

- Hecht, M. K. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proc. R. Soc. Vic.* **87**, 239–250 (1975).
- Price, G. J. & Webb, G. E. Late Pleistocene sedimentology, taphonomy and megafauna extinction on the Darling Downs, southeastern Queensland. *Aust. J. Earth Sci.* **53**, 947–970 (2006).
- Roberts, R. G. *et al.* New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* **292**, 1888–1892 (2001).
- Miller, G. H., Magee, J. W. & Jull, A. J. T. Low-latitude glacial cooling in the Southern Hemisphere from amino-acid racemization in emu eggshells. *Nature* **385**, 241–244 (1997).
- Pelejero, C., Calvo, E., Barrows, T. T., Logan, G. A. & De Deckker, P. South Tasman Sea alkenone palaeothermometry over the last four glacial/interglacial cycles. *Mar. Geol.* **230**, 73–86 (2006).
- Calvo, E., Pelejero, C., De Deckker, P. & Logan, G. A. Antarctic deglacial pattern in a 30 kyr record of sea surface temperature offshore South Australia. *Geophys. Res. Lett.* **34**, doi:10.1029/2007GL029937 (2007).
- Molnar, R. E. *Dragons in the Dust: the Paleobiology of the Giant Monitor Lizard Megalania* (Indiana Univ. Press, 2004).
- Wroe, S. A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader ramifications. *Aust. J. Zool.* **50**, 1–24 (2002).
- Flannery, T. The case of the missing meat eaters. *Nat. Hist.* **102**, 41–45 (1993).
- Gingerich, P. D. Environment and evolution through the Paleocene-Eocene thermal maximum. *Trends Ecol. Evol.* **21**, 246–253 (2006).

doi:10.1038/nature08222

Re-calibrating the snake paleothermometer

Arising from: J. J. Head *et al.* *Nature* **457**, 715–717 (2009)

In a recent study¹ a new proxy for paleoclimate reconstructions was proposed on the basis of a theoretical approach linking the largest body sizes to ambient temperature in extant taxa of air-breathing poikilotherms^{2,3}. The value of the largest fossil snake's body length was used to estimate the mean annual temperature (MAT) for the Palaeocene neotropics of $\Delta T = 3.8\text{--}7.2\text{ }^\circ\text{C}$ above the modern value¹. Here we argue that the reported temperature difference is a twofold overestimate and obtain a corrected estimate of $\Delta T = 1.9\text{--}3.7\text{ }^\circ\text{C}$ using the taxon-specific metabolic scaling exponent $\alpha = 0.17$ for boid snakes. The importance of using relevant taxon-specific information in case of one-taxon-based temperature reconstructions¹ while leaving the theoretically derived generic α values (such as $\alpha = 0.33$ used by Head *et al.*¹) for broad inter-taxonomic analyses^{2,3} is emphasized.

It was proposed and tested against diverse sets of data^{2–7} that there exists a minimum level $q = q_{\min}$ of mass-specific metabolic rate q (energy spent per unit body mass per unit time), the fall below which is not compatible with successful biological and/or ecological performance of species in a given taxon. In poikilotherms, q declines with increasing body mass M but grows with increasing ambient temperature T , $q(M, T) = q_0(M/M_0)^{-\alpha} Q_{10}^{(T-T_0)/10\text{ }^\circ\text{C}}$, in which q_0 is the value at a reference body mass M_0 and temperature T_0 , Q_{10} and α (the metabolic scaling exponent) are constants. Species living in warmer climates can afford larger maximum body sizes, thus offsetting the size-related drop of metabolic rate by a higher temperature.

On a log–log scale, metabolic rates (q) of species living at different temperatures plotted against body length ($L \propto M^{1/3}$) form slanting parallel lines bounded by a common horizontal bottom-line $q = q_{\min}$ (Fig. 1). Metabolic scaling exponent (α) determines the tangent of the angle of slope ϑ , $\tan \vartheta = 3\alpha$. The steeper the allometric lines go, the greater temperature difference ($\Delta T > 0$) is needed to extend body length from L_2 (length of smaller taxon) to L_1 (length of larger taxon) at constant $q = q_{\min}$, $\Delta T = 3\alpha \times (10\text{ }^\circ\text{C}) \times \log_{10}(L_1/L_2)/\log_{10} Q_{10}$. In comparative analysis of a large number of diverse taxa, a representative value of $\alpha = 0.3$ was used² reflecting the debate about possible universality of α at 0.33 or 0.25 (for example, ref. 8). Boid snakes, however, fall on the lower end of the observed range of α values, for them $\alpha = 0.17 \pm 0.04$ (± 2 s.e.m.)⁹. Using the estimated maximum body length of *Titanoboa cerrejonensis* $L_1 = 10.4\text{--}14.9$ m, maximum body length $L_2 = 7.3$ m for the anaconda *Eunectes murinus*¹ and $Q_{10} = 2.65$ for boid snakes⁹, we conclude that the Palaeocene neotropics were $\Delta T = 1.9\text{--}3.7\text{ }^\circ\text{C}$ warmer than at present, Fig. 1. The use of $\alpha = 0.33$ instead of $\alpha = 0.17$ in ref. 1 resulted in a twofold overestimate of ΔT .

Interestingly, comparison of the largest extinct frog *Beelzebufo ampinga* found on Madagascar¹⁰ ($L_1 = 42.5$ cm), and the largest extant frog *Conraua goliath* ($L_2 = 32$ cm) gives a similar estimate for the neotropical MAT of the Late Cretaceous (70.6–65.5 Myr). For anurans $\alpha = 0.20 \pm 0.07$ and $Q_{10} = 2.21$ (ref. 9), which gives $\Delta T = 2.1\text{ }^\circ\text{C}$.

Generally, the approach used by Head *et al.*¹ can be considered a significant extension of the nearest living relative method widely used in paleoclimate studies^{11,12}; for example, when the presence of plant fossils with extant freeze-intolerant relatives is interpreted as indicative of mild winters. The proposed animal framework suggests that if the extant species are consistently smaller than their fossil relatives then the fossil species had probably evolved in a warmer-than-present climate. For example, among the few Palaeocene insect fossils¹³ some very big lacewings¹² and giant ants¹⁴ were found in temperate latitudes, providing further evidence for a warmer Palaeocene climate. Apparently, joint consideration of several 'paleothermometers' built for different taxa will enhance the reliability of climate reconstructions, so the possibility of there being a universal scaling exponent α preferable for a broad inter-taxonomic analysis^{3,4} needs to be further scrutinized. In the meantime, for temperature reconstructions focusing at one particular taxon as the

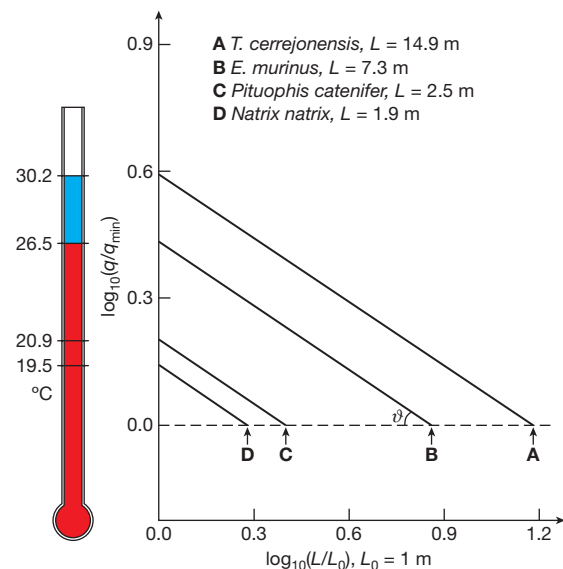


Figure 1 | The snake paleothermometer. Allometric dependencies of mass-specific metabolic rate q on body length L , $q \propto L^{-3\alpha}$, $\alpha = 0.17$, are shown at four different temperatures. Points at which the allometric lines cross the horizontal dashed-line $q = q_{\min}$ correspond to body lengths of the largest snakes^{1,2} in Palaeocene neotropics (A), South America (B), Colorado (C) and the United Kingdom (D). Temperatures reconstructed from the metabolic allometry (assuming that the anaconda lives at $26.5\text{ }^\circ\text{C}$) are marked on the thermometer, with the difference between the modern and Palaeocene neotropics shown in blue. Note that the reconstructed temperature differences pertain to the differences between typical 'lifestyle' temperatures of the considered species that can differ significantly from MAT in seasonal climates.

one performed by Head *et al.*¹ it is plausible to use as accurate taxon-specific information on metabolic allometry as available.

Anastassia M. Makarieva^{1,2}, Victor G. Gorshkov^{1,2} & Bai-Lian Li²

¹Theoretical Physics Division, Petersburg Nuclear Physics Institute, 188300, Gatchina, St Petersburg, Russia.

e-mail: elba@peterlink.ru

²Ecological Complexity and Modeling Laboratory, Department of Botany and Plant Sciences, University of California, Riverside, California 92521-0124, USA.

Received 23 March; accepted 15 April 2009.

- Head, J. J. *et al.* Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* **457**, 715–717 (2009).
- Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. Gigantism, temperature and metabolic rate in terrestrial poikilotherms. *Proc. R. Soc. Lond. B* **272**, 2325–2328 (2005).
- Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos* **111**, 425–436 (2005).
- Gorshkov, V. G. The distribution of energy flow among the organisms of different dimensions. *Zh. Obshch. Biol.* **42**, 417–429 (1981).
- Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. A note on metabolic rate dependence on body size in plants and animals. *J. Theor. Biol.* **221**, 301–307 (2003).

- Makarieva, A. M. *et al.* Size- and temperature-independence of minimum life-supporting metabolic rates. *Funct. Ecol.* **20**, 83–96 (2006).
- Makarieva, A. M. *et al.* Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. *Proc. Natl Acad. Sci. USA* **105**, 16994–16999 (2008).
- White, C. R., Phillips, N. F. & Seymour, R. S. The scaling and temperature dependence of vertebrate metabolism. *Biol. Lett.* **2**, 125–127 (2006).
- Chappell, M. A. & Ellis, T. M. Resting metabolic rates in boid snakes: allometric relationships and temperature effects. *J. Comp. Physiol. [B]* **157**, 227–235 (1987).
- Evans, S. E., Jones, M. E. H. & Krause, D. W. A giant frog with South American affinities from the Late Cretaceous of Madagascar. *Proc. Natl Acad. Sci. USA* **105**, 2951–2956 (2008).
- Greenwood, D. R. *et al.* Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. *Can. J. Earth Sci.* **42**, 167–185 (2005).
- Archibald, S. B. & Makarkin, V. N. Tertiary Giant Lacewings (Neuroptera: Polystoechotidae): revision and description of new taxa from western North America and Denmark. *J. Syst. Paleontol.* **4**, 119–155 (2006).
- Grimaldi, D. & Engel, M. S. *Evolution of the Insects* Ch. 2 (Cambridge Univ. Press, 2005).
- Rust, J. & Andersen, N. M. Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae). *Zool. J. Linn. Soc.* **125**, 331–348 (1999).

doi:10.1038/nature08223

Can the giant snake predict palaeoclimate?

Arising from: J. J. Head *et al.* *Nature* **457**, 715–717 (2009)

In their report on *Titanoboa cerrejonensis*, Head *et al.*¹ propose that the great size of this 58 to 60 million-year-old snake (estimated length = 13 m, mass = 1,135 kg) indicates a mean annual neotropical temperature (MAT) of 30–34 °C, substantially higher than previous estimates for that period. They argue that the high MAT was necessary to compensate for the decreased mass-specific metabolic rate intrinsic to a snake of this size. However, the relationship on which Head *et al.*¹ base their conclusion does not account for the scope of behavioural control over body temperature available to *Titanoboa* due to its huge mass. Our calculations suggest that because of its ability to behaviourally control its body temperature, *Titanoboa* cannot serve as an accurate palaeothermometer.

The metabolic rate of poikilothermic (ectothermic) animals such as snakes depends on both body temperature (T_b) and body mass (m): at a given temperature, mass-specific metabolic rate (M) decreases with increasing size (approximately as $m^{-0.25}$); for a given mass, M increases with increasing body temperature (governed by metabolic Q_{10}). Thus, if there is a minimal M required for cellular maintenance, there must be an upper limit to body size for a given body temperature, and the ratio of maximum body sizes in similar animals can be related to their temperatures². Using a comparison to the mass and known MAT for the largest extant snake (an anaconda), Head *et al.*¹ suggest that the MAT of *Titanoboa*'s environment must have been 1–8 °C higher than earlier estimates.

However, Head *et al.*¹ implicitly assume that the relationship between body temperature and air temperature is constant across body size. This assumption is reasonable for small animals (such as those dealt with by Makarieva *et al.* in the paper on which Head *et al.* base their calculations²), but is questionable for the massive *Titanoboa*. Animals exchange heat with their surroundings across their surface area, whereas metabolic heat is generated by the animal's entire volume^{3,4}. The relatively large surface area to volume ratio (SVR) for small organisms allows them to reach thermal equilibrium (metabolic heat produced = heat shed) with a body temperature only marginally higher than air temperature (Fig. 1). In contrast, the relatively low SVR for an animal as large as *Titanoboa* requires T_b to be increased substantially above air temperature to establish thermal equilibrium. For example, let us assume that *Titanoboa* had a

mass-specific metabolic rate of 0.021 W kg⁻¹ at 28 °C, and a metabolic Q_{10} of 2.63 (values estimated from extant boid snakes⁵). If the snake were to coil itself into a hemispherical mound as it lay on an insulating substratum in a mild breeze (0.5 ms⁻¹), its equilibrium body temperature would be 4.3 °C above ambient. If the breeze were slower, or the snake more massive (the estimates of Head *et al.*¹ range as high as 1,819 kg), body temperature would be even higher. Indeed, if air temperature was 34 °C (the peak of the range estimated by Head *et al.*¹), a coiled *Titanoboa* could dangerously overheat. When uncoiled, *Titanoboa*'s body temperature would still be >0.5 °C above ambient. In contrast, even when coiled, temperature increase in an anaconda would be less than half that of *Titanoboa*. In short, *Titanoboa* could have regulated its body temperature by varying its posture to a much greater degree than extant snakes, potentially changing its relationship to ambient air temperature.

The calculations made here for body temperature are themselves uncertain. For example, we have not taken into account any heat input

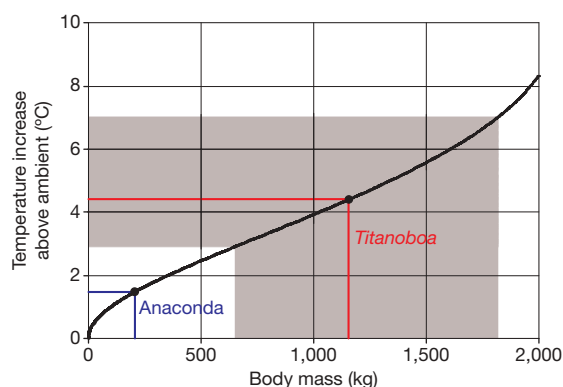


Figure 1 | Body temperature of a coiled snake at thermal equilibrium is increased above ambient air temperature. In this example, wind velocity is 0.5 ms⁻¹. The value for the green anaconda *Eunectes murinus* is calculated for an individual 7.3-m long—the length used by Head *et al.*¹ in their comparisons. The shaded area depicts the range of estimated mass for *Titanoboa* and the associated range of temperature increase.