# Evolution of the Special Senses in Primates: Past, Present, and Future

**NATHANIEL J. DOMINY,**[1]* **CALLUM F. ROSS,**[2] **AND TIMOTHY D. SMITH**[3]
[1]Department of Ecology and Evolution, University of Chicago, Chicago, Illinois
[2]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois
[3]School of Physical Therapy, Slippery Rock University, Slippery Rock, Pennsylvania

### ABSTRACT

The present special issue of *The Anatomical Record* is the result of a symposium entitled Evolution of the Special Senses in Primates. Considered together, the special senses of primates are remarkable because they constitute a singular and definitive suite of mammalian characteristics. Examining their evolution is pivotal for understanding the origin and present-day variation of primate behavior and ecology. Accordingly, the 14 articles assembled here consider the different constraints and opportunities associated with the uptake and use of physical and chemical stimuli. The present issue brings together experts on different primate sensory modalities and stresses events at the sensory periphery, where the organism is exposed to and comes into contact with its environment. Key topics include color vision, the genetics of olfaction, the morphological basis and significance of chemical communication, and the neural organization and scaling of primate sensory systems. The result is a special issue that both reflects our current understanding of primate sensory modalities and challenges certain fundamental assumptions concerning their evolution.    © 2004 Wiley-Liss, Inc.

**Key words: audition; gustation; olfaction; touch; vision; vomeronasal**

This special issue of *The Anatomical Record* is the result of a symposium held during the 73rd annual meeting of the American Association of Physical Anthropologists. The symposium was the suggestion of Timothy D. Smith; the conveners were Nathaniel J. Dominy, Callum F. Ross, and Timothy D. Smith. It was presented in Tampa, Florida, on 17 April 2004. The title of the symposium and the present issue is Evolution of the Special Senses in Primates. We focus on primate special senses (vision, audition, olfaction, and gustation) for the same reasons the topic has already received much attention (Le Gros Clark, 1959; Noback, 1978; Martin, 1990)—because humans are primates and because there is a unique complexity in the expression of primate special senses. Two contributions to this issue consider the evolution of somatosensation, which also bears pivotal importance to the origin of Primates.

Senses represent the anatomical interface between the environment and the behaving organism. The 14 articles assembled here emphasize the constraints and opportunities associated with sensing environmental information. The articles also examine the selective pressures in the evolution and behavioral ecology of primates; after all, the survival and reproductive success of an organism depends on the acquisition of sensory stimuli. In this regard, primates do not eat or reproduce with whatever is available; instead, they show considerable selectivity. A mixture of many analytically separable factors is locked together in a potential food resource or mate. These factors can be conveniently differentiated into two broad categories: physical and chemical. Accordingly, the following synopsis describes the contributions of the present special issue to our understanding of primate sensory systems within these categories.

## SENSING PHYSICAL STIMULI

### Vision

For several reasons, the primate visual system has long attracted attention from neuroscientists, primatologists and evolutionary biologists. First, because light travels extremely quickly in straight lines, providing almost instantaneous information about events at a distance; vision is therefore an extremely useful sense for finding conspecifics, predators, and food. Second, primates have specialized visual systems that differ from those of other mammals in various features, and anthropoid primates are

further distinguished by a suite of visual adaptations (Ross, 2000). Comparative studies of anthropoid primates can therefore provide insight into human visual function. Third, some important aspects of visual system soft-tissue anatomy are also reflected in the anatomy of associated skeletal tissues (Kay and Cartmill, 1977; Kay and Kirk, 2000; Bush et al., 2004a; Kirk and Kay, 2004), providing insight into the visual adaptations of fossil primates. This makes it possible not only to study the visual adaptations of extant primates, but also to investigate the morphological, behavioral, and ecological contexts in which the primate visual system evolved (Martin and Ross, 2005).

Primates as a group are differentiated from other mammals by relatively high degrees of orbital convergence (Le Gros Clark, 1959; Cartmill, 1972). The most persuasive hypothesis for the increased convergence in the primate stem lineage invokes adaptation for nocturnal visual predation (Allman, 1977; Pettigrew, 1978; Cartmill, 1992; Ross et al., 2005), a hypothesis supported by Heesy's (2003) extensive comparative analysis of ecological determinants of orbit orientation in mammals. However, despite considerable attention to the measurement and explanation of orbital convergence over the last 3 decades (Cartmill, 1972; Ross, 1995a; Noble et al., 2000; Heesy, 2003), the relationship between orbital orientation and the orientation of the visual fields has been little studied [but see Ross (2000)]. Heesy's (2004) contribution to this issue demonstrates convincingly that, indeed, the degree of visual field overlap is positively and isometrically correlated with the degree of orbital convergence in mammals, including primates. Interestingly, however, there is some indication that within mammalian orders, the relationship between orbital convergence and visual field overlap is negatively allometric, with clade effects accounting for the isometric relationship across mammals as a whole. Further data on variation in visual field and orbit orientation within different orders are required to evaluate this possibility.

Three articles in this issue deal with changes to the visual system at anthropoid origins. The origin of crown anthropoids was associated with numerous changes to the visual system (Ross, 2000), including the evolution of a retinal fovea (Ross, 2004), increases in the number of retinal ganglion cells and the size of the optic nerve (Kirk and Kay, 2004), lengthening of the eye (Ross, 2000), increased orbital convergence (Cartmill, 1972; Ross, 1995a), and evolution of a postorbital septum (Cartmill, 1980; Ross, 1995b). Kirk (2004, this issue) demonstrates that the decreased relative cornea diameter differentiating anthropoids from other primates also differentiates anthropoids from all other mammals. This confirms suggestions that early primates did not differ from nonprimate mammals in eye shape, but only in relative size of the eye (Ross et al., 2005). This change in eye shape at the origin of crown anthropoids appears to be an adaptation to increased visual acuity (Ross, 2000; Kirk, 2004, this issue). It is also possible to estimate visual acuity from relative optic canal dimensions (Kay and Kirk, 2000; Kirk and Kay, 2004), so it is interesting to note that the earliest fossil anthropoid for which visual acuity can be estimated, *Parapithecus grangeri*, had previously been estimated to have visual acuity similar to that of extant anthropoids (Kirk and Kay, 2004; Bush et al., 2004a). In this issue, Bush et al. (2004b) advance an estimate of retinal ganglion cell number derived from multiple regression of retinal ganglion cell counts on either optic foramen area and

skull length or optic foramen area and orbit area. These regressions produce estimates of ganglion cell number for *Parapithecus* broadly overlapping the strepsirrhine range. Although these predictions are not necessarily at odds with the acuity estimate of Kirk and Kay (2004), they do highlight the need for better data on retinal ganglion cell counts for extant primates.

Bush and Allman (2004b, this issue) also address anthropoid origins in their investigation of scaling relationships of striate cortex, V1, relative to extrastriate cortex and the lateral geniculate nucleus (LGN) of the thalamus. Anthropoids have a relatively larger VI than do strepsirrhines, suggesting that they are doing more with the visual information from the thalamus than strepsirrhines. It is also interesting that in interspecific comparisons within both anthropoids and strepsirrhines, V1 volume scales with positive allometry relative to LGN volume (Stevens, 2001). Two obvious characteristics of anthropoids might be related to these differences between anthropoids and strepsirrhines: the retinal fovea and color vision. It is well known that the representation of the foveal portion of the visual field is amplified in visual cortex and that anthropoids devote 60% of V1 to the central 10° of the visual field, whereas *Otolemur garnetti* and cats devote only around 20% (Rosa et al., 1997). Anthropoids also exhibit at least dichromatic and, in catarrhines, trichromatic color vision, and some color processing does occur in V1 (Kandel et al., 1991). However, precisely how increased acuity and color vision might relate to the positive allometry of V1 relative to LGN remains to be elucidated.

## Audition

Whereas vision takes advantage of the fact that light travels virtually instantaneously in straight lines, hearing allows perception of phenomena that might be out of sight. This property of hearing is doubtlessly of great use in nocturnal and dense tropical rain forest environments, both of which characterize many extant primates and probably the first primates as well (Martin, 1990). Indeed, it has been argued that orbital convergence is not a necessary component of a nocturnal predatory lifestyle because some primates are apparently capable of localizing prey with their ears (Rasmussen, 1990; Sussman, 1991, 1995; Crompton, 1995). While there is no doubt that prey localization is facilitated by the auditory system, this by no means precludes selection for increased visual field overlap to improve image brightness and break crypsis. Indeed, as Heffner (2004, this issue) points out, there is a positive correlation between the width of the field of best vision and the degree of auditory acuity, i.e., animals that devote a very narrow portion of the visual field to high visual acuity also have a well-developed ability to localize a sound source in space. Thus, it is argued that the function of sound localization ability is to inform the visual system where to look. This suggests that selection for increased visual field overlap in early primates would have been associated with increased sound localization ability as well.

Heffner reviews a number of important features of primate hearing performance as measured by audiograms, noting the unusual audiogram of humans compared to other primates, especially in their decreased high-frequency sensitivity. She rejects hypotheses linking this characteristic to human speech, as well as simple allometric explanations for variation in high-frequency sensitiv-

ity. Rather, she suggests that small mammals augment high-frequency hearing to facilitate use of spectral cues in localization of sound sources in the environment and that large animals such as humans and elephants do not retain good high-frequency sensitivity because they do not need it for sound localization.

Despite the fact that primates as a whole have relatively unspecialized hearing systems (Heffner, 2004, this issue), there are significant differences in hearing performance between anthropoids and strepsirrhines (Coleman and Ross, 2004, this issue). Anthropoid audiograms exhibit an unusual W-shaped audiogram compared with strepsirrhines. Although this may reflect a decrease in sensitivity around 4 kHz (Heffner, 2004, this issue), comparisons between anthropoids and strepsirrhines suggest that it is a derived feature of anthropoids, reflecting enhanced low-frequency sensitivity in this clade (Coleman and Ross, 2004, this issue). Coleman and Ross (2004, this issue) also demonstrate that anthropoids have a significantly more symmetrical pinna (height:width) than strepsirrhines and tarsiers, as well as a lower value of T, the percentage of acoustic transmission. Most of the difference in T appears to be due to differences in malleus-incus lever ratio, rather than the relative size of the tympanic membrane and oval window. However, relationships between audiometric variables derived from audiograms and morphological variables are weak, especially when standardized independent contrasts are used rather than data from the tips of the phylogenetic tree (Coleman and Ross, 2004, this issue). This result provides some support for Heffner's hypothesis that the bony morphology of the ear little constrains hearing performance in mammals. Further support for this possibility comes from the observation that although lorisoids resemble anthropoids in having a dual-chambered middle ear cavity, they do not share the double-peaked audiogram and low-frequency sensitivity of platyrrhine anthropoids (Coleman and Ross, 2004, this issue). More detailed work on the relationship between hearing performance and ear morphology in primates is needed.

## Touch

The mammalian somatosensory system permits inferences about the physical properties of the outside world, using information from receptors that respond to touch and vibration, body movement, temperature, and painful stimuli (Kaas, 2004, this issue). Interestingly, anthropoid primates have several unique specializations, first in the density of digital mechanoreceptors, where there is an unusual emphasis on the hand as tactile organ, and then in the thalamus and cortex, where more subdivisions of the brain are devoted to somatosensory perception. Such elaborations and specializations appear to relate largely to the recognition and identification of objects and surfaces by touch. The process of object identification is aided by fine motor control of the hand and digits and modifications in the motor cortex.

Hoffmann et al. (2004, this issue) examine the density of specialized digital mechanoreceptors, Meissner corpuscles (MCs). MCs are reported only from primates and marsupials and are located exclusively in the papillae of glabrous skin. Martin (1990) called attention to the close alignment of MCs beneath epidermal ridges and suggested that the structures were bifunctional; that is, their purpose is both frictional and tactile in order to sense and prevent slippage on arboreal supports. Although an en-

hanced tactile sensitivity on slender locomotor substrates probably conferred strong selective pressures to primate ancestors, the dispersion of MCs in anthropoid digits raises the possibility of a more specialized coopted function. Hoffmann et al. (2004) suggest that the high density of MCs could be related to fruit selection. Softening texture is a salient sensory cue during fruit development and perceiving the textural properties of fruits haptically may provide a rapid means of discerning edibility (Dominy, 2004). Compellingly, primates are reported to palpate fruits during foraging. Accordingly, Hoffmann et al. (2004) examined the digital density of MCs in five anthropoid taxa selected to represent diverse dietary regimes. Results show that greater MC density correlates with the extent to which anthropoids are frugivorous, but locomoter and phylogenetic effects could not be discounted. Although their study cannot support any one particular model of MC evolution, it does provide a novel and exploratory step for generating hypotheses regarding the evolution of primate special senses.

## SENSING CHEMICAL STIMULI
## Olfaction and Other Chemical Senses

Physiological and morphological data suggest that the term "microsmatic" may not be a valid descriptor of primates (Laska et al., 2000; Smith and Bhatnagar, 2004; Smith et al., 2004, this issue). All primates possess at least one olfactory system: a main olfactory system (MOS) and, in numerous primates, a vomeronasal (accessory olfactory) system (VS). The roles of these systems in primates are poorly understood because a functional VS is absent in catarrhines and because its function is uncertain in haplorhines (Bhatnagar and Meisami, 1998; Smith et al., 2001; Dennis et al., 2004, this issue). In mammals generally, the sense of smell (olfaction) is mediated through the MOS, which is specialized to detect airborne (volatile) odorants (Dulac and Torello, 2003). Odorants of heavier molecular weight (nonvolatile) are detected through the VS. Functionally, the division of labor between these systems has been an intense point of discussion for decades (Stephan et al., 1982; Frahm, 1985). Early insights into function of the vomeronasal organ (VNO) in rodents (Wysocki, 1979) have yielded a tendency to generalize that the VS detects pheromones while the MOS detects most other chemical signals. However, it is becoming clearer that in mammals some pheromones are easily detected by the MOS and that the VS is at least capable of detecting odorants that do not have pheromonal function (Wysocki and Preti, 2004, this issue). Early analyses of the VS debated the pheromonal versus nonpheromonal functions of this system in primates (Stephan et al., 1982), and it seems necessary to revisit this discussion based on the functional overlap of the MOS/VS in some other mammals. It is also critical to emphasize that although New World anthropoids apparently possess an intact VS (i.e., possess the receptor organ, vomeronasal nerves, and an accessory olfactory bulb), there is no convincing evidence whatsoever that it is functional for pheromone (or any odorant) detection (Barrett et al., 1990). In strepsirrhines, there is reason to believe the VS is critical for pheromonal communication (Aujard, 1997; Alport, 2004, this issue; Kay et al., 2004, this issue).

Anatomically, structural elements of both systems have played critical roles in the discussion of primate evolution and sensory specializations of extant primates. A number of authors have discussed size differences in the main

olfactory bulb (MOB) between diurnal and nocturnal primates (Baron et al., 1983; Martin, 1990; Kay et al., 2004, this issue; Bush et al., 2004b, this issue). In this issue, Bush et al. (2004b), conclude that *Parapithecus grangeri* had intermediate retinal ganglion cell counts and olfactory bulb volume compared to extant strepsirrhines and anthropoids. Their findings may ultimately affect our understanding of sensory specializations that were present in stem anthropoids. In another study, Kay et al. (2004, this issue) conclude that the fossil platyrrhine *Tremacebus harringtoni* was not nocturnal, which narrows the possible dates for secondary evolution of nocturnality in ancestors of the extant owl monkey.

Broadly speaking, studies of primate olfactory bulb size illustrate some general trends in that visually adapted diurnal species have relatively smaller MOBs than nocturnal species. It may be worth considering that activity patterns offer only indirect correlates of MOB size. For instance, dietary specializations explain some variation in MOB volume in either diurnal or nocturnal species (Barton et al., 1995). It would be equally interesting to know whether varied patterns of social behavior (e.g., scent marking) (Epple et al., 1993; Irwin et al., 2004) relate strongly to MOB size. To date, behavioral correlates of the size of chemosensory structures have usually been discussed in relation to accessory olfactory bulb size (Stephan et al., 1982). There have been few explicit attempts to study social correlates of MOB size in primates.

Thus, a tendency to generalize about these parallel but anatomically distinct olfactory pathways, primarily based on knowledge about mammals with a well-developed VNO (e.g., rodents or opossums) (Halpern and Martínez-Marcos, 2003), obscures an integrated picture of the sensory systems. Recent attempts to understand a possible evolutionary trade-off between vision and olfaction have focused separately on the MOS (Rouquier et al., 2000; Gilad et al., 2004) and the VS (Liman and Innan, 2003; Zhang and Webb, 2003; Webb et al., 2004). Whereas these studies have important implications concerning the evolution of each system, it is difficult to understand the implications concerning particular functions (e.g., pheromonal communication) when it is not clear which olfactory system mediates that function in primates. There is clearly a need for more studies considering multiple permutations for how particular patterns of primate behavior may be mediated by neural structures.

The study by Alport (2004, this issue) is an important departure, examining whether intrasexual competition relates to MOB or neocortical volume in haplorhines. Studies that consider the roles of multiple neural pathways in mediating behavior are scarce (Barton et al., 1995; Alport, 2004, this issue), but may be the best route for dealing with the overlap in function of chemical senses. Regarding primates, this avenue may be especially important when considering that flavor is both gustatory and olfactory (Rolls, 2004, this issue). A similar combinatorial function has been suggested for the MOS and VS (Dennis et al., 2003).

## CONCLUSION

A singular suite of special senses characterizes the primate order. In these 14 articles, the reader will note remarkable advances in knowledge, as well as contrasting points of view. The anatomy of primate sensory systems can reveal much about the importance of environmental information, and vice versa. However, further questions of how sensory information is used remain unanswered. The immediate problem for fresh and continuing researchers is to examine the cognitive and sensory ecology of the primates observed. Primates are selective in virtually all their behaviors—the question is not why they are selective but how do they select. The present issue indicates how much information the observer needs to acquire before this goal can be attempted. Accordingly, an understanding of functional morphology of these sensory modalities is pivotal for understanding the origin and present-day variation of primate behavior and ecology.

## LITERATURE CITED

Allman J. 1977. Evolution of the visual system in the early primates. Prog Psychobiol Physiol Psychol 7:1–53.

Alport LJ. 2004. Comparative analysis of the role of olfaction and the neocortex in primate intrasexual competition. Anat Rec 281A:1182–1189.

Aujard F. 1997. Effect of vomeronasal organ removal on male socio-sexual responses to female in a prosimian primate (*Microcebus murinus*). Physiol Behav 62:1003–1008.

Baron G, Frahm HD, Bhatnagar KP, Stephan H. 1983. Comparison of brain structure volumes in Insectivora and Primates: III, main olfactory bulb (MOB). J Hirnforsch 24:551–558.

Barrett J, Abbott DH, George LM. 1990. Extension of reproductive suppression by person cues in subordinate female marmoset monkeys, *Callithrix jacchus*. Behav Ecol Sociobiol 90:411–418.

Barton RA, Purvis A, Harvey PH. 1995. Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. Phil Trans R Soc Lond B 348:381–392.

Bhatnagar KP, Meisami E. 1998. Vomeronasal organ in bats and primates: extremes of structural variability and its phylogenetic implications. Microsc Res Techn 43:465–475.

Bush EC, Allman JM. 2004. Three-dimensional structure and evolution of primate primary visual cortex. Anat Rec 281A:1088–1094.

Bush EC, Simons EL, Dubwitz DJ, Allman JM. 2004a. Endocranial volume and optic foramen size in *Parapithecus grangeri*. In: Ross CF, Kay RF, editors. Anthropoid origins: new visions. New York: Kluwer Academic/Plenum Publishers. p 603–614.

Bush EC, Elwyn L, Simons EL, Allman JM. 2004b. High-resolution computed tomography study of the cranium of a fossil anthropoid primate, *Parapithecus grangeri:* new insights into the evolutionary history of primate sensory systems. Anat Rec 281A:1083–1087.

Cartmill M. 1972. Arboreal adaptations and the origin of the Order Primates. In: Tuttle R, editor. The functional and evolutionary biology of primates. Chicago: Aldine. p 97–122.

Cartmill, M. 1980. Morphology, function, and evolution of the primate postorbital septum. In: Ciochon RL, Chiarelli AB, editors. Evolutionary biology of the New World monkeys and continental drift. New York: Plenum. p 243–274.

Cartmill M. 1992. New views on primate origins. Evol Anthropol 3:105–111.

Coleman MN, Ross CF. 2004. Primate auditory diversity and its influence on hearing performance. Anat Rec 281A:1123–1137.

Crompton RH. 1995. "Visual predation," habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 11–30.

Dennis JC, Allgier JG, Desouza LS, Eward WC, Morrison EE. 2003. Immunohistochemistry of the canine vomeronasal organ. J Anat 202:515–524.

Dennis JC, Smith TD, Bhatnagar KP, Bonar CJ, Burrows AM, 2004. Morrison EE. Expression of neuron-specific markers by the vomeronasal neuroepithelium in six species of primates. Anat Rec 281A: 1190–1200.

Dominy NJ. 2004. Fruits, fingers, and fermentation: the sensory cues available to foraging primates. Integr Comp Biol 44:29–37.

Dulac C, Torello AT. 2003. Molecular detection of pheromone signals in mammals: from genes to behaviour. Nat Rev Neurosci 4:551–562.

Epple G, Belcher AM, Küderling I, Zeller U, Scolnick I, Greenfield KL, Smith AB III. 1993. Making sense out of scents: species differences in scent glands, scent-marking behaviour, and scent-mark composition in the Callitrichidae. In: Rylands AB, editor. Marmosets and tamarins: systematics, behaviour, and ecology. Oxford: Oxford University Press. p 123–151.

Frahm HD. 1985. Comparison of main olfactory bulb size in mammals. Fortschr Zool 30:691–693.

Gilad Y, Wiebe V, Przeworski M, Lancey D, Pääbo S. 2004. Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates. PLOS Biol 2:1–6.

Halpern M, Martínez-Marcos A. 2003. Structure and function of the vomeronasal system: an update. Prog Neurobiol 70:245–318.

Heffner RS. 2004. Primate hearing from a mammalian perspective. Anat Rec 281A:1111–1122.

Heesy CP. 2003. The evolution of orbit orientation in mammals and the function of the primate postorbital bar. Stony Brook, NY: Interdepartmental Doctoral Program in Anthropological Sciences, State University of New York at Stony Brook.

Heesy CP. 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat Rec 281A:1104–1110.

Hoffmann JN, Montag AG, Dominy NJ. 2004. Meissner corpuscles and somatosensory acuity: the prehensile appendages of primates and elephants. Anat Rec 281A:1138–1147.

Irwin MT, Samonds KE, Raharison J-L, Wright PC. 2004. Lemur latrines: observations of latrine behavior in wild primates and possible ecological significance. J Mammal 85:420–427.

Kaas JH. 2004. Evolution of somatosensory and motor cortex in primates. Anat Rec 281A:1148–1156.

Kandel ER, Schwartz JH, Jessell TM. 1991. Principles of neural science, 3rd ed. Norwalk, CT: Appleton and Lange.

Kay RF, Cartmill M. 1977. Cranial morphology and adaptation of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea? Primates), with a description of a new genus and species. J Hum Evol 6:19–35.

Kay RF, Kirk EC. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. Am J Phys Anthropol 113:235–262.

Kay RF, Campbell VM, Rossie JB, Colbert MW, Rowe TB. 2004. Olfactory fossa of *Tremacebus harringtoni* (platyrrhini, early Miocene, Sacanana, Argentina): implications for activity pattern. Anat Rec 281A:1157–1172.

Kirk EC. 2004. Comparative morphology of the eye in primates. Anat Rec 281A:1095–1103.

Kirk EC, Kay RF. 2004. The evolution of high visual acuity in the Anthropoidea. In: Ross CF, Kay RF, editors. Anthropoid origins: new visions. New York: Kluwer Academic/Plenum Publishers. p 539–602.

Laska M, Seibt A, Weber A. 2000. "Microsmatic" primates revisited: olfactory sensitivity in the squirrel monkey. Chem Senses 25:47–53.

Le Gros Clark WE. 1959. The antecedents of man. New York: Harper.

Liman ER, Innan H. 2003. Relaxed selective pressure on an essential component of pheromone transduction in primate evolution. Proc Natl Acad USA 100:3328–3332.

Martin RD. 1990. Primate origins and evolution: a phylogenetic reconstruction. Princeton, NJ: Princeton University Press.

Martin RD, Ross CF. 2005. The evolutionary and ecological context of primate vision. In: Kremers J, editor. The primate visual system. New York: John Wiley and Sons (in press).

Noback CR. 1978. Sensory systems in primates. New York: Kluwer Academic Publishers.

Noble VE, Kowalski EM, Ravosa MJ. 2000. Orbit orientation and the function of the mammalian postorbital bar. J Zool 250:405–418.

Pettigrew JD. 1978. Comparison of the retinotopic organization of the visual wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. In: Cool SJ, Smith EL, editors. Frontiers of visual science. New York: Springer Verlag. p 328–335.

Rasmussen DT. 1990. Primate origins: lessons from a neotropical marsupial. Am J Primatol 22:263–277.

Rolls ET. 2004. Convergence of sensory systems in the orbitofrontal cortex in primates and brain design for emotion. Anat Rec 281A: 1212–1225.

Rosa MGP, Casagrande VA, Preuss TM, Kaas JH. 1997. Visual field representation in striate and prestriate cortices of a prosimian primate (*Galago garnetti*). J Neurophsyiol 77:3193–3217.

Ross CF. 1995a. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. J Hum Evol 29: 201–227.

Ross CF. 1995b. Muscular and osseous anatomy of the primate anterior temporal fossa and the functions of the postorbital septum. Am J Phys Anthropol 98:275–306.

Ross C. 2000. Into the light: the origin of Anthropoidea. Annu Rev Anthropol 29:147–194.

Ross CF. 2004. The tarsier fovea: functionless vestige or nocturnal adaptation? In: Ross CF, Kay RF, editors. Anthropoid origins: new visions. New York: Kluwer Academic/Plenum Publishers. p 477–537.

Ross CF, Hall MI, Heesy CP. 2005. Were basal primates nocturnal? Evidence of eye and orbit shape. In: Ravosa MJ, Dagosto M, editors. Primate origins and adaptations. New York: Kluwer Academic/ Plenum Publishers (in press).

Rouquier S, Blancher A, Giorgi D. 2000. The olfactory receptor gene repertoire in primates and mouse: evidence for reduction of the functional fraction in primates. Proc Natl Acad USA 97:2870–2874.

Smith TD, Siegel MI, Bhatnagar KP. 2001. Reappraisal of the vomeronasal system of catarrhine primates: ontogeny, morphology, functionality and persisting questions. Anat Rec 265:176–192.

Smith TD, Bhatnagar KP. 2004. "Microsmatic" primates: Reconsidering how and when size matters. Anat Rec Part B (New Anat) 279B:24–31.

Smith TD, Bhatnagar KP, Tuladhar P, Burrows AM. 2004. Distribution of olfactory epithelium in the primate nasal cavity: are microsmia and macrosmia valid morphological concepts? Anat Rec 281A:1173–1181.

Stephan H, Baron G, Frahm HD. 1982. Comparison of brain structure volumes in Insectivora and Primates: II, the accessory olfactory bulb (AOB). J Hirnforsch 23:575–591.

Stevens CF. 2001. An evolutionary scaling law for the primate visual system and its basis in cortical function. Nature 411:193–195.

Sussman RW. 1991. Primate origins and the evolution of angiosperms. Am J Primatol 23:209–223.

Sussman RW. 1995. How primates invented the rainforest and vice versa. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 1–10.

Webb DM, Cortés-Ortiz L, Zhang J. 2004. Genetic evidence for the coexistence of pheromone perception and full trichromatic vision in howler monkeys. Mol Biol Evol 21:697–704.

Wysocki CJ. 1979. Neurobehavioral evidence for the involvement of the vomeronasal system in mammalian reproduction. Neurosci Biobehav Rev 3:301–341.

Wysocki CJ, Preti G. 2004. Facts, fallacies, fears, and frustrations with human pheromones. Anat Rec 281A:1201–1211.

Zhang J, Webb DM. 2003. Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. Proc Natl Acad USA 100:8337–8341.