Cover illustration: A ghost of a chance

The black and white ruffed lemur (*Varecia variegata variegata*) gracing the cover is a diurnal prosimian endemic to Madagascar. The word "lemur" means "ghost" in Latin, and watching these magnificent animals travel through, and seemingly disappear into, the trees may actually make you believe that you have seen a ghost. Lemurs vault from limb to limb and cling to the spiniest and most peculiar trees with the greatest of ease. Even though they do not have prehensile tails, lemurs can hang upside down from their feet and feed with their forelimbs, and are masters of their arboreal domain. The black and white ruffed lemur spends almost all of its life in trees, even building a nest there. These animals are so intricately woven into the forest tapestry that they have become the sole pollinator of the traveller's palm and appear to have co-evolved with the tree. But, despite the aerial ballet, sharp acuity seemingly has not been necessary, as these lemurs are afoveate, and this is important to our story.

The order Primates is divided into three suborders: *Prosimii*, *Platyrrhina*, and *Catarrhina*. The *Prosimii* consists of the lemurs, bushbabies, lorises, pottos, and tarsiers. Most of these are nocturnal or cathemeral (active both day and night), although the black and white ruffed lemur is diurnal. The platyrrhines are New World monkeys, and within the catarrhines there are two divisions, consisting of Old World monkeys and the hominoids. The prosimians ("before the monkeys") are thought to retain more "primitive" characteristics than the higher primates or, at least, were seen earlier in the evolutionary process, and hence are viewed as perhaps preserving features of our early ancestors. So, to compare the nocturnal and diurnal prosimians and the radiation into the other primate suborders is to consider the particulars of our direct early evolution.

There is no consensus on the formation of Madagascar although most authorities believe the continent-like island was carried with India away from Africa as Gondwanaland broke up, some time during the Cretaceous period, approximately 190 to 65 million years ago. At that time, the greater subcontinent of India probably abutted Tanzania, Kenya, and Somalia. This supercontinent of India and Madagascar existed until about 130 to 65 million years ago when they separated, eventually sending India, geologically speaking, headlong into Asia, creating the Himalayas. Placental mammals evolved some time before the Cretaceous period. The early primates or plesidadapiforms are not in evidence until the Palaeocene period, approximately 65 million years ago, but were probably present in the Cretaceous period. Hence, it would appear that the Madagascar lemurs occupy a very special position. They were set towards evolving when an early primate or primate predecessor survived as Madagascar broke away from India. Current evidence suggests that all of the Madagascar primates, including the bizarre aye-aye, evolved from a single predecessor species, although how this animal arrived in Madagascar remains in dispute. This single species evolved and speciated independently without other primate competition, and may provide us with additional information on the evolution of colour vision. Isolated from other primates, the lemurs, through allopatric speciation, have radiated into at least 49 species, although only 33 are extant. All of these are threatened. These elegant animals offer us a glimpse into the evolution of the visual system in the context of primate speciation, as well as the importance of colour vision in species survival.

Currently, we believe that all mammals have a certain population of cones, and they probably were present very early evolutionarily, but colour vision among mammals, and even among primates, is not universal. Briefly and simply, there are three different visual pigments in the Old World monkeys (all catarrhines), presumably previous hominoids and humans. For discussion and explanation, we will describe these pigments according to their wavelength of peak sensitivity at 560 nm (long wavelength), 530 nm (middle wavelength), and 420 nm (short wavelength). For evolutionary discussion purposes, we can consider the catarrhines and hominids as mature ocular equivalents among the primates.

The New World monkeys, except the howler monkey (*Alouatta seniculus* and *A caraya*), do not have consistent visual pigments and may illustrate visual pigment evolution in progress. The howler monkeys are trichromats and each animal has three predictable visual pigments very similar to the three visual pigments of the Old World monkeys and may represent convergent evolution. At least three other species of New World monkeys have been tested and there is considerable variation within these species. Some individuals within each species may be dichromats and some may be trichromats, so colour vision will vary depending on the individual animal. It would appear that these species are evolving trichromacy now.

The diurnal prosimians have been evaluated to some extent and have been found to have visual pigments with peak sensitivity at 543 nm (long/medium wavelength) and 437 nm (short wavelength). These prosimians are dichromats, although the nocturnal prosimians, such as the bushbaby (*Otolemur crassicaudatus*), have only one cone pigment with peak sensitivity at approximately 545 nm. The nocturnal prosimians, and presumably other nocturnal species, do not see in colour. Recently, however, the females of two diurnal lemurs closely related to the black and white lemur have been found to have genetic polymorphisms allowing some individuals to have the visual pigments required for trichromacy. Some individuals within each of these species may actually have three visual pigments.

The distribution of cones is at least as important to colour vision as their spectral sensitivity, and current evidence suggests that lemurs have a relatively low concentration of cones in the macular area, and are afoveate. Furthermore, the prosimians may not have the necessary neural components to process the more complex visual signals of trichromacy, or if they do have the necessary wiring, it is not being used as such currently. When tested against the New World monkeys with known dichromacy, the diurnal prosimians are unable to discriminate spectral variations that are quite apparent to the monkeys. The principal difference between the two species is the higher concentration of cones in the macular region of the New World monkeys.

What, then, are the implications for the evolution of colour vision? While in dispute, one explanation could be as follows. Trichromacy is a useful aid to perceptual colour vision, and the selection and location of a frugivorous diet. The protoprimate that initiated the speciation of lemurs on Madagascar had dichromacy (as do many mammals that preceded the primates), and perhaps the genetic tools for trichromacy, but this potential has never been realised because of the lack of other primate competition. But, in the New World monkeys, primate competition has selected the necessary wiring of the brain, the cone concentrations, and begun moving towards trichromacy in many species, and even succeeded in the howler monkeys. Alternatively, the prosimians may have evolved genetic polymorphisms convergently and in parallel with the New World monkeys. The Old World monkeys had sufficient competition to select the necessary pigments and the neural imperatives for trichromacy long ago. The hominids evolved from the Old World monkeys as trichromats, suggesting that trichromacy may have a very important role in primate evolution. Hence, any lemur or closely allied species competing with other primates would be hard pressed to maintain its niche, and could be replaced by trichromatic successors.

The lemurs are currently threatened by habitat destruction, but could they be threatened by trichromacy as well? Perhaps, they don't stand a ghost of a chance.—*Ivan R Schwab, MD, UC Davis Department of Ophthalmology, 4860 Y Street, Suite 2400, Sacramento, CA 95817, USA (irschwab@ucdavis.edu)*.

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