

Sensory ecology: olfaction

E. CHRISTOPHER KIRK

The University of Texas at Austin, USA

Olfaction plays a key role in the behavioral ecology of many primates. The ability to identify and discriminate between chemicals (odorants) detected by the olfactory organs may be of critical importance in a variety of contexts, including food selection (see *DIETS (PRIMATES)*), predator avoidance, social communication (see *COMMUNICATION*), and mate choice (see *SOCIOSEXUAL BEHAVIOR (NONHUMAN PRIMATES)*). As in other mammals, the sense of olfaction in primates is mediated by two distinct sensory systems: the main olfactory system (MOS) and the accessory olfactory system (AOS). The MOS detects volatile odorants via a specialized sensory epithelium in the posterior nasal cavity. This olfactory epithelium is characterized by the presence of olfactory receptor cells (ORs)—modified neurons that express olfactory receptor proteins (ORPs) on olfactory cilia that project into the nasal cavity. For an odorant to be detected by the MOS, it must bind with a suitable site on the extracellular surface of at least one ORP to initiate a transduction cascade that leads to depolarization of the OR. Each OR has an axon that passes through the cribriform plate of the ethmoid to terminate in the main olfactory bulb (MOB). Input to the MOB is ultimately relayed to other olfactory centers of the brain, such as the amygdala, hypothalamus, hippocampus, and piriform cortex.

Unlike the MOS, which is more generalized in function, the AOS is specialized for the detection of pheromones—chemical signals that elicit stereotyped behavioral, physiological, or hormonal changes in conspecific individuals. The AOS sensory epithelium is located in the vomeronasal organ (VNO)—a tube-shaped sense organ found beneath respiratory mucosa on the floor of each nasal fossa and connected to the nasal and oral cavities via the nasopalatine duct (NPD). Vomeronasal receptor cells (VRs)

express vomeronasal receptor proteins (VNRPs) on microvilli within the fluid-filled lumen of the VNO. The VNO detects both volatile and nonvolatile odorants, which must enter the VNO and bind with a suitable VNRP to initiate transduction. Detection of volatile odorants may be facilitated by retraction of the upper lip (flehmen) to expose the inlet of the NPD. Detection of nonvolatile odorants (e.g., in urine, feces, scent marks, and other bodily secretions) may be facilitated by licking or by direct contact with a rhinarium—a hairless collecting surface surrounding the nares and connected to the NPD via a groove in the upper lip (philtrum). Axons of VRs terminate in the accessory olfactory bulb (AOB), from which afferent signals are relayed to two primary targets in the brain: the amygdala and hypothalamus.

Anatomical and genomic evidence suggests that primates exhibit considerable variation in their olfactory abilities. Strepsirrhines have MOS anatomy that is generally consistent with that observed in many other mammals and inferred for the last common ancestor of living primates (Kirk et al. 2014). Strepsirrhines exhibit a nasal cavity with an olfactory recess that is separated from the main airway (nasopharyngeal meatus) by a transverse bony lamina (Figure 1). Strepsirrhines also possess four major ethmoturbinals and a variable number of minor turbinals that increase the surface area available for olfactory epithelium. Haplorhines, by comparison, share derived reductions of MOS anatomy (Smith, Rossie, and Bhatnagar 2007). Haplorhines have lost many of the bony turbinals that are seen in strepsirrhines and most other mammals, and as a result they typically have a relatively smaller area of olfactory epithelium. The nasal cavities of haplorhines also lack an olfactory recess separated from the main airway. Compared to strepsirrhines, haplorhines have relatively small MOB, and olfactory structures comprise a smaller portion of total brain volume. Genomic data for two species (galago and mouse lemur) suggest that strepsirrhines have at least approximately 350 functional ORP genes (Niimura 2012). These values are comparable to the number of

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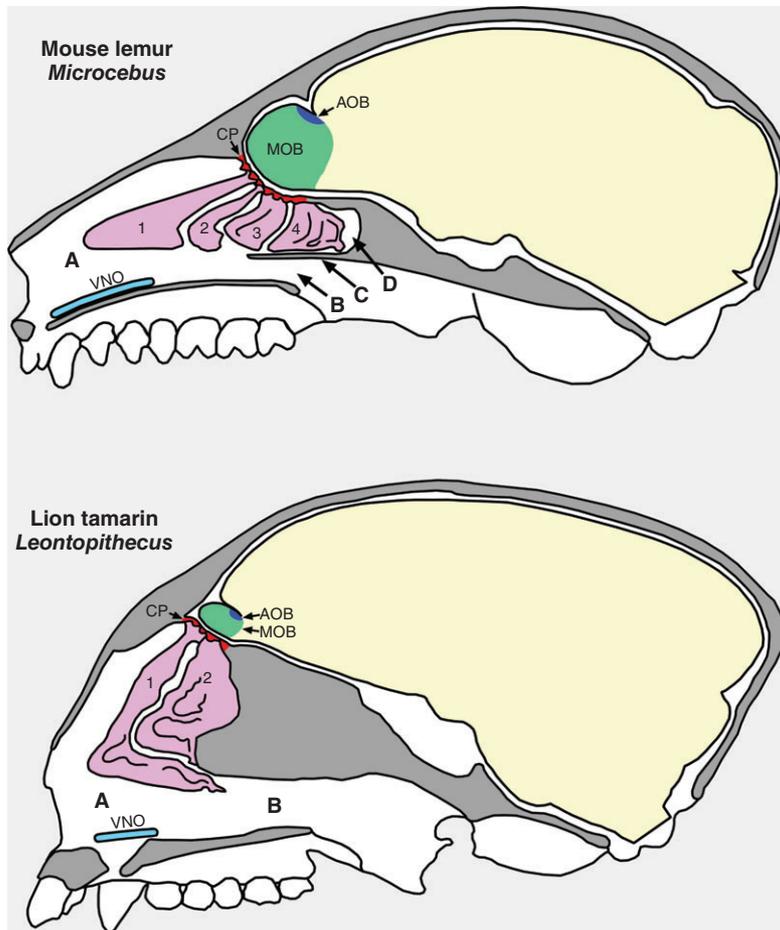


Figure 1 Schematic parasagittal cross-section through the cranium and right nasal fossa of a strepsirrhine (top: *Microcebus*, Lemuriformes) and haplorhine (bottom: *Leontopithecus*, Platyrrhini). Images not to scale. Ethmoturbinals are numbered; maxilloturbinal and nasoturbinal are omitted for clarity. A, Nasal fossa; B, nasopharyngeal meatus; C, transverse bony lamina; D, olfactory recess; AOB, accessory olfactory bulb; CP, cribriform plate; MOB, main olfactory bulb; VNO, vomeronasal organ.

functional ORP genes reported for anthropoids (~ 300–400), but far fewer than that reported for colugos (518), treeshrews (969), and glirans (~ 750–1,200) (Mason et al. 2016). Strepsirrhines also share plesiomorphic AOS anatomy, including the presence of a functional VNO, AOB, and a rhinarium irrigated by a horizontally oriented nasolacrimal duct. Tarsiers and platyrrhines exhibit a functional VNO and AOB, but like all haplorhines they lack a rhinarium and share a derived vertical orientation of the nasolacrimal duct (Rossie and Smith 2007). Catarrhines are highly derived among mammals in lacking a functional VNO

and AOB. Comparative data on VNRP genes are limited at present, but suggest that strepsirrhines and tarsiers exhibit a large number of intact VNRP genes, while anthropoids have lost functionality of most VNRP genes (Young et al. 2010). Reports that marmosets have relatively few functional VNRP genes contrast with the presence of a functional VNO in platyrrhines and the known importance of olfactory communication in callitrichine behavioral ecology. Furthermore, despite lacking a functional VNO, most catarrhines appear to express functional VNRPs and a separate class of pheromone receptors

(trace-amine associated receptors, or TAARs) in the MOS olfactory epithelium.

These comparative data suggest that reductions in olfactory functionality have occurred multiple times in primate evolution (see PHYLOGENY). Although the last common ancestor of living primates probably retained MOS and AOS anatomy that is plesiomorphic for Euarachonta, the origin of crown primates may have been associated with a decrease in the number of functional ORP genes and a corresponding decrease in the number of volatile odorants that could be detected. The origin of crown haplorhines was further associated with the loss of a rhinarium and greatly diminished complexity of peripheral MOS structures. Catarrhines have further lost a functional VNO, and anthropoids generally appear to have lost functionality of most VNRP genes. These derived reductions of the haplorhine MOS and AOS suggest that there has been diminished selection to maintain various aspects of olfactory functionality, perhaps associated with the evolution of high visual acuity in anthropoids and routine trichromatic color vision in catarrhines (see SENSORY ECOLOGY: VISION). By contrast, VNRP genes of strepsirrhines have been the target of positive selection (Hohenbrink, Radespiel, and Mundy 2012), and an entire class of VNRP genes (V1Rstrep) has evolved that is unique to the clade (Yoder et al. 2014). These anatomical and genomic comparisons reinforce the impression that olfaction generally plays a greater role in the behavioral ecology (see SOCIOECOLOGY, PHYLOGENY, AND SOCIAL ORGANIZATION) of strepsirrhines than in haplorhines. Compared to other primates, catarrhines may also be generally less reliant on olfaction and more reliant on visual signals in the context of social communication.

SEE ALSO: Anthropoid origins; Brain evolution (primate); Catarrhine origins; Primate genomics; Primate origins

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