LETTERS

Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures

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The largest extant snakes live in the tropics of South America and southeast Asia[1-3] where high temperatures facilitate the evolution of large body sizes among air-breathing animals whose body temperatures are dependant on ambient environmental temperatures (poikilothermy)[4,5]. Very little is known about ancient tropical terrestrial ecosystems, limiting our understanding of the evolution of giant snakes and their relationship to climate in the past. Here we describe a boid snake from the oldest known neotropical rainforest fauna from the Cerrejón Formation (58–60 Myr ago) in northeastern Colombia. We estimate a body length of 13 m and a mass of 1,135 kg, making it the largest known snake[6-9]. The maximum size of poikilothermic animals at a given temperature is limited by metabolic rate[4], and a snake of this size would require a minimum mean annual temperature of 30–34 °C to survive. This estimate is consistent with hypotheses of hot Palaeocene neotropics with high concentrations of atmospheric CO_2 based on climate models[10]. Comparison of palaeotemperature estimates from the equator to those from South American mid-latitudes indicates a relatively steep temperature gradient during the early Palaeogene greenhouse, similar to that of today. Depositional environments and faunal composition of the Cerrejón Formation indicate an anaconda-like

ecology for the giant snake, and an earliest Cenozoic origin of neotropical vertebrate faunas.

Serpentes Linnaeus 1758
Boidae Gray 1825
Boinae Gray 1825
Titanoboa cerrejonensis gen. et sp. nov.

Etymology. The generic name combines '*Titan*' (Greek, giant) with '*Boa*', type genus for Boinae. The specific name refers to the Cerrejón region, Guajira Department, Colombia. The full translation is 'titanic boa from Cerrejón'.
Holotype. UF/IGM 1, a single precloacal vertebra (Fig. 1a–d).
Locality. La Puente Pit, Cerrejón Coal Mine, Guajira Peninsula, Colombia (palaeolatitude 5.5° N; Supplementary Fig. 1).
Horizon. Single claystone layer, middle segment of the Cerrejón Formation (Supplementary Fig. 2); middle–late Palaeocene epoch (58–60 Myr ago), palynological zone Cu-02 (ref. 11).
Referred material. UF/IGM 2 (paratype), nearly complete precloacal vertebra (Fig. 1g, h). UF/IGM 3–UF/IGM 28, 184 additional precloacal vertebrae and ribs representing 28 individuals (Supplementary Table 1).
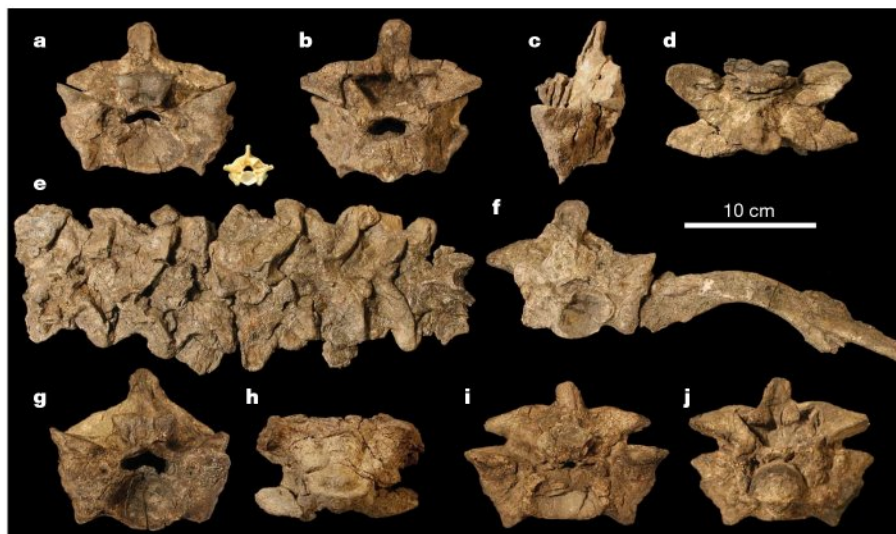

Figure 1 | *Titanoboa cerrejonensis* precloacal vertebrae. a, Type specimen (UF/IGM 1) in anterior view compared to scale with a precloacal vertebra from approximately 65% along the precloacal column of a 3.4 m *Boa constrictor*. Type specimen (UF/IGM 1) shown in posterior view (**b**), left lateral view (**c**) and dorsal view (**d**). Seven articulated precloacal vertebrae (UF/IGM 3) in dorsal view (**e**). Articulated precloacal vertebra and rib (UF/IGM 4) in anterior view (**f**). Precloacal vertebra (paratype specimen UF/IGM 2) in anterior view (**g**) and ventral view (**h**). Precloacal vertebra (UF/IGM 5) in anterior view (**i**) and posterior view (**j**). All specimens are to scale.

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Diagnosis. Extremely large-bodied boine snake with robust precloacal vertebrae possessing a uniquely T-shaped neural spine composed of a transversely expanded posterior margin and distinctly narrow, blade-like anterior process (Fig. 1a–d, i, j). Subcentral and lateral foramina are extremely reduced.

The vertebrae possess a character combination unique to boine snakes. These are: the presence of paracotylar fossae and foramina; straight, posteromedially angled interzygapophyseal ridges; and the vaulted, bi-angled posterior margin of the neural arch. These characters are also present in some madtsoiid snakes; however, all specimens of *Titanoboa* possess short, posteriorly angled prezygapophyseal accessory processes as in boines but unlike madtsoiids, and lack the parazygantral foramina and laterally extensive synapophyses that diagnose Madtsoiidae[12]. Among extant boines, *Titanoboa* is united with *Boa constrictor* on the basis of dorsolaterally positioned paracotylar fossae and foramina.

Vertebrae of *Titanoboa* are the largest recovered for any extant or fossil snake[6–8]. Body size can be predicted from vertebral dimensions in taxa where body length evolved by increasing the size of vertebrae instead of their number. This is true for all extant giant boids and pythonids[13] and is inferred for *Titanoboa* because it is united with *Boa* within Boinae. Vertebral size changes along the vertebral column in snakes, and the position of isolated fossil vertebrae, must be determined before body length can be reconstructed. We estimated vertebral position by matching the vertebral shape of two undistorted specimens of *Titanoboa* to a composite geometric morphometric model vertebral column[14] constructed from extant boines (see Methods). Both vertebrae were estimated to be located 60–65% back along the precloacal vertebral column from the axis–atlas complex. Regressions of vertebral width from this region against body lengths for extant boines indicate a snout–vent length (SVL) of 12.01 ± 2.04 m (39 ft) and a total body length (TBL) of 12.82 ± 2.18 m (42 ft) for *Titanoboa*. Incorporating SVL values of this study into the relationship between length and body mass determined for extant *Eunectes murinus* (green anaconda)[2] and *Python natalensis* (southern African python)[15] results in an estimated mass for *Titanoboa* of 1,135 kg (1.27 ton) with a range of 652–1,819 kg (0.73–2.03 ton).

Body size estimates for *Titanoboa* greatly exceed the largest verifiable body lengths for extant *Python* and *Eunectes*, which are approximately 9 m and 7 m, respectively[1]. Maxima for these taxa are extraordinary, however, and surveys of large populations have not recovered individuals exceeding 6 m TBL for *Python* and 6.5 m TBL for *Eunectes*[2,3,15,16]. Conversely, the record of *Titanoboa* includes eight individuals represented by vertebrae of approximately the same size as the elements used to estimate TBL (Fig. 1, Supplementary Table 1), indicating that extremely large body size was common in the taxon. *Titanoboa* is larger than all other giant fossil taxa, including palaeopheids and madtsoiids[6,9], making it the largest known snake (Fig. 2). Discovery of *Titanoboa* extends the known range of body lengths in snakes by more than two orders of magnitude, between TBLs of 10 cm (*Leptotyphlops carlae*) and 12.8 m. Our estimates of body size also demonstrate that *Titanoboa* is the largest known non-marine vertebrate from the Palaeocene and early Eocene[17].

Large body size in *Titanoboa* provides significant information on equatorial climates during the Palaeogene. Snakes have body temperatures that are dependant on their ambient environment (poikilothermy), and ambient temperature regulates maximum body size in poikilothermic vertebrates[4,5]. Palaeotemperature can be predicted from fossils of poikilothermic taxa using a model for extant taxa[4] that demonstrates that the difference in maximum body size of taxa between two localities is proportional to the difference in ambient temperature for a given mass-specific metabolic rate (see Methods). We used the difference in TBL between *Titanoboa* and *Eunectes murinus*, the largest snake in the modern neotropics, to reconstruct the mean annual temperature (MAT) for the Palaeocene of equatorial South America. The relationship between TBL and temperature in *Eunectes* indicates that the approximate minimum MAT under which a 13-m-long boine
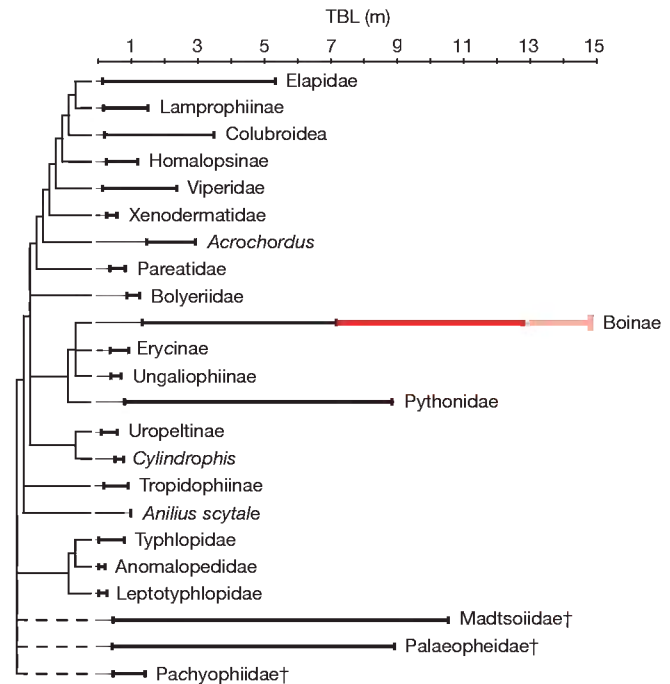

Figure 2 | Body size ranges for major snake clades plotted along phylogeny[28–30] (Supplementary Table 3). Controversial fossil (dagger) lineages Madtsoiidae, Pachyophiidae and Palaeopheidae were placed as an unresolved polytomy at the base of the snake crown. The size range increase in Boinae based on the *Titanoboa cerrejonensis* mean TBL estimate is in dark red; maximum TBL estimate for *Titanoboa* is in pink.

snake could survive is 32–33 °C, ranging between 30 °C and 34 °C for body sizes between 11 m and 15 m (Fig. 3).

These temperature estimates are consistent with hot Palaeogene climate models requiring high atmospheric p_{CO_2} concentrations of approximately 2,000 parts per million[18], and are slightly higher than temperatures derived from planktonic foraminifer oxygen isotopes by 1–5 °C[19]. These estimates exceed MATs derived from coeval Cerrejón palaeofloras by 6–8 °C[20], but palaeotemperatures based on fossil leaf assemblages from riparian and wetland habitats of rainforests are underestimates[21]. Palaeotemperature estimates of 30–34 °C exceed MAT maxima of modern tropical forests[22]. However, the high rainfall estimates from the Cerrejón palaeoflora (~4 m per year[11]) combined with increased p_{CO_2} could have maintained forest floras under higher temperature conditions[23].

Palaeotemperature estimates near the equator allow reconstruction of latitudinal temperature gradients across South America during the Palaeogene. MAT for the middle Palaeocene of Argentina (palaeolatitude ~51° S) is 14.1 °C ± 2.6 °C[24], indicating a latitudinal gradient of 13–22 °C between 5° N and 51° S, with a midpoint of 18 °C (accounting for taphonomic bias[21] suggests MAT of 17.6 °C ± 3.6 °C with a gradient midpoint of 15.4 °C). Our midpoint estimates during the early Palaeogene greenhouse approximate the modern temperature difference across South America (Fig. 3) and are not consistent with the climatic thermostat hypothesis that predicts cooler equatorial temperatures and a shallow temperature gradient during greenhouse intervals[25]. If our Palaeocene estimates are correct, tropical temperatures at the slightly younger (55.8 Myr ago) Palaeocene–Eocene thermal maximum (PETM) could have reached 38–40 °C, resulting in widespread equatorial heat-death as recent models and other proxy data have predicted[26]. However, we still lack empirical evidence of the effects of the PETM on tropical floras and faunas.

Remains of *Titanoboa* were found in depositional environments consisting of coastal plains incised by large-scale river systems within a wet tropical rainforest[11,20] and were associated with an aquatic vertebrate fauna including podocnemidid pleurodire turtles, dyrosaurid
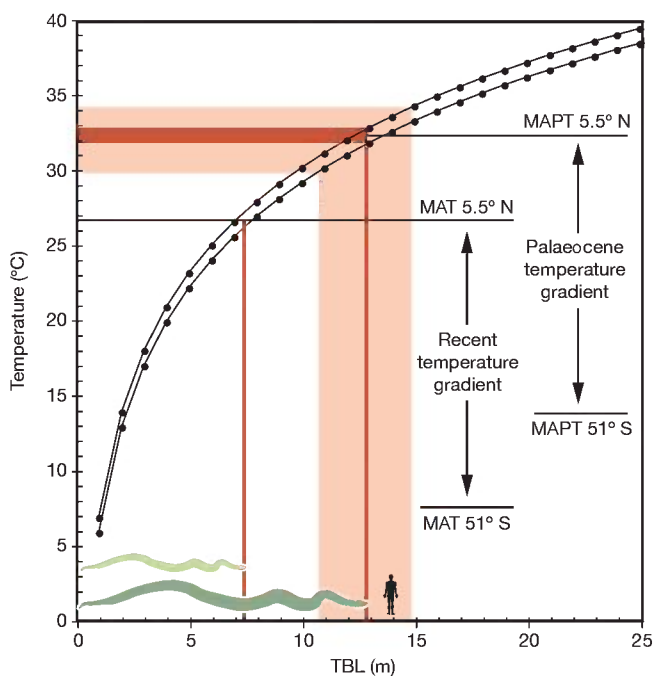
Figure 3 | Mean annual palaeotemperature and Palaeocene latitudinal temperature gradients derived from body size of the green anaconda *Eunectes murinus* (light green) and body size estimates of *Titanoboa cerrejonensis* (dark green). Curves represent model body size increases with temperature in boine snakes based on a maximum TBL for *Eunectes* of 7.3 m at modern neotropical MAT of 26 °C (lower curve) and 27 °C (upper curve). Light red regions indicate error for *Titanoboa* TBLs and resultant temperature ranges. A MAPT gradient of 18 °C from equatorial to mid-latitudes at ~58 Myr ago is equivalent to the modern gradient (18–19 °C). Silhouettes are to scale for *Titanoboa*, *Eunectes* and a 1.85-m-tall adult human male.

mesoeucrocodylians, and elopomorph and dipnoan fishes. Similarities between depositional environments of the Cerrejón Formation and habitats of extant *Eunectes* together with inferred prey taxa (crocodyliforms) indicate a similar ecology of *Titanoboa* to modern anacondas[2,3]. Discovery of *Titanoboa* and the additional Cerrejón Formation fossil record indicates that components of modern neotropical riverine vertebrate faunas were assembled at most six to seven million years after the Cretaceous–Palaeogene extinction event.

METHODS SUMMARY

We estimated SVL and TBL in *Titanoboa* by first determining the intracolumnar position of isolated precloacal vertebrae through maximum likelihood identification of quantified vertebral morphology against morphological change along a model boine vertebral column. We regressed SVL and TBL of extant taxa onto vertebral width (postzygapophyseal width) for the intracolumnar regions corresponding to the positions determined for the fossil elements, and used the resulting equations to calculate SVL and TBL for fossil specimens. We estimated mean annual palaeotemperatures (MAPT) by solving the equation describing size differences across a temperature gradient at a standard coefficient of metabolism $[Q_{10}]^{27}$, TBLs for *Titanoboa* of 10.6–14.9 m, maximum TBL for *Eunectes murinus* of 7.3 m[1], and MAT values for modern neotropical lowland rainforests of 26–27 °C[22].

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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METHODS

Position estimation of fossil vertebrae. We used a maximum-likelihood algorithm to find the most likely position of isolated vertebrae along an anterior–posterior shape gradient derived from the vertebrae of representative extant taxa, a procedure modified from ref. 14. The anterior–posterior morphological gradient was estimated by measuring the shape of vertebrae between the first and last precloacal vertebrae. Vertebral shape was quantified using two-dimensional geometric landmarks that represent morphology in anterior view (Supplementary Fig. 3). The anterior view was chosen because it provides height and width information as well as the most complex vertebral morphology. The number of precloacal vertebrae varies within Boinae[13] (Supplementary Table 2), so we sampled vertebral morphology at 5% intervals along the column for all specimens to standardize comparisons across taxa.

We projected the vertebral landmarks of all the extant species and the isolated fossil specimens into the same shape space by Procrustes superimposition to minimize shape differences among specimens, with orthogonal projection into tangent space. Shapes were rotated to their principal components (PC) axes using singular value decomposition to find the eigenvectors and eigenvalues. The PC axes have the valuable property that the shape variation described by each one is statistically uncorrelated with the shape variation described by the others. Variance is therefore additive across the axes, allowing the PC scores to be used as uncorrelated variables in multivariate statistical analysis.

A multivariate regression of vertebral shape onto position in the vertebral column was used to extract a species-independent anterior–posterior shape gradient from the extant data set. Both a discrete function and a continuous spline function were fit. The discrete function runs through the multivariate means of each of the 5% vertebral positions and is undefined between them. The spline function runs through the 5% multivariate means and is interpolated between them (Supplementary Fig. 4).

These multivariate regression functions and their residual variation were used as likelihood models for estimating the position of the fossil vertebrae. The following function describes the likelihood distribution of shape at vertebral position (pos) k:

$$L(\text{pos}_k|z,\hat{z},\sigma^2) = \prod_{n=1}^{i} \frac{1}{\sqrt{2\pi\sigma_{k,i}^2}} e^{-\frac{(z_i - \hat{z}_{k,i})^2}{2\sigma_{k,i}^2}} \quad (1)$$

where i is the number of principal components, k,i is the score of the unknown vertebra on PC_i, $\hat{z}_{k,i}$ is the expectation of shape at vertebral position k on PC_i along the shape gradient defined by the extant species, and σ^2_i is the residual variance around the estimated shape gradient at position k on PC_i. If the variance is presumed to be equal along the length of the shape gradient, which it is approximately in our data, then the variance term becomes a constant and can be dropped:

$$L(\text{pos}_k|z,\hat{z}) = \prod_{n=1}^{i} e^{-(z_i - \hat{z}_{k,i})^2} \quad (2)$$

The log likelihood equation is then simply:

$$l(\text{pos}_k|z,\hat{z}) = \sum_{n=1}^{i} (z_i - \hat{z}_{k,i})^2 \quad (3)$$

Maximizing this equation for position k gives the best estimate of the position of the unknown vertebrae given its shape (z) and the estimated shape gradient of the extant snakes ($\hat{z}$).

Standard errors (s.e.) for the positional estimates were obtained by cross validation. Isolated vertebrae with a known position were systematically selected from the sample of extant snakes. Each vertebra was submitted to the maximum likelihood procedure and the distance of the estimated position from the true position was noted. s.e. is the mean distance from the true value for the entire sample.

Regression of body size onto vertebral size. We estimated body length for *Titanoboa* by regressing SVL and TBL measured in millimetres onto postzygapophyseal width measured in millimetres for precloacal vertebrae between 60% and 65% intervals along the precloacal vertebral column for the examined sample of extant boines ($n = 21$, Supplementary Table 2), based on results of position estimation, and applying the resultant equation to the holotype (UF/IGM 1, width = 120 mm) and paratype (UF/IGM 2, width = 119 mm) specimens. SVL, TBL and vertebral width data were not log-transformed because they were approximately normally distributed (SVL skewness = 0.63, TBL skewness = 0.49, postzygapophyseal width skewness = 0.64, s.e. skewness for all = 1.07). Least-squares linear regression models produced positive, significant relationships between SVL and width (60%: slope = 95.9, intercept = 262.6, $P < 0.001$, $R^2 = 0.85$; 65%: slope = 100.4, intercept = 226.5, $P < 0.001$, $R^2 = 0.87$), and TBL and width (60%: slope = 100.7, intercept = 436.2, $P < 0.001$, $R^2 = 0.81$; 65%: slope = 106.0, intercept = 390.0, $P < 0.001$, $R^2 = 0.83$). The estimated means of 12.04 m SVL and 12.82 m TBL were obtained by averaging the 60% and 65% estimates. The error for size estimates was determined by subtracting the averaged regression coefficients from a perfect fit for extant taxa.

Palaeotemperature estimation. We estimated palaeotemperature from body size using the equation of ref. 4:

$$\frac{L_1}{L_2} = Q_{10}^{(\Delta T/10^\circ C)/3\alpha} \quad (4)$$

where L_1 is length of the largest taxon, L_2 is length of the smallest taxon, 10 °C is interval of temperature change associated with metabolic rate change (Q_{10}; ref. 5), and $\Delta T =$ temperature$_1$ − temperature$_2$. We solved for the temperature associated with the larger taxon (*Titanoboa*; Fig. 3) as follows:

$$\text{MAPT} = \text{MAT} + 3\alpha 10^\circ C\left(\frac{\log_{10}(\text{TBL}_T/\text{TBL}_E)}{\log_{10}Q_{10}}\right) \quad (5)$$

where MAPT is mean annual palaeotemperature (temperature$_1$ in equation (4)), MAT is modern mean annual temperature (temperature$_2$ of equation (4)), TBL$_T$ is total body length of *Titanoboa* (L_1 in equation (4)), TBL$_E$ is total body length of *Eunectes* (L_2 of equation (4)), Q_{10} is mass-specific metabolic rate of 2.65 for boid snakes[27], and $\alpha = 0.33$ (ref. 5):

$$\text{MAPT} = \text{MAT} + 9.9^\circ C\left(\frac{\log_{10}(\text{TBL}_T/\text{TBL}_E)}{0.42}\right) \quad (6)$$