

Type species: *Coronella fissidens* Günther, 1858.

Glaphyrophis Jan, 1863. Arch. Zool. Anat. Fis. 2:304.

Type species: *Glaphyrophis pictus* Jan, 1863.

Hydrocalamus Cope, 1885 (dated 1884). Proc. Amer. Phil. Soc. 22(1884):176.

Type species: *Homolopsis quinquevittatus* Duméril, Bibron and Duméril, 1854.

Coniophanes (16 species):

Coniophanes alvarezi Campbell, 1989

Coniophanes andresensis Bailey, 1937

Coniophanes bipunctatus (Günther, 1858)

Coniophanes dromiciformis (Peters, 1863)

Coniophanes fissidens (Günther, 1858)

Coniophanes imperialis (Baird, 1859)

Coniophanes joanae Myers, 1966

Coniophanes lateritius Cope, 1862

Coniophanes longinquus Cadle, 1989

Coniophanes melanocephalus (Peters, 1869)

Coniophanes meridanus Schmidt and Andrews, 1936

Coniophanes michoacanensis Flores-Villela and Smith, 2009

Coniophanes piceivittis Cope, 1869

Coniophanes quinquevittatus (Duméril, Bibron and Duméril, 1854)

Coniophanes sarae Ponce-Campos and Smith, 2001

Coniophanes schmidti Bailey, 1937

Coniophanes taylori Hall, 1951

Genus ***Rhadinaea*** Cope

Rhadinaea Cope, 1863. Proc. Acad. Nat. Sci. Phila. 1863:101.

Type species: *Taeniophis vermiculaticeps* Cope, 1863.

Rhadinea Garman, 1883. Mem. Mus. Comp. Zool. 8:71. (Unjustified emendation)

Rhadinella Smith, 1941. Copeia 1941:7.

Type species: *Rhadinella schistose* Smith, 1941.

Rhadinaea (20 species):

Rhadinaea bogertorum Myers, 1974

Rhadinaea calligaster (Cope, 1876)

Rhadinaea cuneata Myers, 1974

Rhadinaea decorata (Günther, 1858)

Rhadinaea flavilata (Cope, 1871)

Rhadinaea forbesi Smith, 1942

Rhadinaea fulvivittis Cope, 1875

Rhadinaea gaigeae Bailey, 1937

Rhadinaea hesperia Bailey, 1940

Rhadinaea laureata (Günther, 1868)

Rhadinaea macdougalli Smith and Langebartel, 1949

Rhadinaea marcellae Taylor, 1949

Rhadinaea montana Smith, 1944

Rhadinaea myersi Rossman, 1965

Rhadinaea omiltemana (Günther, 1894)

Rhadinaea pulveriventris Boulenger, 1896

Rhadinaea quinquelineata Cope, 1886

Rhadinaea sargenti Dunn and Bailey, 1939

Rhadinaea taeniata (Peters, 1863)

Rhadinaea vermiculaticeps (Cope, 1860)

Genus ***Trimetopon*** Cope

Trimetopon Cope, 1885. Proc. Amer. Phil. Soc. 22:177.

Type species: *Ablabes gracilis* Günther, 1872.

Trimetopon (6 species):

Trimetopon barbouri Dunn, 1930

Trimetopon gracile (Günther, 1872)

Trimetopon pliolepis Cope, 1894

Trimetopon simile Dunn, 1930

Trimetopon slevini Dunn, 1940

Trimetopon viquezi Dunn, 1937

Genus ***Urotheca*** Bibron

Urotheca Bibron, 1843. In Cocteau and Bibron, Rept., In de la Sagra, Hist. Fis. Pol. Nat. Isla Cuba 8:130.

Type species: *Calamaria dumerilii* Bibron, 1843.

Pliocercus Cope, 1860. Proc. Acad. Nat. Sci. Phila. 1860:253.

Type species: *Pliocercus elapoides* Cope, 1860.

Elapochrus Peters, 1860. Monats. Akad. Wiss. Berlin 1860:293.

Type species: *Elapochrus deppei* Peters, 1860.

Pleiocercus Salvin (emendation of *Pliocercus* Cope), 1861. Proc. Zool. Soc. London 1861:227.

Pleiokerkos Cope (emendation of *Pliocercus* Cope), 1862. Proc. Acad. Nat. Sci. Phila. 1862:72.

Cosmiosophis Jan, 1863. Arch. Zool. Anat. Phys. 2:289.

Type species: none designated.

Urotheca Savage and Crother, 1989. Zool. J. Linnean Soc. 95:335–362.

Type species: *Urotheca*

Urotheca (11 species):

Urotheca decipiens (Günther, 1893)

Urotheca dumerilli (Bibron, 1840)

Urotheca elapoides Cope, 1860

Urotheca euryzonus Cope, 1862

Urotheca fulviceps (Cope, 1886)

Urotheca guentheri (Dunn, 1938)

Urotheca lateristriga (Berthold, 1859)

Urotheca multilineata (Peters, 1863)

Urotheca myersi Savage and Lahanas, 1989

Urotheca pachyura (Cope, 1875)

Urotheca wilmarai Smith, Perez-Higareda and Chiszar, 1996

Tribe Nov. 4

Contents: *Chersodromus* and *Ninia*. This tribe is sister to the Dipsadini.

Genus ***Chersodromus*** Reinhardt

Chersodromus Reinhardt, 1860. Vidensk. Medd. Naturhist. Foren. Kjöbenhavn 1860:242.

Type species: *Chersodromus liebmanni* Reinhardt, 1860.

Opisthiodon Peters, 1861. Monats. Akad. Wiss. Berlin 1861:460.

Type species: *Opisthiodon torquatus* Peters, 1861.

Chersodromus (2 species):

Chersodromus liebmanni Reinhardt, 1861

Chersodromus rubriventris (Taylor, 1949)

Genus ***Ninia*** Baird and Girard

Ninia Baird and Girard, 1853. Catalogue of North American Reptiles:49.

Type species: *Ninia diademata* Baird and Girard, 1853.

Streptophorus Duméril, Bibron and Duméril, 1854. Erp. Gén. 7:514.

Type species: *Streptophorus bifasciatus* Duméril, Bibron and Duméril, 1854.

Ninia (9 species):

Ninia atrata (Hallowell, 1845)

Ninia celata McCranie and Wilson, 1995

Ninia diademata Baird and Girard, 1853

Ninia espinali McCranie and Wilson, 1995

Ninia hudsoni Parker, 1940

Ninia maculata (Peters, 1861)

Ninia pavimentata (Bocourt, 1883)

Ninia psephota (Cope, 1875)

Ninia sebae (Duméril, Bibron and Duméril, 1854)

Tribe Nov. 5

Contents: *Enuliophis* and *Enulius*. This tribe is sister to a clade containing the sister taxa *Tantalophis* and *Rhadinophanes*.

Genus ***Enuliophis*** McCranie and Villa

Enulius Cope, 1871. Proc. Amer. Phil. Soc. 11:558.

Type species: *Enulius murinus* Cope, 1871.

Leptocalamus Günther, 1872. Ann. Mag. Nat. Hist. (4)9:16.

Type species: *Leptocalamus torquatus* Günther, 1872.

Enuliophis McCranie and Villa, 1993. Amphibia-Reptilia 14(3):261–267.

Type species: *Enuliophis sclateri* McCranie and Villa, 1993.

Enuliophis (1 species):

Enuliophis sclateri (Boulenger, 1894)

Genus ***Enulius*** Cope

Enulius Cope, 1871. Proc. Amer. Phil. Soc. 11:558.

Type species: *Enulius murinus* Cope, 1871.

Leptocalamus Günther, 1872. Ann. Mag. Nat. Hist. (4)9:16.

Type species: *Leptocalamus torquatus* Günther, 1872.

Enulius (4 species):

Enulius bifoveatus McCranie and Köhler, 1999

Enulius flavitorques (Cope, 1868)

Enulius oligostichus Smith, Arndt and Sherbrook, 1967

Enulius roatanensis McCranie and Köhler, 1999

Tribe Nov. 6

Contents: *Hydromorphus* and *Tretanorhinus*. These two highly-aquatic species form a tribe that is sister to a clade containing *Adelphicos*, *Atractus*, *Chersodromus*, *Cryophis*, *Ninia* and the Dipsadini.

Genus ***Hydromorphus*** Peters

Hydromorphus Peters, 1859. Monats. Akad. Wiss. Berlin 1859:276.

Type species: *Hydromorphusi concolor* Peters, 1859.

Hydromorphus (2 species):

Hydromorphus concolor Peters, 1859

Hydromorphus dunni Slevin, 1942

Genus ***Tretanorhinus*** Duméril, Bibron and Duméril

Tretanorhinus Duméril, Bibron and Duméril, 1854. Erp. Gén. 7:348.

Type species: *Tretanorhinus variabilis* Duméril, Bibron and Duméril, 1854.

Tretanorhinus (4 species):

Tretanorhinus mocquardi Bocourt, 1891

Tretanorhinus nigroluteus Cope, 1861

Tretanorhinus taeniatus Boulenger, 1903

Tretanorhinus variabilis Duméril, Bibron and Duméril, 1854

Tribe Nov. 7

Contents: *Rhadinophanes* and *Tantalophis*. These two genera share unusual and highly derived hemipenial morphology and form a tribe that is sister to the genera *Enuliophis* and *Enulius*.

Genus ***Rhadinophanes*** Myers and Campbell

Rhadinophanes Myers and Campbell, 1981. Amer. Mus. Novitat. 2708:2.

Type species: *Rhadinophanes monticola* Myers and Campbell, 1981.

Rhadinophanes (1 species):

Rhadinophanes monticola Myers and Campbell, 1981.

Genus ***Tantalophis*** Duellman

Tantalophis Duellman, 1958. Uni. Kansas Publ. 11(1):1–9.

Type species: *Leptodeira discolor* Günther, 1860.

Tantalophis (1 species):

Tantalophis discolor Günther, 1860.

Dipsadine taxa *incertae sedis*

Köhler et al. (2001) suggested that the genus *Omoadiphas* shares several morphological similarities with members of the Dipsadini and the other invertebrate feeding genera (i.e., *Adelphicos*, *Atractus*, *Chersodromus*, and *Ninia*). However, I was unable to include this taxon in this study. Lacking any compelling evidence for generic or tribal affinities, I relegate this genus to Dipsadinae *incertae sedis*.

Genus ***Omoadiphas*** Köhler, McCranie and Wilson

Omoadiphas Köhler, McCranie and Wilson, 2001. Senckenbergiana Biologica 81:270.

Type species: *Omoadiphas aurula* Köhler, McCranie and Wilson, 2001.

Omoadiphas (3 species):

Omoadiphas aurula Köhler, McCranie and Wilson, 2001

Omoadiphas cannula McCranie and Cruz-Díaz, 2010

Omoadiphas texiguatensis McCranie and Castañeda, 2004

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Bogert, C. M. and W. E. Duellman. 1963. A new genus and species of colubrid snake from the Mexican state of Oaxaca. American Museum Novitates 2I62:1–15.

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BIOGRAPHICAL INFORMATION

Coleman grew up in Richmond, Virginia, where he graduated *summa cum laude* from J. Sargeant Reynolds Community College with an Associate in Science in 2000. He then transferred to the University of Florida (UF), where he graduated *magna cum laude* from the College of Liberal Arts and Sciences with a major in Zoology and a minor in Wildlife Ecology and Conservation in 2002. Coleman continued his studies at UF and in 2006 earned a Masters in Science working on snake ecomorphology with Harvey B. Lillywhite. During his time at UF, Coleman worked extensively on several projects involving 1) the structure and function of tails in snakes, 2) the freshwater requirements of marine sea kraits (*Laticauda* spp) in Taiwan, and 3) the spatial ecology and bird/snake community ecology of an insular population of cottonmouth snakes (*Agkistrodon piscivorus*) in the Gulf of Mexico. He also collaborated with colleagues in the Florida Museum of Natural History (FLMNH) on several projects documenting the occurrence and spread of introduced reptiles and amphibians in Florida. After earning his Masters, Coleman moved to the University of Texas at Arlington (UTA) to work on his PhD with Eric N. Smith on the feeding behavior and molecular phylogenetic relationships of snail-eating snakes of the tribe Dipsadini and the subfamily Dipsadinae. While at UTA, Coleman also worked on projects including 1) the phylogeography of the pelagic sea snake (*Pelamis*) across the Pacific Ocean, 2) the evolution of cardio-pulmonary morphology in snakes, 3) the biodiversity of Mexican reptiles and amphibians, and 3) the description of a new species of snake from Ecuador. Coleman has extensive fieldwork experience in 13 countries, especially Mexico (>6 mo) and Costa Rica (>3 mo). He has gained valuable museum experience from his work at the FLMNH (4 yr) and the Transvaal Museum in South Africa (3 mo). Coleman currently has 26 peer-reviewed publications spanning a wide range of topics and involving

collaborators from eight countries in total. He has presented 12 oral presentations and two posters at national and international meetings, and he was recently invited to present his research at the 2012 SICB meeting as part of an NSF-funded symposium. Coleman has received 11 research-related grants and awards including most recently the W.F. Pyburn Fellowship and the Graduate Dean's Dissertation Fellowship (UTA). He was recently invited to become a member of the IUCN Sea Snake Specialist Group. Coleman has taught laboratories for 13 different courses while in graduate school, and he is committed to providing students with quality education. Coleman participated in the I-Engage undergraduate mentorship program at UTA for two summers, and he was recently awarded the 2012 T.F. Kennerly Award for excellence in teaching. Since earning his PhD, Coleman has returned to UF to work with Harvey Lillywhite as a postdoctoral researcher to continue projects involving 1) sea snake phylogeography and water balance, 2) snake ecomorphology, and 3) bird/snake community ecology on Seahorse Key, Florida. He is also continuing several projects with Eric Smith and colleagues at UTA on dipsadine snake phylogeography and phylogenetic systematics. Coleman hopes to secure an academic faculty position at a university or museum collection where he can pursue his interests in herpetological research and teaching.