Biased reptilian palaeothermometer?

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

Palaeotemperatures can be estimated from characteristics of fossils if their living relatives represent the full evolutionary potential of the larger taxon to which the fossil belongs. By drawing on observations[1,2] that the body size of poikilotherms decreases globally with ambient temperature, Head et al.[3] used the 13 m length of the newly described fossil boid *Titanoboa cerrejonensis* to estimate that the Palaeocene neotropical mean annual temperature (MAT) was 30–34 °C. I question the validity of this palaeotemperature estimate by using the same data and approach as Head et al.[3] to show that *Varanus* (*Megalania*) *prisca*[4], a large extinct lizard that lived in eastern Australia during the Late Pleistocene, was 3–4 times longer than predicted by the largest lizard species in the tropics today. This suggests that the scarcity of large predatory reptiles today may primarily be a function of competition with mammalian carnivores, rather than a function of modern temperatures.

Makarieva et al.[1,2] established that the largest living species within 24 poikilotherm taxa from tropical (ambient temperature (T_a) = 26 °C), temperate (T_a = 14–18 °C) and polar (T_a = 2 °C) climates decrease in length 2–3 times with every 10 °C decrease in temperature. Using this relationship, Head et al.[3] estimated the Palaeocene neotropical MAT from the ratio of the *Titanoboa* total body length (TBL; 10.6–14.9 m) to that of the longest extant neotropical snake—the 7.3-m-long boine *Eunectes murinus*. I tested this approach by using palaeotemperatures experienced by *Varanus prisca*, and its inferred body length, to calibrate curves that predict T_a from body length (see Methods). I then compared these with a curve derived from the TBL of the world's largest extant lizard, equatorial *Varanus komodoensis*, which the analysis of Makarieva et al.[1,2] assumed is the largest lizard possible at current tropical T_a, to make predictions of plausible varanid body lengths at different temperatures.

Varanus prisca occurred across eastern Australia during the Late Pleistocene, but is most abundantly recorded in the Darling Downs district of southeast Queensland[5,6], where luminescence dating demonstrates it survived until at least 40,000 years ago[7], during the last glacial interval when regional temperatures were, conservatively, at least 2 °C lower, and probably much lower than present[8–10]. Modern representative T_a for the Darling Downs (at Warwick, Queensland, T_a = 21.5 °C) therefore indicates that *V. prisca* tolerated $T_a \leq 19.5$ °C. The TBL of *V. prisca* is uncertain[11,12], but Head et al.[4] accepted a range of 5–7 m for large individuals. Curves derived from these values (Fig. 1, large filled red squares) predict that the modern tropical MAT ($\approx T_a$) of 27 °C is capable of supporting a 10–14-m-long varanid (Fig. 1, shaded area L_1), which is much larger than any known fossil or extant lizard. Conversely, the 3.1-m length[1,2] of *V. komodoensis* at a MAT of 27 °C (Fig. 1, large filled black circle) predicts that eastern Australian glacial $T_a \leq 19.5$ °C should have supported varanids no longer than 1.55 m (Fig. 1, L_2), ~3–4 times shorter than *V. prisca*. Moreover, the *V. komodoensis* curve predicts that 5–7-m *V. prisca* would have required $T_a \geq 32–36$ °C to survive (Fig. 1, shaded T_2), which overestimates glacial temperature by 13–16 °C. Conversely, the *V. prisca* curve predicts that 3.1 m lizards could be expected to occur wherever $T_a \geq 10.7–14.3$ °C (Fig. 1, shaded T_1), as cool as or cooler than the United Kingdom where the largest lizard (46 cm) is less than one-sixth of this length[2].

These comparisons show that the 3.1-m length of *V. komodoensis* is not the maximum possible for a varanid at modern tropical temperatures, so its position within the analysis of Makarieva et al.[1,2] as the longest possible modern lizard probably biases the palaeotemperature estimate of Head et al.[3]. Moreover, the *V. prisca* curves indicate that few, if any living lizards are near maximum body size for their ambient temperature. Given the similar body shape of lizards and
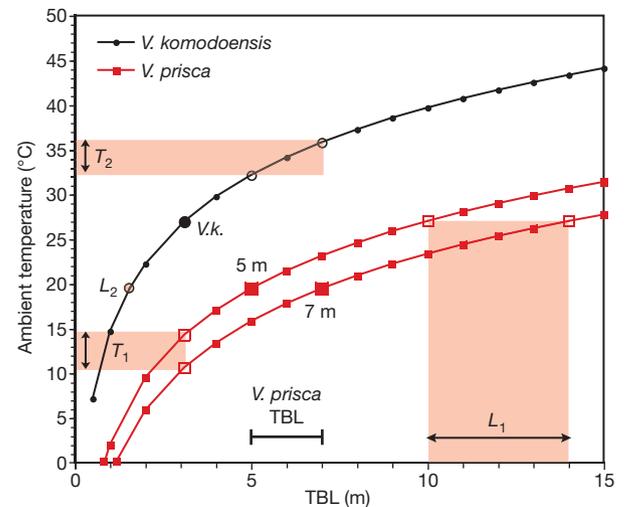

Figure 1 | Ambient temperature and body length relationships predicted from TBL of the komodo dragon *V. komodoensis* (black) and from TBL estimates of *V. prisca* (red). Curves represent model body size increase with temperature in varanids, based alternatively on a maximum TBL for *V. komodoensis* (3.1 m) at a modern tropical MAT of 27 °C (large filled black circle), and on TBL estimates for extinct Pleistocene *V. prisca* (5 and 7 m, representing the range accepted by Head et al.[4]) at glacial ambient temperature of 19.5 °C (large filled red squares). See text for explanation of open circles and squares.

snakes, a snake as large as *Titanoboa* might therefore have experienced tropical temperatures no warmer than today. If so, the lack of such large terrestrial reptiles today, and their scarcity during greenhouse intervals of the Cenozoic, may reflect non-climatic impediments to their evolution. One impediment may be competition with mammals for the large predatory niche, so that reptiles can approach size limits set by metabolic constraints only where this competition is reduced, as it may have been in the Australian Pleistocene[12,13] and more widely in the Palaeocene before the global emergence of large mammalian carnivores[14].

METHODS

Because outside of the tropics poikilotherms may only be active during part of the year, Makarieva et al.[2] compared ambient temperatures (T_a), equivalent to the mean temperature of the warm half-year. I therefore estimated T_a for Warwick, Queensland, as the mean temperature of the six warmest months (Australian Bureau of Meteorology, http://www.bom.gov.au). Curves relating TBL to T_a were calculated from equations (4) and (5) of Head et al.[2], using mean representative values of $Q_{10} = 2.3$, and $\alpha = 0.3$ (ref. 2), based on 3.1-m *V. komodoensis* at $T_a = 27$ °C; and 5- and 7-m *V. prisca* at $T_a = 19.5$ °C.

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Re-calibrating the snake palaeothermometer

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In a recent study[1] a new proxy for palaeoclimate 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 $\Delta T = 3.8$–$7.2\,°C$ above the modern value[1]. Here we argue that the reported temperature difference is a twofold overestimate and obtain a corrected estimate of $\Delta T = 1.9$–$3.7\,°C$ 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 reconstructions[1] 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, $q(M,T) = q_0 (M/M_0)^{-\alpha} Q_{10}^{(T-T_0)/10\,°C}$, 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, tg $\vartheta = 3\alpha$. 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 $q = q_{min}$, $\Delta T = 3\alpha \times (10\,°C) \times \log_{10}(L_1/L_2)/\log_{10}Q_{10}$. In comparative analysis of a large number of diverse taxa, a representative value of $\alpha = 0.3$ was used[2] 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* $L_1 = 10.4$–$14.9\,m$, maximum body length $L_2 = 7.3\,m$ for the anaconda *Eunectes murinus*[1] and $Q_{10} = 2.65$ for boid snakes[9], we conclude that the Palaeocene neotropics were $\Delta T = 1.9$–$3.7\,°C$ 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 Madagascar[10] ($L_1 = 42.5\,cm$), 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 $\Delta T = 2.1\,°C$.

Generally, the approach used by Head *et al.*[1] can be considered a significant extension of the nearest living relative method widely used in palaeoclimate 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 fossils[13] some very big lacewings[12] and giant ants[14] were found in temperate latitudes, providing further evidence for a warmer Palaeocene climate. Apparently, joint consideration of several 'palaeothermometers' 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
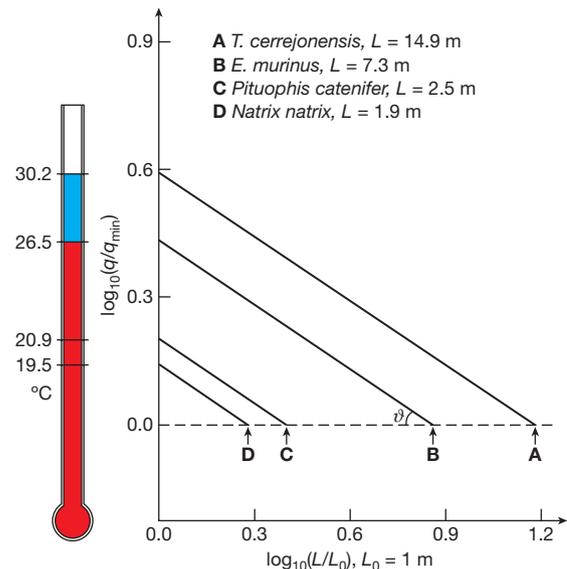

Figure 1 | The snake palaeothermometer. Allometric dependencies of mass-specific metabolic rate q on body length L, $q \propto L^{-3\alpha}$, $\alpha = 0.17$, are shown at four different temperatures. Points at which the allometric lines cross the horizontal dashed-line $q = q_{min}$ correspond to body 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 °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.

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Can the giant snake predict palaeoclimate?

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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 temperatures[2]. 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 calculations[2]), 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 snakes[5]). 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
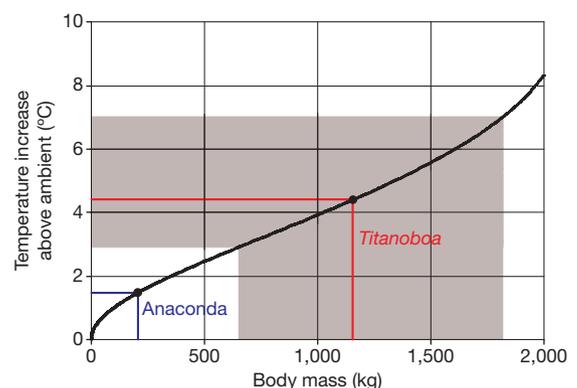

Figure 1 | Body temperature of a coiled snake at thermal equilibrium is increased above ambient air temperature. In this example, wind velocity is 0.5 ms^{-1}. The value for the green anaconda *Eunectes murinus* is calculated for an individual 7.3-m long—the length used by Head *et al.*[1] in their comparisons.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

into the snake from absorbed sunlight, or heat lost by conduction to the substratum. The former depends at least in part on the snake's behaviour, the latter on both the thermal properties of the substratum and the time for which the snake rested in a single spot, both of which would be difficult to quantify accurately for an extinct snake. Furthermore, an aquatic lifestyle would complicate things further, as entry into water would have led to major changes in thermoregulatory relationships. But these uncertainties serve to reinforce our main point: body size alone is an imprecise index on which to base reliable estimates of average habitat temperature. *Titanoboa* is a fascinating discovery, but a palaeothermometer of uncertain accuracy.

METHODS

Heat transfer coefficients (h_c) for a hemisphere and a cylindrical rod (axis parallel to flow, aspect ratio equal to that of *Titanoboa*) were measured in a wind tunnel at varying air speeds (see ref. 6). Objects rested on insulating substrata. Results were expressed as Nusselt/Reynolds number relationships (rod: $Nu = 0.316Re^{0.670}$, hemisphere: $Nu = 0.218Re^{0.587}$) from which h_c of *Titanoboa* and *Eunectes* are

estimated for given wind speeds. Overall heat loss at a given increase in body temperature (ΔT) is then estimated using Newton's law of cooling[3,4]. Metabolic heat production was calculated as $MmQ^{\Delta T/10}$, with $m = 1{,}135$ kg and $Q = 2.63$.

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Head et al. *reply*

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Denny et al.[1] and Sniderman[2] question our use of body size in *Titanoboa cerrejonensis* as an equatorial temperature proxy during the Palaeocene[3], and Makarieva et al.[4] suggest an adjustment to our temperature estimates. Denny et al.[1] misinterpret the physiological model of our study[5,6] and the implications of their body temperature (T_b) estimates relative to the thermal ecology of extant snakes. They assert that our model is inappropriate for large-bodied animals because the relationship between T_b and air temperature (mean annual temperature; MAT[3]) is not constant across different body sizes in poikilotherms. In fact, the model does not assume constancy of T_b relative to MAT. Changes in T_b (and thus body size) relative to MAT resulting from increasing thermal inertia with size are inherent in the model, as evidenced by the scaling of body length and MAT (see Fig. 3 in ref. 3). The model is accurate for the longest extant snake, *Python reticulatus*[6], with a maximum body length ~70% that of *Titanoboa*[3], indicating that it is appropriate to use with animals approximating the sizes of the largest known snakes.

Denny et al.[1] model the T_b for a coiled *Titanoboa* at 4.3 °C above ambient temperature at 28 °C, concluding that increased MAT was not necessary to maintain metabolic efficiency and high T_b could be behaviourally maintained. Increased T_b is not unique to *Titanoboa*—large extant snakes combine high thermal inertia with behavioural thermoregulation to maintain increased T_b relative to ambient temperature at similar magnitudes[7]. Similarly, the *Titanoboa* T_b values predicted by Denny et al.[1] for the MATs we estimate fall within the T_b ranges of extant boids between 30–38 °C[8]. In short, Denny et al.[1] provide a first-order approximation of T_b, but their results do not indicate a unique thermal ecology for *Titanoboa*, and do not falsify our palaeoclimatic reconstructions or the use of body size to estimate palaeotemperature.

The analysis of Sniderman[2] illustrates several fundamental assumptions of our model: body sizes in both extant and fossil taxa are maximized relative to MAT for a given habit and environment, and mass-specific metabolic rates are equivalent to estimate palaeotemperature. We assume this is the case for extant *Eunectes murinus* in the absence of any additionally recognized ecological regulators (resource availability, predation pressure) on body sizes, and conclude that it is an accurate comparison for *Titanoboa* given strong aquatic

habitat similarities between the two[3], a close phylogenetic relationship, and a known mass-specific metabolic rate for boid snakes[9]. The same assumptions cannot be made when comparing *Varanus prisca* to extant varanids or other lizards, as predation pressures are known to restrict body size ranges in extant *Varanus*[10] independently of MAT, and the largest living species, *Varanus komodoensis*, is an island endemic with limited habitat availability. Comparison of *V. prisca* to the semi-fossorial, limbless *Anguis fragilis* from the United Kingdom (and subsequent extension of these results to the rest of Squamata), is inappropriate because these species are not closely related, have different body plans, live in different habitats, and *Varanus* has significantly higher mass-specific metabolic rates than other squamates[11].

We also find the mechanics of Sniderman's analysis[2] problematic. He overestimates body length for *V. prisca* by relying on secondary reports of size maxima[12], despite empirical studies indicating smaller body lengths (snout–vent length = 2.19 m; total body length = 3.5–4.7 m)[13,14]. These smaller lengths reduce his reported temperature to body size discrepancies by half. A smaller than predicted body size in *V. komodoensis* cannot bias our analysis, as neither the theoretical model of Makarieva et al.[4–6], or our derivation of it to estimate palaeotemperature, is based on that datum. We consider Sniderman's results indicative of a complex relationship between size and environment in extant *Varanus*, and not an indictment of our methods.

Makarieva et al.[4] argue for a taxon-specific metabolic scaling exponent in calculating palaeotemperatures based on *Titanoboa*, in contrast to their previous argument that the exponent should be a universal value of 0.33 (ref. 6). If their adjustment is correct, then the estimated MAT for the Palaeocene neotropics would be 28–31 °C—a 2–3 °C decrease from our original analysis. Regardless of which metabolic scaling exponent is most appropriate, we note that the implications for palaeoclimate, related to the hypothesis that equatorial latitudes were much warmer 60-million years ago than today, are the same.

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