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News and Views

A rod cell marker of nocturnal ancestry

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In a recent *Cell* article, Solovei et al. (2009) have shown that the rod cell nuclei of nocturnal and diurnal mammals (including primates) are organized in distinct patterns, and that the nocturnal-associated pattern likely facilitates efficient photon capture by the photoreceptors. Their research underscores the exceptional selective pressures placed on the visual system in low light environments and provides a new marker of nocturnal ancestry. This marker can be used to advance our understanding of activity pattern evolution, potentially including the behavioral ecology of ancestral primates.

Distinct rod nuclear architectures of diurnal and nocturnal mammals

In the interphase cell, DNA is organized at multiple inter-related levels. At one level there are two principal types of chromatin, the structural combination of DNA and proteins (especially histones) of which chromosomes are composed. Gene-poor regions are packed densely as heterochromatin, and gene-rich regions are decondensed as euchromatin. The relative openness of euchromatin may facilitate regulatory transcription factor binding and gene expression, although in heterochromatin these processes are not inhibited completely (Misteli, 2007). At another organizational level, euchromatin typically occupies the nuclear interior while heterochromatin is distributed primarily at the nuclear periphery (Kosak et al., 2007; Misteli, 2007). This particular spatial organization – hereafter referred to as the 'conventional architecture' – is nearly universal among eukaryotic cells (Habermann et al., 2001; Tanabe et al., 2002; Alexandrova et al., 2003; Postberg et al., 2005) and is considered important for the precise control of complex gene expression programs (Schneider and Grosschedl, 2007; Sexton et al., 2007; Finlan et al., 2008; Reddy et al., 2008).

A striking exception to the conventional architecture is found in the mouse rod photoreceptor (Carter-Dawson and LaVail, 1979). In these cells, heterochromatin occupies the center of the nucleus and euchromatin is relegated to the periphery. Solovei et al. (2009) characterized in detail this 'inverted architecture' of mouse rod cells and performed comparisons with a diversity of other mammals. The inverted architecture was observed in the rod cells of other nocturnal species, while the conventional pattern was associated with diurnal activity (Fig. 1a). Among primates, the rod nuclei of the nocturnal pygmy mouse lemur (*Microcebus myoxinus*) and the diurnal long-tailed macaque (*Macaca fascicularis*) are organized in the inverted and conventional architectures, respectively.

What might explain the association of the inverted architecture with nocturnality? Solovei et al. (2009) used quantitative phase contrast microscopy and computer simulations to show that the mouse rod nuclei with dense heterochromatic centers act as converging lenses, achieving a more efficient light transmission (note that photons must pass through the nucleus to the rhodopsin-containing segment of the rod cell), compared to the conventional architecture (Fig. 1b). Therefore, the inverted architecture that characterizes the rod cell nuclei of nocturnal mammals is likely an adaptation that maximizes photon capture in low light environments. The inverted architecture is unique to mammals and probably evolved in a common (nocturnal) mammalian ancestor, followed by independent reversions to the conventional architecture in multiple lineages that have shifted to diurnal activity patterns (Solovei et al., 2009). Absent the intense selective pressures imposed by night vision, the conventional pattern of nuclear architecture is likely advantageous.

Implications for current debates about primate origins

A number of hard and soft tissue phenotypes, now including rod nuclear architecture, are potential indicators of activity pattern in mammals (Table 1). Generally, the primate common ancestor is reconstructed to have been nocturnal (e.g., Martin, 1990; Sussman, 1991; Heesy and Ross, 2001; Ravosa and Savakova, 2004; Ravosa and Dagosto, 2007; Ross et al., 2007; Ross and Kirk, 2007). Recently,

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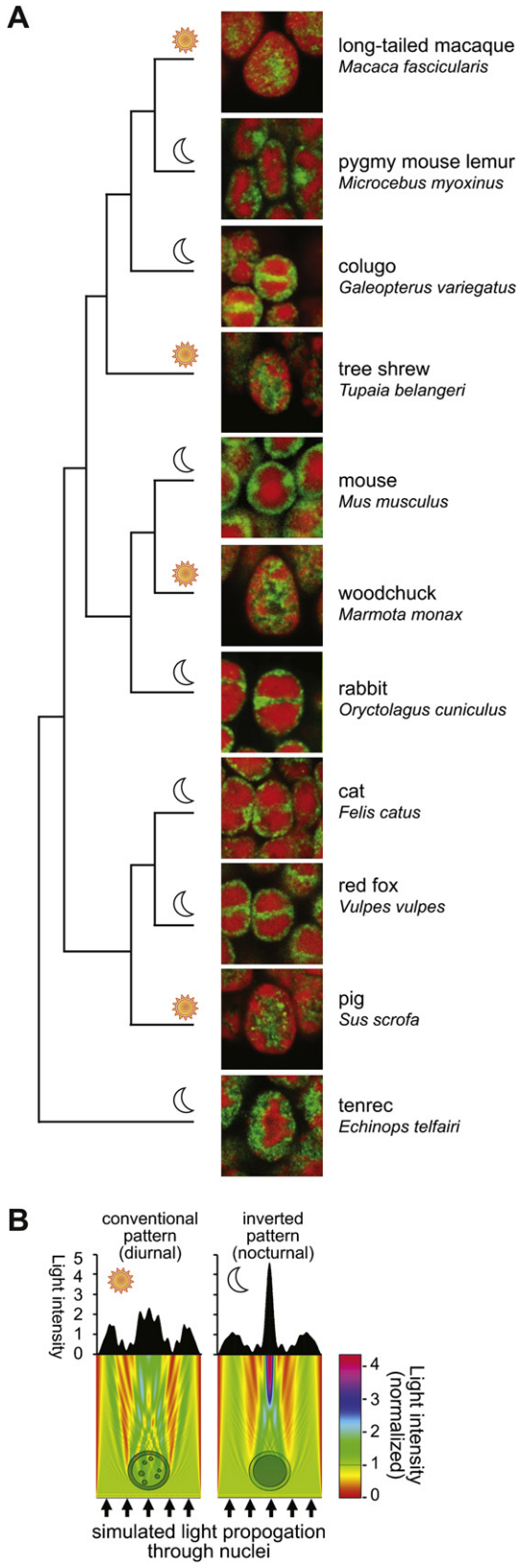

however, this standard view has been questioned (Tan et al., 2005; Lucas et al., 2007; Ankel-Simons and Rasmussen, 2008), in part based on a new appreciation of visual system diversity among extant nocturnal primates. Specifically, some taxa – dwarf lemurs, lorisoids, and night monkeys – probably have monochromatic vision resulting from functional loss of the blue-sensitive opsin gene (Jacobs et al., 1996; Tan et al., 2005). Yet in other lineages – mouse lemurs, *Avahi*, *Lepilemur*, aye-ayes, and tarsiers – both the blue and the green/red-sensitive opsin genes are intact (Tan et al., 2005). The corresponding cone types are present in the retina of at least two of these taxa (Hendrickson et al., 2000; Dkhissi-Benyahya et al., 2001), signifying the functional viability of both opsins and the capacity for dichromacy, which is likely the ancestral mammalian state. Assuming that nocturnality would necessarily lead to monochromacy, Tan et al. (2005) concluded that the primate common ancestor was either diurnal or cathemeral, followed by at least seven independent shifts to nocturnality. Some of these shifts must have been relatively recent, so that mutations that otherwise would disable the blue opsin gene have not had sufficient opportunity to occur and accumulate by genetic drift (Tan et al., 2005).

Based on a population analysis of aye-aye opsin gene sequences, the assumption underlying Tan et al.'s conclusion (2005) has been questioned by the suggestion that color vision may be adaptive for some primates even under nocturnal conditions (Perry et al., 2007). This possibility is supported by recent research on nocturnal bats. While the blue opsin gene has been lost in some lineages, two opsins have been maintained intact over many millions of years in others (Wang et al., 2004; Zhao et al., 2009a; Zhao et al., 2009b), echoing the diversity observed among nocturnal primates. Moreover, if tarsier activity pattern continuity can be inferred from morphological similarities with the middle Eocene fossil *Tarsius eocaenus* (Rossie et al., 2006), then this implies the maintenance of two opsins (and likely dichromacy) in a nocturnal lineage for >45 M.yr.

While the possibility of adaptive color vision for some nocturnal primates may be exciting, this would not necessarily help us to answer questions about primate origins, because the opsin evidence would be compatible with any possible ancestral state: nocturnal, cathemeral, or diurnal. Other soft tissue activity pattern markers are subject to convergence (e.g., Martin and Ross, 2005; Peichl, 2005) and thus may not be useful for ancestral inference based on extant taxa observations, and we lack recognizable fossils from appropriate time periods (Tavare et al., 2002) to address this issue more directly with hard tissue markers.

Can we now use rod cell nuclear architecture to retrodict the likely activity pattern of the primate common ancestor as nocturnal or cathemeral, given that the inverted architecture is observed in

Fig. 1. Phylogenetic and functional analyses of rod cell nuclear organization. Images adapted from Solovei et al. (2009) with permission from Elsevier and the authors. (A) Immunostaining of rod nuclei from retinal sections. Heterochromatin is stained with DAPI (red). An antibody against histone 3 tri-methylated lysine 4 (H3K4me3; green) marks euchromatin (Litt et al., 2001; Noma et al., 2001; Bernstein et al., 2005). Conventionally, heterochromatin localizes predominantly to the nuclear periphery while euchromatin is in the nuclear interior. Such an architecture is observed in the rod cells of diurnal mammals (as well as the nuclei of non-rod cell types, not shown). The inverted architecture is observed in the rod cell nuclei of nocturnal mammals. Depicted phylogenetic relationships are based on the recent literature (Janecka et al., 2007; Murphy et al., 2007). Sun and moon symbols identify diurnal and nocturnal taxa, respectively. (B) Simulated light transmission (wavelength=500 nm, the peak sensitivity of rod photoreceptors) through conventional- and inverted-architecture nuclei. In the illustrated nuclei, darker shading represents heterochromatin (corresponding to the red-stained regions in part A of the figure) while unshaded regions represent euchromatin (green-stained regions in part A). Heatmaps depict light intensities at points beyond the nuclei (arrows indicate light direction), with intensities from the top margin of the heatmap plotted above. Light must pass through the nucleus to reach the rhodopsin-containing segment of the rod cell. Inverted-architecture nuclei act as converging lenses to focus light at relatively increased intensity.