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Artiodactyl 'success' over perissodactyls in the late Palaeogene unlikely to be related to the carotid rete: a commentary on Mitchell & Lust (2008)

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Comment

Artiodactyl 'success' over perissodactyls in the late Palaeogene unlikely to be related to the carotid rete: a commentary on Mitchell & Lust (2008)

Mitchell & Lust (2008) present evidence that the carotid rete of artiodactyls allows for a dissociation between brain and carotid artery temperatures, muting whole body thermoregulatory responses, and thus allowing for energy and water conservation. They argue that this morphological feature provides artiodactyls with a thermoregulatory advantage in extreme habitats, such as the Arctic or in deserts, and that it is the absence of a rete that confines perissodactyls to more tropical environments today. The fossil record shows (see Mitchell and Lust's, fig. 1) that during the late Eocene, coincident with climatic changes, perissodactyl generic diversity decreased while that of artiodactyls increased. While they acknowledge previous explanations for this differential pattern of evolution between artiodactyls and perissodactyls, related to differences in the digestive systems, Mitchell & Lust make a strong case for the importance of thermoregulatory abilities related to the possession of a carotid rete, which they propose would have given artiodactyls a competitive advantage over perissodactyls in the 'highly seasonal post-Eocene climate' (p. 415).

Note, however, that the absence of a carotid rete has not debarred perissodactyls from climatic extreme conditions in the relatively recent past. During the Pleistocene, there was a diversity of high-latitude rhinos and horses, including Arctic forms such as the woolly rhino, and, indeed, horses are found today in the Gobi desert. Additionally, as the rete is found in all modern artiodactyl suborders (Fukuta *et al.* 2007), its absence in tragulids evidently represents secondary loss, and so it must have been acquired prior to 45 Ma (the first appearance of any member of the modern groups). The rete would have been evolved during essentially equable tropical times, predating the Late Eocene climatic deterioration by at least 5 Ma. Thus, whatever advantages the rete may bestow on artiodactyls in extreme climatic conditions today, it cannot have been evolved for that specific purpose.

Although the world became more seasonal in the late Eocene, the major change was from mid-latitude tropical-like forests to seasonal temperate woodland. The present-day types of extreme climates were absent at this time: there was no evidence of ice at the Arctic Circle, nor of deserts, until *ca* 5 Myr ago (Prothero 2006). So the proposed advantage of a carotid rete would not have been relevant at this point in time. Additionally, while many types of perissodactyls (including hyracotheriine horses) became extinct in the late Eocene, so did at least a dozen artiodactyl families. The ungulates that succumbed were mostly similar in size and apparent diet (as determined by craniodental evidence) to inhabitants of tropical forests of low seasonality today (e.g. tragulids). The Oligocene saw the radiation of more derived types of both artiodactyls and perissodactyls, with teeth indicative of a more fibrous diet, including members of modern families. Although artiodactyls remained more generically diverse for the rest of the Cenozoic, the Oligocene world, when their 'takeover' became apparent, was not a time of extreme environmental conditions where thermoregulatory issues would have provided an adaptive advantage.

The post-Eocene relative 'evolutionary success' of artiodactyls, especially at the supposed expense of perissodactyls, is a familiar evolutionary story, but one that is somewhat overrated. The large numbers of artiodactyls today are mainly the result of the relatively recent (Pliocene) explosive radiation of a single group, the African bovids, and the small number of perissodactyls reflects extinctions over the past 5 Myr or so. Perissodactyls were fairly diverse for most of the Cenozoic: e.g. the mid-Miocene (*ca* 15 Ma) savannahs of North America supported not only 38 genera of artiodactyls, but also 21 genera of perissodactyls (Janis *et al.* 1998). Certainly, there were more genera of artiodactyls present, but perissodactyls were hardly dwindling to extinction, and many of these perissodactyls (most of the genera of horses and rhinos) were extremely numerous as fossils and likely highly abundant as individuals in real life. Both groups suffered later extinctions world wide, along with declining high-latitude temperatures, with the end-Pleistocene extinctions being especially hard on the megaherbivores and wiping out the New World horses.

The ruminant digestive system is more efficient than the hindgut system of perissodactyls in processing food of moderate fibre content: however, aspects of ruminant physiology preclude them from eating highly fibrous herbage or from attaining body sizes of greater than approximately 1000 kg (Clauss *et al.* 2003). The post-Eocene radiation of artiodactyls was of mid-sized folivores, while that of perissodactyls was mainly of high fibre specialists (browsing tapirs and grazing horses) and megaherbivores (rhinos) (see discussion in Janis 2007). These evolutionary patterns are explicable by the differences in the digestive systems, but not by the presence or absence of the carotid rete.

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The accompanying reply can be viewed on page 99 or at http://dx.doi.org/doi:10.1098/rsbl.2008.0534.

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