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Artiodactyl success and the carotid rete

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Invited reply

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As Dr Janis emphasizes (Janis 2009), the success of artiodactyls during the post-Eocene period is mainly attributed to the development of a rumen. We agree that this adaptation was important and said so in our paper (Mitchell & Lust 2008). Dr Janis is incorrect in saying that we proposed artiodactyls had a competitive advantage over perissodactyls and that their success was 'at the expense of perissodactyls'. In fact, we discounted this idea and focused on a non-competitive explanation for their success. Environmental and body temperatures are as important in the life of animals as nutrition. Selection for the very complex behavioural and physiological mechanisms of temperature regulation is crucial to the survival of species. These mechanisms include hibernation, migration, evaporative cooling mechanisms, non-shivering thermogenesis and mechanisms that alter the core : shell thickness ratio. Most species have evolved one or more of them, including perissodactyls that have lived in less than congenial climates. Anatomical adaptations that facilitate thermoregulation, such as the carotid rete and the extensive modifications to the anatomy of the blood supply to the nasal mucosa and the venous drainage from it (Carlton & McKean 1977; Johnsen *et al.* 1985), are as important as our data show.

Dr Janis argues that the rete must have been unimportant because horses are found in the Gobi Desert, and the rete is likely to have evolved prior to the Eocene–Oligocene temperature changes. If the Gobi horses are similar to the feral horses of the Namibian deserts we have studied, then they will be significantly smaller, have lower daily water turnover (Sneddon *et al.* 1991), use interstitial fluid (rather than intracellular fluid) to maintain plasma volume (Sneddon *et al.* 1993*a*) and have vasopressin and aldosterone responses to dehydration and rehydration significantly different from those in standard horses (Sneddon *et al.* 1993*b*). Thus, it does not surprise us that horses can live in the Gobi Desert, and that they do illustrates the large range of adaptations that animals can evolve.

We agree with Dr Janis that the rete is likely to have evolved early in artiodactyls as it is present in suids and, in a primitive form, in cetaceans. We do not think that its primary evolutionary purpose was to achieve cooling of the brain or to protect the brain from high temperatures. We indicated that at least three known functions can be attributed to it. One is the regulation of blood flow and pressure to the cerebral circulation. The rete is best developed in those creatures '*who go with their heads hanging down*' so that '*the torrent of blood being divided into small rivulets, its more rapid course may be so far dull'd or broken that it may be but leisurely instilled into the brain*' (Willis 1664). This seems a likely function for the rete in cetaceans (Nagel *et al.* 1968), and Willis's conjecture has been supported by observations in terrestrial mammals (Lluch *et al.* 1985). The rete can also facilitate transfer of substances from venous blood coming from the nasal mucosa to the pituitary (Grzegorzewski *et al.* 1997). In suids, which can be regarded as primitive artiodactyls (Carroll 1988) and which depend heavily on olfactory cues, this function may well be its main function in them: the rete mechanism is insensitive to changes in brain temperature in pigs (Fuller *et al.* 1999). It is highly probable that these two functions were the primary selection pressures in operation at the time of the rete's evolution, and that its recruitment for temperature regulation was a later addition to its functions. Post-Oligocene survivors may well have evolved this function of the rete, while those artiodactyl families that died out were, like tragulids, unable to recruit the rete for thermoregulatory purposes. The absence of the carotid rete in perissodactyls limits their temperature regulation. It seems unreasonable not to conclude, therefore, that the rete may have played a role in artiodactyl success in times of temperature changes to which perissodactyls and other non-rete animals were less well adapted.

In summary, our overall position remains unchanged—'the carotid rete in conjunction with rumination and locomotion contributed to artiodactyl success'—and are confident that, in time, other helpful adaptations also will be discovered.

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The accompanying comment can be viewed on page 97 or at http://dx.doi.org/doi:10.1098/rsbl.2008.0429.

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