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Evolution of Body Size and Ontogenetic Color Change in the Booid Snakes (Superfamily Booidea)

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Abstract

There are currently 66 different recognized species within the superfamily Booidea, whose representatives inhabit six continents, with some of these species being endemic to islands. While we are more familiar with certain species, there are species that we know next to nothing about. By using traits such as body size, which is a measurement that uses the distance between the snout and vent, which is a valuable measurement that can provide insight into the habitat and diet of a species. Along with ontogenetic color change, which is a one-time shift in the colorations and patterns between the juvenile and adult life stages. Using characteristics including body size and ontogenetic color change, we may be able to gain insight into how these characteristics may have evolved and persisted among the different families of Booidea. After collecting DNA samples from 62 different species, excluding *Corallus blombergi*, *Eryx borrii*, *Eryx somalicus*, and *Eryx whitakeri* (which did not have an available DNA sequence), a phylogeny was created in order to visualize the evolution of body size and ontogenetic color change. This study aimed to use a phylogenetic tree based on the current DNA sequences from the aforementioned 62 species to examine the evolution of body sizes and ontogenetic color change in the superfamily Booidea. By doing so, we hope to ascertain patterns of evolution of body size and ontogenetic color change to provide insight into the diversification of traits in the family Booidea.

1. Introduction

Booidea (booids or boas) is a superfamily of generally large-bodied snakes, currently consisting of 66 species (Reynolds and Henderson 2026) in the suborder Serpentes. This superfamily is in the reptile class Lepidosauria, which includes snakes, lizards, amphisbaenians, and tuataras. Within this group, we see the sister lineages of Booidea, Pythonoidea, Uropeltoidea, Typhlopoidea as representative superfamilies of what historically were called "basal" snakes, or macrostoman and scolecophidian snakes. Some of the booid species are highly familiar, such as *Boa constrictor*, and some we know next to nothing about, such as *Eryx borrii*. Within this superfamily we recognize seven families: the Boidae (37 species), Calabariidae (1), Charinaidae (4), Erycidae (12 species), Sanziniidae (4), and Ungaliophiidae (3), Candoiidae (5).

Boas are found nearly circumglobally, occurring in the Americas, Caribbean, Africa, Europe, Asia, Melanesia, and the South Pacific (Reynolds and Henderson 2018). Despite this, 42 species of boas are found on islands and 27 of these species can only be found on islands. When broken down at the family level, 46 of the species fall within three families: Boidae, Sanziniidae, and Candoiidae. Of those, 37 species can be found on islands, and 25 are endemic to islands. The genera *Acrantophis, Candoia, Chilabothrus,* and *Sanzinia* are all entirely restricted to islands. In North America, we see two families present, Charinaidae and Boidae. In Central and South America we see species in the genera *Corallus, Epicrates, Boa,* and *Eunectes,* all of which are in the family Boidae. The West Indies are inhabited by 18 of the 66 species (Reynolds et al. 2023), 14 of which are in the genus *Chilabothrus*, 2 in the genus *Boa,* and 2 in the genus *Corallus*. In Africa, the Mediterranean, the Indian Ocean, and the Middle East, we see an exclusive representation of the genera *Eryx* and *Calabaria*. In Madagascar, we see the endemic family Sanziniidae with two genera, *Actantophis* and *Sanzinia*, and four species. Asia is home to 8 different species all in one genus *Eryx*. In Melanesia, Micronesia, and Polynesia, we see the presence of the genus *Candoia*.

While a fair amount is known about the evolution and phylogenetic relationships of the booids, the evolution of specific traits in the lineage has been poorly studied. We know quite a bit about the evolution of body size in the Booid's sister lineage Pythonoidea (Esquerré et al. 2022), although that is a more modest radiation of just 40 species. Body size evolution in booids (Fig. 1) has been studied at the level of specific genera, such as *Chilabothrus* (Reynolds et al. 2016) and *Boa* (Card et al. 2016), but never at the level of the superfamily (in other words, across all species distributed globally). Body size is often measured in TTL (total body length, including the tail) or SVL (snout to vent length) and is a measurement that has the potential to give insight into the life history of a species (Vitt 1987; Pyron and Burbrink 2009; Reynolds et al. 2016). It can clue researchers in to some of the habitat and diet preferences of these species as we see evidence that the body size evolves with the prey resources (Henderson et al. 1987; Rodriguez-Robles and Greene 1996; Pizatto et al. 2009; Reynolds et al. 2016; Card et al. 2016). However, collecting body size information is challenging for several reasons, including different measurement types based on the preferences of researchers, sexual dimorphism of Booidea as females tend to be larger, general variation in size among individuals, relative rarity of truly large individuals, collection biases, and indeterminate growth (Reynolds and Henderson 2026). Among the Booidea, we see that some of the smallest species is *Eryx borrii* with an SVL of 330 mm, closely followed by *Ungaliophis panamensis* with an SVL of 482 mm and *Exiliboa placata* with an SVL of 500 mm. The largest species, *Eunectes murinus*, has an SVL of 6000 mm, nearly 18 times that of the smallest species, *Eryx borrii*.

Further, boas exhibit a unique set of traits during ontogeny, whereby some species change color from light colors to grays and browns as they age, generally in their first year. Called ontogenetic color change (OCC; Fig. 2), we know nothing about how this trait has evolved in booids. For example, has OCC evolved once or twice, or is it a trait that evolves repeatedly? Is OCC mostly restricted to just one family or genus, or is it widespread without a phylogenetic pattern? Ontogenetic color change is a permanent change in the patterns and coloration from a juvenile state to an adult state, which is often associated with shifts in life history that can be dictated by changes in diet or even habitat (Reynolds and Henderson, 2026). An excellent example of this is the Emerald Tree Boa, *Corallus caninus*, which, as neonates, exhibit a vibrant red, orange, or yellow coloration that will later transition to a vibrant green. In the genus *Chilabothrus*, we see multiple different species that display OCC. During their neonate coloration *Chilabothrus subflavus,* has a bright orange coloration on the dorsal and ventral surfaces with a yellow to brown banding pattern, adult coloration being yellow to orange with black banding on the dorsal scales that expands creating a black tail with slight yellow stippling amd a greenish chin and orange venter (Newman et al 2020, Grant 1940, Tolson and Henderson 1993). Because OCC has never been characterized across the Booidea, it is unclear whether the trait might be evolving randomly with respect to the phylogeny, or whether there is a strong phylogenetic signal (the trait is tied closely to phylogenetic relatedness).

By building a near-complete phylogeny for the superfamily, as well as assembling morphological character databases for these traits, I can directly visualize the evolution of body size and OCC in booids, thereby spurring additional work that could reveal why some lineages evolve large or small bodies, or why some species transition from colorful to drab. Here I present a new phylogenetic hypothesis for the booids, which I then use to map these traits using phylogenetic comparative methods to reveal evolutionary patterns in these traits.

Figure 1. Adult female boas in the genus *Chilabothrus*. Left, an adult *C. ampelophis*, which reaches a maximum body size of under 700 mm. Photo by R. Graham Reynolds. Right, an adult *C. angulifer*, which can reach body sizes exceeding 4000 mm. Photograph by Tomas Rodriguez-Cabrera.

Figure 2. Ontogenetic color change in the Puerto Rican Boa (*Chilabothrus inornatus*). Left) an orange neonate; top right, a transitioning yearling; bottom right, an adult. Photos by R. Graham Reynolds.

2. Methods

2.1 Phylogenetic tree

I obtained a preliminary phylogenetic dataset consisting of DNA sequence data from 56 boas from an unpublished study by Dr. Reynolds. These data are mitochondrial Cytochrome-b (CYTB) sequences, approximately 1100 base pairs long and containing the entire coding region of CYTB. This phylogeny was missing 10 of the 66 boa species currently recognized by Reynolds and Henderson (2026), so I searched GenBank for additional CYTB sequence data that was available for missing species in the original phylogeny. I recovered sequence data from six additional boa species, bringing the total to 61 of 66 species. The only data I was unable to obtain were from the following species: *Corallus blombergi, Eryx borrii, Eryx somalicus*, and *Eryx whitakeri*. *Corallus blombergi* is an endangered species from Ecuador, and a shed skin that Dr. Reynolds was able to obtain from a captive specimen did not yield any usable DNA. *Eryx borrii* and *Eryx somalicus* are two miniature species of sand boas currently known only from Somalia and recorded only from just two specimens each. *Eryx whitakeri* is a poorly studied species from the Western Ghats of India, and no DNA data or tissue samples are yet available.

All computational analyses that follow were conducted using the "CHILABOTHRUS MARKII" HPC (16c, 128gb RAM) running Ubuntu 24.10 at the University of North Carolina Asheville, as well as on my personal Windows® laptop.

I aligned the new sequences with the existing dataset using Geneious®, trimming the ends to align. I then estimated a new phylogenetic tree using the RaxML function in Geneious with the following parameters: GTR Gamma model with 1,000 rapid bootstrap replicates and a thorough maximum likelihood search.

2.2 Phylogenetic comparative methods: body size

I collected body size data from a wide variety of primary and secondary literature, as summarized in Reynolds and Henderson (2026). This included the maximum length of a boa species that had been published previously. Snake body sizes, in particular body lengths, are traditionally measured from the tip of the snout to the opening of the cloaca on the ventral surface, which is called snout-vent length. However, some boa body sizes are reported in the literature as the total length, or a measurement from the snout to the tip of the tail. It is often preferable that the snout-vent length is reported, as the tail length can be altered due to damage to the individual. Tails in boas are typically short relative to the overall body length, rarely exceeding 10% of the total length of the animal. When a species has a maximum size reported as total length, I subtracted 10% from this as an estimate of the snout-vent length and used this measurement for my analyses. I created a vector containing these body sizes and read it as a CSV file into RStudio.

I then loaded the phylogenetic tree into RStudio as a nexus file (.nex) using the *read.nexus()* function from the package ape (Paradis and Schliep 2019). Next, I had to convert the phylogeny from a cladogram into an ultrametric (distance/time calibrated) tree using the *chronopl()* function from ape. I then read in a vector containing the names of the tree tips (boa species names) in the same order as the arrangement of the tips in the phylogeny (I checked this using the function *plot*() from ape). Then, I matched names to tips using *names*() and checked the match by exporting a CSV file using *write*.*csv*(). I then performed a method using stochastic character mapping to map the body size vector to the phylogeny using the contMap() function from the package phytools (Revell 2012). This method matches the phylogeny to the body size vector and then computes ancestral (continuous) character states using maximum likelihood and a tree re-rooting algorithm that reroots the tree at each internal node and then calculates the state at that node. The function then maps (or "paints") character states onto the phylogeny for visualization. I then exported the resulting mapped tree from RStudio as a PDF file.

2.3 Phylogenetic comparative methods: ontogenetic color change

I obtained OCC data from an unpublished senior thesis conducted by a former UNC Asheville student (Ally Brandon, '21), as well as from Reynolds and Henderson (2026). These data were obtained either from primary or secondary literature or from visual examination of neonate offspring of boa species to score them as either having or not having ontogenetic color change. With this, I created a vector of binary data signifying the presence of OCC (1) or absence of OCC (0). From there, I imported the vector into RStudio and matched it to the phylogeny using the procedure outlined above.

Because stochastic character mapping is intended for continuous character data, I needed an alternate way to conduct comparative analysis for the OCC dataset. I used the *make*.*simmap*() function in phytools (Revell 2012), which matches the tree to a discrete dataset (in this case, a binary dataset) and then simulates histories of the character using an "equal rates" model based on what is specified for each tip of the phylogeny. The method then gives probabilities (as pie charts) for whether ancestral nodes were likely to show OCC or no OCC. I then exported the resulting mapped tree from RStudio as a PDF file.

3. Results

Table 1. The morphological dataset used in this study. Included are boa species, maximum body lengths, and ontogenetic color change (OCC) binary coding. Body lengths are in mm,

and OCC is coded as present (1) and absent (0). Boa species for which no DNA was available are listed at the end, and in gray.

Species	Size	OCC	Species	Size	OCC
Acrantophis dumerili	3000	0	*Corallus caninus*	1579	1
Acrantophis madagascariensis	3200	0	*Corallus cookii*	1820	1
Boa constrictor	4800	0	*Corallus cropanii*	1700	0
Boa imperator	2500	0	*Corallus grenadensis*	1625	1
Boa nebulosa	4000	0	*Corallus hortulanus*	1787	1
Boa orophias	3000	0	*Corallus ruschenbergerii*	1870	1
Boa sigma	2730	0	*Epicrates alvarezi*	1443	0
Calabaria reinhardtii	1030	0	*Epicrates assisi*	1420	0
Candoia aspera	930	0	*Epicrates cenchria*	1500	0
Candoia bibroni	2489	1	*Epicrates crassus*	1320	0
Candoia carinata	715	0	*Epicrates maurus*	1280	1
Candoia paulsoni	1365	0	*Eryx colubrinus*	1000	0
Candoia superciliosa	885	0	*Eryx conicus*	940	0
Charina bottae	840	1	*Eryx elegans*	540	0
Charina umbratica	750	1	*Eryx jaculus*	1127	0
Chilabothrus ampelophis	697	0	*Eryx jayakari*	570	0
Chilabothrus angulifer	5650	0	*Eryx johnii*	1300	1
Chilabothrus argentum	1245	1	*Eryx miliaris*	1000	0
Chilabothrus chrysogaster	1345	1	*Eryx muelleri*	800	0

Chilabothrus exsul	810	1	*Eryx sistanensis*	855	0
Chilabothrus fordii	860	0	*Eunectes beniensis*	3240	0
Chilabothrus gracilis	905	1	*Eunectes deschauenseei*	2307	0
Chilabothrus granti	1112	0	*Eunectes murinus*	6000	0
Chilabothrus inornatus	2200	1	*Eunectes notaeus*	4250	0
Chilabothrus monensis	1255	0	*Exiliboa placata*	500	0
Chilabothrus schwartzi	1219	1	*Lichanura roseofusca*	1200	0
Chilabothrus striatus	2489	0	*Lichanura trivirgata*	1100	0
Chilabothrus strigilatus	2180	0	*Sanzinia madagascariensis*	2000	1
Chilabothrus subflavus	2050	1	*Sanzinia volontany*	1800	0
Corallus annulatus	1447	1	*Ungaliophis continentalis*	760	0
Corallus batesii	1710	1	*Ungaliophis panamensis*	482	0

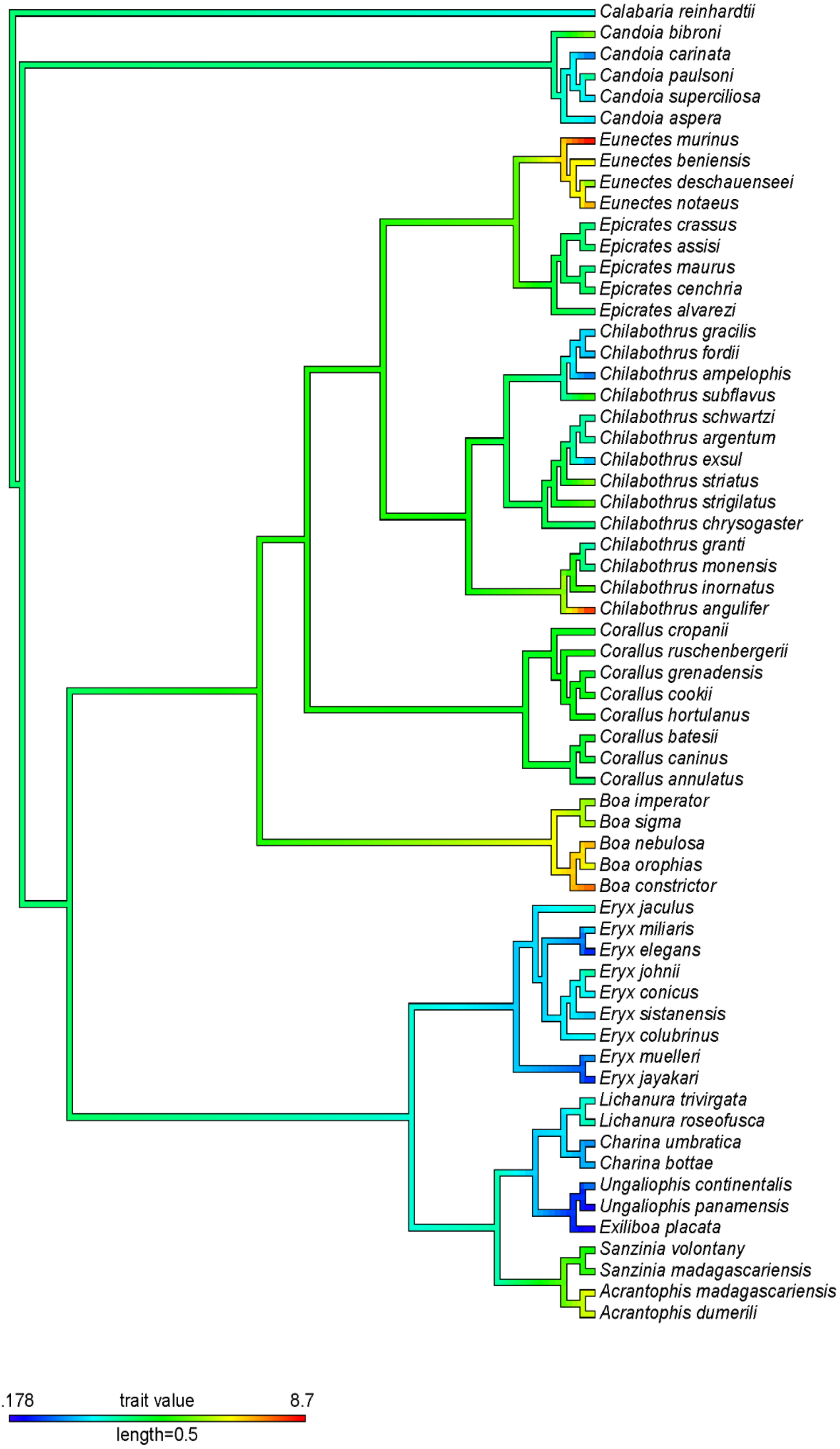

Figure 3. Phylogeny of Booid describing the evolution of body size represented as snout-vent length (SVL). Blue represents a small body size and red indicates a large body size, with lengths given on a log scale.

My analyses show clearly that body size in Booids is a labile trait, with both large and small body size evolving multiple times. For example, the sister taxa *Boa nebulosa* with a SVL of 4000 mm and *Boa constrictor* with a SVL of 4800 mm (table 1, Fig. 3) evolved large body size, as did the sister taxa *Eunectes murinus* with a SVL of 6000 mm and *Eunectes notaeus* with a SVL of 4250 mm (table 1, Fig. 3). Small body size also evolved multiple times. For example, a small-bodied clade includes *Charina umbratica* SVL of 750mm*, Charina bottae* SVL of 840 mm*, Lichanura trivirgata* SVL of 1100 mm*, Lichanura roseofusca* SVL of 1200mm*, Exiliboa placata* 500 mm*,* and *Ungaliophis continentalis* SVL of 760 mm (table 1, Fig. 3). We also see the clade consisting of *Eryx muelleri* SVL of 800 mm, *Eryx elegans* SVL of 540 mm, *Eryx miliaris* SVL of 1000 mm, *Eryx jaculus* SVL of 1127 mm, *Eryx colubrinu*s SVL of 1000 mm, *Eryx johnii* SVL of 1300 mm, *Eryx conicus* SVL of 940 mm (table 1, Fig. 3). The tip with *Chilabothrus exsul* SVL 810 mm is a part of a clade with *Chilabothrus argentum* SVL 1245 mm *and Chilabothrus schwartzi* SVL 1219 mm, which are on the cusp between small and medium body size (Fig. 3). It is also interesting to note that in *Chilabothrus* the we see that *Chilabothrus gracilis* SVL of 905 mm and *Chilabothrus fordii* SVL of 806 mm have a smaller body size in comparison to the rest of the clade which have a medium body size (table 1, Fig. 3).

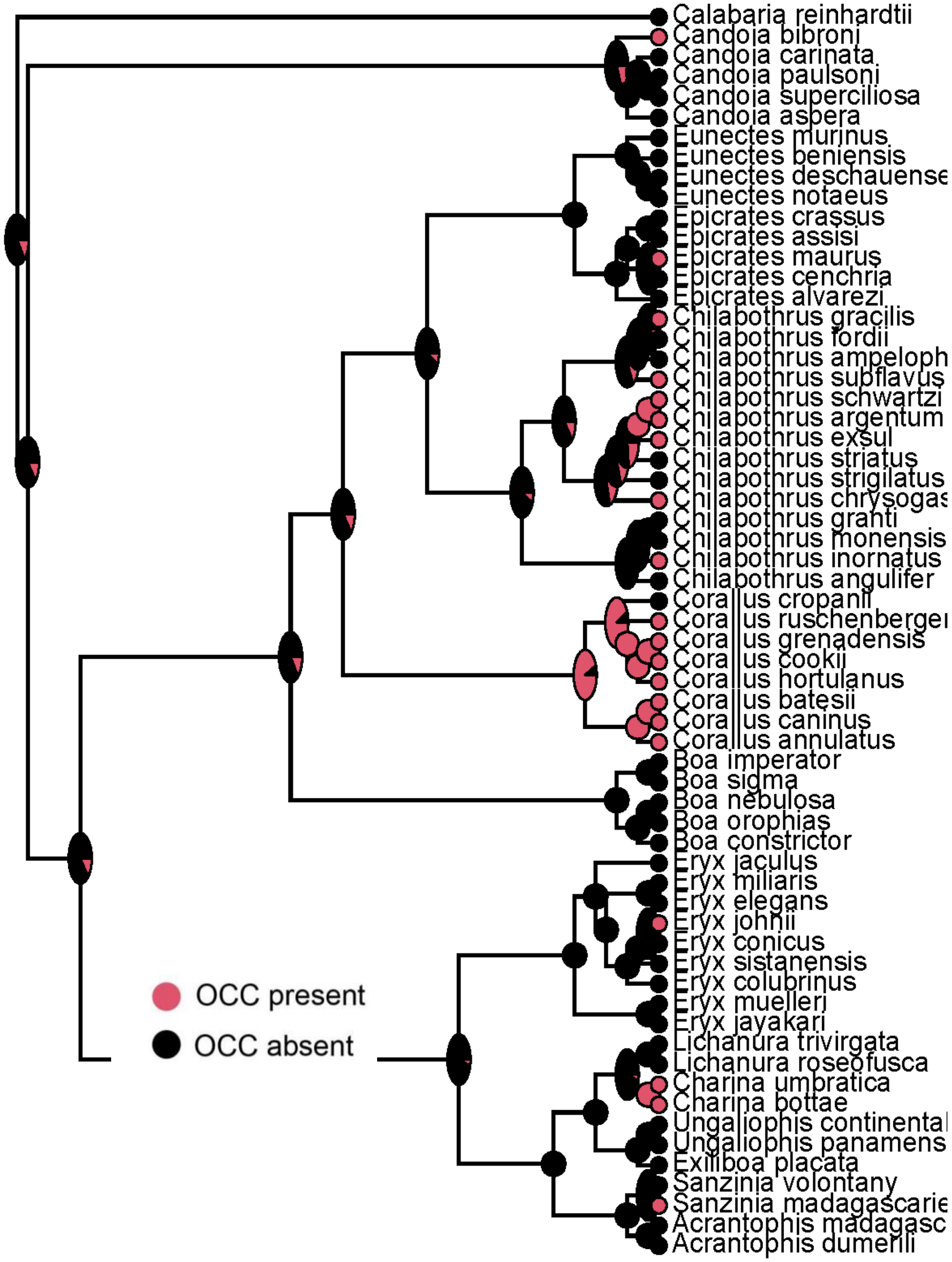

Figure 4. Phylogeny of Booid describing the evolution of ontogenetic color change (OCC), where red represents the presence of OCC and black represents the absence of OCC. Pie charts at ancestral nodes represent the probabilities that the ancestor was either showing OCC or not.

Similarly to body size, we find that 20 of the 66 species have OCC, and the evolution of this trait appears to have occurred at least seven times (Fig. 4). A single representative of the Pacific Boas (family Candoiidae), *Candoia bibroni*, has OCC (Fig. 4). This species is highly arboreal and is also the largest member of the genus, attaining an SVL nearly twice that of other members of the family. In the family Sanziniidae we also see a single occurrence of OCC presence in *Sanzinia madagascariensis*, which is also the arboreal representative of that group of boas. These one-off observations might suggest a connection between arboreality and OCC in these families; however, in the genus *Eryx,* we find that *Eryx johnii* (in the family Erycidae) has OCC yet is a terrestrial species (Fig. 4). Similarly, we find occurrences of OCC in the genus *Charina umbratica* and *Charina bottae* (Fig. 4), both of which are highly terrestrial species.

In the family Boidae we see multiple occurrences of OCC presence in 15 species (Fig. 4). In particular, the genera *Chilabothrus* and *Corallus* have many species that exhibit OCC. In the genus *Chilabothrus*, it is curious that most of the species that show OCC are smaller in body size, with the exceptions being *Chilabothrus inornatus* from Puerto Rico and *Chilabothrus subflavus* from Jamaica, both large-bodied boas (Fig. 4). The Bahamian *Chilabothrus chrysogaster, Chilabothrus schwartzi,* and *Chilabothrus exsul* are all members of the same clade and have OCC (Fig. 4). The small-bodied Hispaniolan *Chilabothrus gracilis* has OCC, but not its sister species *Chilabothrus fordii*. Interestingly, the former species is arboreal and the latter is terrestrial. Among the treeboas (genus *Corallus*), *Corallus caninus, Corallus batesii, and Corallus annulatus* are all in the same clade and have OCC (Fig. 4). *Corallus hortulanus, Corallus grenadensis, Corallus cookii, Corallus ruschenbergerii* also in the same clade and have OCC (Fig. 4). There is only one (of nine) species of *Corallus* that does not have OCC, and that is the enigmatic and extremely rare Atlantic rainforest species *Corallus cropanii*. Among the other South American boas, *Epicrates maurus* has OCC but not *Epicrates cenchria,* its sister taxa. Both species are mildly arboreal, but also readily use the ground. No other species of *Epicrates* show OCC, and all are relatively small-bodied and terrestrial. The largest species of boas (>3m) never show OCC.

4. Discussion

Boas (Superfamily Booidea) represent a modest radiation of snakes, yet they occur in a near-circumglobal distribution and occupy a wide variety of habitats, from desert to rainforest to highly temperate regions. Across these ranges, boas have evolved many adaptations to these environments, and understanding the evolution of the boas will require understanding adaptive evolutionary change. Two traits that are relatively easy to characterize are body size and coloration. Body size is highly correlated with ecology in most snakes, as is coloration (Greene 1997). However, boas (like some other reptiles) can exhibit a dramatic change in coloration as they age, termed ontogenetic color change. While this has been explored in some detail in pythons (another large-bodied group of tropical snakes; e.g., Natusch and Lyone 2021), is has never been characterized nor studied in boas. Here, I wanted to use a phylogeny of the entire family Booidea to explore patterns of evolution of these two traits: body size and OCC. By mapping these traits on the booid phylogeny and inferring ancestral character states, I was able to visualize patterns of evolution of these characters.

Body size and ontogenetic color change have evolved over multiple instances in the phylogeny, showing that these traits are evolutionarily labile traits that are likely responding to selection pressures, such as habitat selection, rather than remaining tied to ancestral character states.

The evolution of body size can give us some insight to the habitat preferences of different species. We see this pattern emerging in the Pythonoidea where we see species specializing in specific habitats based on size, such as the *Liasis mackloti* complex (water pythons), which are large-bodied snakes that inhabit aquatic environments (Esquerré et al. 2022). This also occurs in the booid *Eunectes murinus* (Green Anaconda), which also has an aquatic habitat preference. Green Anacondas are often found in well-vegetated embankments in aguajales or palm wetland, lakes, streams, and rivers, and using free-floating vegetation mats as basking sites, but while not basking they can be found concealed by logs, detritus, or submerged vegetation (Champagne et al. 2025). Similarly to the adult Green Anaconda, neonates are also found in shallow water and share very similar habitat preferences and mobility (Molina et al. 2016). Its sister species, *Eunectes notaeus*, is also mostly observed in aquatic environments, including flooded areas with vegetation, ponds, channels, and flooded areas (Smaniotto et al. 2020). When discussing small body sizes, we see many of the *Eryx* species inhabit desert habitats, where they are typically fossorial. For example *Eryx muelleri* is often found in West African countries with arid tropical climates and long dry seasons with well-vegetated spots with a low percentage of bare soil (Vignoli et al. 2015). *Charina bottae*, the Rubber Boa, a high elevation species, is often located under rock outcrops in fern shrubs or deciduous forests with sun spots and is active during low temperatures (Hoyer et al 2000). We see that body size can be an important clue into habitat preferences.

Ontogenetic color change has also evolved multiple times, which indicates that OCC is maintained by environmental selection rather than evolution. Understanding the selection pressure that results in OCC will be important for understanding the trait. Unlike the booids, OCC in pythons has been explored. In pythons, changes in coloration between juvenile and adult life stages have been suggested to be a result of a shift in their life history as dietary, vulnerability, and habitat may change as the individuals age (Creer 2005; Wilson et al. 2007; Natusch and Lyons 2012,2021). The green python (*Morelia viridis*) changes from a red or yellow color to green, which appears to be related to size as it occurs between 530mm to 590mm, which is about one year of age (Wilson et al 2006a,b; Natusch and Lyons 2012). In the Green python, we see that a difference in habitat occupancy in order to make individuals less conspicuous to bird predators and other conspecifics, the yellow morph is less conspicuous against the non-leafy, the red morph is less conspicuous than the yellow against a non-leafy background (Wilson et al 2017).

Future directions are easy to visualize, with the most approachable path being to further characterize OCC in boas. I modeled this trait as a binary character (OCC present or absent). However, OCC most likely exists as more of a continuum, whereby some species have dramatic color change as they age, while others have a more muted shift in color and/or pattern. Further analysis of these colors and patterns, coupled with a study of the age of onset of OCC could give much more insight into the evolution of this trait. Further, studies should be done on the ecological or adaptive significance of OCC in order to understand why it exists in some species and not others, which will give insight into the ultimate causes for its appearance in some taxa and not others.

5. Acknowledgments

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