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Was climate the prime releaser for encephalization? An editorial comment

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Abstract Kleidon (2009) concludes that warm climates impose important constraints on the evolution of large brains relative to body size, confirming our previous hypothesis (Schwartzman and Middendorf 2000). Here we update the case for our hypothesis and present a first approximation estimate of the cooling required for hominin brain size increase using a simple model of heat loss. We conclude that Pleistocene glacial episodes were likely sufficient to serve as prime releasers for emergence of *Homo habilis* and *Homo erectus*. In addition, we propose that atmospheric oxygen levels may been an analogous constraint on insect encephalization.

We congratulate Axel Kleidon for a provocative and stimulating paper, as well as for creating the opportunity for this intervention. Based on his modeling of maximum heat loss from human metabolic activity, Kleidon (2009) concludes that “warm climates impose important constraints on the evolution of large brains in relation to body size”, i.e., encephalization, supporting our earlier argument (Schwartzman and Middendorf 2000). We now take this opportunity to update and expand on our original proposal.

The long-term cooling history of the Earth’s biosphere correlates with the timing of major events in biotic evolution, such as the emergence of phototrophs, eucaryotes and Metazoa (Schwartzman 1999–2002). These organisms apparently emerged when temperatures declined to the maximum limit that could be tolerated by these organisms, i.e., 70°C (3.5 Ga), 60°C (2.8 Ga) and 50°C (1–1.5 Ga) respectively (Fig. 1). The evidence for this early very warm climate was recently corroborated by the measurement of melting temperatures of proteins resurrected from sequences inferred from robust molecular phylogenies (Gaucher et al. 2008), and is consistent

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Fig. 1 Surface temperature history of biosphere, with the maximum tolerable temperatures (T_{max}) shown for metazoa and vertebrates (Schwartzman 1999–2002). Warm-blooded animals T_{body} near 40°C provides energy for large brain; $T_{body} - T_{climate}$ determines efficiency of heat loss from brain. Temperatures increase in the future because of rising solar luminosity

with the paleotemperatures derived from the oxygen isotopic record of ancient cherts (Knauth 2005).

We proposed that the emergence of vertebrates and their encephalization likewise was similarly constrained by temperature (Schwartzman and Middendorf 2000). Given an upper limit for vertebrate survival being about 40°C (Brock and Madigan 1991), the history of the Earth's surface temperature suggests a narrow window for encephalization, roughly 500 million years ago through the present when climatic cooling became sufficient to allow additional and efficient heat loss from the large energy-intensive brains. Interestingly, it was during this period that encephalization is observed in hominid evolution, as well as for other groups of homeothermic animals including birds and toothed whales in the Cenozoic, and perhaps even for the mammal-like “reptiles” in the Permo-Carboniferous.

1 Hominin evolution

Increases in encephalization quotient (EQ), presumably correlated with enhanced behavioral and cognitive abilities, have been used to measure advances in hominin evolution. EQ (brain mass divided by body mass) was devised by Jerison (1973), to show relative increase in brain size over time. One caveat appended to Jerison's original observations points to the fact that brain size and body mass do not necessarily increase allometrically, e.g. while body size may show rapid change, brain tissue growth may be more conservative, resulting in differential rates of increase (Harvey and Krebs 1990). Finally, in non-human primates absolute brain size rather than encephalization may be the best predictor of cognitive ability (Deaner et al. 2007).

Our earlier explanation prioritizing a temperature constraint on bigger brains contrasted with other, more widely cited climatic hypotheses accounting for hominin evolution. One, the turnover pulse hypothesis emphasizes the impact of growing aridity during a shift from tropical forests to grasslands and the impetus to rapid evolution arising from climatic fluctuations beginning with the modern glacial/interglacial cycle

some three million years ago (Tattersall and Schwartz 2000; for a recent account see Vrba 2007).

Another hypothesis correlates climatic changes (glacial/interglacial cycles) with fossil hominin brain size (Ash and Gallup 2007) where cranial capacity variance was plotted against variation of temperature at 100 and 200 kya intervals (Fig. 2). While significant correlations were noted, the approach failed to account for the likelihood for trend for bigger brains arising from Cope's Rule, i.e., the growing divergence of the maximum cranial size from a smaller baseline value as a result of increasing variance in a trait through evolutionary time (Gould 1988). We argue the critical issue here is not the encephalization during this entire period, but how brain size changed during specific moments during the time period. In other words, we focus on an examination of the fine structure of this trend, i.e., the timing and causation of encephalization.

Foley (1994) found climatic change to correlate with extinction but not with the first dated appearance of hominin taxa. However, the date of first emergence can only be estimated as minimum ages from fossils since older ones may eventually turn up or may be absent from the geologic record. It is doubtful that molecular dating combined with the recovery of ancient hominid DNA will ever give emergence times with sufficient precision to tie appearance to specific glacial or interglacial times during the Pleistocene.

We suggest that an alternative approach that may be more fruitful will be to model the energy budget of the *Australopithecine* to *Homo* transition, testing the hypothesis that a release of climatic temperature constraint was significant for hominin brain enlargement. We envision the following scenario. First, because larger brains are metabolically costly (Aiello and Wheeler 1995), they require a correspondingly

Fig. 2 Marine oxygen isotope record from two East Pacific sites compared with hominid cranial capacity for the last 3 m.y. The oxygen isotope record is a proxy for temperature fluctuations. (Source: Ash and Gallup 2007)

larger heat sink. Because of the metabolic demands of glial cells (Marino 2006; Sherwood et al. 2006; Grossman et al. 2004), higher rates of neocortical energy expenditures become a critical selection factor in the evolution of larger brains. Thus, bigger brain mass necessary for increased complexity and cognitive ability (Marino 2006) results in increased metabolic demand and the corresponding necessity for a major heat sink. There are several possibilities for such—internal cooling mechanisms, external sinks, or even more likely, some combination of the two.

Internal cooling mechanisms, in particular the cranial radiator and changes in posture and locomotion, likely played an important role in facilitating such a heat sink (Falk 1990, 2007; Wheeler 1988). However, in a recent review, Falk (2007) argues that the cranial radiator was a “prime releaser”, not a “prime mover” of human encephalization, where prime movers are aspects of evolving social intelligence, the “social brain” (Dunbar 1998, 2003; Emery et al. 2007) that include hunting, tool production, Machiavellian intelligence and especially language. Thus, if the evolution of the cranial radiator was indeed a prime releaser of thermal constraints on encephalization, then the temperature differential between the ambient environment and the body/brain temperature was likely a prior blocking constraint for each speciation as brain mass increased. External sinks could have been achieved behaviorally through migration to cooler climates and/or shifts in activity, e.g. utilization of dawn and dusk in the African savannah, rather than midday. Alternatively, environmental cooling would have, perhaps even more dramatically rather than incrementally, altered the physical boundary conditions for the possibility of bigger brains. Assuming no profound change in cranial radiator capacity, only a higher, environmental temperature differential could have provided the critical heat sink for a bigger, more energy-intensive brain. Cooler environments could have included the higher elevations in the African Rift as Kingdon suggests (2003, personal communication), even during an interglacial period. If the temperature differential was indeed the first prime releaser, then further morphological and physiological adaptations like strengthening of the cranial radiator could have plausibly occurred as the climate warmed and/or with migration to warmer regions. The relative significance of the external and internal thermal releasers for bigger brains should be tested in a full energy budget model of hominin physiology.

Based on our temperature differential constraint, we predicted emergence of *Homo* in the more temperate Southern Africa, with further speciation during glacial periods with both a drop in climatic temperature and shift to grasslands in Africa (Schwartzman and Middendorf 2000). It is perhaps significant that fossils of *Australopithecus africanus* have only been found in South Africa, not East Africa the source of so many other hominin fossils (Wood and Lonergan 2008). While the debate continues over which australopithecine is proximate or the ancestor to our *Homo* ancestor, we are intrigued by two recent analyses which point to *A. africanus* rather than *A. afarensis*. The first is a cladistic analysis of hominids by Gonzalez-Jose et al. (2008). The second is Falk’s (2007) reassertion of her observation that *A. africanus*, but not *A. afarensis*, shares the human cranial radiator system utilizing the transverse-sigmoid sinuses (see also Kunz and Iliadis 2007).

We computed a first approximation estimate of the cooling required for hominin brain size increase with a simple model of heat loss. Assuming a spherical brain and conductive heat loss, the temperature differential (ΔT) between brain and environment at steady-state (metabolic heat production equals loss to heat sink)

varies with the brain diameter to the 5/4 power (Denny 1993). Hence, ΔT varies with brain volume to the 5/12 power for conductive heat loss from the whole brain. With this relation we computed the ratio of ΔT for the following transitions: *A. africanus* (460) to *H. habilis* (600) and *H. ergaster* (760) to *H. erectus* (1,000) with brain volumes in (cm³) taken from Wood and Lonergan (2008).

For an assumed brain temperature of 37°C and a local mean climatic temperature of 25°C at the time of both transitions, the required cooling (drop in mean local environmental temperature) for emergence of *H. habilis* and *H. erectus* is 1.5°C, a plausible drop in the sub Saharan African venue for a Pleistocene interglacial to glacial shift.

If the cranial radiator dominates as a mechanism for selective heat loss for the hominin brain, then surface rather than volume heat loss is more relevant. Since the ratio of surface area to volume for a sphere is 3/radius, to maintain the same heat flux density (i.e., heat loss/cm²) requires either an expansion of cranial radiator efficiency and/or a cooler environment for brain enlargement. For the same transitions considered above, at the same initial temperatures, the required cooling drops to about only 1°C.

In evaluating the significance of these simple model calculations several caveats are in order. First, we assume no significant differences in physiological, morphological, or behavioral thermoregulation at the initial evolutionary transitions. Second, factors making this computed required temperature decrease a maximum value include the significant contribution of convective and especially evaporative heat loss over and above simple conduction (Denny 1993). Further, any increase in the relative weight of these heat loss mechanisms in the transition to bigger brained hominins would also reduce the computed ΔT s. However it should be noted that the drop in regional temperatures driven by a shift to glacial periods in the Pleistocene occurred with a simultaneous increase in aridity as well as an ecosystem shift to savannah from more humid tropical forests in East Africa (deMenocal 1995; Maslin et al. 2005). These changes in regional and local climate plausibly increased the role of evaporative cooling, especially during foraging and hunting, thereby permitting brain enlargement by boosting the heat sink.

On the other hand, brain reorganization apparently occurred simultaneously with its enlargement, in particular, the growing neocortex with hominin evolution (e.g., see Dunbar 2003). Hence, brain reorganization over and above the enlargement assumed would increase the computed required ΔT since the neocortex is more energy-intensive relative to the rest of the brain (Marino 2006; Sherwood et al. 2006).

2 The mammal-like reptiles

Early mammal-like reptiles, the pelycosaurs followed by the therapsids emerged during the tail end of the great Permo-Carboniferous epoch of ice-ages. Some therapsids, notably the cynodonts, were apparently more encephalized than modern reptiles and were close to being fully homeothermic (Jerison 1985; Bennett-and-Ruben 1986; Turner and Tracy 1986). Parallel with climatic cooling, higher atmospheric oxygen levels during the Permo-Carboniferous likely enhanced body size and body temperature control mechanisms (Bernier et al. 2007; Dudley 1998; Graham et al. 1995), and plausibly encephalization.

3 Cetacean evolution

We also suggested that an increase in encephalization among Odontoceti (toothed whales, dolphins, porpoises) was driven by climatic cooling some 30 mya (Schwartzman and Middendorf 2000). In a recent debate concerning cetacean intelligence, Manger (2006) argued that encephalization was merely an adaptation to cold environment, while Marino et al. (2007) made a robust case for complex cognition going hand in hand with bigger brains. We accept the case for cetacean intelligence being correlated with encephalization (Marino 2007; Marino et al. 2007) but also suggest that Manger (2006) may be correct in proposing that climate cooling set up the conditions for the burst in Cetacean encephalization at the Eocene–Oligocene times. Marino et al. (2007) argue there was no need for odontocetes to respond to climatic cooling by either changes in body size or brain size. This is a curious argument, akin to claiming that there was no need for encephalization in *Homo*. No need perhaps, but cooling of the environment was likely removing a constraint on further encephalization. An odontocete with a smaller body and a bigger, energy-intensive brain was then adapted to both cooler deep water (permitting heat loss from a bigger brain) while still able to exploit still warm tropical waters that

Fig. 3 Termite Mound in Guyana. Photograph taken by Emily Middendorf, daughter of co-author next to mound

demanded more efficient heat loss—as well as benefiting from the increased cognition resulting from encephalization.

4 Atmospheric oxygen levels as a constraint on insect encephalization?

Insect gigantism has been noted at times of elevated atmospheric oxygen levels, especially during the Carboniferous, the time of huge burial of organic carbon that was transformed into coal (Dudley 1998; Graham et al. 1995; Berner et al. 2007). Insect physiology entails the diffusion of oxygen through their tracheal system, thus gigantism, especially for flying insects, imposes an oxygen demand satisfied by higher ambient levels. While correlation of insect brain and body size is problematic because of complex phylogenetic variation in brain structure (Strausfeld et al. 1998), it is recognized that mushroom bodies in the insect brain (there are two in each brain) function as the higher processing centers, particularly for those insects with generalist feeding habits (Farris and Roberts 2005), but also for insects with complex social structures (Molina and O'Donnell 2007). Farris (2008) notes remarkable structural, functional and developmental convergence between insect mushroom bodies and the higher brain centers of vertebrates. Thus, an outstanding question is whether there is an atmospheric oxygen level for insect encephalization that is analogous to the climatic temperature constraint for warm-blooded animals? Did the insect giants of the Carboniferous show a burst of encephalization analogous to that of warm-blooded animals? And on a note of wild speculation, is the emergence of the collective superorganism intelligence of social insects (Gordon 1999; Hölldobler and Wilson 2008), the product of millions of individually-communicating brains, in some colonies, linked to climatic changes? Should we humbly view the marvelous attine ant and termite fungal agriculture and the functional architecture of the termite mound (Fig. 3; Turner 2000), the technology of this superorganism, as the analog of the human technosphere? Can we expect to eventually find insectoid civilizations on some Earth-like planets around sun-like stars?

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