

# UC Riverside

## UCR Honors Capstones 2021-2022

### Title

A POTENTIAL MECHANISM FOR SENSORY PERCEPTION OF UNPLEASANT FLORAL SCENT OF PEAR BLOSSOMS

### Permalink

<https://escholarship.org/uc/item/4jc348xn>

### Author

Atwal, Samreet S

### Publication Date

2021-10-30

### Data Availability

The data associated with this publication are not available for this reason: NA

A POTENTIAL MECHANISM FOR SENSORY PERCEPTION OF UNPLEASANT FLORAL  
SCENT OF PEAR BLOSSOMS

By

Samreet Singh Atwal

A capstone project submitted for Graduation with University Honors

October 30, 2021

University Honors  
University of California, Riverside

APPROVED

Dr. Sachiko Haga-Yamanaka  
Department of Molecular, Cell, and Systems Biology

Dr. Richard Cardullo, Howard H Hays Jr. Chair  
University Honors

## ABSTRACT

The flowers of pear blossoms (*Pyrus calleryana* and *Pyrus kawakamii*) emit a distinctive unpleasant scent often described as a semen-like smell. However, the chemical origin of the smell remains uncharacterized. The knowledge is crucial to explaining the negative response on humans and could potentially explain an evolutionary mechanism. We first conducted an extensive literature search of floral volatile organic compounds (VOCs) in this genus. During this search, other species such as *Castanea mollissima*, *Castanopsis sclerophylla*, *Photinia serrulata*, *Stemona japonica*, and *Xysmalobium parviflorum* were noted to have a similar unpleasant smell. The floral VOCs were identified using mass spectroscopy and gas chromatography. Among the VOCs identified from those plants, 1-pyrroline is known to be perceived as a semen-like smell in humans and, therefore, could be responsible for the pear blossoms' floral scent. We also explored the literature about semen VOCs and identified putrescine, spermidine, and spermine, which contribute to the smell of semen. Interestingly, including 1-pyrroline, all these compounds are nitrogenous amines. Therefore, we expanded to examine how we perceive these amines. As it turns out, trace amine-associated receptors (TAARs) were identified as polyamine receptors. TAARs are expressed in the olfactory epithelium in vertebrate species, and their activation leads to either attractive or adverse behavior in mice. Our literature search suggests that 1-pyrroline to be the source of the smell of pear blossoms and that TAARs are responsible for its perception, which mediates adverse behavior. The mechanism behind this scent illustrates the intricate yet specialized feature of olfactory perception.

## ACKNOWLEDGEMENTS

I would first like to thank my faculty mentor, Dr. Sachiko Haga-Yamanaka, for taking the time to hear my proposal and her support and guidance on how to conduct my project before and especially after COVID-19. I would also like to thank Momo for teaching me about working with mice and conducting fixations in the research lab. I express my thanks to Andrew C. Sanders of the UCR Herbarium for meeting with me and educating me on the pear blossoms. I am grateful to Dr. Clutterbuck and Dr. Wetzel of Thomas Moore University for providing their research poster on the pear blossoms. I especially thank Dr. Stephanie Dingwall for her enthusiastic support of my project and for reviewing my grant proposal. I thank my learning community, peers, and the UCR meme community for their support and inspiration on this project. This research was partially supported by *the UC Riverside Undergraduate Education Mini-Grant Program*.

## INTRODUCTION

In 2017, the Student Voice Committee of UCR presented survey results that 79% of undergraduates found the evergreen pear tree (*Pyrus kawakamii*) smell so repulsive that replacement should be done (Ramos et al., 2017). However, the *Pyrus calleryana* also shared the same sentiment among social feeds. Popular media sources have reported that the blossom's repugnant scents are associated with semen, and the culprits are trimethylamine and dimethylamine (Spector, 2013; Reid, 2015; Van, 2015; SciShow, 2017; Flanagan, 2021; Solomon, 2021). However, no plant volatile organic compound (VOC) analysis has been conducted specifically to confirm the presence of the two amines and the accuracy of the self-ascribed semen smell association.

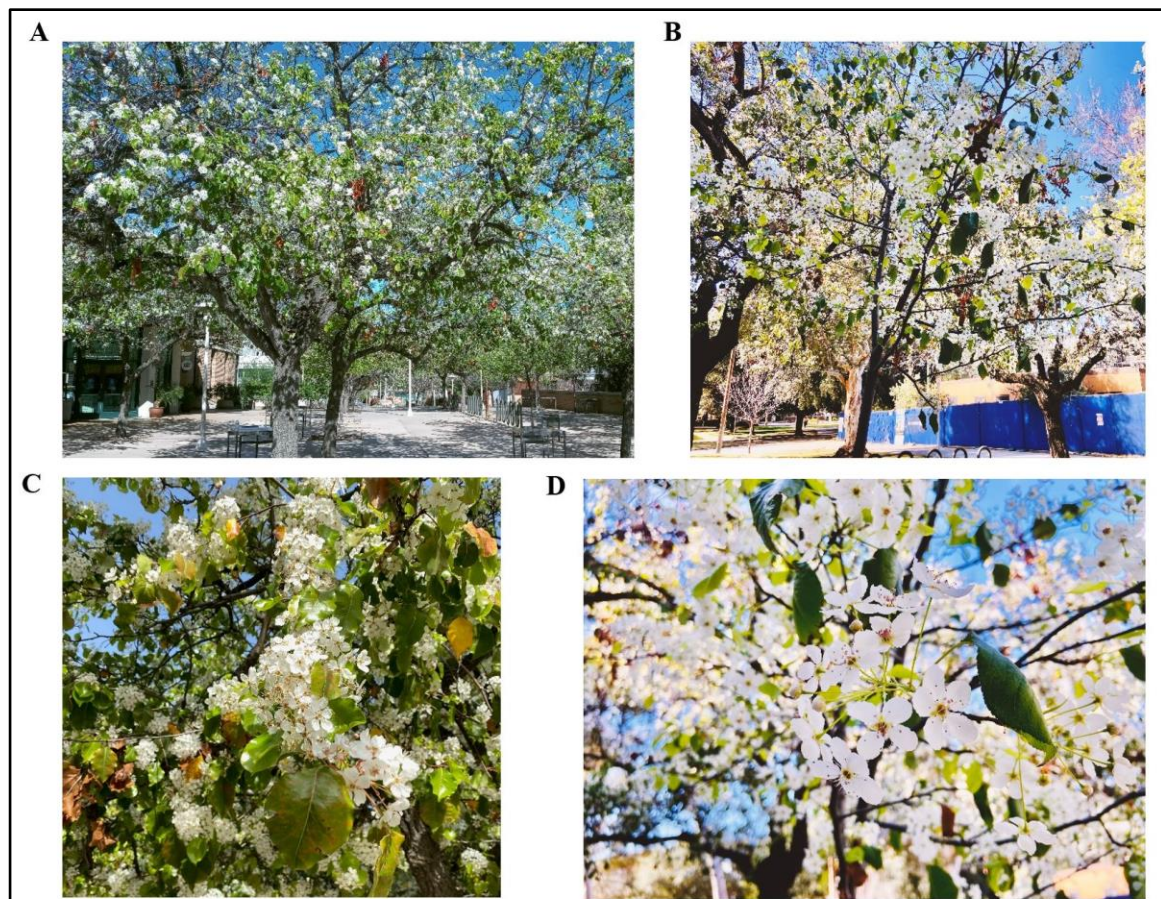
VOCs are molecules that vaporize in the air that allow the perception of a smell. Other plant species had their floral scents analyzed in the literature. (Owen et al., 2001; Li et al., 2013; Ragubeer, 2015). VOC analysis combined with gas chromatography-mass spectrometry (GC-MS) is the primary way to understand the chemical composition of a floral scent and which VOCs are present at higher percentages (Tholl et al., 2006). VOC analysis of *P. calleryana* has been conducted but strictly on leaves (Miller et al., 1989). In addition, several studies found phenolic acid derivatives present from leaves (Challice and Williams, 1968a, 1968b; Nassar et al., 2011). Another found and confirmed the structure of calleryanin and benzylic esters from leaves (Challice et al., 1980). None of which solved what caused the semen-like smell in *P. calleryana* and *P. kawakamii* flowers.

In this review, we provide a comprehensive assessment of the published literature on pear blossom VOCs. We summarize the presence of a semen-like smell in other flora, semen VOCs, and compare the VOC flora culprit to semen VOCs. This paper aims to reveal what possible

VOC in pear blossoms is responsible for the semen-like smell and the mechanism involved in perceiving the scent. We also discuss how the mechanism can modulate behavior not just in humans but also in mice.

### The Pear Blossoms

*P. kawakamii* is initially found in Taiwan and China (UFEI, 1995a). As shown in **Figures 1A, C**, the leaves' shape is oval, and the flowers are white. In addition, the crown of the tree is a vase (**Figure 1A**). *P. calleryana* is found initially in China and is considered an invasive species in California (UFEI, 1995b). As shown in **Figures 1B and D**, the leaves' shape is ovate, and the flowers are white. In addition, the crown of the tree is rounded (**Figure 1B**). Both trees produce



**FIGURE 1** | Photos of the pear blossoms and their scent emitting flowers. *Pyrus kawakamii* tree taken by Lily Wins (**A**). *Pyrus calleryana* tree taken by Dubin Zheng (**B**). *P. kawakamii* flowers by Daisy Sanchez (**C**). *P. calleryana* flowers also by Dubin Zheng (**D**).

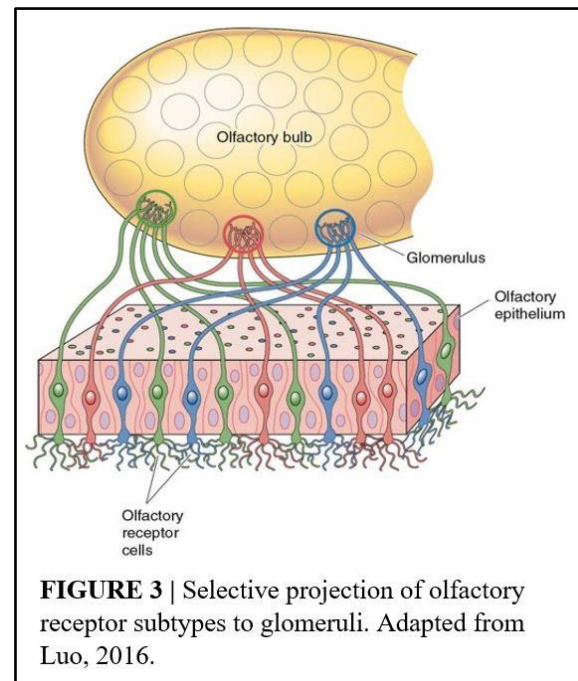
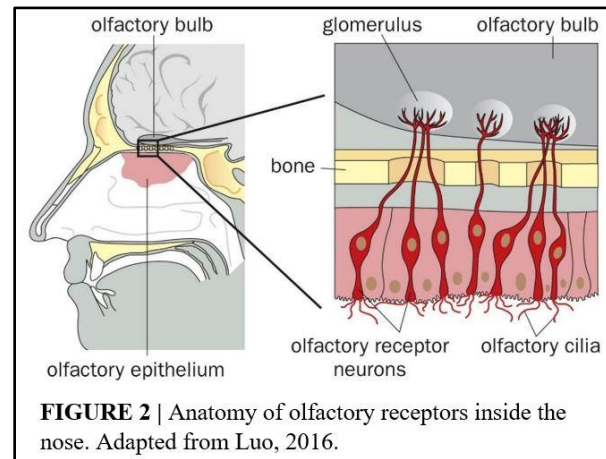
flowers in Winter or Spring with a strong unpleasant scent. In addition, no actual pear fruits are produced.

## Olfaction

Before examining the pear blossom VOCs, we should review how we perceive VOCs as a smell. VOCs/odorants first travel into the nasal passage, which binds to odorant-binding proteins (OBPs) in the nasal epithelia. These OBPs transport the odorants through the mucus to

the odorant receptors (ORs) (Castro et al., 2021). The ORs are a seven-transmembrane G protein-coupled receptor (GPCR) (Buck and Axel, 1991). Each olfactory receptor neuron (ORN) expresses one OR gene allele (Malnic et al., 1999; Serizawa et al., 2004). As seen in **Figure 2**, ORNs converge axons to glomeruli in the olfactory bulb (Ressler et al., 1994; Vassar et al., 1994; Mombaerts et al., 1996). In

**Figure 3**, ORNs expressing the same OR project their axons to the same glomerulus (Luo, 2016). The chemical structure of the odorant determines the number of ORs it binds to, and ORNs activated (Takahashi et al., 2004; Ma et al., 2012). The identities of different odorants are encoded by different populations of ORNs combinatorically activated (Malnic et al., 1999; Luo, 2016). As a result, each odorant elicits a specific spatial pattern of glomerulus activation (Ressler et al., 1994; Rubin and Katz, 1999; Oka et al., 2006).



Second-order neurons called mitral cells then transmit olfactory information from glomeruli to several cortical and limbic areas, including the piriform cortex and cortical amygdala (Haberly and Price, 1977; Scott et al., 1980; Luskin and Price, 1982; Buonviso et al., 1991; Sosulski et al., 2011; Root et al., 2014; Luo, 2016). No spatial pattern of activity for different odorants is observed in the piriform cortex. (Rennaker et al., 2007; Stettler and Axel, 2009; Luo, 2016). Spatially stereotyped activity has been observed in the amygdala (Sosulski et al., 2011; Luo, 2016). Higher-order processing in the cortex completes the process allowing the sense of smell of numerous VOCs.

### PEAR BLOSSOM VOCs

Currently, to our knowledge, only two studies analyzed the VOCs from the pear blossoms (Clutterbuck and Wetzel, 2011; Daley et al., 2013). Only *P. calleryana* was analyzed. The preliminary study that provided the bulk of the VOC profile was by Clutterbuck and Wetzel

**TABLE 1** | Proposed (black) and confirmed (red) major VOCs reported in pear blossoms.

| Compound                                | Source   |
|---|--|
| Vinyl furan                             | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Guaiacol                                | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Palmitic acid                           | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Methyl linolenate                       | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Linolenic acid                          | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Phytol                                  | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Linoleic acid                           | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| 1-mono-linolenin                        | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Sitosterol                              | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| $\alpha$ -amyrin                        | (Clutterbuck and Wetzel, 2011; Daley et al., 2013) |
| Cyclopentanol                           | (Clutterbuck and Wetzel, 2011)                     |
| Pyran                                   | (Clutterbuck and Wetzel, 2011)                     |
| 5-methyl-4-octanone                     | (Clutterbuck and Wetzel, 2011)                     |
| 3-n-propyl-5-methylhexan-2-one          | (Clutterbuck and Wetzel, 2011)                     |
| Pentanoic acid                          | (Clutterbuck and Wetzel, 2011)                     |
| n-heneicosane                           | (Clutterbuck and Wetzel, 2011)                     |
| n-tetracosane                           | (Clutterbuck and Wetzel, 2011)                     |
| n-pentacosane                           | (Clutterbuck and Wetzel, 2011)                     |
| n-heptacosane                           | (Clutterbuck and Wetzel, 2011)                     |
| n-triacontane                           | (Clutterbuck and Wetzel, 2011)                     |
| 1,2-benzenediol                         | (Clutterbuck and Wetzel, 2011)                     |
| Glucopyranoside                         | (Clutterbuck and Wetzel, 2011)                     |
| 3-isopropyl-5-methylhexan-2-one         | (Clutterbuck and Wetzel, 2011)                     |
| Butyl heptyl ketone                     | (Clutterbuck and Wetzel, 2011)                     |
| n-docosane                              | (Clutterbuck and Wetzel, 2011)                     |
| n-tricosane                             | (Clutterbuck and Wetzel, 2011)                     |
| Heptaconsanol                           | (Clutterbuck and Wetzel, 2011)                     |
| n-octacosane                            | (Clutterbuck and Wetzel, 2011)                     |
| n-nonacosane                            | (Clutterbuck and Wetzel, 2011)                     |
| n-dotriacontane                         | (Clutterbuck and Wetzel, 2011)                     |
| (9Z)-9-octadecenyl (9Z)-9-hexadecanoate | (Clutterbuck and Wetzel, 2011)                     |

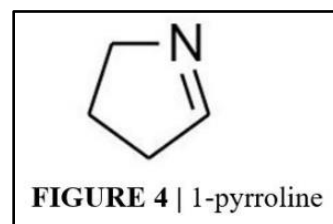


(2011) (**Table 1**). In the study, 50 g of flower blossoms were combined in a 1:5 g:mL ratio of methanol or n-hexane. 3 mL aliquot of the extracted fraction was pressurized by nitrogen gas to make a more concentrated fraction. In total, four individual 1 $\mu$ L aliquots (non-concentrated methanol, n-hexane; concentrated methanol, and n-hexane) were analyzed with GC-MS. The VOCs were confirmed with existing standards and mass spectra. No presence of trimethylamine or dimethylamine that is purported to cause the semen-like smell was confirmed. However, due to the study's design, the extraction of the amines may have been missed.

## **PRESENCE OF SEMEN-LIKE SMELL IN OTHER SPECIES**

### ***Castanea mollissima***

The Chinese chestnut (*Castanea mollissima*) flowers were noted to have a characteristic odor reminiscent of human semen (Zhang et al., 2019). Like the current review on pear blossoms, no compounds were reported to be responsible for the semen-like odor of chestnut flowers. The paper employed neutral desorption extractive atmospheric pressure chemical ionization mass spectrometry (ND-EAPCI-MS) rather than GC-MS because it is less efficient in analyzing some nitrogen-containing VOCs (amines). 20 VOCs were identified as primarily nitrogen-containing. The major VOC responsible for the semen-like odor was purported to be 1-pyrroline, which had the most abundant signal in all the MS spectra (**Figure 4**). 1-pyrroline was confirmed from previously synthesized 1-pyrroline as a standard for identification (Zhang et al., 2017). Further evidence of 1-pyrroline to the semen-like odor were olfactory experiments in which male participants failed to discriminate between 1-pyrroline and the chestnut blossoms.



### ***Castanopsis sclerophylla***

*Castanopsis sclerophylla*, a plant in subtropical Eastern Asia, is well known for the pronounced semen-like odor of its flowers. The chemical origin of semen-like odor emitted by *C. sclerophylla* flowers also remains unknown (Zhang et al., 2018). The authors employed direct ambient corona discharge ionization mass spectrometry (MS). The analysis is done directly on the freshly collected flowers without any VOCs collection being required. The MS used is a variation of atmospheric pressure chemical ionization (APCI). Six new VOCs were identified, and most were nitrogenous VOCs. 1-pyrroline was attributed as the primary source of the semen-like odor. Olfactory discrimination test also confirmed.

### ***Photinia serrulata***

Like *Castanopsis sclerophylla*, the flowers of *Photinia serrulata* emit a strong odor reminiscent of human semen (Zhang et al., 2018). No compounds were reported to be responsible for the semen-like odor. From the same paper analyzing *C. sclerophylla* flowers, 18 VOCs were identified. Most of the identified VOCs belong to nitrogen-containing compounds. Once again, their results indicate the abundant release of 1-pyrroline as the major cause of the semen-like odor in *P. serrulata* flowers. Olfactory discrimination test between 1-pyrroline and flowers also confirmed the results.

### ***Stemona japonica***

While investigating species of the Stemonaceae in China, it was noted that flowers of *Stemona japonica* had a strong, unpleasant foul, and semen-like smell (Chen et al., 2015). The floral scent of *S. japonica* was collected via solid-phase micro-extraction (SPME) and analyzed by GC-MS. VOCs identified were 1-pyrroline (59.2 %), 2-methyl-1-butanol (27.2 %), and 3-methyl-1-butanol (8.8 %). The combined result was a semen-like odor—a smell test with

participants were unable to distinguish blossom from odorant. Zhang et al. (2018) also conducted VOC analysis on the flowers using ambient corona discharge ionization MS. Their paper revealed five new VOCs that have not been observed in *S. japonica* and agreed with Chen et al. (2015) that 1-pyrroline is the main VOC responsible for the semen-like odor.

### ***Xysmalobium parviflorum***

*Xysmalobium parviflorum* is present in grasslands from the Eastern Cape Province to Limpopo Province, South Africa (Shuttleworth, 2016). During fieldwork, it was noticed that flowers had a powerful semen-like odor. Shuttleworth used dynamic headspace extraction methods and GC-MS. Thirty-four compounds were detected from the Lake Merthley X. *parviflorum* population. The composition mainly was by benzaldehyde, several common floral monoterpenes (particularly limonene, b-myrcene, both (E)- and (Z)-b-ocimene, and a-pinene) and 1-pyrroline. 1-Pyrroline was identified by comparison with the mass spectrum for this compound presented in Chen et al. (2015).

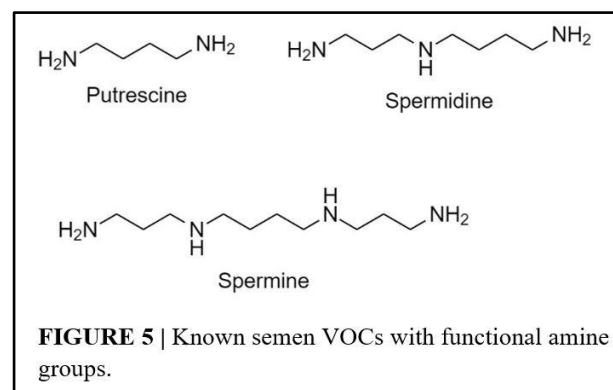
### **1-Pyrroline**

1-pyrroline remains very poorly studied. Despite VOC profiles of various plant species proving the presence of 1-pyrroline, 1-pyrroline is not mentioned in comprehensive reviews of floral volatiles (Knudsen et al., 2006; Pichersky and Dudareva, 2020). The primary reason may be difficulty in identifying its presence via MS. The compound has poor chemical stability (Zhang et al., 2017). No 1-pyrroline analytical standards commercially exist. All VOC analyses of plant species mentioned prior employed in-house 1-pyrroline synthesis. Silver (I)-catalyzed oxidation of pyrrolidine (Ogawa et al., 1982; Shvekhgeimer, 2003; Mores et al., 2008), acid hydrolysis of 4-aminobutanal diethyl acetal (Yoshikawa et al., 1965; Baxter et al., 1991), and denitrogenative ring expansion of cyclobutyl azides (Miki et al., 2021) are various means of

synthesizing 1-pyrroline. Olfaction discriminatory tests of 1-pyrroline and the floral blossoms were practical because the human nose is susceptible to 1-pyrroline (Amoore et al., 1975). Anosmia studies proved human sensitivity (Amoore, 1977; Hirth et al., 1986). 1-pyrroline resembles human semen very closely and possibly a vestigial pheromone (Amoore et al., 1975).

## SEMEN ODORANTS

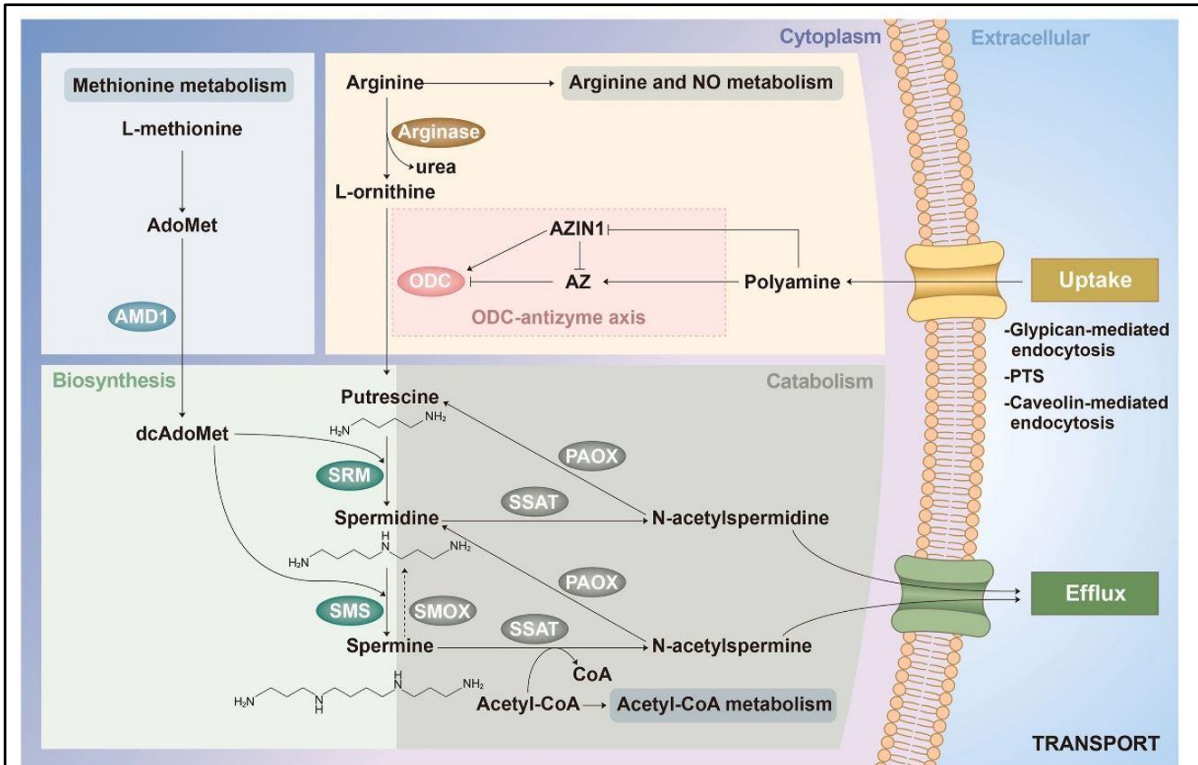
The first mentioned study was by Antonie van Leeuwenhoek in 1679, observing crystals in the seminal fluid (Leeuwenhoek, 1679). 1924 saw the crystal's chemical structure solved (Dudley and Rosenheim, 1925), and two years later, the products were synthesized chemically (Dudley et al., 1926). These studies in the early 20<sup>th</sup> century confirmed the presence of spermine as well as the two precursors, triamine (spermidine) and a diamine (putrescine) (Bachrach, 2010). All three compounds have a linear conformation and multiple amino groups, hence polyamines (**Figure 5**). The polyamines in mammalian semen were essentially from prostatic secretion (Williams-Ashman and Lockwood, 1970). The spermine



concentration in human semen is higher than in most animal tissue (Jänne et al., 1973). High-performance liquid chromatography also confirmed the presence of putrescine, spermidine, and spermine in human semen (Oefner et al., 1992). The polyamines putrescine, spermidine, and spermine were synthesized from the amino acid ornithine or derived from the diet (Sieckmann and Kirschner, 2020). These polyamines are an integral part of metabolism (**Figure 6**).

By the mid-20<sup>th</sup> century, aside from the VOCs associated with semen, polyamines were essential in gametogenesis, embryogenesis, and postnatal development (Sheth and Moodbidri, 1977; Lefèvre et al., 2011; Lenis et al., 2017). In addition, clinical applications for cancer

prevention therapy have been discovered because polyamines are necessary for normal cell viability; inhibiting polyamine production is used as an anti-cancer strategy (Sieckmann and Kirschner, 2020; Novita Sari et al., 2021).

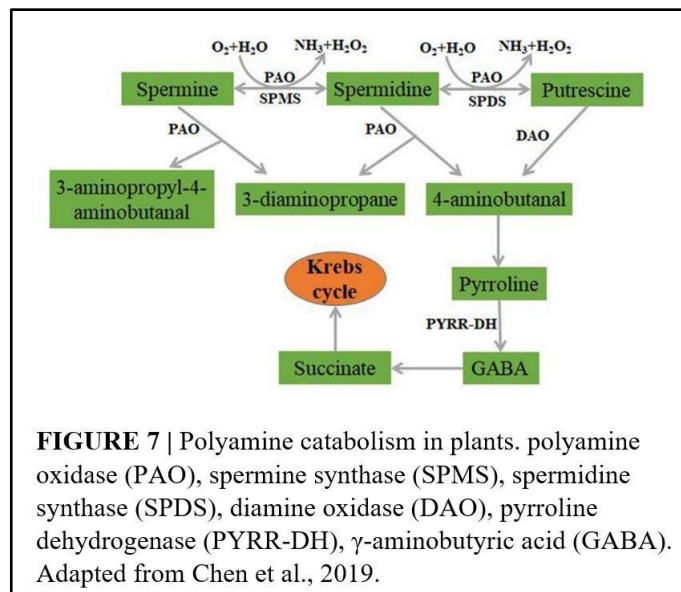


**FIGURE 6** | Metabolic pathway of polyamines and its connections with other metabolic pathways. S-adenosylmethionine (SAM or AdoMet), decarboxylated S-adenosylmethionine (dcSAM or dcAdoMet), S-adenosylmethionine decarboxylase 1 (SAMDC; or adenosylmethionine decarboxylase 1, AMD1), antizyme (AZ), antizyme inhibitor (AZIN), ornithine decarboxylase (ODC), spermidine synthase (SRM), spermine synthase (SMS), spermine oxidase (SMOX), spermidine/spermine N1-acetyltransferase (SSAT), peroxisomal N1-acetylpolyamine oxidase (PAOX), polyamine transport systems (PTS). Adapted from Novita Sari et al., 2021.

### Relationship to Plants

Polyamines are not exclusive to the semen of mammals but plants as well. Putrescine, spermidine, and spermine are also present in plants (Chen et al., 2019). Putrescine is the principal end product of plant polyamine biosynthetic pathways (Chen et al., 2019). The catabolism of the polyamines in plants leads to the production of 1-pyrroline (**Figure 7**). In

Zhang et al. (2019)'s paper, 1-pyrroline was possibly formed via the oxidative deamination of putrescine by observing the signal from protonated 4-amino-butanal intermediate, which yields 1-pyrroline by spontaneous cyclization. 4-amino-butanal has also been reported in *Photinia serrulata* flowers (Zhang et al., 2018). 1-pyrroline synthesis proves that the precursor of 1-pyrroline and 4-amino-butanal in plants is putrescine (Zhang et al., 2018; Chen et al., 2019). There now



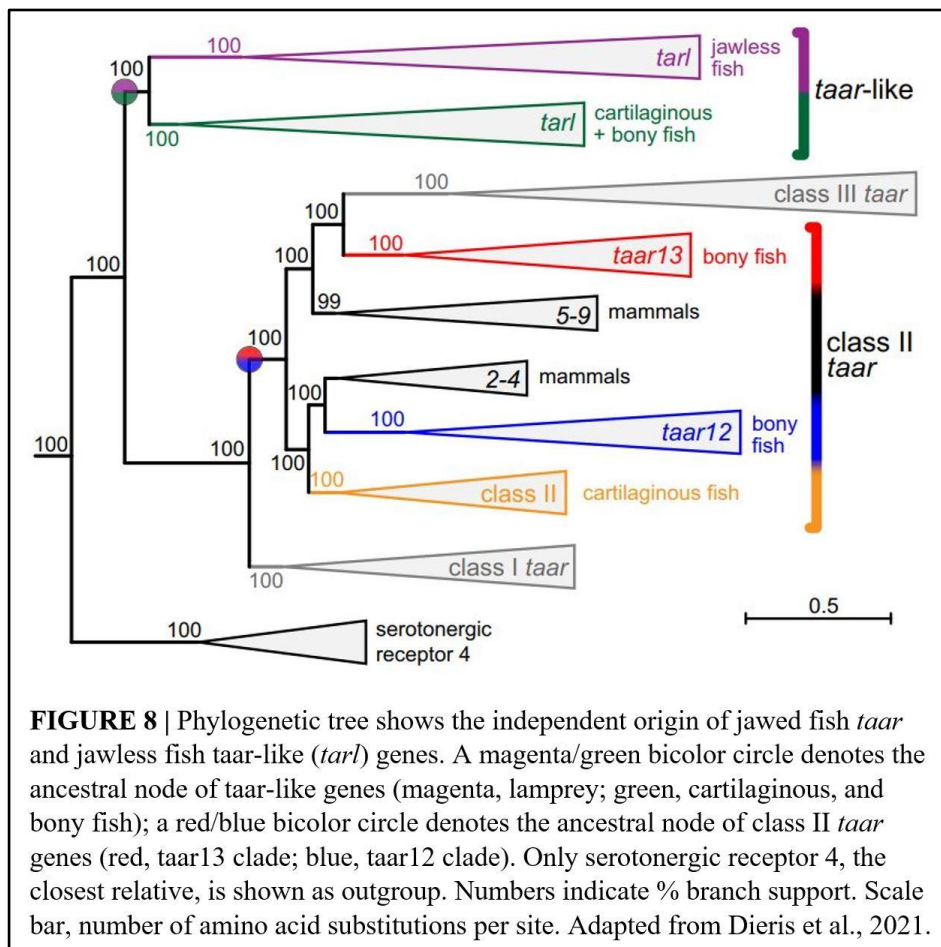
exists a relationship between polyamine VOCs of semen and 1-pyrroline of plants that emit a semen-like odor. Much like polyamines of mammals, plant polyamines play a diverse and critical role. These include flowering, embryo development, senescence, and responses to several (mainly abiotic) stresses (Chen et al., 2019).

## RECEPTOR RESPONSIBLE

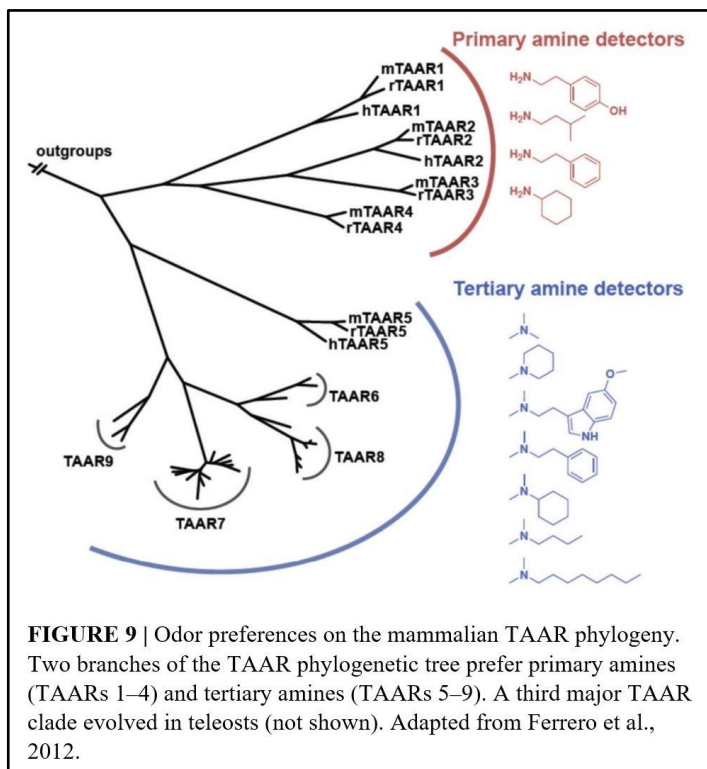
Despite that 1-pyrroline (**Figure 4**) is a cyclic imine, putrescine, spermidine, and spermine are polyamines. Cyclization of 1-pyrroline's double bond forms cyclic amines 2-pyrroline and 3-pyrroline. 1-pyrroline and the polyamines share amine groups; as such, trace amine-associated receptors (TAARs) are responsible for perceiving the smell of the pear blossoms. TAARs were first discovered in 2001 as GPCRs detecting trace amines (Borowsky et al., 2001; Bunzow et al., 2001). The TAARs were demonstrated as chemosensory receptors in mice for volatile amines (Liberles and Buck, 2006) and present in all vertebrates, including humans (Lindemann et al., 2005). TAARs in ORNs project to specific glomeruli just like GPCRs (Johnson et al., 2012; Pacifico et al., 2012; Xu and Li, 2020).

## Evolution of Mammalian TAARs

The TAAR family evolved olfactory functionality twice independently from jawed and jawless fish (Dieris et al., 2021). Homologous genes missing the TAAR motif were named Taar-like genes (Hussain et al., 2009; Eyun et al., 2016; Scott et al., 2019). The most ancestral TAAR genes containing the TAAR motif were in cartilaginous fishes (Hussain et al., 2009; Sharma et al., 2019). However, Dieris et al. (2021) purported that the most recent ancestral TAAR is further back. They identified the evolutionary origin of both taar and tarl genes in vertebrates' most recent common ancestor as a duplication of the serotonergic receptor 4. Two ancestral genes in bony fish (TAAR12, TAAR13) gave rise to the mammalian olfactory taar genes and class II of teleost fish's taar repertoire (Dieris et al., 2021). **Figure 8** shows the two points of independent evolution, TAAR5-9 of mammals shares a recent ancestor with TAAR13, and



TAAR2-4 of mammals shares a recent ancestor with TAAR12. **Figure 9** expanded the mammalian TAAR clades into agonist preferences for primary or tertiary amines for humans, mice, and rats (Ferrero et al., 2012).



## Mammalian TAARs

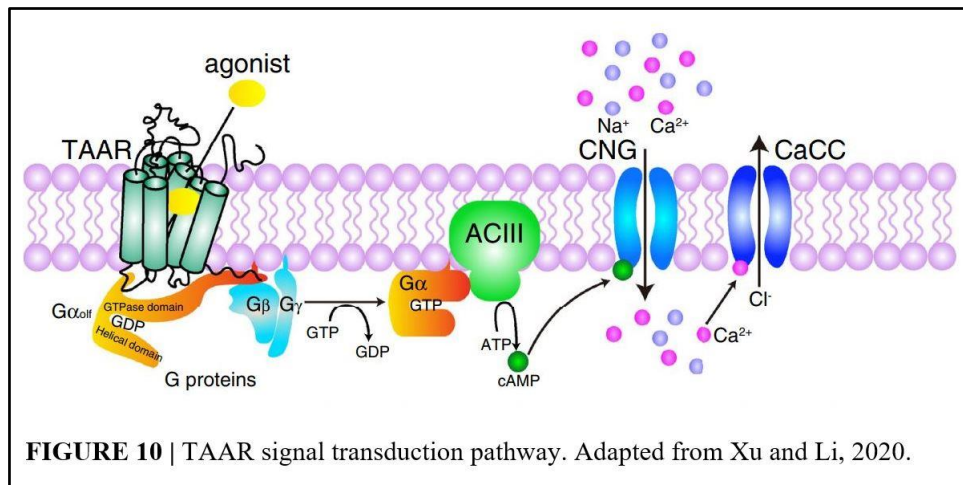
Up to 26 subtypes of TAARs have been identified in mammalian species (Hashiguchi and Nishida, 2007; Hussain et al., 2009; Eyun et al., 2016). All 26 belong to nine sub-families (TAAR1-9) (Gloriam et al., 2005; Lindemann et al., 2005; Hashiguchi and Nishida, 2007). Humans express one variant of 6 of the TAAR family members (TAAR1, 2, 5, 6, 8, and 9). TAAR3, 4, and 7 are human pseudogenes (Lindemann et al., 2005; Berry et al., 2017). In total, 6 TAARs function in humans, 15 in mice, and 17 in rats (Lindemann et al., 2005; Liberles and Buck, 2006; Hussain et al., 2009). TAAR2-9 except TAAR1 are highly expressed in olfactory sensory neurons located in the olfactory epithelium and have an olfactory role (Liberles and Buck, 2006; Johnson et al., 2012; Pacifico et al., 2012; Xu and Li, 2020). Only tertiary amines



can activate hTAAR5 like trimethylamine (Wallrabenstein et al., 2013; Liberles, 2015). Spermine and spermidine activate TAAR9 (Xu and Li, 2020). Putrescine possibly binds to TAAR6 and TAAR8 (Xu and Li, 2020).

### TAAR Signal Mechanism

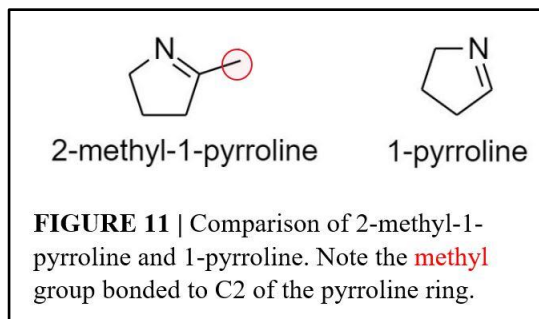
In the olfactory system, TAARs are to the olfactory type  $G\alpha$  proteins ( $G\alpha_{olf}$ ) that activate adenylyl cyclase type III (ACIII) and increase the cAMP production (Liberles and Buck, 2006). cAMP directly activates cyclic nucleotide-gated channels (CNG) to permit  $Na^+$  and  $Ca^{2+}$  entry. The influx of positive ions depolarizes olfactory sensory neurons and is further amplified by  $Cl^-$  efflux through opening calcium-gated chloride channels (CaCCs) (**Figure 10**) (Xu and Li, 2020). Other olfactory TAARs use different  $G\alpha$  proteins. For instance, TAAR8 uses  $G\alpha_i$  to reduce the cAMP levels (Mühlhaus et al., 2014). TAAR5 via  $G\alpha_q/11$ - and  $G\alpha_{12/13}$ -dependent MAP kinase cascades (Dinter et al., 2015).



### BEHAVIOR MODULATION OF MICE VIA RECEPTOR ACTIVATION

The olfactory system in some vertebrates, especially mice, is vital to detect predators and potential mates. As a result, olfaction study methodology on mice behavior manipulates this innate and adaptive behavior (Papes et al., 2018). Knockout studies of mice's olfactory sensory neurons demonstrated a lack of innate responses to aversive odorants (Kobayakawa et al., 2007).

However, learned responses were intact, revealing a separate olfactory network at hand. The TAAR olfactory network is no exception. Spermidine and spermine via mTAAR9 induced attractive behavior (Saraiva et al., 2016). 2-methyl-1-pyrroline via mTAAR5 induced neutral behavior (Saraiva et al., 2016).



From **Figure 11**, 2-methyl-1-pyrroline is not vastly different from 1-pyrroline, which is the suspected VOC of the pear blossoms. As such, 1-pyrroline may be an agonist for TAAR5. In addition, 3-pyrroline is an agonist for mTAAR5 (Xu and Li, 2020). Although the TAAR agonists mainly elicit innate behaviors, the induced behaviors can be context-dependent (Saraiva et al., 2016). Complex behaviors can be made by combining distinct olfactory inputs from different activated TAARs (Saraiva et al., 2016).

## CONCLUSIONS AND FUTURE PROSPECTS

This paper represents a comprehensive review of the published literature on the pear blossom VOCs, VOC composition of other plants with a semen-like smell, and VOCs of human semen. We explored the role of polyamines in humans and plants, the relationship of 1-pyrroline to polyamines, the TAAR responsible with evolutionary background, and that TAAR activity induces innate behavior in mice. This information allows a reference for future research on the role of 1-pyrroline on vertebrate olfactory systems and VOC analysis on other flora that have a semen-like smell. Current VOC profile data on 1-pyrroline in plants remains scarce and understudied. There are still many questions to answer regarding the presence of 1-pyrroline in *P. calleryana* and *P. kawakamii*. Further research is required to confirm the presence of 1-pyrroline and which TAAR is activated in humans should be a primary research direction in the future.

## REFERENCES

- Amoore, J. E. (1977). SPECIFIC ANOSMIA AND THE CONCEPT OF PRIMARY ODORS. *Chem Senses* 2, 267–281. doi:10.1093/chemse/2.3.267.
- Amoore, J. E., Forrester, L. J., and Buttery, R. G. (1975). Specific anosmia to 1-pyrroline: The spermous primary odor. *J Chem Ecol* 1, 299–310. doi:10.1007/BF00988831.
- Bachrach, U. (2010). The early history of polyamine research. *Plant Physiology and Biochemistry* 48, 490–495. doi:10.1016/j.plaphy.2010.02.003.
- Baxter, G., Melville, J. C., and Robins, D. J. (1991). Stabilisation of 3,4-Dihydro-2H-pyrrole (1-Pyrroline) by Complexation with Zinc Iodide. *Synlett* 1991, 359–360. doi:10.1055/s-1991-34733.
- Berry, M. D., Gainetdinov, R. R., Hoener, M. C., and Shahid, M. (2017). Pharmacology of human trace amine-associated receptors: Therapeutic opportunities and challenges. *Pharmacology & Therapeutics* 180, 161–180. doi:10.1016/j.pharmthera.2017.07.002.
- Borowsky, B., Adham, N., Jones, K. A., Raddatz, R., Artymyshyn, R., Ogozalek, K. L., et al. (2001). Trace amines: identification of a family of mammalian G protein-coupled receptors. *Proc. Natl. Acad. Sci. USA* 98, 8966–8971. doi:10.1073/pnas.151105198.
- Buck, L., and Axel, R. (1991). A novel multigene family may encode odorant receptors: a molecular basis for odor recognition. *Cell* 65, 175–187. doi:10.1016/0092-8674(91)90418-x.
- Bunzow, J. R., Sonders, M. S., Arttamangkul, S., Harrison, L. M., Zhang, G., Quigley, D. I., et al. (2001). Amphetamine, 3,4-methylenedioxymethamphetamine, lysergic acid diethylamide, and metabolites of the catecholamine neurotransmitters are agonists of a rat trace amine receptor. *Mol Pharmacol* 60, 1181–1188. doi:10.1124/mol.60.6.1181.
- Buonviso, N., Revial, M. F., and Jourdan, F. (1991). The Projections of Mitral Cells from Small Local Regions of the Olfactory Bulb: An Anterograde Tracing Study Using PHA-L (Phaseolus vulgaris Leucoagglutinin). *Eur J Neurosci* 3, 493–500. doi:10.1111/j.1460-9568.1991.tb00836.x.
- Castro, T. G., Silva, C., Matamá, T., and Cavaco-Paulo, A. (2021). The Structural Properties of Odorants Modulate Their Association to Human Odorant Binding Protein. *Biomolecules* 11, 145. doi:10.3390/biom11020145.
- Challice, J. S., Loeffler, R. S. T., and Williams, A. H. (1980). Structure of calleryanin and its benzylic esters from Pyrus and Prunus. *Phytochemistry* 19, 2435–2437. doi:10.1016/S0031-9422(00)91043-4.
- Challice, J. S., and Williams, A. H. (1968a). Phenolic compounds of the genus Pyrus—I. The occurrence of flavones and phenolic acid derivatives of 3,4-dihydroxybenzyl alcohol 4-glucoside in Pyrus calleryana. *Phytochemistry* 7, 119–130. doi:10.1016/S0031-9422(00)88214-X.
- Challice, J. S., and Williams, A. H. (1968b). Phenolic compounds of the genus Pyrus—II. A chemotaxonomic survey. *Phytochemistry* 7, 1781–1801. doi:10.1016/S0031-9422(00)86651-0.
- Chen, D., Shao, Q., Yin, L., Younis, A., and Zheng, B. (2019). Polyamine Function in Plants: Metabolism, Regulation on Development, and Roles in Abiotic Stress Responses. *Front. Plant Sci.* 9, 1945. doi:10.3389/fpls.2018.01945.
- Chen, G., Jürgens, A., Shao, L., Liu, Y., Sun, W., and Xia, C. (2015). Semen-Like Floral Scents and Pollination Biology of a Sapromyophilous Plant *Stemona japonica* (Stemonaceae). *J Chem Ecol* 41, 244–252. doi:10.1007/s10886-015-0563-0.
- Clutterbuck, A. A., and Wetzel, W. C. (2011). Methods for Separation and Identification of Volatile Oils in Bradford Pear Blossoms by GCMS.
- Daley, J. C., Clutterbuck, A. A., Galbraith-Kent, S. L., and Wetzel, W. C. (2013). Construction and Utilization of a Y-Tube Olfactometer to Determine Honeybee Preferences.
- Dieris, M., Kowatschew, D., and Korsching, S. I. (2021). Olfactory function in the trace amine-associated receptor family (TAARs) evolved twice independently. *Sci Rep* 11, 7807. doi:10.1038/s41598-021-87236-5.
- Dinter, J., Mühlhaus, J., Wienchol, C. L., Yi, C.-X., Nürnberg, D., Morin, S., et al. (2015). Inverse Agonistic Action of 3-Iodothyronamine at the Human Trace Amine-Associated Receptor 5. *PLoS ONE* 10, e0117774. doi:10.1371/journal.pone.0117774.
- Dudley, H. W., and Rosenheim, O. (1925). The Chemical Constitution of Spermine. *Biochemical Journal* 19, 1032–1033. doi:10.1042/bj0191032.
- Dudley, H. W., Rosenheim, O., and Starling, W. W. (1926). The Chemical Constitution of Spermine. *Biochemical Journal* 20, 1082–1094. doi:10.1042/bj0201082.

- Eyun, S., Moriyama, H., Hoffmann, F. G., and Moriyama, E. N. (2016). Molecular Evolution and Functional Divergence of Trace Amine-Associated Receptors. *PLOS ONE* 11, e0151023. doi:10.1371/journal.pone.0151023.
- Ferrero, D. M., Wacker, D., Roque, M. A., Baldwin, M. W., Stevens, R. C., and Liberles, S. D. (2012). Agonists for 13 trace amine-associated receptors provide insight into the molecular basis of odor selectivity. *ACS Chem Biol* 7, 1184–1189. doi:10.1021/cb300111e.
- Flanagan, B. (2021). Why do Bradford pear trees smell like...that? *al*. Available at: <https://www.al.com/life/2021/03/why-do-bradford-pear-trees-smell-likethat.html> [Accessed May 10, 2021].
- Gloriam, D. E. I., Bjarnadóttir, T. K., Schiöth, H. B., and Fredriksson, R. (2005). High Species Variation within the Repertoire of Trace Amine Receptors. *Annals of the New York Academy of Sciences* 1040, 323–327. doi:10.1196/annals.1327.052.
- Haberly, L. B., and Price, J. L. (1977). The axonal projection patterns of the mitral and tufted cells of the olfactory bulb in the rat. *Brain Research* 129, 152–157. doi:10.1016/0006-8993(77)90978-7.
- Hashiguchi, Y., and Nishida, M. (2007). Evolution of Trace Amine-Associated Receptor (TAAR) Gene Family in Vertebrates: Lineage-Specific Expansions and Degradations of a Second Class of Vertebrate Chemosensory Receptors Expressed in the Olfactory Epithelium. *Molecular Biology and Evolution* 24, 2099–2107. doi:10.1093/molbev/msm140.
- Hirth, L., Abadianian, D., and Goedde, H. W. (1986). Incidence of Specific Anosmia in Northern Germany. *Hum Hered* 36, 1–5. doi:10.1159/000153591.
- Hussain, A., Saraiva, L. R., and Korsching, S. I. (2009). Positive Darwinian selection and the birth of an olfactory receptor clade in teleosts. *PNAS* 106, 4313–4318. doi:10.1073/pnas.0803229106.
- Jänne, J., Hölttä, E., Haaranen, P., and Elfving, K. (1973). Polyamines and polyamine-metabolizing enzyme activities in human semen. *Clinica Chimica Acta* 48, 393–401. doi:10.1016/0009-8981(73)90418-X.
- Johnson, M. A., Tsai, L., Roy, D. S., Valenzuela, D. H., Mosley, C., Magklara, A., et al. (2012). Neurons expressing trace amine-associated receptors project to discrete glomeruli and constitute an olfactory subsystem. *Proceedings of the National Academy of Sciences* 109, 13410–13415. doi:10.1073/pnas.1206724109.
- Knudsen, J. T., Eriksson, R., Gershenzon, J., and Ståhl, B. (2006). Diversity and distribution of floral scent. *Bot. Rev* 72, 1. doi:10.1663/0006-8101(2006)72[1:DADOF5]2.0.CO;2.
- Kobayakawa, K., Kobayakawa, R., Matsumoto, H., Oka, Y., Imai, T., Ikawa, M., et al. (2007). Innate versus learned odour processing in the mouse olfactory bulb. *Nature* 450, 503–508. doi:10.1038/nature06281.
- Leeuwenhoek, A. V. (1679). Observationes D. Anthonii Lewenhoeck, de natis'e semine genitali animalculis. *Phil. Trans. R. Soc.* 12, 1040–1046. doi:10.1098/rstl.1677.0068.
- Lefèvre, P. L. C., Palin, M.-F., and Murphy, B. D. (2011). Polyamines on the Reproductive Landscape. *Endocrine Reviews* 32, 694–712. doi:10.1210/er.2011-0012.
- Lenis, Y., Elmetwally, M., Maldonado-Estrada, J., and Bazer, F. (2017). Physiological importance of Polyamines. *Zygote* 25. doi:10.1017/S0967199417000120.
- Li, G., Jia, H., Wu, R., and Teng, Y. (2013). Changes in volatile organic compound composition during the ripening of 'Nanguoli' pears (*Pyrus ussuriensis* Maxim) harvested at different growing locations. *The Journal of Horticultural Science and Biotechnology* 88, 563–570. doi:10.1080/14620316.2013.11513007.
- Liberles, S. D. (2015). Trace amine-associated receptors: ligands, neural circuits, and behaviors. *Current Opinion in Neurobiology* 34, 1–7. doi:10.1016/j.conb.2015.01.001.
- Liberles, S. D., and Buck, L. B. (2006). A second class of chemosensory receptors in the olfactory epithelium. *Nature* 442, 645–650. doi:10.1038/nature05066.
- Lindemann, L., Ebeling, M., Kratochwil, N. A., Bunzow, J. R., Grandy, D. K., and Hoener, M. C. (2005). Trace amine-associated receptors form structurally and functionally distinct subfamilies of novel G protein-coupled receptors. *Genomics* 85, 372–385. doi:10.1016/j.ygeno.2004.11.010.
- Luo, L. (2016). *Principles of Neurobiology*. New York: Garland Science.
- Luskin, M. B., and Price, J. L. (1982). The distribution of axon collaterals from the olfactory bulb and the nucleus of the horizontal limb of the diagonal band to the olfactory cortex, demonstrated by double retrograde labeling techniques. *J Comp Neurol* 209, 249–263. doi:10.1002/cne.902090304.
- Ma, L., Qiu, Q., Gradwohl, S., Scott, A., Yu, E. Q., Alexander, R., et al. (2012). Distributed representation of chemical features and tunotopic organization of glomeruli in the mouse olfactory bulb. *Proc Natl Acad Sci U S A* 109, 5481–5486. doi:10.1073/pnas.1117491109.
- Malnic, B., Hirono, J., Sato, T., and Buck, L. B. (1999). Combinatorial receptor codes for odors. *Cell* 96, 713–723. doi:10.1016/s0092-8674(00)80581-4.

- Miki, Y., Tomita, N., Ban, K., Sajiki, H., and Sawama, Y. (2021). Synthesis of 1-Pyrroline by Denitrogenative Ring Expansion of Cyclobutyl Azides under Thermal Conditions. *Advanced Synthesis & Catalysis* 363, 3481–3484. doi:10.1002/adsc.202100329.
- Miller, R. L., Bills, D. D., and Buttery, R. G. (1989). Volatile components from Bartlett and Bradford pear leaves. *J. Agric. Food Chem.* 37, 1476–1479. doi:10.1021/jf00090a005.
- Mombaerts, P., Wang, F., Dulac, C., Chao, S. K., Nemes, A., Mendelsohn, M., et al. (1996). Visualizing an olfactory sensory map. *Cell* 87, 675–686. doi:10.1016/s0092-8674(00)81387-2.
- Mores, A., Matziari, M., Beau, F., Cuniasse, P., Yiotakis, A., and Dive, V. (2008). Development of Potent and Selective Phosphinic Peptide Inhibitors of Angiotensin-Converting Enzyme 2. *J. Med. Chem.* 51, 2216–2226. doi:10.1021/jm701275z.
- Mühlhaus, J., Dinter, J., Nürnberg, D., Rehders, M., Depke, M., Golchert, J., et al. (2014). Analysis of Human TAAR8 and Murine Taar8b Mediated Signaling Pathways and Expression Profile. *Int J Mol Sci* 15, 20638–20655. doi:10.3390/ijms151120638.
- Nassar, M. I., Mohamed, T. K., El-Toumy, S. A., Gaara, A. H., El-Kashak, W. A., Brouard, I., et al. (2011). Phenolic metabolites from *Pyrus calleryana* and evaluation of its free radical scavenging activity. *Carbohydrate Research* 346, 64–67. doi:10.1016/j.carres.2010.11.007.
- Novita Sari, I., Setiawan, T., Seock Kim, K., Toni Wijaya, Y., Won Cho, K., and Young Kwon, H. (2021). Metabolism and function of polyamines in cancer progression. *Cancer Letters* 519, 91–104. doi:10.1016/j.canlet.2021.06.020.
- Oefner, P. J., Wongyai, S., and Bonn, G. (1992). High-performance liquid chromatographic determination of free polyamines in human seminal plasma. *Clinica Chimica Acta* 205, 11–18. doi:10.1016/0009-8981(92)90349-U.
- Ogawa, K., Nomura, Y., Takeuchi, Y., and Tomoda, S. (1982). Silver(I)-catalyzed oxidation of cyclic secondary amines with peroxodisulphate. *J. Chem. Soc., Perkin Trans. 1*, 3031–3035. doi:10.1039/p19820003031.
- Oka, Y., Katada, S., Omura, M., Suwa, M., Yoshihara, Y., and Touhara, K. (2006). Odorant Receptor Map in the Mouse Olfactory Bulb: In Vivo Sensitivity and Specificity of Receptor-Defined Glomeruli. *Neuron* 52, 857–869. doi:10.1016/j.neuron.2006.10.019.
- Owen, S. M., Boissard, C., and Hewitt, C. N. (2001). Volatile organic compounds (VOCs) emitted from 40 Mediterranean plant species: VOC speciation and extrapolation to habitat scale. *Atmospheric Environment* 35, 5393–5409. doi:10.1016/S1352-2310(01)00302-8.
- Pacifico, R., Dewan, A., Cawley, D., Guo, C., and Bozza, T. (2012). An Olfactory Subsystem that Mediates High-Sensitivity Detection of Volatile Amines. *Cell Reports* 2, 76–88. doi:10.1016/j.celrep.2012.06.006.
- Papes, F., Nakahara, T. S., and Camargo, A. P. (2018). “Behavioral Assays in the Study of Olfaction: A Practical Guide,” in *Olfactory Receptors*, eds. F. M. Simoes de Souza and G. Antunes (New York, NY: Springer New York), 289–388. doi:10.1007/978-1-4939-8609-5\_21.
- Pichersky, E., and Dudareva, N. eds. (2020). *Biology of Plant Volatiles*. 2nd ed. Boca Raton: CRC Press.
- Ragubeer, C. (2015). The emission of volatile organic compounds (VOCs) from rotting fruits and wilting flowers. Available at: <https://researchspace.ukzn.ac.za/handle/10413/13940> [Accessed September 6, 2021].
- Ramos, J., Tran, M., Turan, D., and Rodriguez, M. (2017). Student Voice Committee ASUCR Presentation.
- Reid, L. (2015). What’s That Smell? The Beautiful Tree That’s Causing Quite A Stink. Available at: <https://www.npr.org/2015/04/24/401943000/whats-that-smell-the-beautiful-tree-thats-causing-quite-a-stink> [Accessed October 29, 2019].
- Rennaker, R. L., Chen, C.-F. F., Ruyle, A. M., Sloan, A. M., and Wilson, D. A. (2007). Spatial and temporal distribution of odorant-evoked activity in the piriform cortex. *J Neurosci* 27, 1534–1542. doi:10.1523/JNEUROSCI.4072-06.2007.
- Ressler, K. J., Sullivan, S. L., and Buck, L. B. (1994). Information coding in the olfactory system: Evidence for a stereotyped and highly organized epitope map in the olfactory bulb. *Cell* 79, 1245–1255. doi:10.1016/0092-8674(94)90015-9.
- Root, C. M., Denny, C. A., Hen, R., and Axel, R. (2014). The participation of cortical amygdala in innate, odour-driven behaviour. *Nature* 515, 269–273. doi:10.1038/nature13897.
- Rubin, B. D., and Katz, L. C. (1999). Optical Imaging of Odorant Representations in the Mammalian Olfactory Bulb. *Neuron* 23, 499–511. doi:10.1016/S0896-6273(00)80803-X.
- Saraiva, L. R., Kondoh, K., Ye, X., Yoon, K., Hernandez, M., and Buck, L. B. (2016). Combinatorial effects of odorants on mouse behavior. *Proc Natl Acad Sci USA* 113, E3300–E3306. doi:10.1073/pnas.1605973113.
- SciShow (2017). Why Do We Keep Planting Trees That Smell Like Semen? Available at: <https://www.youtube.com/watch?v=6Vj4DCGnynQ> [Accessed May 10, 2021].

- Scott, A. M., Zhang, Z., Jia, L., Li, K., Zhang, Q., Dexheimer, T., et al. (2019). Spermine in semen of male sea lamprey acts as a sex pheromone. *PLoS Biol* 17, e3000332. doi:10.1371/journal.pbio.3000332.
- Scott, J. W., McBride, R. L., and Schneider, S. P. (1980). The organization of projections from the olfactory bulb to the piriform cortex and olfactory tubercle in the rat. *J Comp Neurol* 194, 519–534. doi:10.1002/cne.901940304.
- Serizawa, S., Miyamichi, K., and Sakano, H. (2004). One neuron–one receptor rule in the mouse olfactory system. *Trends in Genetics* 20, 648–653. doi:10.1016/j.tig.2004.09.006.
- Sharma, K., Syed, A. S., Ferrando, S., Mazan, S., and Korsching, S. I. (2019). The Chemosensory Receptor Repertoire of a True Shark Is Dominated by a Single Olfactory Receptor Family. *Genome Biol Evol* 11, 398–405. doi:10.1093/gbe/evz002.
- Sheth, A. R., and Moodbidri, S. B. (1977). Significance of polyamines in reproduction. *Adv Sex Horm Res* 3, 51–74.
- Shuttleworth, A. (2016). Smells like debauchery: The chemical composition of semen-like, sweat-like and faintly foetid floral odours in *Xysmalobium* (Apocynaceae: Asclepiadoideae). *Biochemical Systematics and Ecology* 66, 63–75. doi:10.1016/j.bse.2016.03.009.
- Shvekhgeimer, M.-G. A. (2003). Methods for the Synthesis of 3,4-2H-Dihydropyrroles ( $\Delta^1$ -Pyrrolines) and Their Chemical Transformations. (Review). *Chemistry of Heterocyclic Compounds* 39, 405–448. doi:10.1023/A:1024753027533.
- Sieckmann, T., and Kirschner, K. M. (2020). Polyamines, metabolites and metabolomics. *Acta Physiologica* 229, e13480. doi:10.1111/apha.13480.
- Solomon, S. (2021). Why those beautiful, white-blossomed trees around Sacramento smell. *abc10.com*. Available at: <https://www.abc10.com/article/life/smell-trees-sacramento-bloom-ornamental-pear/103-571abd5b-9574-4c88-aa1e-2cabbdbc3c5> [Accessed April 5, 2021].
- Sosulski, D. L., Bloom, M. L., Cutforth, T., Axel, R., and Datta, S. R. (2011). Distinct representations of olfactory information in different cortical centres. *Nature* 472, 213–216. doi:10.1038/nature09868.
- Spector, D. (2013). Why all of New York City smells like sex these days. *Business Insider*. Available at: <https://www.businessinsider.com/bradford-pear-tree-semen-sex-smell-2013-4> [Accessed October 29, 2019].
- Stettler, D. D., and Axel, R. (2009). Representations of Odor in the Piriform Cortex. *Neuron* 63, 854–864. doi:10.1016/j.neuron.2009.09.005.
- Takahashi, Y. K., Kurosaki, M., Hirono, S., and Mori, K. (2004). Topographic Representation of Odorant Molecular Features in the Rat Olfactory Bulb. *Journal of Neurophysiology* 92, 2413–2427. doi:10.1152/jn.00236.2004.
- Tholl, D., Boland, W., Hansel, A., Loreto, F., Röse, U. S. R., and Schnitzler, J.-P. (2006). Practical approaches to plant volatile analysis. *The Plant Journal* 45, 540–560. doi:10.1111/j.1365-313X.2005.02612.x.
- UFEI (1995a). SelecTree: A Tree Selection Guide. *Pyrus kawakamii Tree Record*. Available at: <https://selecttree.calpoly.edu/tree-detail/1222> [Accessed May 7, 2021].
- UFEI (1995b). SelecTree: A Tree Selection Guide. *Pyrus calleryana Tree Record*. Available at: <https://selecttree.calpoly.edu/tree-detail/1214> [Accessed May 7, 2021].
- Van, S. (2015). Conversation blossoms about tree scent. *Highlander*. Available at: <https://www.highlandernews.org/16505/conversation-blossoms-about-tree-scent/> [Accessed May 10, 2021].
- Vassar, R., Chao, S. K., Sitcheran, R., Nuñez, J. M., Vosshall, L. B., and Axel, R. (1994). Topographic organization of sensory projections to the olfactory bulb. *Cell* 79, 981–991. doi:10.1016/0092-8674(94)90029-9.
- Wallrabenstein, I., Kuklan, J., Weber, L., Zborala, S., Werner, M., Altmüller, J., et al. (2013). Human Trace Amine-Associated Receptor TAAR5 Can Be Activated by Trimethylamine. *PLOS ONE* 8, e54950. doi:10.1371/journal.pone.0054950.
- Williams-Ashman, H. G., and Lockwood, D. H. (1970). Role of Polyamines in Reproductive Physiology and Sex Hormone Action\*. *Annals of the New York Academy of Sciences* 171, 882–894. doi:10.1111/j.1749-6632.1970.tb39395.x.
- Xu, Z., and Li, Q. (2020). TAAR Agonists. *Cell Mol Neurobiol* 40, 257–272. doi:10.1007/s10571-019-00774-5.
- Yoshikawa, K., Libbey, L. M., Cobb, W. Y., and Day, E. A. (1965). 1-Pyrroline: The Odor Component of Strecker-Degraded Proline and Ornithine. *Journal of Food Science* 30, 991–994. doi:10.1111/j.1365-2621.1965.tb01875.x.
- Zhang, X., Chingin, K., Zhong, D., Liang, J., Ouyang, Y., and Chen, H. (2017). On the chemistry of 1-pyrroline in solution and in the gas phase. *Sci Rep* 7, 7675. doi:10.1038/s41598-017-08217-1.

- Zhang, X., Chingin, K., Zhong, D., Luo, L., Frankevich, V., and Chen, H. (2018). Deciphering the chemical origin of the semen-like floral scents in three angiosperm plants. *Phytochemistry* 145, 137–145. doi:10.1016/j.phytochem.2017.11.001.
- Zhang, X., Ji, Y., Zhang, Y., Liu, F., Chen, H., Liu, J., et al. (2019). Molecular analysis of semen-like odor emitted by chestnut flowers using neutral desorption extractive atmospheric pressure chemical ionization mass spectrometry. *Anal Bioanal Chem* 411, 4103–4112. doi:10.1007/s00216-018-1487-7.