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The carotid rete and artiodactyl success

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Since the Eocene, the diversity of artiodactyls has increased while that of perissodactyls has decreased. Reasons given for this contrasting pattern are that the evolution of a ruminant digestive tract and improved locomotion in artiodactyls were adaptively advantageous in the highly seasonal post-Eocene climate. We suggest that evolution of a carotid rete, a structure highly developed in artiodactyls but absent in perissodactyls, was at least as important. The rete confers an ability to regulate brain temperature independently of body temperature. The net effect is that in hot ambient conditions artiodactyls are able to conserve energy and water, and in cold ambient conditions they are able to conserve body temperature. In perissodactyls, brain and body temperature change in parallel and thermoregulation requires abundant food and water to warm/cool the body. Consequently, perissodactyls occupy habitats of low seasonality and rich in food and water, such as tropical forests. Conversely, the increased thermoregulatory flexibility of artiodactyls has facilitated invasion of new adaptive zones ranging from the Arctic Circle to deserts and tropical savannahs.

Keywords: carotid rete; artiodactyls; evolution

1. INTRODUCTION

The evolution of artiodactyls began in the Eocene (*ca* 55 Myr ago) stimulated by the Early Eocene climatic optimum (Bininda-Emonds *et al.* 2007). They have become a very successful diverse group of 10 families and 90 living genera. Their evolutionary success has been attributed to improved locomotion and their later (Miocene) development of a specialized ruminant gastrointestinal tract (Janis 1976). The rumen facilitated fermentation of fibrous vegetation and acted as a water reservoir, thus allowing them to forage long distances away from water points. Their radiation coincided with a decrease in perissodactyl, hindgut fermenters, from a peak of 66 genera in Late Eocene, a decline associated with the near extinction of equids (Janis 1989, 1993). Since the Middle Miocene the number of perissodactyl families has remained fairly constant, and perissodactyls now consist of three families and five living genera, all of which, except for the domestic horse (*Equus caballus*), live in restricted tropical or subtropical habitats. By contrast, the number of artiodactyl families increased in parallel with the perissodactyls throughout the Eocene, but from the Oligocene onwards continued to increase to the present time (figure 1).

This contrasting pattern has been attributed to competitive interaction, but Cifelli (1981) has shown that competition was not a factor. Janis (1989) offered climate change as an alternative explanation because the contrasting changes in the artiodactyl and perissodactyl fauna began at the Eocene/Oligocene boundary. This boundary marked the beginning of profound seasonal differences in the availability and abundance of vegetation that have persisted to the present. Janis (1976) suggested that artiodactyls responded by evolving a ruminant digestive tract and different modes of food selection, and their improved locomotion facilitated adaptation to open habitats where the vegetation grew. Thus, while a climate of low seasonality supported a greater diversity of hindgut fermenters, highly seasonal climates were more favourable to ruminants because ruminants had better access to and made better use of limited quantities of sparse fibrous vegetation.

We advance here the idea, based on recent evidence we have obtained (Lust *et al.* 2007; Hébert *et al.* 2008), that an additional factor was a difference in the ability to thermoregulate, magnified by the changing climate. Adaptation and evolution are constrained by cold and hot environments that limit food and water supplies and impose temperature stress. Evolution of mechanisms that minimize the effects of these constraints, such as an ability to grow a thick winter pelage, results in radiation. Our data suggest that evolving a carotid rete, an anatomical structure best developed in artiodactyls while being completely absent in perissodactyls, was another physiological/anatomical adaptation that, in conjunction with rumination and locomotion, contributed to artiodactyl success.

2. MATERIAL AND METHODS

Our hypothesis is based on contemporaneous measurements of carotid artery blood (T_{carotid}) and brain temperature (T_{brain}). To obtain true body temperatures of animals, they must be free living in their natural habitat and able to use all their thermoregulatory mechanisms, from behavioural to physiological, over all environmental conditions to which they are exposed. In addition, temperatures must be recorded frequently and for several months at a time. Using implanted thermistors and data loggers, we and colleagues measured brain and carotid artery blood temperatures for long periods of time in free-living animals that have a carotid rete, including wildebeest (*Connochaetes gnou*: Jessen *et al.* 1994); oryx (*Oryx gazella*: Maloney *et al.* 2002); eland (*Taurotragus oryx*: Fuller *et al.* 1999); and pronghorn (*Antilocapra americana*: Lust *et al.* 2007, Hébert *et al.* 2008), and in free-living non-rete animals including horse (*E. caballus*: Mitchell *et al.* 2006) and zebra (*Equus burchelli*: Fuller *et al.* 2000) in hot conditions in summer in the Southern Hemisphere but in both summer and winter in the Northern Hemisphere in pronghorns.

The methods used were similar in all cases and have been described in detail in the references cited above. Approval for the studies was given by the appropriate ethics committees in each case. Briefly, using aseptic surgical techniques, miniature data logger/thermistor assemblies were implanted to record temperatures. The thermistors were small bead thermistors (GE Thermometrics; ABOE3-BR11KA103N/K-L10). The loggers (Onset Computer Corporation) had a resolution of 0.04°C. Scan interval was 5 min. One thermistor was inserted 100 mm into the common carotid artery to record the temperature of blood as a measure of body temperature (T_{carotid}) and the other was placed near the hypothalamus (T_{brain}). After surgery, the animals were released into large enclosures (at least 60 ha) where they had access to food and water and could use all their thermoregulatory mechanisms.

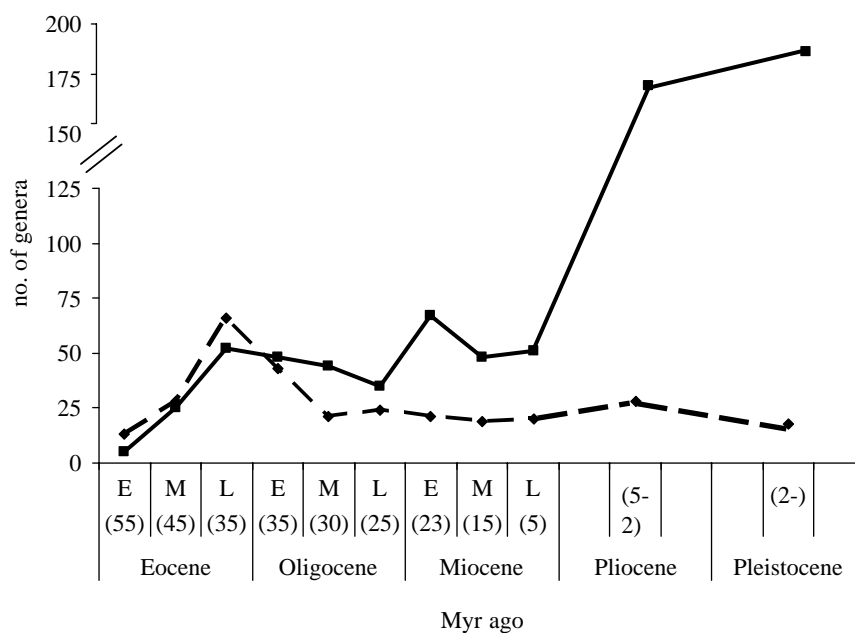


Figure 1. Generic diversity of perissodactyl (diamonds) and artiodactyl (squares) families that have evolved since the Eocene (redrawn from Cifelli 1981). E, Early; M, Middle; L, Late; Myr ago, millions of years ago.

3. RESULTS

Examples of typical recordings of T_{brain} and T_{carotid} from each of the species are shown in figure 2. Figure 2*a,c,e* shows the patterns of T_{brain} relative to T_{carotid} in three rete animals (wildebeest, pronghorn and oryx) in summer conditions and figure 2*b,d,f* in two non-rete animals (zebra and horse) in summer conditions and pronghorn in winter conditions.

These figures show clearly that the possession of a rete results in a quite different relationship between T_{brain} and T_{carotid} compared with that of the non-rete animals. It is characterized by the dissociation of T_{brain} from T_{carotid} at high T_{carotid} when the brain is cooled ($T_{\text{brain}} < T_{\text{carotid}}$), at low T_{carotid} owing to brain warming ($T_{\text{brain}} > T_{\text{carotid}}$), which is especially conspicuous in pronghorn, and evidence of brain cooling at normal body temperatures. The dissociation and separation of T_{brain} and T_{carotid} is associated with a wide range of T_{carotid} in each of the rete animals. If a rete is absent (horse and zebra) then changes in T_{carotid} and T_{brain} are more tightly linked and variation in body temperatures is reduced. Our observation of the relationship between T_{carotid} and T_{brain} in winter in pronghorns (Hébert *et al.* 2008; figure 2*f*) is particularly important. It shows that in winter the effect of the rete can be suppressed and the relationship between T_{brain} and T_{carotid} then becomes identical to that of the non-rete animals. Thus, animals with a rete can alternate between rete and non-rete types of thermoregulation.

4. DISCUSSION

In artiodactyls, the carotid rete arises from the external carotid artery as hundreds of small arterioles. These vessels are surrounded by a cavernous venous sinus containing blood returning from the nasal mucosa. The presence of a rete facilitates regulation of blood flow to the brain (Willis 1664) and transfer of pheromonal signals to the pituitary gland that it

surrounds (Grzegorzewski *et al.* 1997). Heat exchange between the rete carrying warm blood to the brain and venous blood cooled by its previous passage through the nasal mucosa, cools arterial blood destined for the brain, and can lower T_{brain} to a temperature below the carotid artery blood temperature. This observation led to the concept of selective brain cooling (SBC). After the discovery of SBC (Baker & Hayward 1968), it was assumed that the biological purpose of the rete was to protect the brain from thermal damage when body temperatures increased, e.g. during exercise (Taylor & Lyman 1972).

This function of the rete was disproved by studies done in Southern Hemisphere animals exposed to hot and arid conditions (Mitchell *et al.* 2002), and in reindeer in cold conditions (Aas-Hansen *et al.* 2000), which showed that brain temperature was not cooled below arterial temperature during exercise. Moreover, the rete mechanism functions mostly in the normal range of T_{carotid} and not at its extremes. Thus, the alternative proposal developed was that the rete mechanism modulated responses to changes in body temperature and limited thermoregulatory costs (Maloney & Mitchell 1997). Maximal thermoregulatory responses occur when T_{brain} and T_{carotid} change simultaneously (Jessen & Feistkorn 1984). If they are dissociated then responses are muted. Therefore, at low T_{carotid} , when rete activity is reduced and T_{brain} is relatively high, there is reduced heat gain. At high T_{carotid} , when T_{brain} is cooled by the rete, heat loss mechanisms are not activated. The net effect is a relatively wide variation in body temperature, but conservation of energy (at low T_{carotid}) and conservation of water (at high T_{carotid}). Conversely, in non-rete animals T_{brain} and T_{carotid} change together and ranges of body temperature become narrower because whole body cooling or warming occurs at temperatures that do not activate these responses in rete animals. If T_{carotid} falls so does T_{brain} stimulating

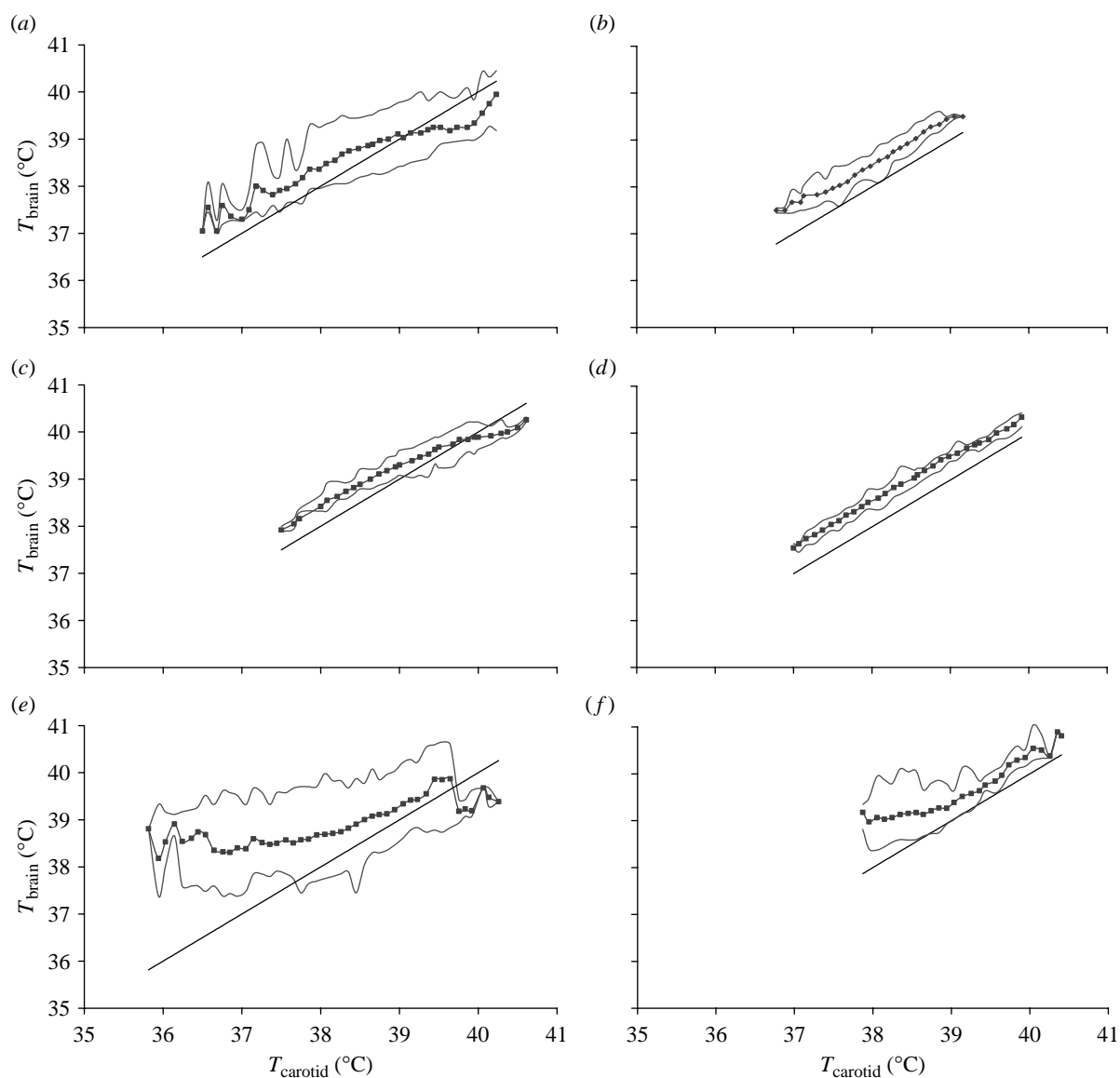


Figure 2. The relationship between T_{brain} and T_{carotid} in (a) wildebeest (Jessen *et al.* 1994); (b) zebra (Fuller *et al.* 1999); (c) oryx (Maloney *et al.* 2002); (d) horse (Mitchell *et al.* 2006); (e) pronghorn in summer (Lust *et al.* 2007); and (f) pronghorn in winter (from Hébert *et al.* 2008). T_{brain} (squares) and its 95% confidence limits are shown in relation to the line of identity.

metabolism and energy consumption. If T_{carotid} increases so does T_{brain} and sweating or respiratory evaporative heat loss is required to reduce it. Thermoregulatory responses of this kind have to be supported by abundant resources to warm or cool the body, which are the features of a low seasonality tropical environment.

Hence, animals that have a rete have an additional weapon in their thermoregulatory arsenal denied to non-rete animals. The rete, by allowing brain and body temperatures to dissociate when conditions are hot, mutes thermoregulatory responses and energy and water conservation follow. In winter, when large fluctuations in body temperature like those that occur in summer could expose the animal to potentially disastrous hypothermia, the rete mechanism is bypassed and body temperature conserved. Clearly, the range of thermal niches an animal can inhabit with this degree of thermoregulatory flexibility will be wider than it is for non-rete animals. The range of habitats occupied by artiodactyls, from the Arctic

Circle to deserts and equatorial forests, is convincing evidence of this advantage.

If this interpretation of our data is correct then animals that do not have a rete will prefer thermal environments that vary little, their habitats will provide abundant food and water and seasonality will be low. This prediction is generally true for perissodactyls and specifically true for the most primitive of artiodactyls, mouse deer (*Tragulus javanicus*, *Tragulus napu*) that do not have a rete (Fukuta *et al.* 2007). They are small (approx. 2 kg) and are therefore at a thermoregulatory disadvantage and are not well adapted to heat or cold. They rely on low variation in environmental temperature to maintain their body temperatures (Whittow *et al.* 1977). Small size alone, however, does not explain the dependence of mouse deer on a forest environment. The next smallest artiodactyl, the dik-dik (*Madoqua kirkii*) weighs approximately 5 kg and is also at an allometric disadvantage, but is not confined to equatorial forests. Thus, our data suggest that it is the absence of a rete

in mouse deer and their inability to regulate T_{brain} which is the critical disadvantage, and may explain why, in the seasonal Mid-Miocene, tragulids were reduced to four species restricted to the forests of the old world tropics of southeast Asia and West Africa (Janis 1989). We have concluded, therefore, that the thermoregulatory flexibility conferred by the rete is as important for the success of artiodactyls as is their ruminant digestive tract and improved locomotion.

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