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An Overview of the Past, Present, and Future of the Cuban Boa, *Chilabothrus angulifer* (Squamata: Boidae): A Top Terrestrial Predator on an Oceanic Island

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Abstract.—On oceanic islands, where carnivorous mammals are frequently absent, the niches of large predators are often filled by raptors and reptiles. Cuban Boas (*Chilabothrus angulifer*), along with Cuban Crocodiles (*Crocodylus rhombifer*) and large birds of prey, were the top predators in the Cenozoic terrestrial ecosystems of Cuba until the arrival of *Homo sapiens* in the region about 6,000 years ago. This ecological scenario of large boas in the genus *Chilabothrus* functioning as top predators in terrestrial ecosystems is repeated on each of the largest islands of the Greater Antilles. The evolution of very large size in the Cuban Boa is best explained as phyletic giantism (Cope's Rule), although other paleo-ecological selective factors might have maintained or even accentuated the evolutionary trend toward large body size (insular giantism). However, this seems not to be the case for all species of *Chilabothrus*, since the evolution of a small body size is repeated in several lineages, a phenomenon that is best explained by autapomorphic nanism (Island Rule). Unfortunately, the negative effects of humans on natural populations of the Cuban Boa apparently have induced a dramatic reduction in maximum body size even during the relatively short period since the first reliable measurements were recorded in the 19th century. Such a reduction in body size is consistent with that reported for other West Indian reptiles and is probably indicative of rapid evolution in response to a highly modified environment with new selective pressures.

The boid snake genus *Chilabothrus*, distributed throughout the Greater Antilles and the Bahamian Archipelago, comprises 12 currently recognized species (Reynolds et al. 2013, 2016a; Rodríguez-Robles et al. 2015). Of the islands where species of *Chilabothrus* occur, only Hispaniola (three) and Puerto Rico (two) support multi-species assemblages (Tolson and Henderson 1993; Henderson and Powell 2009; Reynolds et al. 2013, 2016a; Rodríguez-Robles et al. 2015). The species in this clade have historically been placed into two main groups based on body size. The smaller species (e.g., *C. fordii*, *C. gracilis*, *C. monensis*) rarely exceed one meter in total length, whereas the large species (e.g., *C. angulifer*, *C. striatus*, *C. subflavus*) usually exceed two meters in total length (Sheplan and Schwartz 1974; Tolson 1987; Kluge 1989; Reynolds et al. 2016b). Evidence based on molecular data (e.g., Reynolds et al. 2013, 2016a) indicates that the evolution of small or large body size in the genus is independent of the phylogenetic relationships among the different species and is probably more dependent on the ecological characteristics of the landmasses inhabited by the various taxa (Reynolds et al. 2016b).

The endemic Cuban Boa, *C. angulifer* (Cocteau and Bibron 1840; Fig. 1) is the only species of *Chilabothrus* and the only boid that occurs in Cuba (Tolson and Henderson 1993; Henderson and Powell 2009; Reynolds et al. 2013). This generalist snake is widely distributed across the archipelago, where it occupies a great variety of habitats at elevations that range from sea level to above 1,200 m (Tolson and Henderson 1993; Henderson and Powell 2009; Rodríguez et al. 2010, 2013; Estrada 2012). Two distinct color patterns exhibit clinal variation from western to eastern Cuba, with the dorsal pattern in the western region more faded, undefined, and generally lacking dark coloration, whereas the patterns in progressively more easterly populations are characterized by increasingly darker, well-defined angulate markings and secondary lateral blotches (Fig. 2; Schwartz and Henderson 1991; Tolson and Henderson 1993; Henderson and Arias 2001).

Chilabothrus angulifer generally is considered the least derived species of the genus, with unique plesiomorphic characters shared only with the closely related continental genera *Epicrates* and *Eunectes* (Fig. 3): (1) presence of labial pits, (2)

Fig. 1. The Cuban Boa (*Chilabothrus angulifer*) constitutes an early-diverging lineage of the *Chilabothrus* radiation in the West Indies and also is the largest and stoutest snake in the Insular Caribbean. Photographs © Tomás M. Rodríguez-Cabrera.

supralabials separated from the eye, and (3) a shorter tail with a lower number of subcaudals (45–55) versus 66–93 in all other species of *Chilabothrus* (e.g., Tolson 1987; Tolson and Henderson 1993; Henderson and Arias 2001). How boids arrived in the Greater Antilles has been extensively discussed (e.g., Tolson 1987; Kluge 1988, 1989; Tolson and Henderson 1993), although at least some aspects of that history remain unclear. What seems certain, however, is that once they arrived, this lineage underwent a notable adaptive radiation that included taxa with extreme body sizes and very different body shapes (Sheplan and Schwartz 1974; Tolson 1987; Reynolds et al. 2013, 2016a, 2016b; Rodríguez-Robles et al. 2015). Some boas evolved as large-bodied generalist species, whereas others evolved as small-bodied specialists (Sheplan and Schwartz 1974; Tolson 1987; Tolson and Henderson 1993; Reynolds et al. 2016b). Herein we use the Cuban Boa (*C. angulifer*) as a model to discuss the different evolutionary routes that some of these species could have taken, with special emphasis on the large species that became the top ectothermic predators on many islands. We also discuss the ongoing impact of human activities on the evolutionary trends of large predators like the Cuban Boa on oceanic islands.

What do the old chronicles reveal?

Most scientists are skeptical about the veracity of West Indian chronicles dating from the 15th and 16th centuries, and certainly much of that information is anecdotal, exaggerated, and/or speculative. However, in some cases, when the information is properly vetted, those accounts provide insights into various aspects of the natural history of many species. Such information is especially important because it presents life history data in a very different historical context, under different environmental conditions, and reflecting very different selective pressures. Indeed, anthropologists and ethnographers have obtained valuable information regarding native humans from West Indian chronicles concurrent with the arrival of Spanish conquerors to the region in October 1492. In the case of the native West Indian fauna, the most valuable accounts certainly come from the Captain Gonzalo Fernández de Oviedo y Valdés, considered "the first naturalist of America" (Carlos de la Torre *in* Álvarez 1958), due to his detailed descriptions of species and natural phenomena.

Boid snakes were undoubtedly among the most impressive animals encountered by Europeans when they first arrived in the region and during the subsequent decades of conquest (early 16th century). In particular, references pertaining to "Isla Fernandina" or Cuba repeatedly mentioned the large size of snakes (or *culebras*) inhabiting the island. Christopher Columbus mentioned in his logbook of the first voyage to the West Indies (summarized by Las Casas 1875) that a boy told him that he saw a large snake ("*que vido una grande culebra*"). Las Casas (1875) commented that many snakes were disproportionately large and stout, but very tame and cowardly ("*Culebras había muchas y muy desproporcionadas de grandes y gordas, pero muy mansas y cobardes…*"). The

Fig. 2. Extreme examples of the clinal variation in dorsal patterns of the Cuban Boa (*Chilabothrus angulifer*) from west to east: A western snake with a faded pattern from the Cueva del Cable, Viñales, Pinar del Río Province (left); an eastern snake with a well-defined pattern from the Sierra de Cubitas, Camagüey Province (right). Photographs © Rolando Teruel.

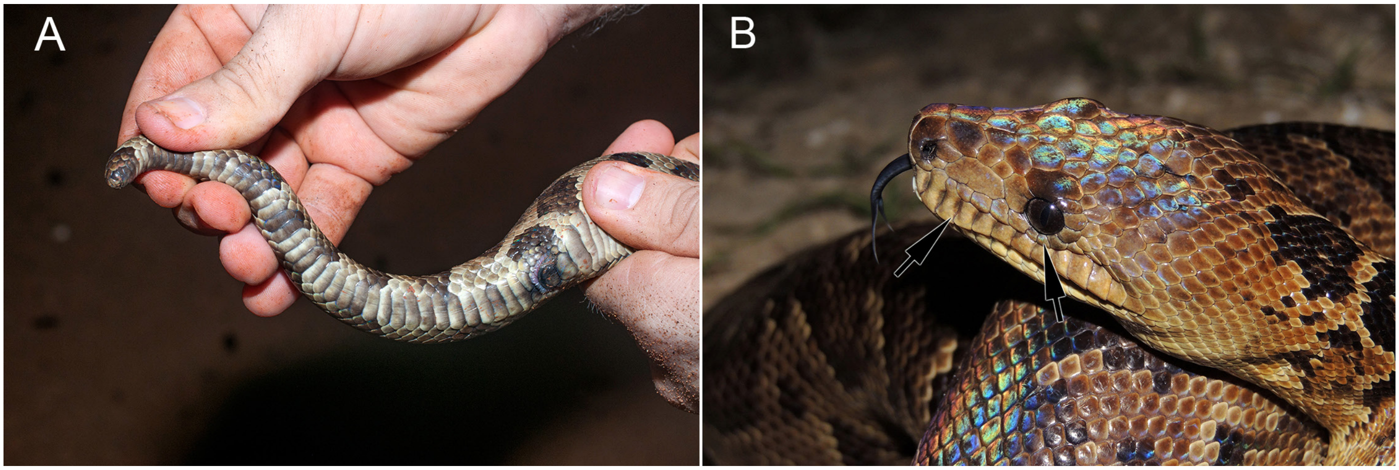

Fig. 3. The Cuban Boa (*Chilabothrus angulifer*) is the only species of the genus that shares some plesiomorphic characters with continental South American Rainbow Boas (genus *Epicrates*) and the anacondas (genus *Eunectes*): (A) A short, blunt tail; (B) labial pits (left arrow) and the eye separated from supralabials (right arrow). Photographs © Rosario Domínguez (A) and Tomás M. Rodríguez-Cabrera (B).

most detailed description by Fernández de Oviedo (1535, officially published in 1851a) commented (in the middle or golden Spanish of the 15th to 17th centuries):

> "*Pero en espeçial en las culebras se han visto en la isla de Cuba muy mayores culebras ó sierpes, porque se han muerto algunas tan gruesas ó mas que el muslo de un hombre, y tan luengas como veynte é çinco é treynta piés é mas; pero son muy torpes é mansas é no enconadas, é cómenlas los indios: é hállanles muchas veçes en el buche seys é siete é más de aquellos animales que he dicho que se llaman guabiniquinax, juntos, que han tragado enteros, aunque son mayores que conejos.*"

> "Very large snakes have been seen, especially on the island of Cuba; some as stout as a man's thigh and as long as twenty-five or thirty feet [7.62–9.14 m] and more have been killed. But they are very lethargic and tame and non-venomous, and the Indians eat them. Sometimes six or seven and more of those animals they call *guabiniquinax* [= hutias; see below] have been found in their stomachs together, swallowed whole, despite that they are larger than rabbits."

Carlos de la Torre (*in* Álvarez 1958) arrived at the conclusion that the large snakes from Cuba mentioned by Fernández de Oviedo and other West Indian chroniclers must be *C. angulifer* (referred therein as *Epicrates angulifer*, but see Reynolds et al. 2013). Despite the fact that this 500-year-old anecdotal report might be exaggerated, the endemic Cuban Boa is by far the largest and stoutest snake in the West Indies (Tolson and Henderson 1993; Henderson and Powell 2009). Gundlach (1875, 1880) stated that he had seen individuals of about "7 varas" (i.e., yards) in total length (6.40 m, the maximum size officially reported for the species), and mentioned one specimen 5 "varas" (4.57 m) in length kept in captivity by him and collected at the Zapata Swamp, Matanzas Province. Rodríguez (1876) commented that the oldest and most massive specimens can measure 10 to 11 in. (25–28 cm) in diameter and six "varas" (5.49 m) in total length. Barbour (1914) mentioned that the Cuban Boa "grows commonly to be twelve feet [3.66 m] long and to be as large in circumference as any boa, or as a Python of far greater length." Other authors also commented on the large size attained by these boas, all referring to individuals exceeding three meters in total length (Barbour and Ramsden 1919; Sheplan and Schwartz 1974). However, the most recent report of a very large Cuban Boa was in Tolson and Henderson (1993), who mentioned a large female "15 ft., 11 in." (4.85 m) in total length that had been killed on a road at the U.S. Naval Base at Guantanamo Bay in 1989. The largest boas thereafter captured at the Naval Base have been only a little over 3.6 m in total length (P.J. Tolson, in litt. 2008).

During recent decades, continuous persecution by humans (Tolson and Henderson 2006; Henderson and Powell 2009), coupled with accelerated habitat loss and the introduction of mammalian predators (Hedges 2006a; Tolson and Henderson 2006), has apparently affected this species to such an extent that snakes exceeding three meters in total length are now very rare in most parts of Cuba (Fig. 4; see also below). As early as the 19th century, Gundlach (1880) commented on the absence of large individuals in cultivated areas because of continuous human persecution. He also mentioned that very large individuals were rare and restricted to mountainous zones and the higher terrains ("*Cayos*") within the Zapata Swamp.

Regarding Oviedo's (1851a) description of *guabiniquinax* or *guaminiquinar* (= *guaminiquinax* of Las Casas 1875), the animals frequently found in the stomachs of those large snakes, Poey (1851) and C. de la Torre (*in* Álvarez 1958) concluded that he was referring to the endemic Cuban capromyid rodents known as hutias (*jutías* in Spanish). In Cuba, hutias comprise at least seven extant species in three genera (*Capromys*, *Mesocapromys*, and *Mysateles*; Silva et al. 2007; Borroto-Páez and Mancina 2011), some of which are the largest native land mammals on the archipelago. Hutia body masses sometimes approach 7 kg (Silva et al. 2007; Borroto-Páez 2011). However, West Indian hystricomorph rodents were much more diverse in the past than today; in Cuba, they included an entire family (Echimydae), three capromyid genera (*Geocapromys*, *Macrocapromys*, *Zazamys*), and at least nine species now extinct (Woods et al. 2001; Silva et al. 2007; Borroto-Páez and Mancina 2011). Some of these genera contained species (i.e., *Ge. columbianus* and *Ma. acevedoi*) as large as or even larger than the largest extant capromyid, the Cuban Hutia (*Ca. pilorides*; Fig. 5). Some of those extinct species (i.e., *Ge. columbianus*) are thought to have disappeared soon after the European conquest (see Silva et al. 2007 for a review). Many if not all of these species could have been prey of Cuban Boas.

Fig. 4. Cuban Boa (*Chilabothrus angulifer*) approaching three meters in total length observed in recent years: (A) Female from the Península de Guanahacabibes, Sandino, Pinar del Río Province (16.IV.2008; currently preserved as a taxidermied specimen in the Parque Zoológico Nacional de Cuba); (B) male from Boca de Jaruco, Santa Cruz del Norte, Mayabeque Province (22.XII.2012); (C) female from Los Hondones, Ciénaga de Zapata, Matanzas Province (1.VII.2015). Photographs © Randol Menéndez (A), Ernesto Testé (B), and Rafael A. Pérez (C).

Oviedo's (1851a) report is not only the first reference regarding the feeding habits of Cuban Boas, but also the first reference to the diet of any identifiable snake in the West Indies. It provides evidence for large hutias (*Ca. pilorides* and/

Fig. 5. With a body mass sometimes approaching 7 kg, the Cuban Hutia (*Capromys pilorides*) is the largest extant native land mammal of Cuba. Although it does climb into trees, it more frequently uses limestone areas with abundant caves. Photographs © Raimundo López-Silvero.

or the extinct *Ge. columbianus*) serving as prey of this snake. Cuban Hutias, particularly *Ca. pilorides*, have been repeatedly mentioned as prey of this boa since the 19th century (e.g., Gundlach 1875, 1880; Rodríguez 1876; Schwartz and Henderson 1991; Witmer and Lowney 2007), but only a few papers report actual observations of predation (e.g., Hernández and Pimentel 2005; Tolson and Petersen 2008). Referring to an unpublished long-term field research project on the Cuban Boa at the U.S. Naval Base at Guantanamo Bay, Tolson and Henderson (2006) and P.J. Tolson (*in* Henderson and Powell 2009) commented that predation on *Ca. pilorides* by this boa is very common, adding that "every adult boa examined had hutia hair in its feces." Consistent with Tolson's observation, Rodríguez-Cabrera et al. (2014) found that *Ca. pilorides* constitutes by far the most frequent prey item for adult snakes exceeding two meters in total length in natural ecosystems (Fig. 6). Those authors also repeatedly found large snakes (> 2.70 m) with two or three hutias in their stomachs, which coincides with Oviedo's (1851a) report of multiple prey items per snake.

A similar paleo-ecological scenario probably was repeated on Hispaniola, the second largest island in the Greater Antilles. Fernández de Oviedo (1851b) said he found a very large dead snake in 1515 around the mouth of the "Neyva" [Neiba] River, in the foothills of the "Pedernales" range:

> *"… la qual yo medí y tenia más de veynte piés de luengo, é lo mas grueso della era mucho mas que un puño çerrado: é debieran averla muerto aquel dia ó*

Fig. 6. A female Cuban Boa (*Chilabothrus angulifer*) approaching three meters in total length from Los Hondones, Ciénaga de Zapata, Matanzas Province, captured just after swallowing a Cuban Hutia (*Capromys pilorides*), the most frequent prey item of adult snakes exceeding two meters (note the bulge at midbody). Photograph © Rafael A. Pérez.

> *pocas horas antes, porque no hedia y estaba fresca la sangre della, que le avie salido de tres ó quatro cuchilladas que tenía."*
>
> "… which I measured and was more than twenty feet [> 6.1 m] in length, and on its stoutest part it was much thicker than a clenched fist. It might have been killed a few hours earlier that same day, because it did not stink and fresh blood was still coming out from the three or four stab wounds it had."

Only one extant species, the Hispaniolan Boa (*C. striatus*), could possibly correspond to Oviedo's (1851b) description. However, the maximum total length reported for this snake is 2.49 m (Ottenwalder 1985; Henderson et al. 1987). It also is an opportunistic predator that feeds on a wide variety of vertebrates, including introduced carnivores and one of the largest native land mammals of the island, the Hispaniolan Hutia (*Plagiodontia aedium*; Ottenwalder 1985; Henderson et al. 1987; Henderson and Powell 2009).

Paleoecological and biogeographical inferences

Molecular phylogenetic reconstructions have suggested that the Cuban Boa either diverged first in the West Indian boa radiation (Reynolds et al. 2013) or that it forms a sister clade to Puerto Rican species (Reynolds et al. 2014, 2016a, 2016b); although neither study resolved this node with strong confidence. Nevertheless, Cuban Boas likely diverged from other West Indian species approximately 16.9–26 Mya (i.e., late Oligocene to early Miocene). This places *C. angulifer* in a context where all living and extinct lineages of native terrestrial mammals (orders Soricomorpha, Pilosa, Rodentia, and Primates) are thought to have been present in the Greater Antillean region (see Silva et al. 2007 for a review). Both Cuba and Hispaniola, as the largest Caribbean islands and hence with the highest productivity (as suggested by size and the adaptive radiation of medium-sized to large herbivores that included capromyid rodents and megalonychid sloths; see White and MacPhee 2001), sustained a greater mammalian diversity than the remaining Greater Antillean islands (for a review on species diversity related to island area see Ricklefs and Bermingham 2008) and shared most taxa belonging to the four orders present in the region (Silva et al. 2007). This diverse mammalian fauna also included forms ranging in size from small bats, shrews, and echimyid rodents (< 0.1 kg) to medium-sized capromyid rodents and pitheciid monkeys (1 to < 10 kg) and medium-sized to large megalonychid sloths (< 10 to ≥ 200 kg) (Silva et al. 2007; Borroto-Páez and Mancina 2011). Additionally, several medium-sized to large birds, some of them with reduced flight capacity (e.g., *Bubo*, *Grus*, *Nesotrochis*, *Ornimegalonyx*), were abundant in Cuba mainly during the Quaternary (e.g., Olson 1974; Acevedo and Arredondo 1982; Arredondo 1982, 1984; Arredondo and Olson 1994). Inferring that such medium-sized to large mammals and some birds may have constituted important components in the diet of large Cuban Boas is reasonable. A comparable pattern can be observed today in areas where other living giant constrictors (e.g., *Boa*, *Eunectes*, *Malayopython*, *Python*) feed on large herons, storks, antelope, deer, monkeys, capybaras, porcupines, wild pigs, and others (Shine et al. 1998; Rivas et al. 2007; see the review of Reed and Rodda 2009).

Boback (2003) developed what he called the "diet alteration hypothesis," which states that the size of available prey on islands is the main factor affecting body size in gape-limited predators like snakes. Also, the theory of island biogeography (MacArthur and Wilson 1967; see also Ricklefs and Bermingham 2008) predicts an increase in species diversity with an increase in island area and/or a decrease in distance from a mainland. However, island biodiversity also is directly related to the diversity of habitats and thus of ecological opportunities (Lack 1976; Ricklefs and Lovette 1999; Ricklefs

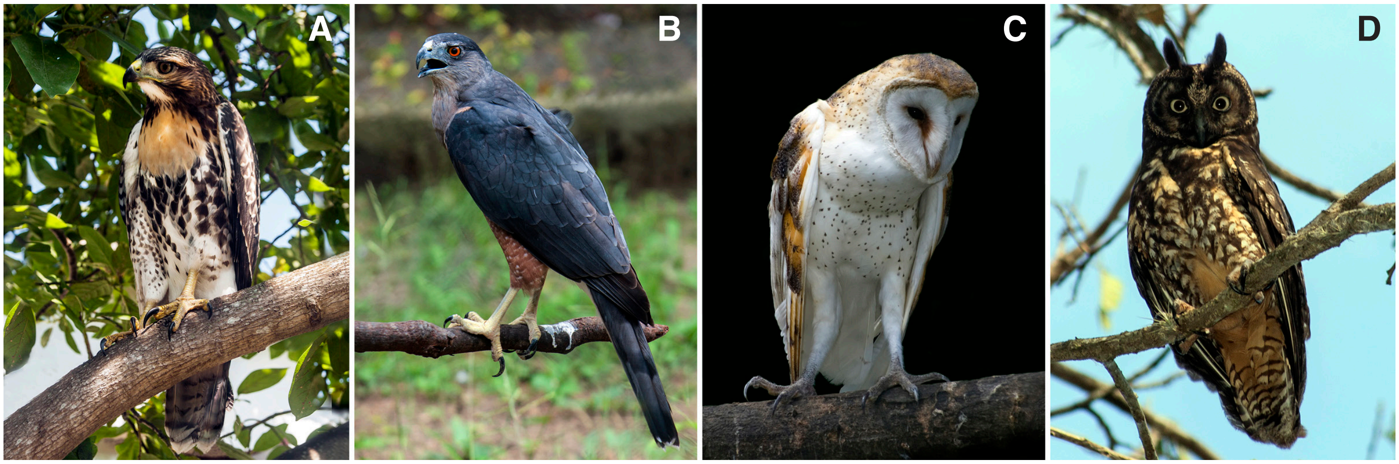

Fig. 7. The principal large raptors extant in Cuba that prey on land vertebrates include: (A) Red-tailed Hawks (*Buteo jamaicensis*), (B) Gundlach's Hawks (*Accipiter gundlachi*), (C) Barn Owls (*Tyto alba*), and (D) Stygian Owls (*Asio stygius*). Photographs © Raimundo López-Silvero.

and Bermingham 2008). According to those hypotheses, the development of the largest sizes in West Indian snakes is expected to have occurred on the largest islands (such as Cuba and Hispaniola), with the highest diversity of species and thus of body sizes of potential prey and with the greatest population densities. This prediction, combined with the absence of large carnivorous mammals in the Greater Antilles, supports the idea that larger species in the genus *Chilabothrus* probably functioned as top predators in the terrestrial ecosystems of the islands they inhabited until at least the arrival of the first humans to the region about 6,000 years ago (for reviews on the structure and function of food webs in oceanic islands, see Flannery 1993; McNab 1994, 2001; Silva et al. 2007).

In Cuba, as well as on other islands, this high trophic position in the various food webs was probably shared with large diurnal and nocturnal raptors (*Amplibuteo*, *Bubo*, *Buteogallus*, *Gigantohierax*, *Ornimegalonyx*, *Titanohierax*, *Tyto*; Arredondo 1972, 1976, 1984; Arredondo and Olson 1994; Suárez 2000, 2004; Arredondo and Arredondo 2002a, 2002b; Suárez and Olson 2007, 2015) and crocodiles (Crocodylidae, Sebecidae) with special morphological and behavioral adaptations to predate on land (Ross 1998; Thorbjarnarson et al. 2008; Jiménez et al. 2014). Raptors are known to have reached very large sizes in Cuba during the Quaternary; for example, *Ornimegalonyx oteroi*, the largest owl ever known, had an estimated height of 1.1 m, a mass of about 13.5 kg, and strong legs armored with powerful claws adapted for subduing relatively large prey like hutias and possibly even young sloths (Kurochkin and Mayo 1973; Acevedo et al. 1975; Arredondo 1976, 1982; Feduccia 1999; Alegre 2002). Nevertheless, none of those birds could have even approached the body mass of a large adult *C. angulifer*, which can easily attain a mass of more than 20 kg after reaching 3.5 m in total length (Petersen et al. 2015). Moreover, the largest extant raptors in Cuba that prey on land vertebrates (i.e., Red-tailed Hawks, *Buteo jamaicensis*; Gundlach's Hawks, *Accipiter gundlachi*; Cuban Black Hawks, *Buteogallus gundlachi*; Barn Owls, *Tyto alba*; and Stygian Owls, *Asio stygius*; Fig. 7) never exceed 2 kg. Some of these extant raptors (e.g., the Red-tailed Hawk, the largest of the species mentioned above) can even serve occasionally as prey of Cuban Boas exceeding 2.5 m in total length (Rodríguez-Cabrera et al. 2014).

Fig. 8. The Cuban Crocodile (*Crocodylus rhombifer*) developed special morphological and behavioral adaptations to predate on land mammals like extinct sloths and hutias, but it remains mostly associated with aquatic ecosystems. Photographs © Raimundo López-Silvero.

Living Cuban crocodiles (*Crocodylus acutus* and *C. rhombifer*) are mostly associated with aquatic ecosystems (see Alonso-Tabet et al. 2014 for a review; Fig. 8). Sebecid crocodiles (which were specially adapted for a terrestrial lifestyle; Gasparini 1981, 1984; Jiménez et al. 2014) are very scarce in Cuban fossil deposits and date from the early Miocene (Jiménez et al. 2014), when *C. angulifer* is thought to have split from the other Caribbean boas (see above, Reynolds et al. 2013). Therefore, little if any overlap in space and time existed between sebecids and the Cuban Boa. These realities, combined with the fact that the largest living native mammal on the island (*Ca. pilorides*; see above) constitutes the main prey of adult Cuban Boas in modern times, support the idea that *C. angulifer* was and remains a top predator in the terrestrial ecosystems of Cuba (see also Petersen et al. 2007, 2015).

One might expect that the rate of predation by a large ectotherm like the Cuban Boa would not exert substantial pressure on prey populations, but population density of this snake might adjust to the abundance and availability of trophic resources in each type of ecosystem. For instance, aggregations approaching 30 individuals have been repeatedly reported in a single hot cave harboring large bat populations (e.g., Berovides and Carbonell 1998; Linares et al. 2009; Rodríguez-Cabrera et al. 2015; Fig. 9), indicating a strong density-dependent predator-prey relationship. Despite the lack of studies on non-cave-dwelling populations of Cuban Boas, this snake likely responds in a similar way to high densities of other prey species such as hutias. These rodents, particularly *Ca. pilorides*, have the potential to explode demographically when associated with highly productive ecosystems in the absence of natural controllers and/or without human predation pressure (i.e., as many as 57 hutias/ha and up to 153 hutias/ha have been reported in inland secondary forests and in mangroves, respectively; Comas et al. 1989; Berovides and Comas 1997), often severely damaging the vegetation (Comas et al. 1989, 1994; Comas and Berovides 1990). However, the greatest predation pressure on hutia populations probably came from endothermic predators, such as the giant raptors that inhabited Cuba — and this scenario probably was repeated throughout the Greater Antilles and the Bahamian Archipelago. For example, the giant owl *Tyto pollens* (Tytonidae), fossil remains of which are always associated with those of Bahamian Hutias (*Ge. ingrahami*), suggesting a close predator-prey relationship during the late Pleistocene (Suárez and Olson 2015). The great diversity of giant raptors in Cuba during the Quaternary (see references above) is indicative of a great prey availability, which must have included hutias.

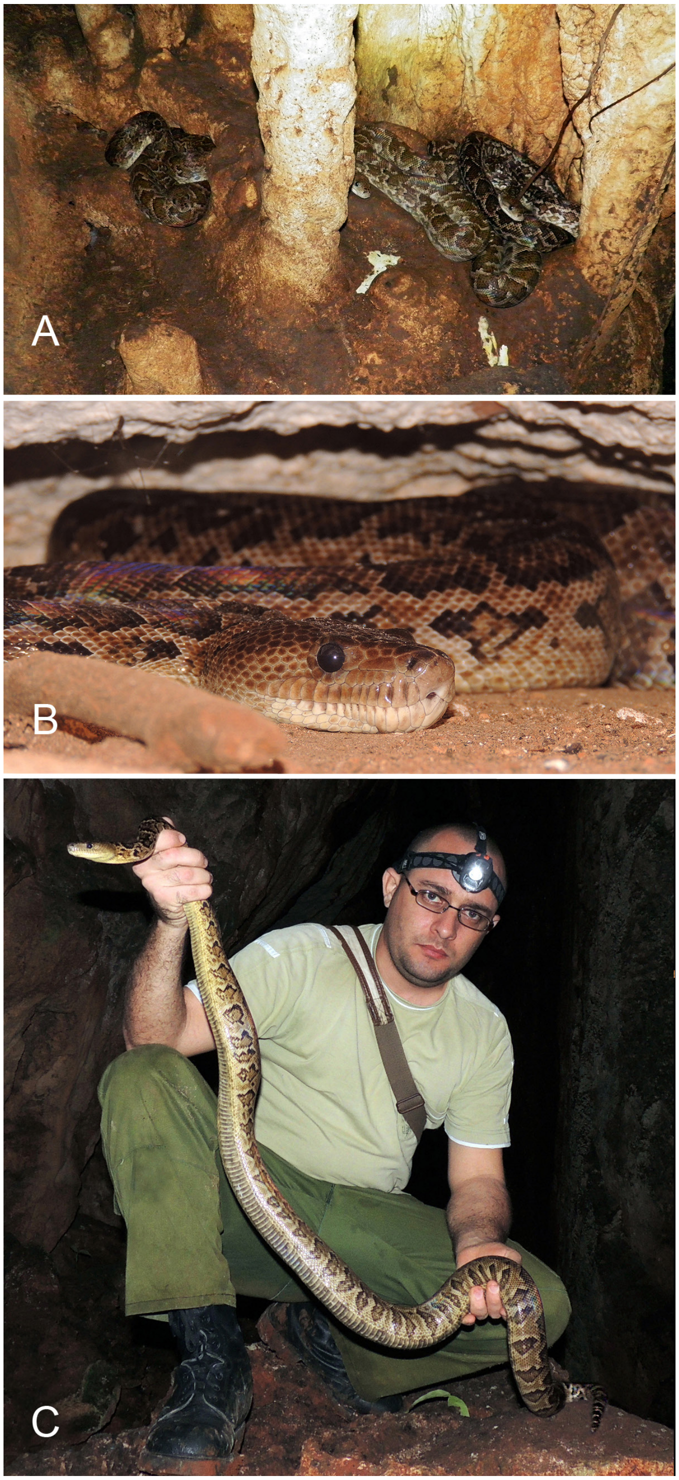

Fig. 9. Aggregations approaching 30 individuals of the Cuban Boa (*Chilabothrus angulifer*) have been repeatedly reported in bat caves: (A) Boas in the Cueva de los Majaes at Galalón, La Palma, Pinar del Río Province, the site with the greatest concentration of this species ever reported; (B) a female Cuban Boa resting during the day in the Cueva del Mudo, Güines, Mayabeque Province; (C) the senior author working with Cuban Boas in a hot cave near Jaruco, Mayabeque Province. Photographs © Armando R. Longueira (A) and Tomás M. Rodríguez-Cabrera (B & C, with tripod).

Petersen et al. (2007, 2015) considered the Cuban Boa to be an ecological keystone species critical for maintaining the balance and diversity of natural ecosystems. Consequently, the fact that each of the largest islands in the Greater Antilles has a large species of *Chilabothrus* (*C. angulifer* on Cuba, *C. inornatus* on Puerto Rico, *C. striatus* on Hispaniola, and *C. subflavus* on Jamaica; Henderson and Powell 2009; Reynolds et al. 2013; Fig. 10) would not appear to be coincidental (although see discussion below on the Bahamian *C. strigilatus*). These four species are the largest snakes on the islands they inhabit. Also, with the exception of *C. striatus* and *C. inornatus*, which coexist on Hispaniola and Puerto Rico, respectively, with other much smaller and ecologically segregated *Chilabothrus* species (< 100 cm SVL, see below), the remaining species are the only boids on their respective islands (e.g., Tolson and Henderson 1993; Henderson and Powell 2009; Powell 2012; Reynolds et al. 2016b). However, the only true giant is *C. angulifer*, the maximum verifiable sizes reported for the remaining non-Cuban *Chilabothrus* rarely exceed 2.5 m in total length (Fig. 10; see also Henderson and Powell 2009 and Reynolds et al. 2016b for reviews, but see also Fernández de Oviedo 1851b for references to very large Hispaniolan Boas).

The case of the Great Bahama Bank-dwelling *C. strigilatus* (Fig. 10), which at first sight would seem to contradict the "large-boa-large-island rule" (i.e., populations are highly fragmented into many small islets and keys), deserves special consideration. Indeed, the largest specimens of *C. strigilatus* have been reported from the small Bimini Island populations (*C. strigilatus fosteri*: 2.33 m SVL; Sheplan and Schwartz 1974). Recent lines of evidence using molecular tools suggest that *C. strigilatus* is among the most recent lineages within the *Chilabothrus* clade and is the sister species to both the Abaco Boa (*C. exsul*) from the Little Bahama Bank (Reynolds et al. 2013, 2014, 2016b) and the Hispaniolan Boa (Reynolds et al. 2016a). Despite a few remaining incongruencies regarding the phylogenetic relationships of Bahamian species of *Chilabothrus*, the general consensus supports the hypothesis of multiple colonization events to the Bahamas from Hispaniola, with *C. strigilatus* the most recent arrival (Reynolds et al. 2013, 2016a). Some of the remaining Bahamian species (*C. argentum* and *C. chrysogaster*) seem to constitute earlier-diverging lineages probably resulting from one or more independent colonization events (Reynolds et al. 2013, 2016a). Using a fossil-calibrated multilocus phylogeny, Reynolds et al. (2013) hypothesized that *C. strigilatus* diverged from Hispaniolan stock during the late Pliocene or early Pleistocene (2.6 Mya). This species (or a proto *strigilatus* + *exsul* lineage) probably arrived on the Great Bahama Bank as an already large generalist boa, similar to the closely related *C. striatus*. This large size might have been favored later by successive drops in eustatic sea level (to 120 m below the mean present level) during the last glacial maximum in the late Pleistocene (about 17,000 years ago), which must have exposed most of the Great Bahama Bank (e.g., Pregill and Olson 1981; Olson and Pregill 1982; Lambeck and Chappell 2001). These drops in sea level likely resulted in a continuous emergent landmass with an area comparable to or even larger than most of the Greater Antillean islands except Cuba (Fig. 10; Pregill and Olson 1981; Olson and Pregill 1982), with corresponding changes in the configuration of its terrestrial habitats. This hypothesis places *C. strigilatus* on a paleo-island with a much higher productivity than those inhabited by any other Bahamian *Chilabothrus* (including its probable sister species, *C. exsul*). Also, the presence of relatively large vertebrates, like iguanas in the genus *Cyclura*, medium-sized to large aquatic birds (e.g., *Burhinus*, *Eudocimus*, *Nyctanassa*, *Rallus*, *Sula*), and the Bahamian Hutia (Olson and Hilgarther 1982; Olson and Pregill 1982; Pregill 1982; Steadman et al. 2007; Henderson and Powell 2009; Buckner et al. 2012; Reynolds et al. 2016b), that once were more or less widespread on the Bahamas, might have favored the subsistence of a large boid on such a paleo-island. Indeed, *C. strigilatus* is known today as the "fowl snake" throughout the Bahamas, because of its predilection for preying on relatively large introduced avian prey (Sheplan and Schwartz 1974). All of these factors combined may have selected the maintenance (versus development) of large body size in this snake. This assumption is supported also by the fact that all remaining Bahamian species of *Chilabothrus*, which inhabit smaller banks, evolved toward smaller body sizes (autapomorphic nanism; in this

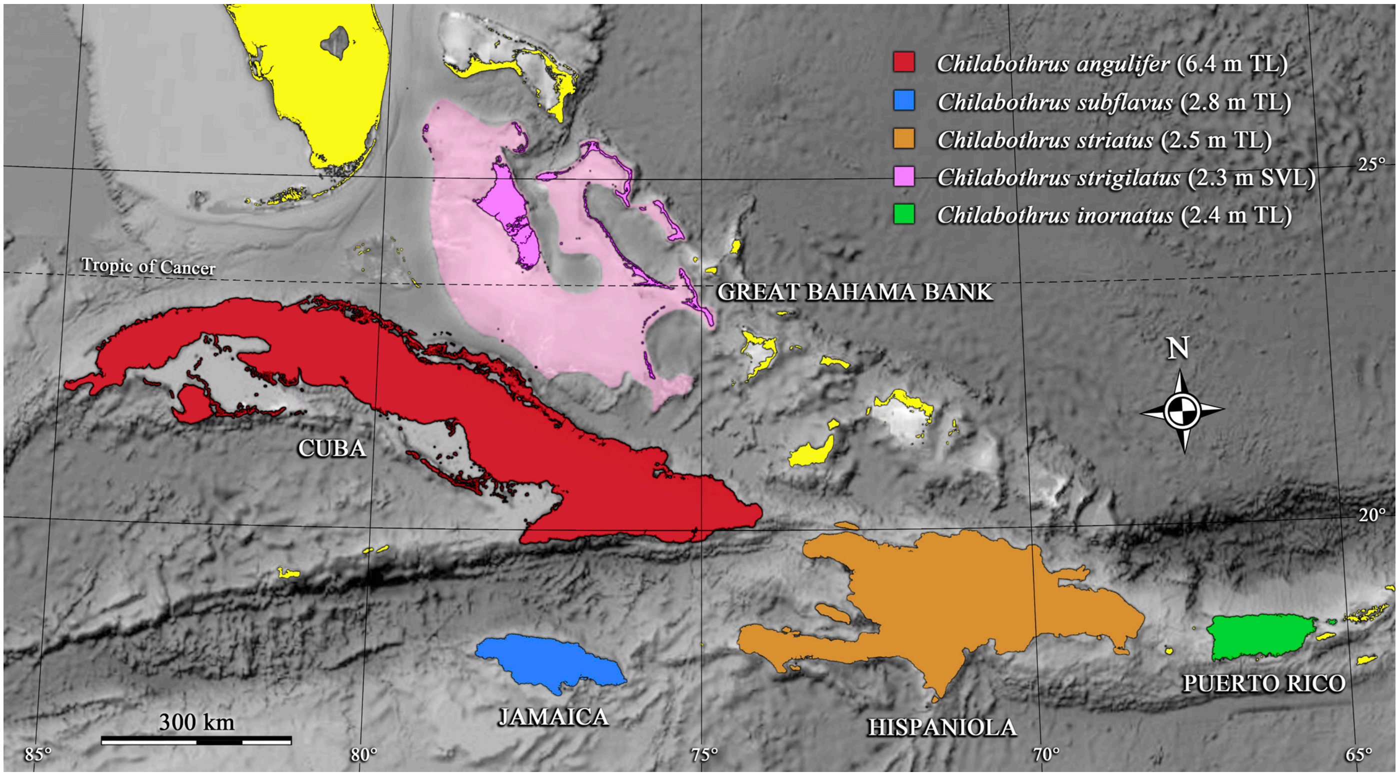

Fig. 10. Map of the Greater Antilles and the Bahamian Archipelago depicting the distribution of those species in the boid genus *Chilabothrus* that reach total lengths exceeding two meters (modified from Reynolds et al. 2013), with the maximum size (TL = total length or SVL = snout-vent length) reported for each species; the remaining landmasses are depicted in yellow. Note the extent of the shallow Great Bahama Bank (light pink area) with respect to other Greater Antillean islands and the current fragmented distribution of *C. strigilatus* around it. Sources for maximum body sizes: Gundlach 1880; Grant 1940; Sheplan and Schwartz 1974; Henderson et al. 1987; Wiley 2003.

case, more properly "synapomorphic" nanism). Reduced landmasses must have favored the subsistence of populations of smaller vertebrate prey (e.g., anoles, small birds), hence selecting for a reduction of the body size of their main snake predators, in contrast to larger and probably more productive landmasses like the emergent Great Bahama Bank, where relatively large herbivores like the Bahamian Hutia might have attained high population densities (this rodent is known to occur at high population densities under suitable conditions; Clough 1969, 1972; Campbell et al. 1991). Consequently, maintaining a large body size would be selectively favored in an opportunistic snake like *C. strigilatus*. However, after the last rise in sea level during the early Holocene, that population was fragmented into subpopulations isolated on small islets and cays as seen today. This isolation apparently reduced gene flow among subpopulations in recent millennia to account for the incipient genetic and phenotypic differentiation currently recognized at the subspecies level (Sheplan and Schwartz 1974; Tolson and Henderson 1993; Reynolds et al. 2013). However, the relatively recent presence of hutias and large iguanas on these islands might not have provided enough time for the snakes to adapt to new ecological conditions (prey consisting primarily of lizards, small birds, and rats) by reducing body sizes to a smaller optimum.

What factors might have favored the differential adaptive radiation of *Chilabothrus* on the neighboring and smaller island Hispaniola when compared to Cuba? Marine currents must have favored overwater dispersal to Cuba from Hispaniola as well as to the Bahamas from Hispaniola (Hedges 2001, 2006a, 2006b; Reynolds et al. 2013, 2016a). Thus, some factors must have impeded further colonization events from Hispaniola to Cuba. First, as mentioned previously, the niche of a large boid is developed by a single species on each of the larger islands throughout the Greater Antilles (Reynolds et al. 2016b). On those islands where more than one species occurs (Puerto Rico, Hispaniola), they have segregated toward very different niches (Reynolds et al. 2016b). On Puerto Rico, the large, generalist *C. inornatus* is sympatric with the smaller, arboreal *C. granti* (A.R. Puente-Rolón *in* Reynolds et al. 2015). Although *C. granti* is today restricted to a single location of less than 2 km^2 at Río Grande on the northeastern portion of the main island of Puerto Rico, it is thought to have been widely distributed throughout the main island in the past (Reynolds et al. 2015; Rodríguez-Robles et al. 2015), with a much larger area of sympatry. On Hispaniola, the large, generalist *C. striatus* is sympatric with two smaller species, the ground-dwelling *C. fordii* and the slender, highly arboreal *C. gracilis* (the most morphologically specialized of all species of *Chilabothrus*; Sheplan and Schwartz 1974; Henderson et al. 1987; Tolson 1987; Tolson and Henderson 1993; Henderson and Powell 2002; Reynolds et al. 2016b; Fig. 11). However, the evolutionary history of a lineage of large generalist *Chilabothrus* on Hispaniola seems to be short and recent (see the discussion below) when compared with the earlier-diverging lineages, comprised of smaller species, previously established on the island (Reynolds et al. 2013, 2016a). The early establishment of a large, generalist and widespread boid in Cuba potentially prevented any further colonization of another lineage of large generalist boids from Hispaniola or elsewhere, contrary to what occurred on the Great Bahama Bank, where this niche apparently remained available. Glor et al. (2005) commented on the probability of a similar phenomenon operating in the evolution of lizards in the genus *Anolis* (family Dactyloidae) in the West Indies. Those authors noted that established populations often prevent close relatives from expanding into their ranges, thus later colonists are unlikely to become established even if the rate of over-water dispersal remained constant through time. Similarly, the previous establishment and adaptive radiation of Dwarf Boas (genus *Tropidophis*, family Tropidophiidae) in Cuba likely prevented later colonization and/or *in situ* evolution of lineages of smaller specialist *Chilabothrus*. The family Tropidophiidae constitutes an ancient group within alethinophidians (Vidal and Hedges 2002, 2004; Pyron et al. 2013; Reynolds et al. 2014), with Cuba as the center of diversification of the most diverse genus, *Tropidophis*, comprised of 16 currently recognized species (Hedges 2002; Domínguez et al. 2006). On Cuba, they fill all available niches for small, nocturnal, constricting snakes, from stout ground-dwelling forms (e.g., *T. pardalis*) to gracile arboreal forms (e.g., *T. semicinctus*) and generalist forms (*T. melanurus*; Fig. 12; Tolson and Henderson 1993; Hedges 2002; Henderson and Powell 2009). Indeed, species within each of these three main groups show strong specializations in substrate use, foraging strategies, and diet (Rodríguez-Cabrera et al. in prep.), leading to the evolution of true "ecotypes." This segregation seems much less accentuated outside Cuba, where the diversity of dwarf boas (and hence interference competition) is much lower (Hedges 2002; Henderson and Powell 2009; Powell and Henderson 2012). This fact probably led Reynolds et al. (2016b) to cite *Tropidophis* as an example of a speciose West Indian genus without extreme morphological and ecologi-

Fig. 11. The highly arboreal Hispaniolan Vineboa (*Chilabothrus gracilis*) is the most morphologically specialized species in the genus. Photograph © Raimundo López-Silvero.

cal diversification. The evolutionary history of these snakes in Cuba seems quite different than that on other Caribbean islands, and ecological segregation is concurrent, although less extensive (probably reflecting their higher trophic position), than that observed in other squamate groups in the region (e.g., Losos 2009). Conversely, a single species of *Tropidophis* (*T. haetianus*) occurs on Hispaniola (Tolson and Henderson 1993; Henderson and Powell 2009; Powell 2012), providing an opportunity for smaller species of *Chilabothrus* to exploit some of those niches and thus leading to some convergence with "ecotypes" evident among Cuban *Tropidophis* (Fig. 13).

Oceanic islands are well known for the frequent evolution of extreme sizes among the species inhabiting them (e.g., Brown and Lomolino 1998; McNab 1994, 2001; Lomolino et al. 2010). However, the development of "giantism" on islands depends on the combination of two main selective pressures: (1) abundance of trophic resources (directly related to island size and productivity), and (2) absence of predators and competitors (Brown and Lomolino 1998; McNab 1994; Lomolino et al. 2010). Otherwise (i.e., low availability of trophic resources, in this case prey of the appropriate size for large predators), the result is the opposite and apparently leads to the development of "nanism" (Brown and Lomolino 1998; McNab 1994; Gould and MacFadden 2005). The evolution of giant sizes on oceanic islands allows avian and reptilian predators to have access to trophic resources that would be exploited by mammalian carnivores in mainland ecosystems (e.g., Brown and Lomolino 1998; Silva et al. 2007). This phenomenon has favored the "replacement" of endotherms by ectotherms on many oceanic islands (e.g., Flannery 1993; McNab 1994). Also, the lower metabolic rates per gram of body mass in ectotherms predicts that their body masses for a given landmass (assuming similar productivity) will be 5–16 times greater (for carnivores and herbivores, respectively) than that of endotherms (Burness et al. 2001). For example, if we consider that the mean body mass estimated for the top endothermic carnivore in Cuba (the giant owl, *O. oteroi*) is about 13.5 kg (Alegre 2002), then the mean body mass of the top ectothermic carnivore (the Cuban Boa) would exceed 60 kg. That estimate certainly would translate to a very large snake, likely exceeding 5–6 m in total length, comparable to some of the largest extant pythons (see review of Reed and Rodda 2009). These estimates also are consistent with the relationship in body size between the top Cuban endothermic herbivores (the terrestrial sloths *Megalocnus rodens* and *Parocnus browni*; Paula 1967; see Silva et al. 2007 for a review), which exceeded 250 kg, and the top endothermic carnivore (*O. oteroi*), about 20 times smaller. Moreover, these relatively large sizes in top endothermic herbivores and carnivores (both giant forms) are unequivocally indicative of high productivity, consistent also with a relatively large landmass (see McNab 2009).

The combination of factors described above could have served as the main selective forces driving the evolution of a large size in at least one species of *Chilabothrus* inhabiting each of the larger landmasses. Nonetheless, another factor that presumably affected the evolution of a large size in these snakes was a genetic capacity to develop large size. The genus *Chilabothrus* forms a monophyletic clade with *Epicrates* and *Eunectes* (Burbrink 2005; Rivera et al. 2011; Reynolds et al. 2013, 2014), which includes anacondas, the world's heaviest and stoutest snakes (see Reed and Rodda 2009 for a review). Therefore, whether the evolution of very large size

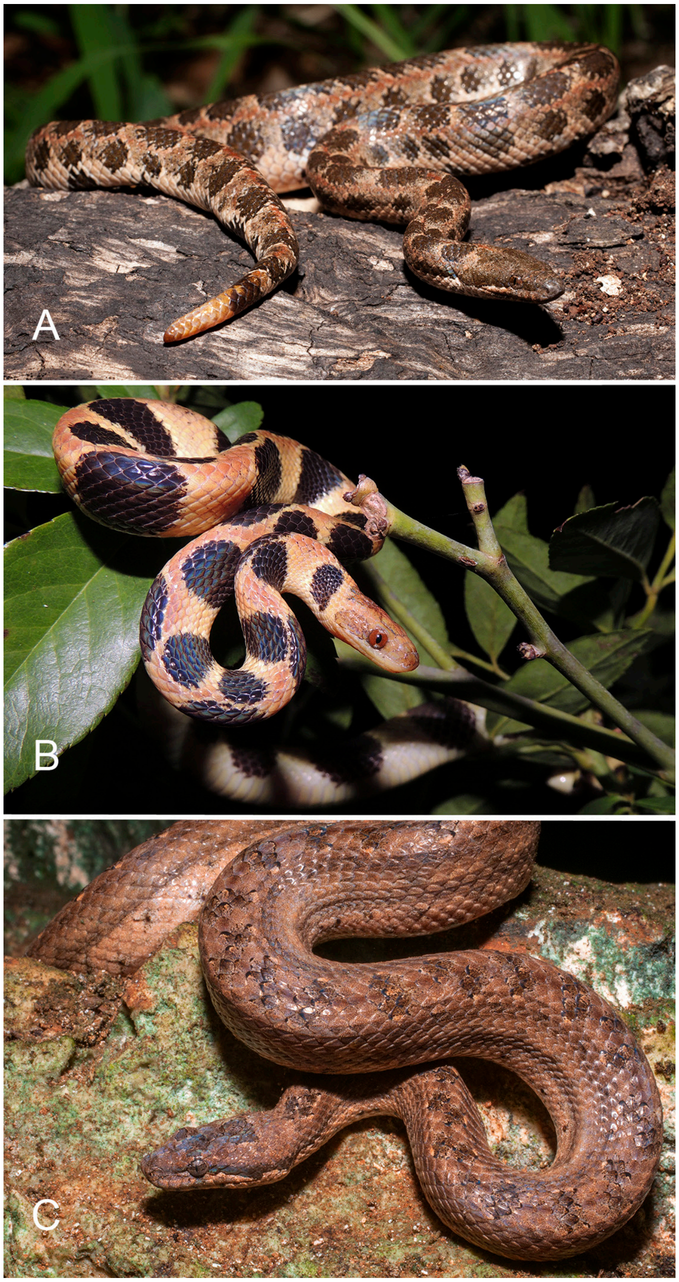

Fig. 12. The dwarf boas or tropes of the genus *Tropidophis* (family Tropidophiidae) have undergone an impressive adaptive radiation in the Cuban Archipelago, leading to the evolution of three main ecotypes: (A) ground-dwelling (e.g., *T. pardalis*), (B) arboreal (e.g., *T. semicinctus*), and (C) generalist (*T. melanurus*); a similar radiation occurred within the genus *Chilabothrus* on Hispaniola, albeit on a much smaller scale. Photographs © Raimundo López-Silvero (A), Tomás M. Rodríguez-Cabrera (B), and Rosario Domínguez (C).

Fig. 13. Strong convergence exists between the Hispaniolan Vineboa (*Chilabothrus gracilis*; left) and the arboreal ecotype of *Tropidophis* in Cuba, such as this Yellow-banded Trope (*T. semicinctus*; right). Photographs © Raimundo López-Silvero (top two and lower left) and Tomás M. Rodríguez-Cabrera (lower right).

in the Cuban Boa is best explained by autapomorphic giantism (Island Rule) or by phyletic giantism (Cope's Rule) or some combination of both remains uncertain. The continental stock, from which the genus *Chilabothrus* split, might already have been comprised of large generalist snakes when it first arrived in the Proto-Greater Antilles (Tolson 1987) — but then the ecological conditions on each island might have driven the further evolution of different body sizes, in some instances enhancing that primary trend toward large size on the larger landmasses or the evolution of smaller forms on smaller landmasses (see Reynolds et al. 2016b). Based on these assumptions, that the Cuban Boa is the largest species in the West Indies is not surprising. First, it constitutes the most basal lineage of the *Chilabothrus* radiation, the closest relative to the continental stock, and hence the species with the strongest genetic component for large size. Second, it evolved on the largest and most biodiverse island, probably with the highest productivity within the region and with a considerably longer history of ecological predator-prey interactions. The evolution of large and small body sizes within the genus *Chilabothrus* has occurred several times during its evolutionary history, probably reflecting the differential ecological scenarios on each island (Reynolds et al. 2016b). Size convergence is supported by the presence of large sizes in both early and later diverging lineages (e.g., *C. angulifer*, possibly the oldest lineage, and *C. striatus* and *C. strigilatus*, among the most recent lineages), with intermediate-aged smaller species (Reynolds et al. 2013, 2016a, 2016b). In the cases of *C. striatus* and *C. strigilatus*, large size seems to constitute a synapomorphy attributable to reversion to a large ancestor, as this character appears to be the plesiomorphic condition in the group (*Eunectes* + *Epicrates* + *Chilabothrus*) that was lost, apparently as autapomorphic nanism, on smaller landmasses or by segregating from the niches of smaller specialized forms to avoid interference competition (see also Reynolds et al. 2016b).

A classic example for comparison is the Komodo Dragon, *Varanus komodoensis* (Varanidae). This species was thought to have evolved toward large size on Flores and nearby islands as a specialized predator of the largest mammal on the island, the Pygmy Elephant (*Stegodon florensis insularis*; Auffenberg 1981; Diamond 1987; Burness et al. 2001). However, a study by Hocknull et al. (2009) revealed that *V. komodoensis* originally inhabited continental Australia during the middle Pleistocene and dispersed northward to Flores and other Indonesian islands as an already large lizard. Also, fossil evidence demonstrated that, even in the absence of moderate-sized prey subsequent to the extinction of *Stegodon* but before the introduction of pigs (a span of over 5,000 years), *V. komodoensis* was able not only to persist on Flores, but its size remained relatively constant (Hocknull et al. 2009). This suggests a strong genetic component for large size, characterized by relative stasis, in this lineage of lizards. This might be what we are seeing in the case of isolated subpopulations of the Bahamian Boa (see above). Hocknull et al. (2009) concluded that varanids can evolve giantism independently of landmass size and can compete with placental carnivores either on islands or continental areas. Also, they stated that: "The stability of *V. komodoensis* body size over a long temporal sequence and during periods of major ecological change implies that insular evolutionary processes had limited effect, and more important illustrate the adaptive flexibility and resilience of a generalist carnivore, rather than a specialist predator of the island's pygmy *Stegodon*." The boid clade comprising *Epicrates* + *Eunectes* + *Chilabothrus* might present a similar scenario. Species within the genus *Eunectes* have evolved the largest sizes within the family while in direct competition with carnivorous mammals in continental South America. Once the lineage arrived in the Greater Antilles, most species retained the original large body size. Adaptation to different and abundant food resources (notably lizards in the genus *Anolis*; e.g., Reynolds et al. 2016b) might have driven the evolution of some populations toward a smaller body size that better matched the ecological conditions. However, one should not rule out the possibility that selective pressures imposed by the very small sizes of some resource-limited islands and the interference competition with congeneric species on some larger islands (Hispaniola, Puerto Rico) broke the stasis by favoring smaller optimal body sizes. A similar situation has been described for some populations of Boa Constrictors (*Boa imperator*) that inhabit very small cays (0.05–0.24 km^2) off the coast of Belize (Boback 2005, 2006; Card et al. 2016; see also Boback 2003 for a review of other cases).

Human-induced reduction in body size and conservation implications

Humans, as predators and competitors, plus the accompanying destruction and alteration of habitats and the introduction of mammalian predators have radically changed the structure and function — and therefore the conditions — of essentially every natural ecosystem in the West Indies, forcing the native biota to adapt or perish (e.g., McNab 2001; Latta et al. 2007). The rate of evolutionary change in species under anthropogenic pressure can be considerably higher than the basal rate, especially on islands. For instance, Sasaki et al. (2008) found that populations of the Japanese Mamushi Pitviper (*Gloydius blomhoffii*, Viperidae) can respond very quickly to human predation pressures with changes in body size, vertebral number (positively correlated with body size), life-history traits, and defensive behaviors. Furthermore, these changes seem to be genetically based, which suggests a rapid evolutionary rate in at least this one species of snake. However, evidence of rapid human-induced evolution have been reported in other vertebrate groups like fish under intense fishing pressure (e.g., Olsen et al. 2004; Reznick and Ghalambor 2005; Walsh et al. 2006) and reptiles (e.g., Pregill 1986; Jiménez et al. 2014). Pregill (1986) reported reductions in body sizes from 6–46% when comparing fossil (Pleistocene or Holocene deposits) and extant populations of some West Indian lizards. Jiménez et al. (2014) compared maximum sizes reported for Cuban Crocodiles (*C. rhombifer*) from Quaternary fossil evidence (">20 ft" [> 6 m total length]; Ross 1998), from 19th-century reports ("16$^1/_2$ feet" [5 m in total length]; Gundlach 1880), and living specimens (3.5 m in total length; Varona 1966; Morgan et al. 1993). This represents a proportional reduction in body size of 17–42% (Fig. 14) and is consistent with the proportion of reduction in maximum body size observed in Cuban Boas reported between the 19th century and the present day (23–42%; Gundlach 1880; Tolson and Henderson 1993; Fig. 14).

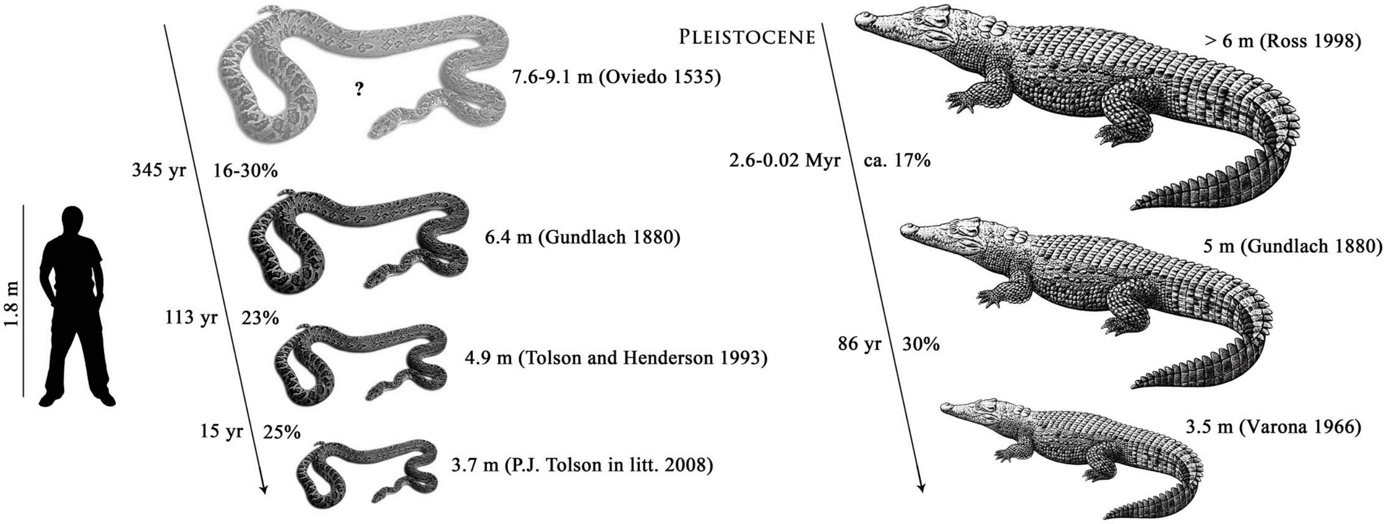

Fig. 14. The reduction in maximum body size evident in the Cuban Boa (*Chilabothrus angulifer*) is comparable to that reported for the Cuban Crocodile (*Crocodylus rhombifer*). Arrows represent the timeline to present, with the spans among records (left) and the proportion (%) in reduction of maximum body size (right). The faded image of the upper boa represents the uncertain (?) sizes reported by Fernández de Oviedo in 1535. Image of the boa © Ansel Fong; image of the crocodile modified from Lafleur et al. (1995).

As a consequence of the human presence in the West Indies (e.g., Tolson and Henderson 2006; Wilson et al. 2006; Hedges and Díaz 2011), we suspect that the current evolutionary trend in most populations of the Cuban Boa and other large species of *Chilabothrus* might be the gradual reduction in body size toward a new optimum (see Boback 2003; Boback and Guyer 2003). Whether due to phenotypic plasticity or genetic change, a new fitness optimum based on body size reduction probably translates into higher survival rates in a rapidly changing and highly modified environment with new selective pressures (i.e., shifts in trophic resources, presence of new predators and competitors). In part due to their greater conspicuousness and high rate of predation on domestic animals, large boas probably have been killed more frequently than their smaller relatives since the arrival of humans to the region, selecting against phenotypic traits advantageous under natural conditions in the past (large size) and effectively reversing directional selection (e.g., Johnson and Porter 2000; Clegg et al. 2002; Clegg 2010; Futuyma 2013). Rapid human-induced evolution could explain the present rarity of very large Cuban Boas, which might not necessarily interfere with reproductive output because reproductive size is less than two meters in total length for both sexes (Rodríguez-Cabrera et al. in press).

However, the dramatic decline in the maximum body size of Cuban Boas in such a brief span calls into question Oviedo's descriptions of boas attaining lengths greater than 7 m in the 16th century. If true, that would imply a proportional reduction in maximum body size of 16–30% when compared to reports from the 19th century, which is consistent with the reductions observed between the 19th century and today (Fig. 14). Also, was it physiologically and ecologically possible for a boa to reach such a large size on an oceanic island like pre-Columbian Cuba? Although on a much larger island, southern Sumatran Reticulated Pythons (*Malayopython reticulatus*, Pythonidae) can approach 7 m in length and 75 kg in mass and frequently consume wild pigs, monkeys, and porcupines (Shine et al. 1998). Visualizing a giant boa in the genus *Chilabothrus* as a supreme predator in a pristine Cuba, with no natural predators or competitors, feeding on juvenile sloths (including adults of smaller species like *Neocnus gliriformis*), hutias, and birds, seems to fall within the realm of possibility — but determining whether such giants ever existed will depend on the discovery of new fossil evidence.

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