



What can studying anacondas tell us about *Titanoboa* *cerrejonensis*? Exploring the life of an extinct giant snake using an extant pretty big snake

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The maximum size that snakes can reach has been a matter of long held debate until the discovery of *Titanoboa cerrejonensis* (Boidae). It was an aquatic predator that lived 60–58 million years ago in what is currently eastern Colombia, occupying tropical swamps. It was calculated to measure 12.82 metres and it was speculated that it grew so much due to a warmer planetary weather. Its life history and ecology are speculated to be very similar to that of current day anacondas. Using data from a long-term study involving hundreds of green anacondas *Eunectes murinus*, this study makes inferences about aspects of the natural history of *T. cerrejonensis* that perhaps will not be easily available by studying the fossil record. Drawing parallels with anaconda's biology, I estimate that a non-breeding female *T. cerrejonensis* weighed approximately 1,232 kg, and 1,465 kg when pregnant. It would have started breeding at 480 cm SVL, weighing 95 kg. New-born *Titanoboa* were between 181 and 215 cm. Its average meal was estimated to be 505 kg, with a potential maximum of 1,799 kg. I estimate that *Titanoboa* had a growth rate of 0.046 mm/day compared with 0.036 in anacondas; which does not support the notion that it grew more due to a warmer planet. Although the results are largely speculative, they help give a better idea of what the life of an extinct snake was like.

Keywords: Gigantism, prey size, reproductive biology, life history, palaeothermometer, giant snake, allometry, palaeoecology

INTRODUCTION

The study of palaeontology has given us great insights into the lives of extinct organism but it is limited by the availability of fossils and how incomplete the fossil record is (Dzik, 2005; Wang & Marshall, 2016; Darwin, 1859). The field has advanced in leaps and bounds lately due to sophisticated technologies that allow more details analysis of the fossil remains we have (Mallison et al., 2009). However, recruiting the assistance of other disciplines can help shed light on the life of extinct organism that analysis of fossils might not. It is possible to use our knowledge of the ecology of extant species that used similar habitat, or that are phylogenetically related to our target extinct species, to make educated guesses about their lives. This approach has been used successfully studying body size of crocodylians (Godoy & Turner, 2020), the evolution of wing morphology (Burch, 2014) and tails in birds (Pittman et al., 2013), as well as gliding among vertebrates (Socha et al., 2014) even among fairly distantly related organisms.

The heart of this approach is based on the assumption that different organisms will respond in similar ways when exposed to a particular set of evolutionary and ecological pressures, especially if they share recent

common ancestors and share a given blueprint that sets them in similar tendencies and constraints. This is the reason that adaptations of natural history traits among vertebrates have shown remarkably similar trends across taxa and variety of habitats (Meiri et al., 2021). Case in point, in birds as distantly related as penguins (Sphenisciformes) and puffins (Charadriiformes) that co-opt their wings in a very similar manner when they evolved diving, despite having split more than 70 m.y.a (Kimball et al., 2019). Simply put, the body plan of a bird will predispose the bearer to swimming in a similar manner even if Charadriiformes are nowhere closely related to penguins. Similarly, data from great white shark *Carcharodon carcharias* has been used to reconstruct the biology of the extinct giant relative megalodon *Carcharocles megalodon* (Pimiento & Balk, 2015). Thus, approaches to use extant species to understand the lives of extinct ones are not limited to very closely related individuals; and still allows us to gain insights on the lives of extinct species that we would not be able to gain using only palaeontological evidence.

One such extinct species which biology is very unknown is *Titanoboa cerrejonensis*, a giant snake that lived 60–58 m.y.a in what is now eastern Colombia (Head et al., 2009). The maximum size a snake can reach

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has been a long held debate among herpetologists, and among those interested in megafauna. There are numerous reports about the maximum size snakes can attain. Some of them are more reliable than others (Murphy & Henderson, 1997). There might be natural limits on the maximum size set by the “blueprint” of a snake (Rivas, 2020a). The finding of *T. cerrejonensis* gave the scientific community undisputable evidence that a snake can reach at least 13 metres in total length (Head et al., 2009).

Titanoboa lived in tropical swamps, surrounded by rainforest, that was likely part of an extensive wetlands that scattered over western South America resulting from the damming of the Palaeo-Amazonas river, by the rise of the Andes. This process would have started since the late Cretaceous, and lasting until the Neogene creating an extensive flooded system of estuaries and marshlands in most of northern South America. This swamp would have fluctuated from freshwater to marine-like conditions on occasions when local weather resulted in higher evaporation rates, in a system that may have been intermittently disconnected from the ocean (Rivas, 2020b). *Titanoboa* belonged to the group of Neotropical Constrictores (Georgalis & Smith, 2020). Vertebrae and skull morphology places *Titanoboa* firmly within the family Boidae, with an association with Madagascar boas (Head et al., 2013) and *Boa constrictor* (Head et al., 2012); however, no formal phylogenetic analyses have been done on the species (Smith & Georgalis, 2022). The taxonomy within the family is problematic because only the use of cranial material can provide the most reliable phylogenetic information (Georgalis et al., 2021) and the only skull known is incomplete (Head et al., 2013); Boinae genera are not diagnosable by vertebrae morphology alone (Head et al., 2006). However, the vertebral evidence is strong enough to consider *Titanoboa* within the family Boinae (Head et al., 2013; 2009). *Titanoboa* may have lived in excess of 60 years based on Lines of Arrested Growth (LAGs) in the vertebrae, but the authors express uncertainty on this estimate based on the lack of complete breaks in tissue deposition between some of the LAGs (Werning et al., 2014). *Titanoboa* was hypothesised to have fed on a variety of fish, crocodiles, and turtles that inhabited the swamps where it lived (Bloch et al., 2005; Head et al., 2009; Cadena & Jaramillo, 2015; Hastings et al., 2010). Its size was estimated to be 1,201 cm long in snout-vent length (henceforth SVL) and 1,282 cm in total length using morphological data from extant boas. Head et al. (2009) argued that it grew so large because of higher global temperatures that promoted faster growth, but this notion has been challenged based on biases of the sample used that fail to predict other Squamata reptiles (Sniderman, 2009), conflict with other estimations of other species (Shackleton & Boersma, 1981), and the fact that it ignores the behavioural abilities of animals to regulate their own temperature (Huber, 2009; Denny et al., 2009; Sniderman, 2009).

Although we do not know exactly how closely related they were, they were related enough that

the ecological similarities and phylogenetic proximity between anacondas and *Titanoboa* offers the possibility to use anacondas as a proxy to understand parts of the ecology of *Titanoboa* that perhaps are very difficult to learn from palaeontological methods. To use data from anaconda biology as a model to understand the biology of *Titanoboa* is well justified because of the following reasons. First, they are closely related phylogenetically, belonging to the same family. It is reasonable to expect that their shared ancestry results in similar responses to environmental variables. Second, they share a similar ecological niche and their ecological interactions with other members of their community would have produced similar selection pressures. Both are top predators living in tropical aquatic environments, mostly swamps. There are some similarities and differences in the diet of adult female anacondas and what *Titanoboa* was hypothesised to feed on. They both were aquatic predators, that preyed in crocodyliforms and other riverine vertebrate fauna (Head et al., 2009; Rivas, 2020a); however, there were also difference in that *Titanoboa* likely included fish in their diet, as evidenced by abundant palatine teeth, (Head et al., 2013) while fish are conspicuously absent in anacondas diet (Rivas, 2020a; Miranda et al., 2016). So, it is reasonable to expect that they faced comparable ecological and evolutionary pressures. Third, anacondas are, by far, the best studied genus of the family Boidae (Rivas, 2015; 2020a). In fact, the authors that described *Titanoboa* used an anaconda dataset to estimate its mass. So, using knowledge on anacondas to predict other aspects of *Titanoboa* biology is consistent with existing patterns in the literature. Thus, this study used data on anaconda biology to make predictions about the life of *Titanoboa*. Specifically, this anaconda dataset facilitates data-based speculation about its size and morphometric relationships, reproductive biology, size at first reproduction, and aspects of its natural history such as neonate size, prey size, growth rate, and demography. I analyse this information in light of the ecological and evolutionary landscape of the time.

MATERIALS & METHODS

Morphometry

Since 1992, I have conducted a long-term study on the life history of anacondas in the Venezuelan Llanos, addressing aspects of its ecology, such as its mating system (Rivas et al., 2007a; Rivas & Burghardt, 2001), reproductive biology (Rivas, 2015), diet, mobility and habitat use (Rivas et al., 2007b; 2016; Rivas, 2020a). As part of this study, I have caught in excess of 800 animals from which I have gathered representative morphometric information (Table 1, and supplementary material). I measured the animals by stretching a non-elastic string over the middle line of their body and later measuring the string on a measuring tape (Rivas et al., 2008) after muzzling them for ease of handling (Rivas et al., 1995). Data were analysed using histograms and linear regression models. I log-transformed the data of SVL and mass to better model their relationship (Huxley,

Table 1. Summary of the measures of 823 anacondas caught between 1992 and 2014 years. N = sample size, SVL = snout-vent length, NP = non-pregnant adult females, P = pregnant adult females. All the measures of length are given in cm and all the masses are given in grams.

Measure	Mean	STD	Max	Min	N	Regression from SVL	R ²
Total length	263.6	83.1	522	64.5	823	$y = 1.1068x \text{ (SVL)} + 10.571$	0.99
SVL	228.0	75.0	477	54.7	813	n/a	
Mass	11437.1	13316.2	97000	107	794	$\text{Log}(y) = 2.9813x \text{ (LogSVL)} - 3.1141$	0.94
Tail length	35.9	10.3	64	10.8	231	$y = 0.115x \text{ SVL} + 91479$	0.86
Perimeter	28.42	12.09	85	10	91	$\text{Log}(y) = 1.0345x \text{ Log(SVL)} - 1.0081$	0.79
Head	86.4	20.49	150	45.6	82	$y = 0.3149x + 9.1166$	0.92
Females							
Total length	304.1	101.2	522	64.6	458	$y = 1.1065x \text{ SVL} + 8.388$	0.996
SVL	267.3	91.2	477	54.7	458	n/a	
Mass	19407.3	17518.6	97000	107	458	$\text{Log}(y) = 2.9629x \text{ Log(SVL)} - 3.0336$	0.95
Tail length	36.4	12.7	64	10.8	114	$y = 0.1203 \text{ SVL} + 5.1685$	0.96
Perimeter	36.15	14.39	85	14.5	39	$\text{Log}(y) = 1.0562x \text{ (log(SVL))} - 1.0268$	0.73
Mass (NP)	22496.4	14699.4	54000	4700	104	$\text{Log}(y) = 2.9386x \text{ Log(SVL)} - 3.1103$	0.99
Mass (P)	26413	18046	97000	7250	235	$\text{Log}(y) = 2.9843x \text{ Log(SVL)} - 3.0245$	0.93
Males							
Total length	238.6	51.2	339.0	68.8	460	$y = 1.1432x \text{ (SVL)} + 5.0762$	0.99
SVL	204.3	44.6	293.7	58	460	n/a	
Mass	5678.6	2906.9	17000	180	460	$\text{Log}(y) = 2.6471x \text{ (LogSVL)} + 2.3927$	0.92
Tail length	35.3	7.3	46	11.3	117	$y = 0.1601x \text{ SVL} + 2.4007$	0.88
Perimeter	22.63	4.86	34.5	10	52	$\text{Log}(y) = 0.8014x \text{ (log(svl))} - 0.4991$	0.82

1932). No fossil specimens were measured in this study. All data from fossil snakes were obtained from the literature (Head et al., 2009).

For the predictions in this study I used a specific dataset that best applied to the category I was trying to predict. For instance, for maximum mass, I used a dataset that included only females with complete tails, as they may suffer injuries that shorten their tails. Additionally, the decision to only use females in the regression is justified because, among boas, larger females are the rule (Shine, 1994), so it is reasonable to assume that the largest *Titanoboa* was female. Males have longer tails and slimmer bodies, so using an only-female dataset is more appropriate to predict the dimensions of the largest, likely female, *Titanoboa*.

General natural history

For most of my calculations I assume than the largest reported size of *Titanoboa*, of 1,201 cm in SVL, is the maximum size it reached (but see below). Data from current snakes show that snake maximum size is between 1.5 to 2.5 the length at which they start breeding (Pritchard, 1994). My data on reproduction of anacondas confirm that females grow up to 2.27 of the size at which they start reproducing (Rivas & Burghardt, 2001; Rivas et al., 2007a; Rivas, 2015; 2020a; 2020b). I thus use the Pritchard's 2.5 ratio to make predictions about *Titanoboa* in terms of its size and first reproduction, clutch size, and neonates size.

In my calculations I use two approaches. First, I scale up what I know about anaconda biology to the size that

Titanoboa was reported to be and speculate about clutch size and neonate size. Second, and more realistically, I assume that *Titanoboa* was not merely a scaled up anaconda but rather the ecological equivalent of current anacondas (the largest aquatic snake of its time). Likely, a young female *Titanoboa* ready to breed was faced with the same decisions as our current anacondas. She had to be able to produce offspring that were ready to survive in terms of both avoiding predation and finding food, as well as having some energy for her own metabolic needs and growth. Natural selection would have shaped the natural history of *Titanoboa*, like that of anacondas, so they would breed as soon as they could produce a viable clutch, both to increase their reproductive output and to secure some offspring in case she was preyed upon before the next breeding opportunity (Rivas, 2020a). Therefore, I assume the investment per offspring for *Titanoboa* was the same as for anacondas at different parts of their ontogenetic developments.

Growth rate

Having the estimated size of neonates, the maximum reported size, and the estimated life span of 60 years, I calculated the growth rate. While the authors that estimated its lifespan to more than 60 years express doubts about the accuracy of their estimate based on LAGs, no better estimate of age has been attempted. In this contribution I use their estimation of 60+ years as the potential life span of *Titanoboa*, since LAGs are a well established method to estimate age in fossils (Castanet et al., 1993)

Maximum size

Last, because *Titanoboa* lived in tropical swamps that regularly have acidic water (Rivas, 2020b) where fossil formation is unlikely, I assume that the individuals found are not necessarily the largest they reached but a representation of the most common size of the population (the average) of *Titanoboa*. Thus, I use the size distribution of existing anacondas to speculate about the maximum size *Titanoboa* could reach. Given their close phylogenetic association and similar ecological roles, these assumptions are well granted.

RESULTS

Body size and body mass estimations

Using an only-female dataset, I calculate that an average *Titanoboa* would have weighed 1,232 kg and measured 168 cm in circumference at its widest point. A non-pregnant female, just after giving birth, would have weighed 870 kg because of a strong investment in reproduction. Conversely, a pregnant female would have weighed an amazing 1,465 kg. Using data from the general population (males and females), I calculate that its head (from the end of the quadrate to the tip of the nasal scale) would have been 38 cm long (Table 1).

At first glance *Titanoboa* may come across as having a very short tail to the trained eye. Current day anacondas of 500 cm SVL have tails in excess of 50 cm. So their tail length is 0.16 % of the total body size. However, in *T. cerrejonensis* it is 0.06 %. At the size *Titanoboa* reached, one would expect it to have a much larger tail if the proportion of tail to body size were the same in both species (Fig. 1A). However, looking at the allometric relationship of tail and body length it is possible to see that as anacondas grow larger, the relative tail length decreases. If a current day anaconda were to grow to the size of *Titanoboa*, it would have a comparably shorter tail (Fig. 1B).

Reproductive biology

Using the 2.5 factor proposed by Pritchard (1994), if *Titanoboa* grew to a maximum of 1,201 cm SVL, it must have started to breed at 480 cm SVL. At this size it would have weighed 95 kg (Table 1). This is about the maximum size reached by current anacondas in the hyper-seasonal savannah of the Venezuelan Llanos (Rivas, 2020a).

If a current day anaconda were to grow to the size of *Titanoboa*, she would produce 1,321 neonates (clutch size = $0.0009 \times \text{mass} + 2.5327$, $R^2 = 0.8421$) weighing 513 g each. She would invest 55 % of her body mass in babies amounting to 678 kg (Rivas, 2020b; Rivas et al., 2016). However, this figure assumes that *Titanoboa* was just a scaled up anaconda, which is likely not the case. For a more responsible calculation, I assume that the neonates of *Titanoboa* were under the same selection pressure as current day neonate anacondas, so its neonates had to be the same proportional size as the neonates of current anacondas. If a *Titanoboa* new mother had babies 4 % of her non-pregnant mass, as anacondas do (Rivas, 2020a; 2015), her babies will weigh 4.0 kg at birth and

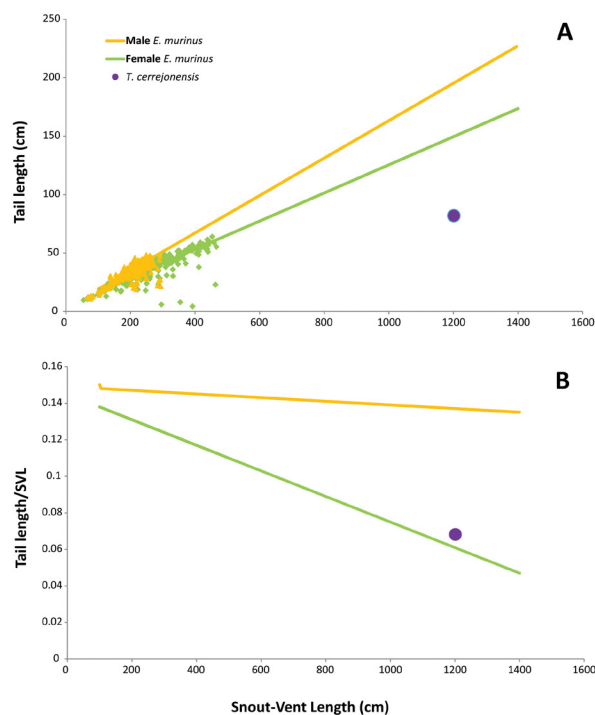


Figure 1. (A) regression of tail length vs snout-vent length in male ($R^2=0.88$) and female ($R^2=0.96$) green anacondas. The scatter plot in the lower values shows data from actual green anacondas (yellow triangles males; green squares females). The regression lines offer predictions for males (green) and females (yellow) on the larger sizes. The purple dot represent the tail of *Titanoboa*. **(B)** regressions showing the allometric relationship between relative tail length (tail length/SVL) and SVL in male and female anacondas. In the size range of current day anacondas it is not obvious to see the shortening of the tails as they get larger (females relative tail length = $-0.0001 \times \text{SVL} + 0.1664$, $R^2 0.53$). The purple dot shows where *Titanoboa* fell in this relationship. This chart shows that *Titanoboa*'s tail/SVL proportions were just on par with those of current day anacondas.

measure 1.81 metres SVL (Log (SVL) = $0.3141x + 1.1265$, $R^2 = 0.94$). Using a similar reasoning it is possible to estimate neonate size from a 12.82 m long *Titanoboa*. The relative investment per offspring declines as the animals gets larger. In anacondas it drops to 0.56 % of the female's mass (Rivas, 2020a; 2015). At 1,232 kg of mass, a *Titanoboa* would have had neonates weighing 6.9 kg and measuring 2.15 m in SVL at birth.

Prey size

Average prey size of a neonate is about 32 % of their body weight (Rivas et al., 2016). So, neonatal prey items must have ranged between 1.3 and 2.2 kg. The average prey size for adult females is 41 % (Rivas, 2020a; 2015), so the average *Titanoboa* meal would have been in average 505 kg. Furthermore, data on the diet of anacondas suggests that anacondas can go for prey as large as 146 % of its body weight (Rivas, 1998). If a large *Titanoboa*, at 1,232 kg, had been able to attack prey of this size, this prey would have weighed 1,799 kg.

Last, using the current size distribution of anacondas, it is possible to speculate about the size distribution of *Titanoboa* under the assumption that the animals recovered from the fossil record were representative of the average *Titanoboa*. Figure 2 shows the current distribution size of female anacondas (Fig. 2A) and the hypothetical distribution size of *Titanoboa* (Fig. 2B).

Growth rate

Bone histology suggests that *Titanoboa* had a lifespan in excess of 60 years (Werning et al., 2014). If neonate *Titanoboa* was born between 181 cm and 215 cm SVL, it would have experienced a growth rate between 0.046 and 0.047 mm per day to reach 1,201 cm in 60 years.

Maximum size

Figure 2A shows the distribution of female anacondas from my study, suggesting a typical normal distribution. If *Titanoboa* had a similar size distribution, it is not impossible that the largest snake that ever lived was much larger than the 13 m long *Titanoboa* found. If the *Titanoboa* specimens that have been found were average in size, the theoretical maximum *Titanoboa* could have reached in excess of 20 m in total length (Fig. 2B). At this size it would have had a mass of 5,091 kg.

DISCUSSION

This study offers educated guesses on the life of *Titanoboa* that would be difficult to obtain using other methods. Studying the life of extinct animals is fraught with limitations from the nature of the evidence that can be found in the fossil record (Darwin, 1859). However, using an extant organism that is closely related phylogenetically, and that plays the same ecological role as the extinct one, may offer unprecedented opportunities to make educated guesses on the biology of the extinct one, thereby aiding our capacity to understand better the life and ecology of the extinct organism (Kimball et al., 2019; Pimiento & Balk, 2015).

The original paper describing *Titanoboa* calculated its mass to be 1,135 kg using available regressions from pythons and anaconda sizes (Head et al., 2009). However, the anaconda dataset used in that study included males, which are thinner than females (Rivas, 2015; Rivas et al., 2007a; Rivas & Burghardt, 2001). It also included terrestrial pythons, that are slimmer than aquatic snakes. An aquatic lifestyle releases the organism from constraints of gravity and allows for the development of a larger body mass (Denny, 1990; Andersson, 1994). Taken together, I believe that a dataset only including female anacondas is more appropriate to predict *Titanoboa*'s mass and body proportions.

I assume that the ecology of *Titanoboa* was comparable to that of anacondas and thus used what we know of anacondas to speculate about the life of *Titanoboa*. *Titanoboa*'s world was likely filled by large predators, several species of crocodiles and predatory fish that abounded in the waters (Bloch et al., 2005; Hastings et al., 2010; Hastings & Bloch, 2007). There would have

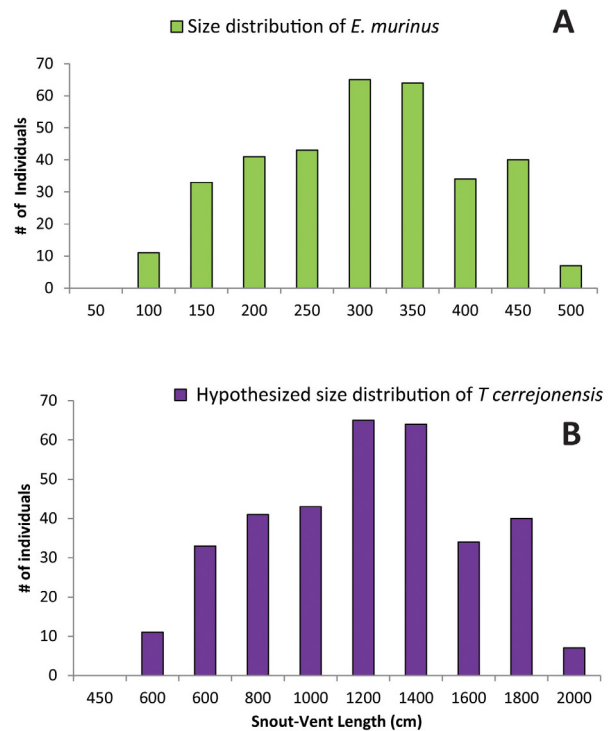


Figure 2. (A) Size distribution of female anacondas in the Venezuelan Llanos. (B) Hypothetical size distribution of *Titanoboa* assuming their demographic distribution was similar.

been a size after which a juvenile *Titanoboa* would have outgrown its predators. But until then, predation was expected to be high if the biology of anacondas and other large reptiles is any indication (Rivas et al., 2016). During *Titanoboa* times, a neonate 350 g in mass and 90 cm SVL (the largest anaconda neonate) would have faced a large amount of very large predators for a long time. This probably would have prevented a large proportion of them from reaching adulthood and reproducing. Furthermore, the assemblage of prey we have in current times provides a variety of smaller prey, including many birds, that neonate anacondas feed on (Rivas et al., 2016). Likely, smaller prey items were not that common in *Titanoboa*'s time, as *Titanoboa* predated the radiation and diversification of Neornithes birds (Claramunt & Cracraft, 2015). Therefore, a neonate *Titanoboa* the size of a neonate current-day anaconda, scaled up as it may be, would really have faced very hard odds, both for finding small food items they could prey on and also by facing strong predation during their long time of vulnerability. Because of this, I believe that the first calculation of clutch size of 1,321 neonates is unrealistic. Rather, assuming conservatism in the proportions of female mass to neonate mass yields sounder estimates (0.56–4 % of female's mass). Furthermore, the relationships of clutch size and reproductive investment is similar in *Boa constrictor* (Cardozo & Chiaraviglio, 2011), suggesting that these natural history traits are conserved within the family.

My data suggest that the average prey size of a 1,282 cm SVL *Titanoboa* was approximately 505 kg. Clearly an

animal as large as *Titanoboa* had to consume very large prey. There were a whole assortment of crocodiles, turtles, and fish at the time that likely were common in its diet (Cadena et al., 2010; Bloch et al., 2005; Hastings et al., 2010; Hastings & Bloch, 2007). Furthermore, many snakes that feed on very large prey are able to shut down their metabolism when they are not foraging. Allowing its digestive system atrophy saves energy when digestive tissue is not being used (Secor & Diamond, 1997; 2000). Moving from feast to famine is common among many snakes, and certainly among Boidae. This may be the reason that anacondas drop smaller prey from their diet as they grow larger (Rivas, 2020a; 2015). It does not pay for a very large snake to restart its large metabolic machinery for a prey that is not big enough to warrant the investment. If *Titanoboa* shared this physiological adaptation, that seems to be common among basal snakes (Secor & Diamond, 2000), it would have been also advantageous for it to drop smaller prey items from its diet. So, an average human being weighing 70 kg would weigh only 5.7 % of *Titanoboa* mass. Anacondas hardly ever take a prey this small (Rivas, 2020a; 2015). So, a full size *Titanoboa* might not have been interested in eating a person!

Studies from wild anacondas show that wild neonates may have a growth rate of 0.071 mm per day (Rivas et al., 2016). Captive bred neonates may grow as fast as 0.14 to 2.15 mm per day (Rivas et al., 2016; Lamonica et al., 2007). However, these figures are not comparable because they are from neonates fed *ad libitum* and the calculated growth rate of *Titanoboa* is over its 60-year lifespan; neonates are supposed to experience a higher growth rate than adults. A more reasonable comparison would be comparing growth rate of adult anacondas in the wild with that of *Titanoboa*, since neonatal growth rate is supposed to last a relatively short period. Female adult anacondas have an average growth rate of 0.036 mm/day (Rivas, 2020a) which seems very similar to the growth rate found in *Titanoboa* along its lifespan.

The original paper that described *Titanoboa* (Head et al., 2009) speculated that its large size was associated with faster growth due to the higher temperature of the planet at the time. My data suggest that the contribution of higher temperature to *Titanoboa*'s size might have been marginal, at best. While 0.047 mm per day seems higher than 0.036 mm per day, the seemingly higher growth rate in *Titanoboa* could be the combination of faster juvenile growth and slower adult growth. If *Titanoboa* was born at, for example, 200 cm SVL and grew at the same growth rate as neonate anacondas (0.071 mm per day) until it reached adulthood (at 480 cm SVL), it would take 10.8 years to reach that size. If then it grew at the same growth rate of adult anaconda (0.036 mm per day) it will take her another 54.9 years to reach 1,201 cm, needing a total of 65.9 years to reach that size. This calculation suggests that *Titanoboa* experienced a comparable growth rate as current day anacondas. Its large size can be explained by its long lifespan alone, without invoking higher global temperatures.

Last, I will speculate about the maximum size *Titanoboa* could have reached. Palaeontologists know all too well how difficult it is to find fossils. The odds that an organism would fossilise are low to begin with. Furthermore, the fossil then needs to be found by someone who can identify it properly. Considering that *Titanoboa* lived in tropical swamps that likely had acidic black water (Rivas, 2020b) that dissolves the calcium phosphate from the bones, we are lucky to have any fossils at all. All of the knowledge the scientific community accepts, regarding the size of the largest snake that ever lived, is the calculated size based on the fossils found. But what are the odds that the largest *Titanoboa* is the one found? It is unlikely that the *Titanoboas* found represent really the largest of its kind. The largest individual is only one, and the top largest are only few. In fact, in the Cerrejón mines where *Titanoboa* was found, they have found several individuals of about the same size. So it is quite possible that the 13 m long *Titanoboas* found might have been just your run-of-the-mill, regular-size, impress-nobody individuals. Supporting this notion is the later finding of a partial skull whose owner was estimated to be 14.3 m in total length (Head et al., 2013). If the size distribution of *Titanoboa* was similar to that of anacondas and the animals found are average size individuals, the maximum possible size of *Titanoboa* would have been in excess of 20 m. We may never find a fossil of a snake quite that large. However, this calculation shows at least the theoretical maximum that a snake could reach.

While the results of this study are speculative, they are based on well justified assumptions and a solid dataset. Using the ecology of extant anacondas allows us to speculate about the biology of *Titanoboa* and create sound predictions on their biology and life history. There is no doubt that fossil studies will continue to yield sound information about extinct species but this study shows that cross-pollination with other disciplines can help better understand the lives of extinct organisms.

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REFERENCES

- Andersson, M. (1994). Sexual selection. Princeton University Press, New Jersey.
- Bloch, J., Cadena, E., Herrera, F., Wing, S.L. & Jaramillo, C.A. (2005). Paleocene vertebrates from the Cerrejón Formation, Guajira Peninsula, northeastern Colombia.

- Journal of Vertebrate Paleontology*, 25, 37A–38A.
- Burch, S.H. (2014). Complete forelimb myology of the basal theropod dinosaur *Tawa hallae* based on a novel robust muscle reconstruction method. *Journal of Anatomy*, 225, 271–297.
- Cadena, E., Bloch, J. & Jaramillo, C.A. (2010). New podocnemidid turtle (Testudines: Pleurodira) from the Middle–Late Paleocene of South America. *Journal of Vertebrate Paleontology*, 30, 367–382.
- Cadena, E. & Jaramillo, C.A. (2015). Early to Middle Miocene Turtles from the Northernmost Tip of South America: Giant Testudinids, Chelids, and Podocnemidids from the Castilletes Formation, Colombia. *Ameghiniana*, 52, 188–203.
- Cardozo, G. & Chiaraviglio, M. (2011). Phenotypic plasticity of life history traits in relation to reproductive strategies in *Boa constrictor occidentalis*. *Evolutionary Ecology*, 25, 1163–1177.
- Castanet, J., Francillon-Vieillot, H., Meunier, F.J. & de Ricqlès, A.D. (1993). Bone and individual aging. In *Bone growth*. Hall, B.K. (Ed.) Bone, Vol. 7. CRC Press, London. 245–283 pp.
- Claramunt, S. & Cracraft, J. (2015). A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advancement*, 1(11), e1501005.
- Darwin, C. (1859). *On the Origin of the Species by means of Natural Selection or the Preservation of favoured races in the struggle for life*. John Murray, Albemarle Street, London.
- Denny, M.W. (1990). Terrestrial versus aquatic Biology: the medium and its message. *American Zoologist*, 30, 111–121.
- Denny, M.W., Lockwood, B.L. & Somero, G.N. (2009). Can the giant snake predict palaeoclimate? *Nature*, 460, E3–E4.
- Dzik, J. (2005). The chronophyletic approach: Stratophenetics facing an incomplete fossil record. *Special Papers in Palaeontology*, 159–183.
- Georgalis, G.L., Rabi, M. & Smith, K.T. (2021). Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology*, 140, 1–140.
- Georgalis, G.L. & Smith, K.T. (2020). Constrictores Opperl, 1811 – the available name for the taxonomic group uniting boas and pythons. *Vertebrate Zoology*, 70, 291–304.
- Godoy, P.L. & Turner, A.H. (2020). Body Size Evolution in Crocodylians and Their Extinct Relatives. *Els* 1, 442–452.
- Hastings, A.K. & Bloch, J. (2007). New short-snouted dyrosaurid (Crocodylomorpha) from the Paleocene of Northern Colombia. *Journal of Vertebrate Paleontology*, 27, 87A–88A.
- Hastings, A.K., Bloch, J., Cadena, E. & Jaramillo, C.A. (2010). A new small short-snouted dyrosaurid (Crocodylomorpha, Mesoeucrocodylia) from the Paleocene of Northeastern Colombia. *Journal of Vertebrate Paleontology*, 30, 139–162.
- Head, J.J., Bloch, J., Moreno-Bernal, A., Rincon-Burbano, F. & Bourque, J. (2013). Cranial Osteology, Body Size, Systematics and Ecology of the Giant Paleocene Snake *Titanoboa cerrejonensis*. *Journal of Vertebrate Paleontology*, 33, 140–141.
- Head, J. J., Bloch, J.I., Hastings, A.K., Bourque, J.R., Cadena, E.A., Herrera, F.A., Polly, P.D. & Jaramillo, C.A. (2009). Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature*, 457, 715–717.
- Head, J.J., Rincón, A.F., Suarez, C., Montes, C. & Jaramillo, C.A. (2012). Fossil evidence for Earliest Neogene American Faunal Interchange: *Boa* (Serpentes, Boinae) from Early Miocene of Panama. *Journal of Vertebrate Paleontology*, 32, 1328–1334.
- Head, J.J., Sánchez-Villagara, M.R. & Aguilera, O.A. (2006). Fossil snakes from the Neogene of Venezuela (Falcón state). *Journal of Systematic Palaeontology*, 4, 233–240.
- Huber, M. (2009). Snakes tell a torrid tale. *Nature*, 457, 669–671.
- Huxley, J. (1932). *Problems of relative growth*. Methuen, London.
- Kimball, R.T., Oliveros, C.H., Wang, N., White, N.D., Barker, F.K., Field, D.J., Ksepka, D.T., Chesser, R.T. et al. (2019). A Phylogenomic Supertree of Birds. *Diversity*, 11, 109.
- Lamonica, R.C., Abrahão-Charles, H., Loguercio, M.F.C. & Rocha-Barboas, O. (2007). Growth, shedding and food intake in captive *Eunectes murinus* (Linnaeus, 1758) (Serpentes: Boidae). *International Journal of Morphology*, 25, 103–108.
- Mallison, H., Hohloch, A. & Pfretzschner, H.U. (2009). Mechanical Digitizing for Paleontology - New and Improved Techniques. *Palaeontologia Electronica*, 12, 1–41.
- Meiri, S., Murali, G., Zimin, A., Shak, L., Itescu, Y., Caetano, G. & Roll, U. (2021). Different solutions lead to similar life history traits across the great divides of the amniote tree of life. *Journal of Biological Research (Greece)*, 28, 1–17.
- Miranda, E.B.P.D., Ribeiro-Jr, R.P., Camera, B.F., Barros, M., Draque, J., Micucci, P., Waller, T. & Strüssmann, C. (2016). Penny and penny laid up will be many: large Yellow anacondas do not disregard small prey. *Journal of Zoology*, 301(4), 301–309
- Murphy, J.C. & Henderson, R.W. (1997). *Tales of Giant Snakes: A historical natural history of anacondas and pythons*. Krieger Publishing Company, Malabar, Florida.
- Pimiento, C. & Balk, M.A. (2015). Body-size trends of the extinct giant shark *Carcharocles megalodon*: a deep-time perspective on marine apex predators. *Paleobiology*, 41, 479–490.
- Pittman, M., Gatesy, S.M., Upchurch, P., Goswami, A. & Hutchinson, J.R. (2013). Shake a Tail Feather: The Evolution of the Theropod Tail into a Stiff Aerodynamic Surface. *Plos One*, 8(5), e63115.
- Pritchard, P.C. (1994). Letters to the editors: The tympanum. *Bulletin of the Chicago Herpetological Society*, 29, 37–39.
- Rivas, J.A., Ascanio, R.E. & Muñoz, M.D.C. (2008). What Is the Length of a Snake? *Contemporary Herpetology*, 2008, 1–3.
- Rivas, J.A. (1998). Predatory attack of a green anaconda (*Eunectes murinus*) on an adult human. *Herpetological Natural History*, 6, 158–160.
- Rivas, J.A. (2015). *Natural History of the Green Anaconda: with emphasis on its reproductive biology*. CreateSpace Independent Publishing Platform, South Carolina.
- Rivas, J.A. (2020a). *Anaconda, The Secret Life of the World's Largest Snake*. Oxford University Press, Oxford.
- Rivas, J.A. (2020b). Climate Change and speciation pulses in a nearly flooded continent: Tackling the Riddle of South America's High Diversity. *Ecotropicos*, 32, 1–21.
- Rivas, J.A. & Burghardt, G.M. (2001). Sexual size dimorphism in

- snakes: wearing the snake's shoes. *Animal Behaviour*, 62, F1–F6.
- Rivas, J.A., Molina, C.R., Corey-Rivas, S.J. & Burghardt, G.M. (2016). Natural History of Neonatal Green Anacondas (*Eunectes murinus*): A Chip Off the Old Block. *Copeia*, 104, 402–410.
- Rivas, J.A., Muñoz, M.C., Thorbjarnarson, J.B., Holmstrom, W. & Calle, P.P. (1995). A safe method for handling large snakes in the field. *Herpetological Review*, 26, 138–139.
- Rivas, J.A., Muñoz, M.D.C., Burghardt, G.M. & Thorbjarnarson, J.B. (2007a). Mating system and sexual size dimorphism of green anaconda (*Eunectes murinus*). In *Biology of Boas, Pythons, and Related Taxa*. Henderson, R.W. & Powell, R. (Eds.) Eagle Mountain Publishing Company, Eagle Mountain. 461–473 pp.
- Rivas, J.A., Muñoz, M.D.C., Thorbjarnarson, J.B., Burghardt, G.M., Holmstrom, W. & Calle, P.P. (2007b). Natural History of the green anacondas in the Venezuelan llanos. In *Biology of Boas, Pythons, and Related Taxa*. Henderson, R.W. & Powell, R. (Eds.) Eagle Mountain Publishing Company, Eagle Mountain, 128–138 pp.
- Secor, S.M. & Diamond, J.M. (1997). Determinants of the postfeeding metabolic response of Burmese pythons, *Python molurus*. *Physiological Zoology*, 70, 202–212.
- Secor, S.M. & Diamond, J.M. (2000). Evolution of Regulatory Responses to Feeding in Snakes. *Physiological and Biochemical Zoology*, 73, 123–141.
- Shackleton, N. & Boersma, A. (1981). The climate of the Eocene ocean. *Journal of the Geological Society*, 138, 153–157.
- Shine, R.G. (1994). Sexual size in snakes revisited. *Copeia*, 1994, 326–346.
- Smith, K.T. & Georgalis, G.L. (2022). The diversity and distribution of Palaeogene snakes - a review, with comments on vertebral sufficiency. In *The Origin and Early Evolution of Snakes*. Gower, D. & Zaher, H. (Eds). Cambridge University Press, Cambridge. 55–84 pp.
- Sniderman, J.M.K. (2009). Biased reptilian palaeothermometer? *Nature*, 460, E1–E2.
- Socha, J.J., Jafari, F., Munk, Y. & Byrnes, G. (2014). How animals glide: From trajectory to morphology. *Canadian Journal of Zoology*, 93, 901–924.
- Wang, S.C. & Marshall, C.R. (2016). Estimating times of extinction in the fossil record. *Biology Letters*, 12(4), 20150989.
- Werning, S., Head, J.J. & Bloch, J.I. (2014). Bone Histology and Growth in the Largest Known Snake, *Titanoboa cerrejonensis*. *Journal of Vertebrate Paleontology*, 35, 254.

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