Species-Specific Duplications of Trace Amine-Associated Receptors in Vertebrate Genomes
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Chemosensory receptors (CRs) are used to detect a wide range of chemicals and are a crucial gateway between perception and environment. Expansion or loss of CRs would reflect the adaptation to the organism's life at the molecular level. Life-history traits such as foraging behavior and type of foods are expected to play a central role in driving variation in the number of CRs. Evolution of CRs may also be correlated with that of other detection functions (e.g., vision and audition). CRs, especially the olfactory receptors (ORs), represent the largest gene family in animal genomes (Nei et al., 2008). Vertebrate ORs are predominantly expressed in the main olfactory epithelium (MOE) in the nasal cavity. Interestingly, Liberles and Buck (2006) demonstrated that mouse Trace Amine-Associated Receptors (TAARs) are also expressed in the MOE and can function as ORs for volatile amines found in urine. TAAR-expressing olfactory sensory neurons could be involved in the detection of social pheromone cues such as β-phenylethylamine, isoamylamine, and trimethylamine that elicit innate behaviors. In order to examine how the number of TAARs varies among vertebrates and elucidate the evolutionary history of these proteins, we identified all TAARs from twenty two vertebrate genomes. We found that the number of TAAR genes is much smaller than the number of ORs. On the other hand, extremely large variation in the number of TAARs among vertebrate species was observed. For example, while the megabat (Pteropus vampyrus) genome carries the largest number of TAARs (26 genes and 10 pseudogenes) among the mammals we studied, the dolphin (Tursiops truncatus) genome has no TAAR gene (3 pseudogenes). The chicken and lizard (Gallus gallus and Anolis carolinensis) genomes have also smaller numbers of TAAR genes (4 and 3, respectively). The numbers of TAARs in this study showed 13-fold difference among the tetrapod mammals, ranging from 2 in dog to 26 in megabat. This range is much larger than that of OR genes, which showed only 4-fold difference, from ~326 in macaques to 1,259 in rats (Nei et al., 2008). Gene duplication has been counted as a major mechanism in molecular evolution. We found that four TAAR paralogs (TAAR6, TAAR7, TAAR8, and TAAR9) are characterized with recent and extensive tandem duplications. For instance, the gene duplication rate of TAAR7 in rat is 0.043 (duplications per gene per million years), which is 16 to 33-fold higher than their average gene duplication rate (0.0013 - 0.0026 per gene per million years; Gibbs et al., 2004). Although many of the GPCR families are characterized with gene duplication and divergence, TAARs show the case of extreme. All TAARs identified in this study form a monophyletic clade and are clearly distinguishable from other biogenic amine receptors. Although TAARs are regarded as a second class of ORs, their sequences are similar to classical biogenic amine receptors but not to ORs. Two TAARs are present in the elephant shark genome (Callorhinchus milii). A lamprey, two tunicates, and a lancet genomes do not contain TAARs, although they have biogenic amine (serotonin) receptors. Therefore, the origin of TAARs seems to be traced back to the common ancestor of jawed vertebrates (cartilaginous fishes). The pairwise distances calculated from CRs are normally distributed except for TAARs, whose distribution is bimodal (P < 1 × 10⁻⁶) implying that TAARs are highly conserved among orthologs but diverged between paralogs. While ORs are scattered among many chromosomes, the TAARs and other adjacent genes are located in a gene cluster in vertebrates. The syntenic relationships of these genes are highly conserved among vertebrates, although the order is inverted in mammalian.

References