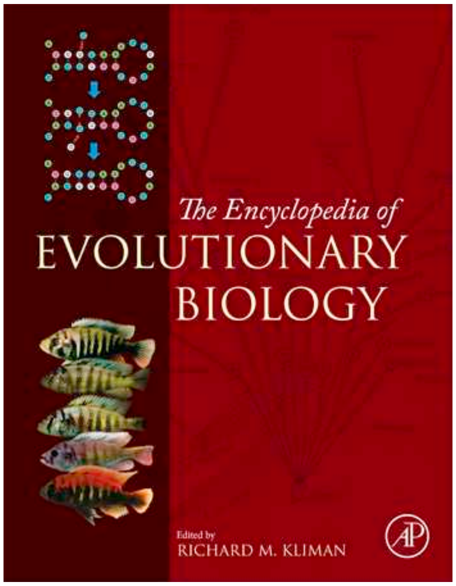

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Sensory Systems: Molecular Evolution in Vertebrates

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Introduction

Vertebrates are a strikingly diverse group occupying a wide variety of niches and environments, some astonishingly extreme. Because distinct environmental conditions pose different selective constraints, natural selection is expected to have influenced sensory evolution, shaping the way vertebrates perceive, interact, and respond to their natural surroundings. This has resulted in extraordinary examples of sensory adaptation, such as electroreception in fishes, thermoperception in snakes, and the echolocation abilities of whales and bats. The last few decades have been particularly fruitful in expanding our knowledge of how different sensory systems are structured and how they operate at the level of genes and proteins. Even more remarkable have been the advances in our understanding of the molecular mechanisms underlying sensory receptor physiology as well as the evolutionary processes driving sensory adaptation in vertebrates. This review summarizes our current knowledge of the molecular underpinnings of the diverse array of sensory systems found in vertebrates.

Photoreception

Amidst the diverse array of vertebrate sensory modalities, vision is among the best understood. At the molecular level, all of the components underlying the visual transduction cascade within the photoreceptors of the eye have been identified in model species. Comparative molecular studies have largely centered on visual pigments, light-sensitive receptors found within the highly specialized rod and cone photoreceptor cells of the retina. Visual pigments are G protein-coupled receptors that form the first step in visual transduction, and mediate vision under different light intensities. They are comprised of an opsin protein covalently bound to a vitamin A-derived chromophore in a region known as the binding-pocket. Upon stimulation by light, the chromophore isomerizes, leading to conformational changes in the opsin structure that initiates a biochemical cascade through activation of the G protein transducin.

Five classes of spectrally distinct visual pigments are present in vertebrates, and there is impressive variation in opsin complement across species (**Figure 1**). While rhodopsin (RH1) is expressed in rod cells and mediates vision under dim-light, up to four classes of opsins (RH2, SWS1, SWS2, and LWS) have been identified in cone cells, which are active under bright-light conditions and ultimately mediate color vision. Interactions between the chromophore and amino acids lining the binding-pocket affect the wavelength of maximal absorbance of a visual pigment, which may be shifted to different wavelengths of light as a result of amino acid substitutions in this region. In vertebrates, it is known that the proportion and number of spectral classes of photoreceptors in the eye, and the wavelengths at which they are maximally sensitive (λmax) can vary enormously (**Figure 1**), and are generally thought to represent adaptations to aspects of the light environment such as spectral composition and light intensity (Bowmaker, 2008).

Visual pigment genes evolved through successive duplications from a single ancestral gene. As a result, four classes of visual pigments were thought to be present in the lineage leading to ancestral vertebrates. *RH1* and *RH2* originated later in the evolutionary history of vertebrates emerging from a duplication event that probably occurred before the divergence of agnathans and gnathostomes (Pisani *et al.*, 2006). While several opsin genes were lost in cartilaginous fishes, visual pigments further diversified in bony fishes following a whole genome duplication (WGD) event. This may have spurred the evolution of additional spectrally distinct pigments, allowing bony fishes to explore more varied, spectrally complex environments, and to evolve in concert with sexually dimorphic coloration. For instance, six distinct copies of *LWS* have been found in the adult guppy (Weadick and Chang, 2007), a model system for the study of sexual selection and mate choice. Neotropical cichlids have a reduced number of cone opsin classes (Weadick *et al.*, 2012) relative to their African sister clade famous for their extravagance and diversity in coloration (Seehausen *et al.*, 2008; Miyagi *et al.*, 2012; Weadick *et al.*, 2012). However, ecological factors associated with spectrally distinct fresh water environments may underlie the evolution of *RH1* in both cichlid lineages (Schott *et al.*, 2014). In contrast, deep-sea teleost and cottoid fishes display a reduced visual pigment repertoire and blue-shifted RH1 pigments that match the wavelengths of available light at extreme depths (Hunt *et al.*, 1996; Hunt *et al.*, 2001).

In tetrapods, opsin genes underwent several major evolutionary events that resulted in extremely diverse distributions among lineages. In amphibians, frogs, and salamanders there persists two classes of rod cells, in which *RH1* and *SWS2* are expressed, whereas *LWS*, *SWS1*, and *SWS2* are expressed in cones (Hisatomi *et al.*, 1998; Hisatomi *et al.*, 1999; Ma *et al.*, 2001). Among reptiles, crocodiles and snakes have a reduced cone opsin repertoire while lizards and turtles have retained all five classes of visual genes. In birds, vision is known to have played an important role in the evolution of colored plumage and social communication. Single photoreceptor cells in birds express all five classes of vertebrate opsins, whereas LWS is also expressed in double cones. Interestingly, certain amino acid residues mediating ultraviolet (UVS) to violet sensitivity (VS) in birds may differ from those in other vertebrates. These amino acid substitutions account for large spectral tuning shifts in SWS1, the short wavelength-sensitive visual pigment, in birds, and have been suggested to underlie shifts from a VS ancestor to UVS in a number of bird lineages (Wilkie *et al.*, 2000; Carvalho *et al.*, 2007; Van Hazel *et al.*, 2013). While the influence of particular single amino acid substitutions mediating UVS and VS sensitivity in birds

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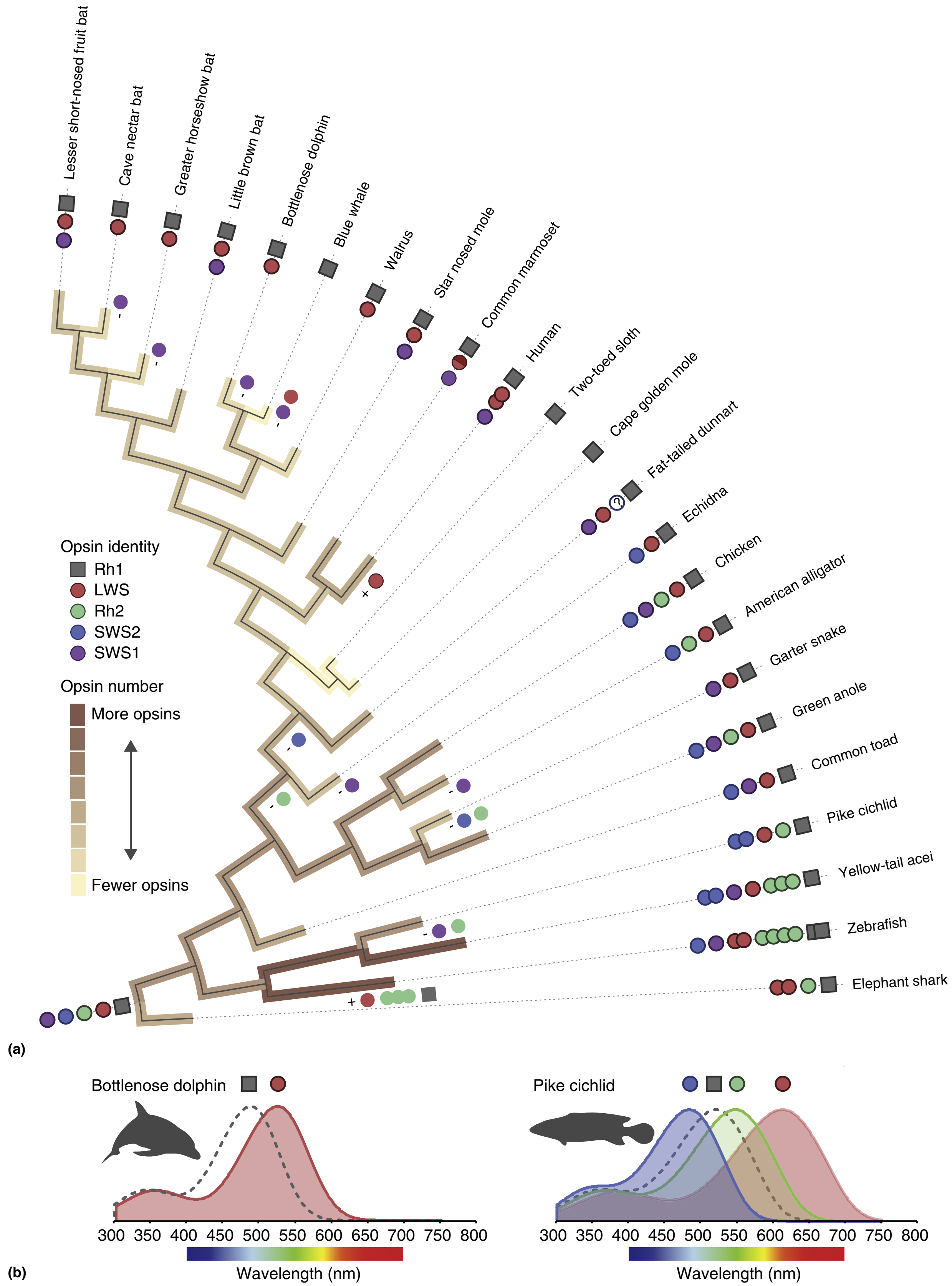

Figure 1 Diversity of vertebrate opsin complements. (a) Phylogeny depicting the gains and losses of specific opsin genes across vertebrate taxa. Branch length and color are indicative of opsin number, and duplications and losses are shown below branches. Cone opsins represented as circles, and rod opsins as squares. Cone opsins with question marks represent the yet-uncharacterized opsin classes, and bicolored cone opsins represent allelic variants providing distinct spectrally sensitive pigments. (b) Spectral sensitivity curves for the bottlenose dolphin (Fasick *et al.*, 1998) and pike cichlid (Weadick *et al.*, 2012).

has been well-characterized, in other vertebrate groups, such as mammals, these substitutions are much more variable and do not predictably shift λmax (Hauser *et al.*, 2014).

Relative to other vertebrates, mammals have a reduced set of opsin genes. While monotremes have functional copies of *LWS* and *SWS2* genes, the majority of marsupials and eutherians have only retained LWS and SWS1 cone pigments (Jacobs, 2009). Intriguingly, a third class of spectrally distinct cones has been identified in some Australian marsupials (Arrese *et al.*, 2002), although the molecular basis of this pigment remains unknown (Cowing *et al.*, 2008).

Within terrestrial eutherian mammals, nocturnality appears to play an important role in the evolution of visual pigments, particularly the *SWS1* gene, which has become pseudogenized in many nocturnal carnivores and nocturnal primates. Curiously, bats, which have long occupied the nocturnal niche, exhibit a complex distribution of the *SWS1* gene; though it is functional in most microbats, *SWS1* became pseudogenized in some megabats and a few related microbat lineages, likely as result of the evolution of refined high-duty cycle (HDC) echolocation as well as cave-roosting behavior (Zhao *et al.*, 2009a). Interestingly, RH1, which mediates dim-light vision, does not appear to have undergone adaptive evolution in bats as a consequence of the photic limited niche, although convergent evolution has occurred between lineages of highly visual bats (Shen *et al.*, 2010; Zhao *et al.*, 2009b).

Remarkably, subterranean eutherian mammals also exhibit variable opsin gene repertoires, ranging from the typical mammalian arrangement in the star-nosed mole to only a functional *RH1* copy in the Cape golden mole (Emerling and Springer, 2014). Nevertheless, a number of visual genes have become pseudogenized in phylogenetically distant lineages, which likely occurred after those lineages invaded subterranean environments (Emerling and Springer, 2014). In contrast, xenarthrans (armadillos, sloths, and anteaters), which diverged very early in the eutherian lineage and occupied a variety of ecological niches, have nonfunctional *SWS1* and *LWS* genes, probably the result of a subterranean lifestyle in the early history of the group (Emerling and Springer, 2015).

Aquatic environments are also thought to have shaped visual pigment evolution in mammals. Pinnipeds and cetaceans have independently lost functional *SWS1* genes, possibly due to relaxation of selective constraints (Levenson *et al.*, 2006). *LWS* is also pseudogenized in most baleen whales and in some deep-diving toothed whale lineages whose representatives inhabit depths in which light is dim and dominated by short-wavelengths (Meredith *et al.*, 2013). Curiously, the RH1 pigment is blue-shifted in most cetacean species (Bischoff *et al.*, 2012), showing functional variation that is likely associated with diving depth.

Unlike the majority of mammals, diurnal primates have regained a middle-wavelength sensitive (MWS) class of cone opsin through evolutionary modification of the *LWS* gene. While this occurred through gene duplication in Old World primates (Nathans *et al.*, 1986), in New World primates it evolved through a polymorphism of the *LWS* gene by allelic variants on the X-chromosome (Williams *et al.*, 1992). Thus, MWS is present in both male and female Old World monkeys, whereas only heterozygous female New World monkeys have a copy of the MWS pigment (Bowmaker, 2008). Opsin polymorphism linked to the X-chromosome has also been identified in diurnal and cathemeral prosimians (Jacobs *et al.*, 2002; Veilleux and Bolnick, 2009). Remarkably, MWS also evolved in Neotropical howler monkeys (Jacobs *et al.*, 1996), though through unequal crossover that allocated two different alleles of the polymorphic New World gene onto a single chromosome (Hunt *et al.*, 1998). Although the adaptive significance of a three-cone opsin system remains unclear, many have argued that it improves the detection and assessment of ripe fruits (Sumner and Mollon, 2000a,b), new leaves (Dominy and Lucas, 2001), and predators (Pessoa *et al.*, 2014) through a better discrimination of red and green signals.

Chemoreception

Odorant Perception

Although not as well studied as vision, the molecular mechanisms of odorant perception are starting to be revealed in detail. Three classes of odorant GPCRs have been identified in vertebrates: olfactory receptors (OR), vomeronasal receptors (V1R and V2R), and the recently discovered trace amine associated receptors (TAAR). Typically, ORs are expressed in the main olfactory epithelium (MOE), and are activated by volatile odorant molecules that enter the olfactory cavity, whereas VNRs are expressed in the vomeronasal organ (VNO) and respond to social odors such as pheromones (Niimura, 2012). The recently identified TAARs are also expressed in the MOE and have the ability to recognize volatile amines present in urine and molecules linked to stress (Liberles and Buck, 2006).

Olfactory receptors

Compared to other sensory receptors, which are tuned to respond to a specific stimulus, OR function in a combinatorial manner: multiple ORs may be sensitive to a single odorant or a single OR may detect multiple odorants. This makes the study of olfactory mechanisms very complex. Two types of ORs have been identified in vertebrates and are predicted to detect odorants with different chemical properties. While ORs that respond to water-soluble molecules are present in fishes and amphibians, ORs sensitive to airborne components have diversified predominantly in tetrapods. Interestingly, amphibians also exhibit a particular group of ORs that likely detect odorants that dissipate both in the air and water, such as alcohols (Niimura, 2012).

In mammals, *OR* genes form a surprisingly high proportion of the genome, but also contain a great deal of pseudogenization. It is broadly accepted that the numerous families of *OR* genes evolved through the process of birth-and-death evolution, in which gene duplication followed by mutation may result in fixation or deletion in the genome, varying the number of functional genes as well as pseudogenes (Nei *et al.*, 2008). Interestingly, expansion and retraction of the mammalian *OR* gene repertoire is thought to be closely associated with ecological factors. For instance, mammals that occupy similar ecological niches but are phylogenetically distant exhibit similar patterns of contraction or expansion of the OR gene families, such as in aquatic, terrestrial and flying groups

(Hayden *et al.*, 2010). Among bats, several *OR* gene families have been linked to frugivory in New World and Old World lineages, indicating another example of niche specialization in the *OR* gene repertoire (Hayden *et al.*, 2014). Primates, on the other hand, have *OR* gene repertoires that are markedly reduced compared to other terrestrial mammals, which has been linked to a trade-off between olfaction and the presence of three classes of cone opsins in some lineages (Gilad *et al.*, 2004; but see Matsui *et al.*, 2010).

Vomeronasal receptors

Unlike ORs, vomeronasal receptors are encoded by only two multigene families, *V1R* and *V2R*, and play an important role in pheromone detection. Upon activation, V1Rs and V2Rs couple with specific G proteins, which leads to the opening of TRPC2 channels, ultimately resulting in signal transduction (Nei *et al.*, 2008). While VNRs are expressed in the vomeronasal system, which is exclusive to tetrapods, genes of the vomeronasal-signaling pathway are expressed in the olfactory epithelium of fishes (Grus and Zhang, 2006).

V1R genes and *Trpc2* genes evolved early in the vertebrate lineage and are less diverse compared to *V2R* genes, which originated after the divergence of agnathans and gnathostomous (Grus and Zhang, 2009). Though *V1R* genes are under strong purifying selection among several fish lineages, sites at putative ligand-binding regions are under positive selection within African cichlids, suggesting an adaptive function of V1Rs for reproductive behavior or social communication (Nikaido *et al.*, 2014). Contrary to *V1R*s, *V2R* genes are much more diverse in teleost fishes and play important roles in feeding behavior and social communication. Although the ligand-binding region of V2Rs exhibits impressive sequence variation within several fish lineages, suggesting adaptation to different ligands, studies have failed to detect signals of positive selection, indicating that sequence variation likely emerges from relaxation of selective constraints or genetic drift (Nikaido *et al.*, 2013).

The transition from aquatic to terrestrial environments in tetrapod evolution was followed by the emergence of the VNO resulting in enormous expansion of VNR genes in some tetrapod lineages as well as numerous pseudogenization events in others. Frogs, which have a rudimentary VNO, display the largest *V2R* gene repertoire among tetrapods and only small number of *V1R* genes. In contrast, no *V1R* genes are observed in birds and the VNO is absent (Grus *et al.*, 2005). Within mammals, there is great variation in VNR gene repertoire. Generally, the *V1R* gene family expanded in lineages that exhibit a morphologically complex VNO, such as in monotremes and rodents where adaptive evolution likely contributed to gene diversification. Nevertheless, no functional V1Rs are observed in several bats, cetaceans, and humans, due to pseudogenization of *Trpc2* (Liman and Innan, 2003; Young *et al.*, 2010; Zhao *et al.*, 2011). Although most *V1R* genes also became pseudogenized in Old World monkeys, several functional copies are observed in New World monkeys and are even more numerous in prosimians. Interestingly, sites at the ligand-binding region of V1Rs in prosimians are under strong positive selection, indicating adaptation of the *V1R* gene repertoire and emphasizing the ecological importance of the VNS in this primate lineage (Hohenbrink *et al.*, 2012; Yoder *et al.*, 2014). Comparatively, *V2R* genes are less diverse and became pseudogenized in several mammalian lineages, likely through relaxation of selective constraints (Shi and Zhang, 2007).

Gustatory Perception

Taste receptors (TRs) are encoded by two multigene families that are in close phylogenetic proximity to *VNR* genes. TRs are expressed in cells located in taste buds on the tongue and palate and respond to organic compounds associated to the perception of sweet, umami (savory), and bitter taste. Similar to other GPCRs, stimulation of TRs mediates the activation of receptor-specific G proteins, leading to a biochemical cascade that ultimately results in the gating of a transduction channel, in this case TRPM5 (Chandrashekar *et al.*, 2006). Conversely, the perception of salty and sour taste is mediated by direct entry of Na^+ and H^+ in taste receptor cells (TRC) through specific ion channels, although molecular mechanisms underlying these gustatory modalities have just begun to be elucidated (Liman *et al.*, 2014). While great variability in TRs is observed among vertebrates, shifts in gene copies numbers, and pseudogenization of *TR* genes generally reflect adaptation to ecological niches and diet, as a way to better assess the quality and nutritional value of food.

T1Rs mediate the perception of umami and sweet taste through different sets of heterometric receptors. Subunits T1R1 and T1R3 form a receptor that detects L-amino acids and nucleotide enhancers (IMP, GMP, AMP), which are perceived as a savory taste known as umami (Nelson *et al.*, 2002), whereas the T1R2 + T1R3 heterodimer responds to simple sugars, artificial sweeteners, and D-amino acids, mediating sweet taste (Nelson *et al.*, 2001). *T1R* genes evolved in the ancestor of cartilaginous and bony fishes, along with the taste-transduction channel gene *Trpm5*. Whereas T1R1 and T1R3 are encoded by single copy genes in bony fishes, T1R2 further diversified through multiple gene duplications (Shi and Zhang, 2006). Interestingly, sites at ligand-binding region of T1R2 are positively selected, indicating that the duplicate genes likely adapted to respond to different tastants (Hashiguchi *et al.*, 2007). Relative to fishes, great divergence is observed in *T1R* genes among tetrapods. Amphibians, for instance, have lost all *T1R* genes and detection of amino acids is mediated by V2Rs, whereas *T1R2* genes were lost in all avian lineages, resulting in inability to perceive sweets (Shi and Zhang, 2006). Intriguingly, this ability was recovered in nectar-eating hummingbirds. In this group, the T1R1 + T1R3 umami receptor has been repurposed by substitutions at the ligand-binding domain of the T1R3 subunit, acquiring a new adaptive function (Baldwin *et al.*, 2014). Similarly, diet specialization and diverse ecological niches act as strong selective pressures on the evolution of T1Rs in mammals. The giant panda is related to carnivorous bears, but lacks the ability to perceive amino acids through umami receptors due to pseudogenization of *T1R1* gene, which occurred concomitantly to a dietary switch to bamboo in the evolution of the species (Zhao *et al.*, 2010b), though other molecular adaptations might also be involved in diet specialization in pandas (Jin *et al.*, 2011). Conversely, *T1R2* became pseudogenized in several carnivores, rendering them unable to detect carbohydrates, which is likely a result of a dietary specialization to obligatory carnivory (Jiang *et al.*, 2012). Curiously, *T1R2* has also undergone pseudogenization in hematophagous bats (Zhao *et al.*, 2010a), and loss of umami taste is widespread among bats, regardless of diet (Zhao *et al.*, 2012). The most striking example of gustatory loss is observed in sea lions and cetaceans, in which feeding behavior and niche specialization contributed to relaxation of selective constraints, resulting in pseudogenization of all *T1R* genes (Jiang *et al.*, 2012; Feng *et al.*, 2014; Zhu *et al.*, 2014).

Unlike other chemosensory receptors, several *T2R* genes are expressed at different levels in a single TCR, rendering taste cells sensitive to a variety of bitter molecules, which maximizes the ability to detect potentially harmful substances, characterized by bitter taste (Yarmolinsky *et al.*, 2009). Compared to T1Rs, T2Rs originated much later in the evolution of vertebrates, just before the divergence of teleosts and tetrapods, in which T2Rs became more diverse through lineage-specific gene duplications (Grus and Zhang, 2009). Amphibians, reptiles, and mammals have large *T2R* gene repertoires, though fewer copies are observed in some avian lineages (Dong *et al.*, 2009). Interestingly, T2Rs in some birds are broadly tuned to a variety of agonists, which compensates for the low diversity of bitter receptors (Behrens *et al.*, 2014). Within mammals, reintrogression into aquatic environments accompanied by a switch in feeding ecology led to pseudogenization of *T2R* genes in sea lions (Jiang *et al.*, 2012) and cetaceans (Jiang *et al.*, 2012; Feng *et al.*, 2014; Wang *et al.*, 2014). In terrestrial mammals, diet plays a major role in the evolution of T2Rs. Herbivorous and omnivorous mammals generally exhibit a larger *T2R* repertoire compared to carnivorous mammals, as a way to detect harmful bitter tasting compounds in plants. However, a large proportion of the *T2R* repertoire of cows and horses became pseudogenized, likely the by-product of extensive artificial selection in these lineages (Dong *et al.*, 2009).

Auditory Perception

Prestin (SLC26A5) is a voltage-sensitive membrane protein expressed in the outer hair cells (OHC) of the auditory system that underlies hearing sensitivity and frequency range through amplification of signal input. This is particularly relevant for bats and whales, in which the ability to acoustically sense the environment, known as echolocation, convergently evolved. The *Prestin* gene has undergone parallel evolution in echolocating bats and continued to undergo adaptive selection in the lineage leading to the more derived HDC echolocating bats (Li *et al.*, 2008). *Prestin* is also thought to have undergone adaptive evolution in toothed whales, suggesting that adaptive changes in *Prestin* are linked to the evolution of echolocation in this group (Liu *et al.*, 2010b). Remarkably, it appears that *Prestin* evolved convergently in HDC bats and echolocating cetaceans, as result of strong selective constraints to detect high-frequency sounds in both lineages (Li *et al.*, 2010; Liu *et al.*, 2010a). More recently, substitutions at two amino acid sites have been identified as critical for functional convergence among high-frequency echolocating mammals (Liu *et al.*, 2014). In addition to *Prestin*, several genes involved in OHC function (*Kcnq4*, *Pjkv*, *Cdh23*, *Pcdh15*), maturation (*Tmc1*) and signal transduction (*Otof*) also experienced adaptive selection and convergent evolution in echolocating bats and dolphins to account for high-frequency hearing (Liu *et al.*, 2011; Davies *et al.*, 2012; Liu *et al.*, 2012; Shen *et al.*, 2012a).

Electroreception and Electrogenesis

The ability to detect electric fields is conferred by electroreceptors, which exhibit a complex pattern of evolution across vertebrate lineages and achieved greater specialization following the evolution of the electrogenic organs in some taxa. Electroreceptors transduce electric signals into action potentials that are processed in the central nervous system, and can convey information of relevance for social communication, navigation, hunting, and defense (Albert and Crampton, 2005). Electroreceptors evolved in the common ancestor of all vertebrates as a submodality of the lateral line system, which also encodes mechanosensory information in fishes and amphibians through specialized neuromast hair cells. In some amphibians, cartilaginous fishes, and non-teleost bony fishes, electroreceptors are organized into ampullary organs that respond to passive low-frequency environmental electric fields (Jørgensen, 2005).

Electroreceptors were lost in amniote and teleost fish ancestors. Air is a poor conductor of electricity, explaining the absence of electroreceptivity in terrestrial taxa. Within amniotes, electroreception was independently regained in aquatic monotremes and river dolphins through neofunctionalization of mechanosensory organs (Pettigrew, 1999; Czech-Damal *et al.*, 2012). Multiple lineages of teleost fishes have independently regained electroreception. In two orders of electrogenic fishes, the South American Gymnotiformes and African Mormyriformes, a sophisticated electrosensory system is mediated by a second class of tuberous electroreceptors. These electroreceptors are sensitive to the higher frequency of self-generated electric fields, enabling fishes to covertly communicate and navigate using electric fields. The waveforms of the electric organ discharges (EODs) vary substantially across gymnotiform and mormyriform species. Avoidance of electroreceptive predators and sexual selection have likely contributed to the evolution of EOD diversity (Stoddard, 1999; Crampton *et al.*, 2013).

The waveform of an EOD is modulated by the rate of depolarization and repolarization of the stacked electrocyte cells forming the electric organ, which is in turn controlled by ion channels lining the anterior and posterior faces of each individual cell. The *scn4aa* and *scn4ab* genes (duplicates of the mammalian *Scn4a* gene), respectively encode the sodium channel proteins Nav1.4a and Nav1.4b, which play a role in determining properties of the EOD (Ferrari *et al.*, 1995). In most teleost fishes, *scn4aa* and *scn4ab* are expressed in muscle; however, in most Gymnotiformes and Mormyriformes, *scn4aa* is exclusively expressed in the electric organ (**Figure 2**; Zakon *et al.*, 2006). This phylogenetic pattern of expression is accompanied by increased rates of molecular evolution and elevated dN/dS values in *snc4aa* from electrogenic fish lineages (**Figure 2**; Arnegard *et al.*, 2010), likely due to natural selection associated with diversification of EODs. Sites found to be positively selected in these lineages likely affect the kinetics of channel activation and inactivation, and

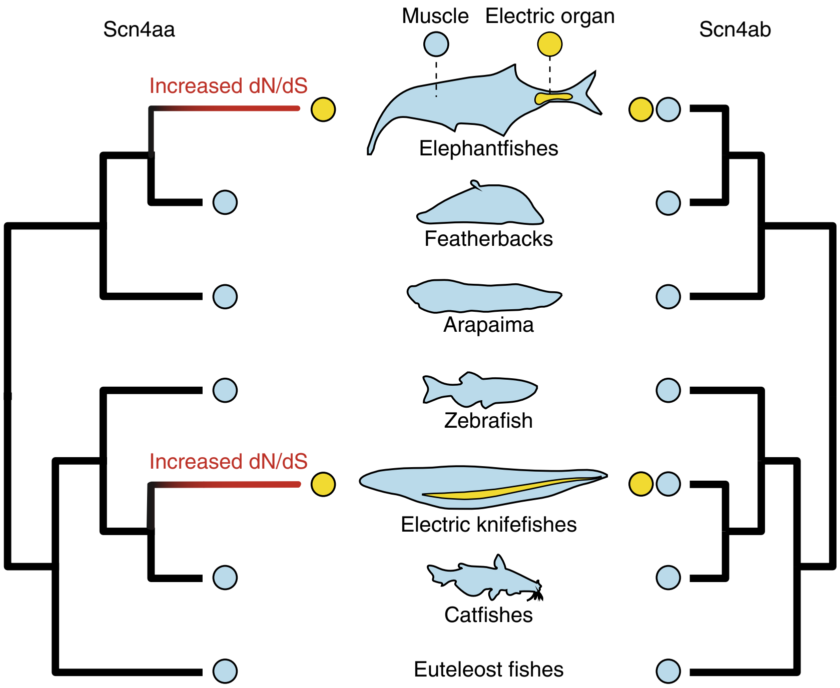

Figure 2 Expression of *scn4aa* and *scn4ab* in teleost fishes. Branch lengths and color are schematic representations of nonsynonymous to synonymous rate variation. Blue and yellow circles identify tissue type where the *scn4a* gene is expressed. Based on data presented in Zakon *et al.* (2006).

thereby EOD waveform parameters. Thus, convergent neofunctionalization of a duplicated sodium channel gene likely contributed to the evolution and diversification of independently derived electrosensory systems.

Thermoreception

The TRP superfamily of ion channels, expressed in neurons of the somatosensory system, responds to temperature changes in peripheral tissues. Remarkably, some *TRP* genes have gained a new function in specialized organs on the faces of snakes and bats, conferring infrared sensing abilities that are crucial for food acquisition. The TRPA1 calcium channel, expressed in the pit organs of snakes, detects infrared radiation, which is transduced into electric signals that are processed in the optic tectum, resulting in a 'thermal vision' (Gracheva *et al.*, 2010). This ability evolved independently in pythons, boas, and venomous snakes through adaptive selection of sites at different domains of the TRPA1 channel, becoming crucial for prey detection and predator avoidance (Geng *et al.*, 2011). Interestingly, infrared perception also evolved in vampire bats, though through a different mechanism. In the leaf pit organs located on the face of vampire bats, a shorter splice variant of the *Trpv1* gene is expressed. TRPV1-S is truncated at the C-terminus end, lowering the threshold to which the leaf pits respond, allowing vampire bats to detect areas where blood flows closer to the skin (Gracheva *et al.*, 2011).

Concluding Remarks and Future Research

Studies throughout the last decade have greatly developed our understanding of the diverse molecular mechanisms underlying the remarkable sensory adaptation observed in vertebrates. This outstanding progress has been particularly fruitful in identifying molecules that act as sensory receptors responsible for transducing a variety of environmental stimuli into neural signals that ultimately result in physiological and behavioral responses. Interestingly, the nature of vertebrate somatosensory mechanoreceptors that mediate our sense of touch remains largely puzzling, although much progress has been made in invertebrates (Schuler *et al.*, 2015). It is also important to note that although vision and particularly visual pigments have been studied in a comparative context (Shen *et al.*, 2012b; Lin *et al.*, 2013; Shen *et al.*, 2013; Emerling and Springer, 2014; Emerling and Springer, 2015), other sensory systems have not received the same degree of attention, and remain largely understudied from a molecular evolutionary perspective. The recent developments in next generation sequencing technologies provide an unprecedented opportunity to not only identify candidate genes that may play a role in sensory transduction pathways (Gracheva *et al.*, 2010, 2011; Gerhold *et al.*, 2013), but also to expand our understanding of the complex mechanisms underlying vertebrate sensory perception. Finally, future research should also be devoted to the intricate interactions among different sensory systems, many of which have likely coevolved to result in the exquisite examples of sensory adaptation observed in nature.

See also: Genome Organization, Evolution of. Systems in Evolutionary Systems Biology

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