NDC E-BIOS (Online) Volume 4, pp - 82-99, (2024) ISSN: 2583-6447
DOI: https://doi.org/10.5281/zenodo.15817391

REVIEW ARTICLE

SEMIOCHEMISTRY IN HIGHER ANIMALS: PERCEPTION AND EXPRESSIVE PHYSIOLOGY

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Abstract: *Odor biology has accomplished conformist role in shaping co-evolution of plant-animate existence of the planet ensconced upon inter communicating linkages other than audio-visual reciprocation. Semiochemicals comprising significant fractionation of Volatile Organic Compounds (VOCs) constitute pool of natural odor be classified as pheromones and allelochemicals with subclasses. Objective of the review lies in pointing out brief insight of the formative and transducing mechanism for conventional plant originated volatile molecules (not aiding the purpose of sex) in higher animals and manifestation of inhalation in their physiological kinesics emphasizing onto cat (Felis catus) attractant molecules from various plant families discovered till present along with comparative behavioral analysis. The illustrative methodology of olfaction in vertebrates and higher brain structure for semiochemicals of plant origin frame the distributary pathways of odorant perception via main olfactory bulb for conventional VOCs and accessory olfactory organs like vomeronasal organ (VNO) for pheromones entrusting G-protein coupled receptor (GPCR) dependency especially in mammals. The numbers of intron-less coding sequences for olfactory receptors (OR I and OR II) considerably reduces in high end mammalian evolutionary stem leading to pseudogene constitution. The decade old story of distinct behavioral concoction found in subfamilies of Felidae with response to cis- trans configured active compound (Nepetalactone) from the genus Nepeta and matatabilactone, actinidine like hallucinogen from species other than Nepeta was correlated with recent discovery of prolonged drug like response of cat to iridoid compounds (Isodihydronepetalactone and isoiridomyrmecin) and seven Gas-Chromatography (GC) identified Non-steroidal anti- inflammatory drug (NSAID) compounds from non-aerial portion of Acalypha indica plant. With the analysis of unit behavioral aspect elaborated in literature and performed bioassay, it was found that though the reactive function to the latter was analogous to 'catnip response', the exact pathway for olfactory signal transduction yet not clear especially for character like the genital licking which was not found earlier and also the same to be tested for other members of Felidae as well to draw the continuum.*

Key words: Semiochemicals, conventional VOCs, olfaction, GPCR, catnip response, *Acalypha indica*, NSAID

Communicated:18.06.2024 Revised:30.08.2024 Accepted:15.09.2024

1. INTRODUCTION

Following chemotactic principle of motility for survival in living kingdom, Semiochemicals have established a pool of informatory molecules carrying high end potentiality for intraspecific and interspecific communications panning wide range of species in the ecosystem. The mechanism of signaling by producing chemical attractant or deterrent establishes a third channel for plant-plant, plant-animal or animal-animal interaction beyond audiovisual trajectory of responsiveness. Semiochemicals could be classified in broader groups of Pheromones (intraspecific) and allelochemicals (interspecific) where in the latter be sub-grouped further into Allomone, emitter friendly and Kairomone, receiver friendly in nature [1]. Many-a-times, these signaling molecules are volatile in nature with low-molecular weight and comprises considerable percentage of Volatile Organic Compounds (VOCs). The science of odor has shaped wide array of communication taking from host-parasite interaction, induction of behavioral changes in pollinator insects and aphids, direct and indirect defense mechanism in plants, pest controlling agriculture [2] to mother-child interrelation, acceleration of puberty and block pregnancy, mediating as mighty sex attractant in higher animals [1], which contributed in structuring plant-animal co-evolution since time immemorial framing the ecological skeleton. Though the scientific repository provides illustrative studies on insect behavior in response to chemical signals from plants, such studies are less in comparison in case of higher animals or mammals in particular. Deterrent effect of monoterpenes like camphor and α-pinene on *Flourensia cernua* DC (tarbush) pellet consumption by sheep explained differential herbivory impacted by individual volatile compound or amalgamated form produced by shrubs [3, 4]. The study comprised of spraying selected chemicals such as α-pinene, camphor, limonene, cis-jasmone, β-caryophyllene and borneol individually on Alfalfa pellets for sheep consumption. Long back, induction of P450 oxidases in rat was established with response to α-pinene and borneol [5]. Probably such exclusive detoxification mechanism retained monoterpene consumption "Generally Recognized as Safe" for the mammals while toxic to insect community [6]. However, Estell's study revealed production of few leaf monoterpenes led to differential use of Alfalfa in selection of diet by the ruminants. Deviated adaptive mutualistic behavior of few *Nepenthes* sp. from simple carnivorous food habit have been shown just to accommodate the need of specific vertebrate species revealing unpredicted avenue for plant-animal coevolution [7]. *Nepenthes hemsleyana*, found in low land forest of Brunei Darussalam has developed alternate pitcher with elongated tube and low-level fluid to provide roosting space for *Kerivoula hardwickii* (woolly bats) [8, 9]. Similarly, *N. lowii* produces white jelly-like secretion that attracts *Tupaia montana* (tree shrews) [10]. Also, it has been reported that *N. rajah*, another *Nepenthes* species of higher mountain has been adopted itself to successfully capture faeces of *T. montana* and *Ratus baluensis* (summit rats) in its pitcher by virtue of their positioning while accessing the nectar [11,12]. The story of cat attracting plant *Nepeta cataria* is well known to humanity for decades. Such behavioral attribute called "catnip response" has been proved to be a manifestation of Nepetalactone, an insect repellent as the first identified cat attractant chemical from the plant reported but without performing bioassays [13]. Later an unpublished research work [14] reported a group of lactones containing epinepetalactone, iridomyrmecin, neonepetalactone, isodihydronepetalactone, dihydronepetalactone and isoiridomyrmecin along with nepetalactone itself eliciting such response in domestic cats. This interesting plant-mammal interaction indulged many researchers in recent time to investigate if any other cat attractant plant present in nature.

Figure 1. tree shrew (*Tupaia minor*) collecting nectar from the lower lid surface of *Nepenthes gracilis* pitchers [7] with a gesture of positioning their faeces inside the altered designed pitcher.

Mechanism of olfactory transduction for general odorants

Science of olfaction constitute an obvious pathway of plant-animal coevolution by means of odor perception mediated by transducers and amplifying receptors. Plant odorants are integral component of semiochemistry though their mechanism of functionality differs in the range of animal taxa. Plant-pollinator relationship was well established conventionally as a derivative of odor biology [15] where it is indispensable to manifest important life cycle phenomena sometimes involving volatile semiochemicals of floral microbiome too, aiding the methodology of perception for insect community [16] but the nitty gritty for complex processing of any plant originated odorant in higher brain structure of the vertebrates and its expressive concoction brings the nuance in the study. In mammals, such perception of plant volatile ligand is occurred by Odorant Receptors (ORs), the largest family of heptahelical [17, 18] G-protein coupled receptor that spans the epithelial layer of Olfactory Sensory neurons (OSNs) in the posterior nasal cavity and is responsible for strong olfactory activity in mammals by converting chemical information into electric impulse and opening of nonselective cation channels with production of cyclic AMP (cAMP) pool [19] and neuron depolarization [20]. OSNs are bipolar neurons with dendritic end in nasal cavity and axon in olfactory bulb of higher brain [21, 22]. Odorant Binding Proteins (OBPs) containing lipocalins with β- barrel foldings [23] play significant role in passive transportation of hydrophobic odorant ligands through epithelial mucus layer by formation of OBP-odorant (ligand) complex [24] that selectively detected by olfactory neurons [25-27]. Whereas the epithelial activity of OSNs is an established hypothesis of first line response for smell sensitization in higher animals especially in mammals [28, 29], many advanced studies have demonstrated the chemosensory process to be more complex and tightly regulated [30, 31]. Trace amine-associated receptors (TAAR) expressed on olfactory epithelium are able to sensitize odorants containing volatile amines [32], similarly some members of guanylyl cyclase D(GC-D) expressing OSNs [33, 34] of dorsal olfactory bulb (OB), sensory neurons in the septal organ (SO) of nasoplatine duct [35, 36], mature Grueneberg ganglion (GG) of olfactory bulb (OB) expressing olfactory marker protein are functional instruments [37] for odor discrimination from the natural pool.

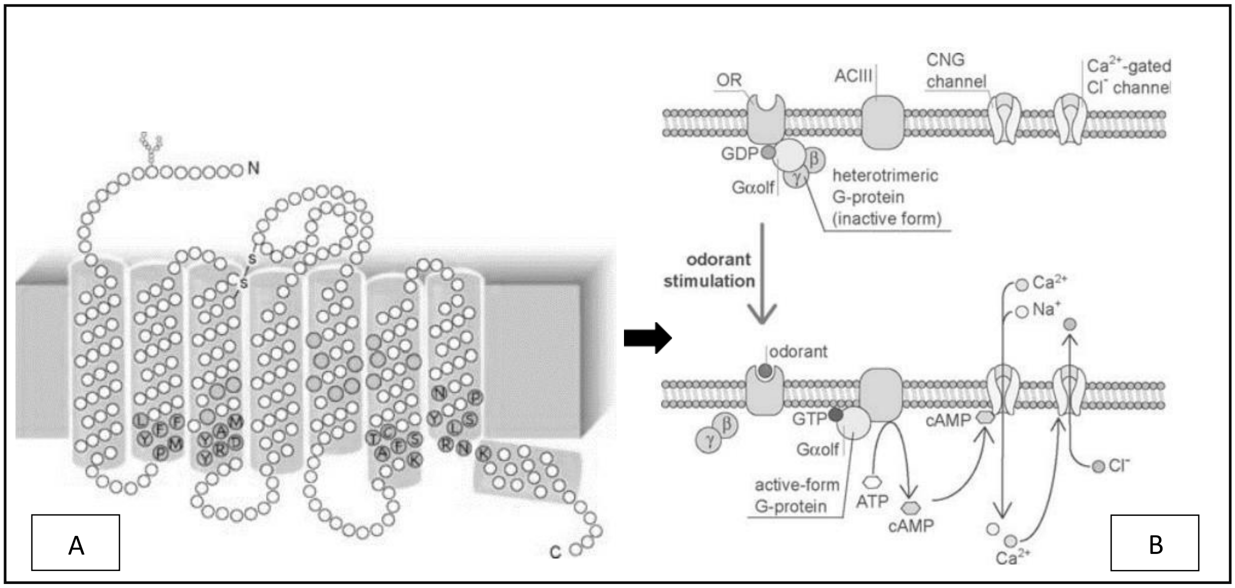

Figure 2. Canonical pathway of olfactory signal transduction in OSNs[B] via activation of heptahelical Olfactory Receptors [B] spanning posterior nasal cavity of mammals [22].

Table1. Cell signaling pathways responsible for transduction of some common plant originated volatile molecules [48]

Sl No.	Plant Volatiles (VOCs)	Source Plant	Regulator Pathway After Detection
1	Zerumbone	*Curcuma zerumbet*	• Downregulating hedgehog (Hh/GLI) signaling pathway • Upregulating TNF-related apoptosis-inducing ligand pathway • Interference in NF-κB signaling Pathway
2.	Phytol	Common plants	• Interferon (TNF-β) signaling pathway
3.	β-caryophyllene	Edible plants	• Selectively binds with cannabinoid type-2(CB_2) receptor • Inhibition of toll-like receptor complex CD14/TLR4/MD2 pathway
4.	Carvacrol	Unknown	• Activation of peroxisome proliferator-activated receptor gamma (PPAR-γ) • Downregulation of COX-2 pathway
5.	Thymoquinone	*Nigella sativa* L.	• Active in cyclooxygenase and lipoxygenase activity
6.	D-Limonene	Citrus fruit	• Binds with transient receptor potential melastatin-8(TRPM8) described as prostate cancer marker

Mechanism of olfaction had been well studied for decades in insect model organism *Drosophila melanogaster* [38], worm *Caenorhabditis elegans* [39] and zebrafish *Daniorerio* [40] amongst which insect model attracts highest interest where antennal lobe behaves as equivalent of the Olfactory Bulb to the mammals. Here, both antenna and maxillary pulp [41, 42] containing the sensory hairs called sensilla [43, 44] express Olfactory Receptor Neuron (ORNs) responsible for transduction of chemical information to higher brain structure like protocerebrum [45], therefore, constituting a G-protein coupled receptor (GPCR) independent pathway of scent perception [46]. Despite of bearing absolute different architecture for olfactory receptor organs, higher mammals (human) and insects show commonness in detecting volatile enantiomers of carvone, menthol, D-limonene, α-pinene etc. Similarly, S-(+)-carvone is sensed like caraway whereas R-(-)-carvone is detected like spearmint in human [47]. However, perception of odorants other than VOCs again constitute an GPCR pathway where Vomeronasal Organ (VO) acts as mediator to carry forward chemosensory response from Accessory Olfactory Bulb (AOB) to higher brain structure [21, 22].

2. GENETICS OF ODORANT RECEPTORS

Discovered in rat for the first time with extreme diverse amino acid sequences [49], Olfactory Receptor (OR) genes are also widely dispersed in mammal genome majorly into tandem cluster [50] and are intron less. They are encoded by multigene family ensuring higher diversity and broad distribution [51] except chromosome 18 and Y in mouse [52, 53] and chromosome 20 and X [54]. Depending on sequence and evolutionary track, the OR genes are categorized into two separate classes like OR I and OR II genes. 80-90% OR genes in mammals is made up of class II [55]. Though OR I genes were thought to be able to discriminate water-soluble odorants only with exclusive distribution in catfish [56] and amphibians [57], their presence was reported later in mammals too [58]. These genes contain ~1kb coding region with OR sequence motifs [59]. Number of intact OR genes vary considerably in different mammal species from ~1000 in mouse and ~800 in dog to ~370 in human [59] and those who are unable to code functional OR proteins are termed as OR pseudogenes. However, the olfactory sensitivity in higher animals is much correlated with number of glomeruli present on each Olfactory Bulb rather than total number of intact OR genes in organism [60] and quantity of functional OR gene decreases in higher evolutionary stem [61].

The receptive mechanism of semiochemicals like pheromone by higher group of animals is initiated primarily by G-protein coupled receptors of V1R (Vanilloid type 1 receptor) and V2R (Vanilloid type 2 receptor) on vomeronasal epithelium. While V1Rs expressing $G_{\alpha 12}$ are dominant in the apical neurons of vomeronasal organ, V2Rs are explicitly located in the basal neurons of the same with expression of Gαo subunit. Presence of functional V1R receptors have significantly diminished in higher group of mammal e.g., human genome consists of several V1R pseudogenes except only five functional genes. Dogs are able to perform exceptionally well functioned olfaction with only eight functional V1R genes. Phylogenetic analysis shows both of the gene families emerged to complement the basic olfactory requirements in rodents, however they underwent countable gene losses in carnivores in long run and also multiple mutations in their subfamilies to the level of non-functional pseudogenes [62].

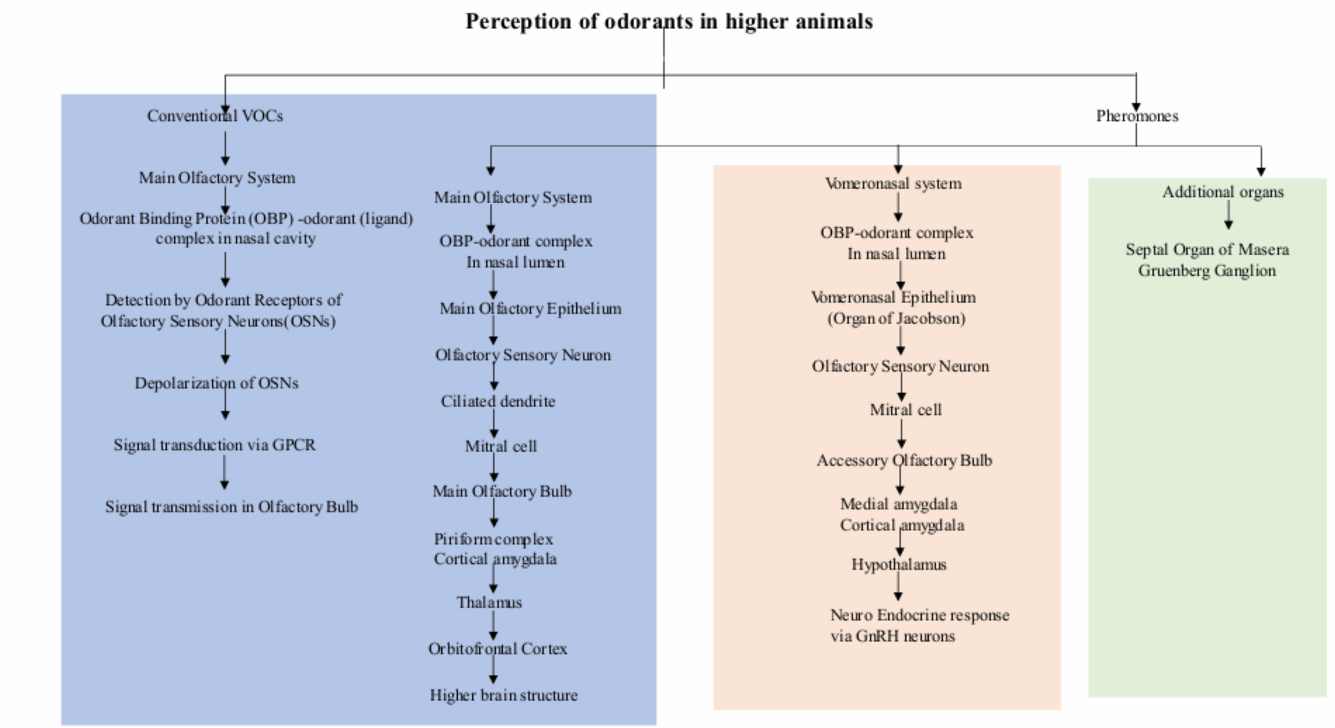

Figure 3. Schematic presentation of olfaction in higher animals [62]. Color blocks represent division of olfaction like Main Olfactory Bulb is involved in transmission of both conventional VOCs and pheromone (blue colored); Vomeronasal Organ (VNO), Septal Organ of Masera (SO) and Gruenberg Ganglion (GG) are involved in olfaction of pheromone (red and green block).

3. BIOSYNTHETIC PATHWAYS FOR CONVENTIONAL PLANT VOLATILES

Unlike plant produced primary metabolites used in growth, development and reproduction, the volatile compounds including semiochemicals comprise major percentage (~1%) of plant secondary metabolites [63] that play significant role in ecological communication. In addition to plants, major metabolic pathways in human, microbes (mVOC) and other animals are also responsible to emit airborne volatile compounds [2]. VOCs are sequestered carbons of lower molecular weight with higher vapor pressure for which cellular membranes of living organism show high permeability [64]. Being lipophilic in nature [63], the resultants of Lipoxygenase (LOX) pathway [48] include release of hydrophilic counterparts, reduction, hydroxylation/oxidation, methylation, acetylation reaction to furnish their biosynthesis [64] and are classified in distinct groups like terpenoids, alkaloids, carotenoids, fatty acid derivatives, phenyl propanoids and several amino acid derivatives. Four pathways namely mevalonate pathway (MVA), shikimate pathway, Methyl erythritol (MEP) and acetate pathway with spatial subcellular localization are responsible for origin of pool of volatile compounds. Amongst them only MEP pathway explicitly marks its presence in plastid with all its enzyme subset [65] that give rise to mainly monoterpenes, hemiterpenes and diterpenes. The MVA pathway considered for development of triterpenes and sesquiterpenes is conventionally localized in cytosol whereas some present study reports its distribution within cytoplasm, peroxisome and endoplasmic reticulum [66, 67]. Both these pathways contribute isopentyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP) [68], the two five carbon isoprene building blocks those units for synthesis of further precursor molecules in the pathway like geranyl diphosphate (GPP) for monoterpenes, farnesyl diphosphate (FPP) for sesquiterpenes and geranylgeranyl diphosphate (GGPP)for diterpenes [69]. The precursors of shikimate pathway originate from pentose phosphate and glycolytic pathway to the formation of Phenylalanine (Phe) for giving rise to phenylpropanoid and benzenoid group of VOCs [70]. Though Phenylalanine formation occurs inside plastid [71], rest of the pathway is localized in cytosol. The group of fatty acid derivative volatile compounds are generated from Acetyl-CoA, the end product from glycolytic pathway through lipoxygenase (LOX) biochemical reactions using 13-Hydroperoxylelonic acid as an intermediate compound [72].

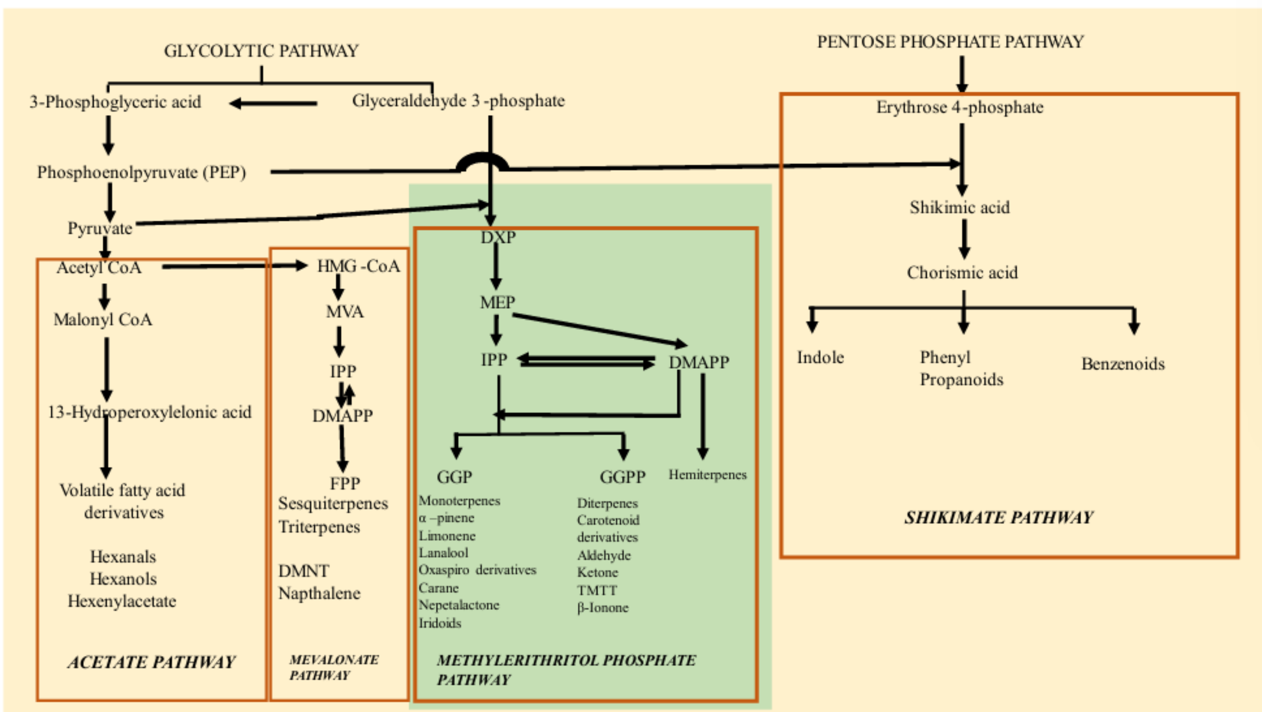

Figure 4. Schematic representation of biosynthetic pathway of plant Volatile Organic Compounds (in brief) with spatial organization in cellular compartments [2, 48, 63] mentioning formative pathways for cat [86, 90] and sheep attractant molecules [3]. Color blocks represent cellular compartments of plastid (green block) and cytoplasm (yellow block)

Figure 5. Hallucinogenic response to non-aerial portion (root) of *Acalypha indica* found in feral cats (*Felis catus*) similar to catnip [86].

4. PLANT-HIGHER ANIMAL COMMUNICATION FOLLOWING THE TERMS OF PLANT ODORANTS

Researches have revealed plant originated volatile compounds establishes direct liaison with stimulated behavioral responses in higher animals. The fundamental and pioneering credit of findings in the direction must go to the discovery of *Nepeta cataria* (catnip) elicited response in *Felis catus* (domestic cat) almost 200 years ago [73]. The term 'catnip responses' include a group of behavioral expression [Table 2] independent of any sexual aspect [74] regulated by autosomal gene. Such kind of response had also been tested in wide range of animals within subfamilies of Felidae for which positive results were found in Pantherinae subfamily only [75] in *Panthera leo* (lion), *Panthera tigris* (tiger), *Panthera pardus*(leopard), *Panthera onca* (Jaguar), *Panthera uncia* (snow leopard) and in *Neofelis nebulosa* (clouded leopard) amongst which lions and jaguars were found to be extremely sensitive to catnip [76]. Chemical study of the plant revealed more than one molecule with cat attracting property, the principal compound being nepetalactone (cis-trans isomer, 70-99.9%) and epinepetalactone (trans-cis isomer, 0.1-30%) of essential oil obtained from catnip [77]. Differential combination of these two molecules was found in other species of *Nepeta* like *Nepeta nepetella* L., *Nepeta sibthorpii* Benth. and *N. hindostana* Haines and also in species other than *Nepeta* like *Actinidia polygama, A. kolomikta, Valeriana officinalis* L., *Teucrium marum* L. *Menyanthes trifoliata* L. and *Menyanthes trifoliata* L. Amongst these cat attractant molecules, matatabilactone, actinidine [78] and many indole compounds were classified as hallucinogens, potent inhibitors of acetylcholinesterase. Amazingly smoking of catnip was found to be pleasurable for human being [79] with a hint of its hallucinogenic effect [Table 2]. The operation of functionality explores that smell is the sole determinant of catnip originated cat attractant behavior where vomeronasal organ is not involved directly in the process [80] but the ventromedial nucleus of hypothalamus was found to be responsible to respond to such olfactory stimulation [81]. Interestingly each unit of 'catnip response' is apparently juxtaposed to sexual or ingestive behavior [82] whereas the removal of amygdala expressed no effect on such response to *Actinidia polygama* [83] suggesting a probable cross-reactive analysis of such response with some sort of naturally originated social odor in the family of Felidae like various glandular secretion and odor of urine and feces [84]. Study in recent decade revealing drug like activity of *Acalypha indica* or Indian nettle root on feral cat introduced a new chapter to the story of plant elicited cat attractant molecules wherein the interesting chemical analysis by the researchers has identified (4R,4aR,7S,7aR)-isodihydronepetalactone and (4S,4aS,7S,7aR)-iridomyrmecin from *Acalypha indica* dried root those matched with prepared synthetic hydrogenated oil from *Nepeta cataria* containing *cis*-fused and *trans*-fused nepetalactone [85]. Also, an Indian patent entitled 'A METHOD FOR ISOLATING THE CHEMICAL COMPOUNDS FROM THE FRESH ROOTS OF *ACALYPHA INDICA* LINN' [86] has identified group of hallucinogenic, anti-spasmatic attractants of cat. Strong olfactory activity is well known in pig for distinguishing social odor, utilizing such recognition for reproduction [87, 88] and also respond to odor from non-social origin has reported [89].

Table 2. Higher animal responses to odor of plant origin

SL No	Molecules	Responses
1.	Odor from Aniseed, Cedarwood, Pine, Thyme, Lavendel, Cinnamon bark, Ginger	Repeated scratching of head and neck, flopping on either side of body with or without rubbing, sniffing in pig. [89]
2.	Alfalfa pellet mixed with volatiles of limonene, jasmone, β-caryophyllene, borneol	Enhancement of consumption by sheep [3].
3.	Smashed leaves of *Nepeta cataria* (catnip) releasing nepetalactone, epinepetalactone, dihydronepetalactone, isodihydronepetalactone, neonepetalactone, 5,9-dehydronepetalactone	Sniffing the odor, chewing leaves, licking with head shaking, body rubbing, head-over and side by side body rolling, paw licking and salivating, scratching soil [90]. In totality these behavioral expressions are called 'catnip response'.
4.	N. *hindostana* Haines (native to India) leaves contain traces of nepetalactone	Excites cat [91]
5.	Leaves and galls of *Actinidia polygama* silver vine) and A. *kolomikta* containing Matatabilactone which is a mixture of iridomyrmecin and isoiridomyrmecin [92], actinidine and beta-phenylethyl alcohol.	'Matatabi' reaction [82] and salivation in cat

6.	N-(2-p-hydroxy-phenyl) ethyl-actinidine isolated from dried roots of *Valeriana officinalis* L. [93]; dolicholactone C and D from essential oil of *Teucrium marum* L. [94]; boschniakine and boschnialactone from *Boschniakia rossica* [95]; mitsugashiwalactone from *Menyanthes trifoliata* L. [95]	Induce catnip response
7.	Isodihydronepetalactone and isoiridomyrmecin from *Acalypha indica* L. dried root [85]	Induce catnip response
8.	Group of seven compounds (1- Oxaspiro [2.5] octane, 4,4- Dimethyl l-8-methylene;1-Napthalenol, decahydro-4a- methyl; Carane, 4,5–epoxy-, trans; Naproxen, Nabumetone, Carpofen and Piperidine 2,6-dimethyl-1- nitroso) from fresh roots of *Acalypha indica* L. [86]	Hallucinogenic, drug-like, anti-spasmatic and anti-inflammatory symptoms in cat apparently similar to catnip response. In addition to this licking of genital area was recorded by the inventors.
9.	*Nepeta cataria* smoking through cigarettes or pipes or sprayed on tobacco	Makes human happy and helps for intoxication [96]. Has antispasmodic activity in humans.

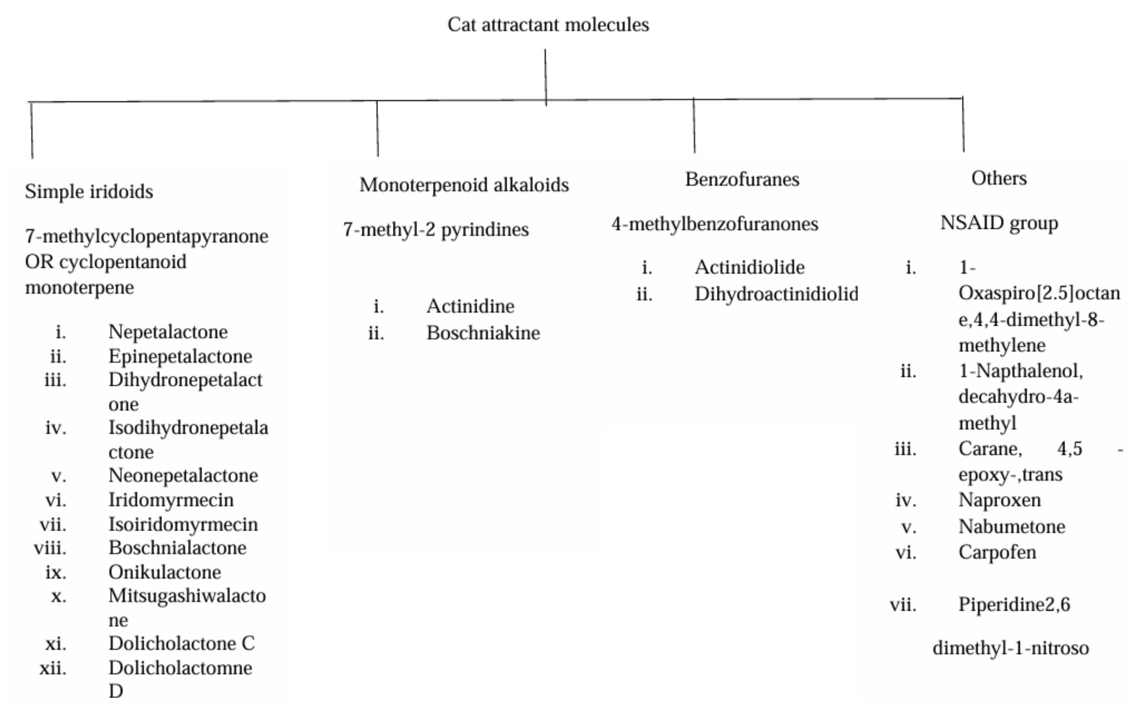

Figure 6. Classification of plant elicited cat attractant molecules [86, 90]

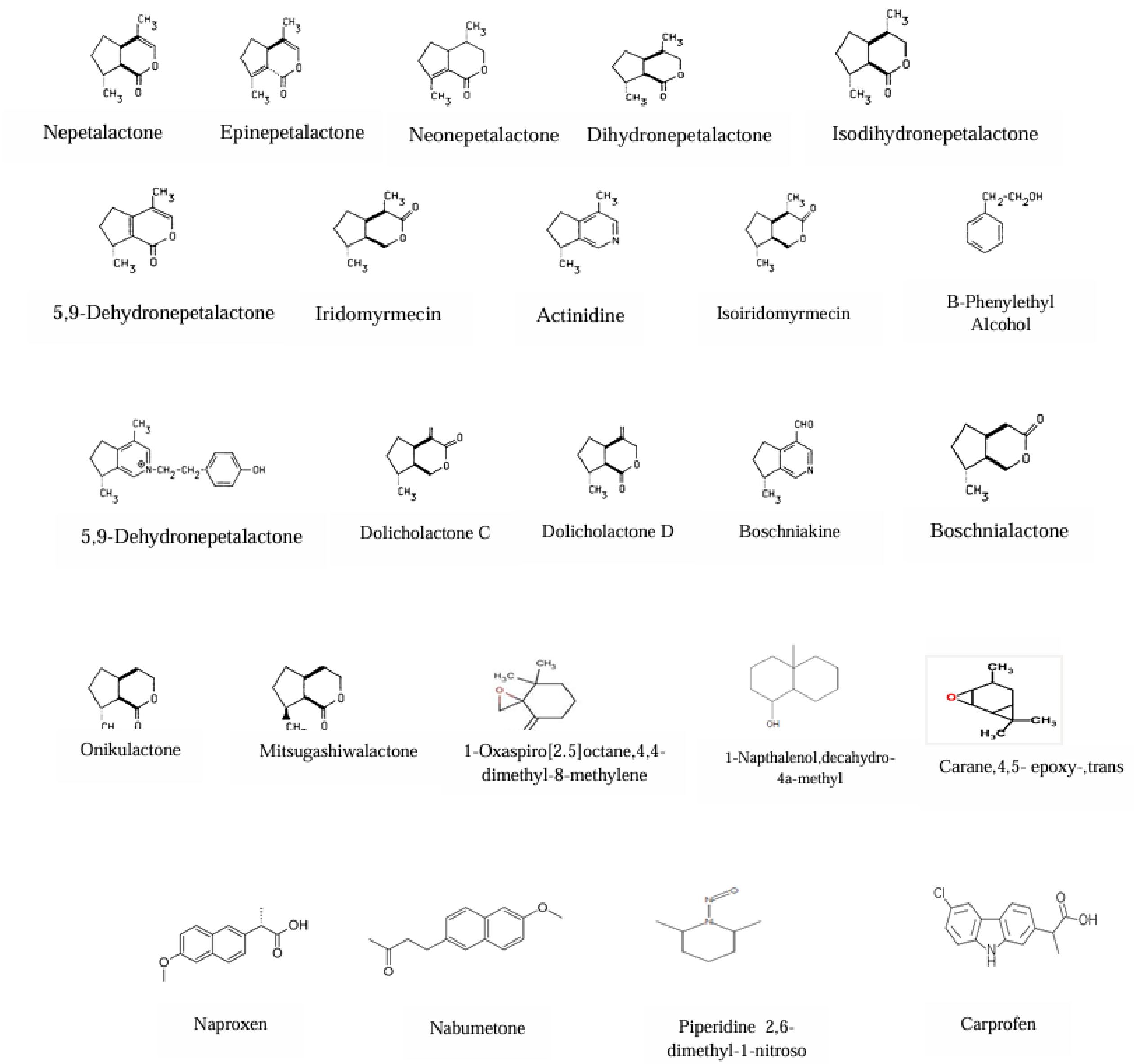

Figure 7. Chemical structure of potent cat attractants discovered till present [85, 86, 90]

5. CONCLUSION

The pool of all natural perfumes (odor) sourced to the environment could be discussed under two broad systems of general odorants and pheromones [97] aiding communication between living organism to its external world. In case of vertebrates and other higher animals, such communication is prerogative of an elaborative mechanism called olfaction, a type of chemo-sensation involving wide array of receptors expressed on peripheral sensory neurons transmitting chemical information to the main olfactory system of brain, principally for general odorants and accessory olfactory system (vomeronasal organ, SO and GG) for pheromone mostly [Figure 2], depending upon the nature of receptors. The odorant molecules function as ligands to such receptors by forming odorant-receptor complexes could be assessed chemically based on their volatility where the olfactory epithelium is entrusted for detecting highly volatile compounds in relation to the vomeronasal organ [98] that requires direct contact with the source for initiation of olfaction. The unique response to the elicited volatile compounds from catnip by some of the members of Felidae had been demonstrated long back as an activity of main olfactory system, were anesthetized olfactory mucosa [75] and olfactory bulbectomy [80] had abandoned catnip behavior in totality eliminating the notion of vomeronasal organ (VNO) to be connected with such response. As oral administration of active compounds from *Nepeta cataria* failed to induce 'catnip response' [99], it became thoroughly clear that 'the smell' and not 'the taste' was key to such response to occur [100]. Discovery of similar responses of feral cat to the root (non-aerial part unlike catnip) elicited compounds from *Acalypha indica* Linn. undoubtedly explores a novel domain in the direction with some differences of identified compounds from dried [85] and fresh root [86] of the plant. The compounds primarily identified from the fresh root determined a strong drug like effect [Table2] as shown in the bioassay which comprises all sort of behavior like catnip except the licking of genital area [86] which was not reported in case of catnip response and also longer interaction time was recorded in comparison to catnip [101]. Now, some unit behavior of catnip response like body rubbing and overhead rolling soon after chewing of the source were conventionally seen as sexual response in cat, thus linking of such behavior to activity of vomeronasal organ was an easy hypothesis to build up until the experiment of olfactory bulbectomy was successfully performed. Therefore, the exact pathway of response against *Acalypha* root in higher brain structure of cat is yet to establish in order to understand its real nature like whether it is an ingestive response, a pleasure response comprising of sexual unit behavior or mixing of any sort of social odor (saliva, genital secretion, urine etc.) thereto is involved to the process. Presence of Isodihydronepetalactone and isoiridomyrmecin [85] in the dried root system of *Acalypha* could not merely answer all and full elucidation of this chapter of neuroscience is required to understand the unknown co-evolutionary stems of life.

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