应用昆虫学报 *Chinese Journal of Applied Entomology* 2025, 62(4): 851–866. DOI: 10.7679/j.issn.2095−1353.2025.081

前沿与综述

昆虫嗅觉编码的分子功能研究进展*

黄敏君[1,2**] 唐 睿[1***]

（1. 广东省科学院动物研究所，广东省动物保护与资源利用重点实验室，
广东省野生动物保护与利用公共实验室，广州 510260；2. 仲恺农业工程学院，广州 510225）

摘 要 昆虫依靠嗅觉定位寄主、躲避天敌、寻找配偶，从而适应不断变化的环境。近半个世纪以来，通过神经行为学和分子生物学的结合，昆虫外周嗅觉系统的神经结构和分子基础得到了深入研究。大多数昆虫中嗅觉感觉神经元位于相应的感器中检测气味，然后将其轴突投射到触角叶中的神经纤维球，位于神经元树突上的气味受体/气味受体共受体复合物在气味识别中起着关键作用。一般来说，昆虫的嗅觉系统可以通过一个经典原则总结：一类嗅觉感觉神经元上表达气味受体家族的一个成员，并汇聚投射到触角叶的同一个神经纤维球。近年来，随着对昆虫嗅觉蛋白功能和进化研究的不断深入，昆虫的嗅觉编码机制受到越来越广泛的关注。昆虫不仅有多种器官充当"鼻孔"，而且一些非气味受体家族如味觉受体、离子通道型受体和瞬时受体电位通道等也被发现参与昆虫的嗅觉活动。最近的研究表明人类世界的空气污染物会扰乱昆虫的嗅觉定位。因此，昆虫的嗅觉如何在人类世界中进化和适应将是未来重要的研究方向。

关键词 嗅觉；感器；气味受体；触角叶；神经纤维球；适应性

Advances in research on the molecular basis of insect olfactory coding

HUANG Min-Jun[1,2**] TANG Rui[1***]

(1. Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou 510260, China; 2. Zhongkai University of Agriculture and Engineering, Guangzhou 510225, China)

Abstract Insects rely on olfaction to locate hosts, avoid enemies, find mates, and more importantly, to adapt to an ever-changing environment. The integration of neuroethology and molecular biology over the last half-century has led to the neural architecture and molecular basis of the peripheral insect olfactory system being better understood. Normally, the olfactory sensory neurons (OSNs), housed in corresponding sensilla, detect odorants and then project their axons into the glomeruli of the antennal lobe. The odorant receptor/odorant receptor co-receptor (OR/ORco) complex on the OSNs' dendrite plays a key role in odorant recognition. In most cases, insect olfactory systems can be summarized via a classic formula; one class of OSN expresses one member of the OR family, and converges to the same glomerulus in the brain. However, recent advances in research on receptor deorphanization and evolution suggest that this process of olfactory coding is more complex. Not only do multiple organs act as the 'nostrils' of insects, but also some non-OR receptor families, such as the gustatory receptors (GRs), ionotropic receptors (IRs), and transient receptor potential (TRP) channels, are involved in olfaction. Some studies have found that air pollutants are interfering with insect olfaction. How insect olfaction evolves and adapts to such anthropogenic factors should become an increasingly important topic of research.

Key words olfaction; sensillum; odorant receptor; antennal lobe; glomerulus; adaptation

---

*资助项目 Supported project：国家重点研发计划（2023YFC2606900）

**第一作者 First author，E-mail：2260432036@qq.com

***通讯作者 Corresponding author，E-mail：tangr@giz.gd.cn

收稿日期 Received：2024-04-18；接受日期 Accepted：2024-06-09

昆虫利用多种感觉系统来响应各种刺激，包括化学物质、视觉、触觉、声音、温度和湿度等。与其它刺激不同的是，化学信号具有结构多样性、隐蔽性等优势，因此也可能包括环境中的持久性污染物。昆虫主要通过嗅觉和味觉感受辨别化学信号，与水溶性/接触性化合物相比，空气中的气味更易扩散和传递信息。为了感知来自寄主、天敌和同类的信息，昆虫进化出了复杂的嗅觉系统，可以在数千种化学物质中区分有意义的气味（Haverkamp *et al*., 2018）。昆虫的嗅觉随环境压力而进化，其中涉及大量行为决策，在行为背景下比较生态和进化框架中的神经元回路的研究方法被称为神经行为学（Neuroethology），通常这一类研究涉及自然行为，是通过演化与比较等方法对动物行为及其神经系统机制进行研究的学科（Hoyle, 1984）。近几十年来，随着神经和分子生物学技术的发展，昆虫嗅觉系统的研究已从形态和分子功能角度得到了深入的探索（杨斌等, 2020）。

1 昆虫嗅觉系统的神经基础

触角在昆虫嗅觉感知过程中起着关键作用。为了满足昆虫的生态需求，触角在不同类群中表现出形态多样性（Keil, 1999）。此外，在长期的进化过程中，近缘物种触角形态的多样性也在发生改变。例如，在白垩纪中期的琥珀标本中，缘蝽科 Coreidae 显示出宽阔的叶状触角，这与它们的现代亲属不同（Du *et al*., 2020）。嗅觉感器位于触角上，是昆虫嗅觉的基本单位。基于它们的形状，感器被分为不同的类别，包括毛形感器、锥形感器、中间形感器和腔锥形感器等（Stocker, 1994; Shanbhag *et al*., 1999）。不同的感器类别均具有相似的内部神经结构，其中的嗅觉感觉神经元（Olfactory sensory neurons, OSNs）和支持细胞在嗅觉感器中被区隔开来（Zacharuk, 1980; Kaissling, 1986）。感器中的神经元数量也显示出多样性，黑腹果蝇 *Drosophila melanogaster* 感器中的 OSN 为 2-4 个，而沙漠蝗 *Schistocerca gregaria* 则为 20-50 个（Ochieng *et al*., 1998）。

气味通过感器角质层上的孔隙或狭缝进入感器淋巴，并与其中的气味结合蛋白（Odorant binding protein, OBP）对接（Steinbrecht, 1997），由 OBP 将气味送达树突膜上的气味受体（Odorant receptor, OR）和气味受体共受体（Odorant receptor co-receptor, ORco）复合物，并引发非选择性阳离子通道打开，产生去极化神经电信号（Gao and Chess, 1999; Malnic *et al*., 1999; Vosshall *et al*., 1999; Larsson *et al*., 2004; Benton *et al*., 2006; Butterwick *et al*., 2018; Fleischer *et al*., 2018），而后气味被气味降解酶（Odorant-degrading enzyme, ODE）降解（Ishida and Leal, 2005; Leal, 2013）。通常，OR/ORco 复合物对于昆虫识别气味是必须的（Vosshall *et al*., 1999; Elmore *et al*., 2003; Krieger *et al*., 2003; Larsson *et al*., 2004; Sato *et al*., 2008; Wicher *et al*., 2008），但最近在石蛃目中的研究表明，早期物种中的 OR 可以不依赖 ORco 独立完成嗅觉功能（del Mármol *et al*., 2021）。与高度保守的 ORco 不同，OR 在昆虫物种中的数量和功能有较大变化（Touhara and Vosshal, 2009; 胡颖颖等, 2013）。此外，昆虫本身也已进化出不同的气味编码模式，以满足其生态需要。因此，对 OR 进行大规模的功能验证可以提供关于物种生态适应性的重要信息（Hallem *et al*., 2004; Hallem and Carlson, 2006; de Fouchier *et al*., 2017; Di *et al*., 2017; Hou *et al*., 2021）。

在 OR/ORco 复合物被相应的气味配体激活后，电位信号从树突逐级传递到轴突和触角叶（Antennal lobe, AL）。昆虫的 AL 与脊椎动物的嗅球同源，且都由神经纤维球组成（Hildebrand and Shepherd, 1997; Touhara and Vosshall, 2009; Hansson and Stensmyr, 2011; 张瑜等, 2016）。表达同一 OR 的 OSN 会聚于相同的神经纤维球，这是昆虫嗅觉系统的一个 OR-一个 OSN-一个神经纤维球法则（Vosshall, 2000; de Bruyne and Baker, 2008）。在鳞翅目昆虫中，AL 的性别差异现象明显，雄性特异的巨大神经纤维球复合体（Macroglomerular complex, MGC）位于触角的入口处，并主要处理信息素信号，调控种内和种间行为（Boeckh and Boeckh, 1979; Koontz and Schneider, 1987; Hansson *et al*., 1992; Ignell *et al*., 1998）。神经纤维球数量因物种而异（Vosshall *et al*.,

2000），如在沙漠蝗的 AL 中分布有超过 1 000 个神经纤维球，而鳞翅目蛾类昆虫中一般不超过 80 个，黑腹果蝇则为 43 个（Hansson *et al*., 1996; Anton *et al*., 2002）（表 1）。OR-OSN-AL 调控的昆虫外周嗅觉编码气味有两种方式：具有耗时评估的广谱调谐气味的组合编码方式和用于要求即时/先天响应的窄谱调谐气味的线性编码方式（Dethier, 1982; Haverkamp *et al*., 2018）。昆虫普遍遵循上述法则且同时存在两种嗅觉编码策略来区分不同来源化感物质，介导特异的行为模式。但是，有的物种进化出了特化的嗅觉系统以适应环境，例如东亚飞蝗 *Locusta migratoria* 的气味受体普遍具有窄识别谱（Chang *et al*., 2023）。又如埃及伊蚊 *Aedes aegypti* 进化出了独特的嗅觉系统，通过在同一 OSN 上表达多种受体，提升对关键气味的识别性（Herre *et al*., 2022）。

2　基于信息素的嗅觉编码

昆虫对信息素的感受通过典型的线性编码实现，阐明信息素感受机制对解析昆虫与环境的化学通讯具有重要参考。信息素由昆虫感器淋巴内的信息素结合蛋白（Pheromone binding protein, PBP）捕获，然后被转运到 OSN 的神经元膜蛋白 1（Sensory neuron membrane protein 1, SNMP 1）和信息素受体（Pheromone receptor, PR）/ORco 复合物（Fleischer *et al*., 2018）。SNMP 1 被认为将结合配体的 PBP 定位在识别配体的 PR 附近和/或参与信息素向 PR 的释放（Benton *et al*., 2007; Gomez-Diaz *et al*., 2016）。自 60 多年前蚕蛾醇的发现以来（Butenandt *et al*., 1961），鳞翅目昆虫一直是研究性信息素嗅觉调控的重要类群，目前已知大约 75%的物种利用 I 型信息素，其包括 C10-C18 乙酸酯、醇和醛（Ando *et al*., 2004; Löfstedt *et al*., 2016）。I 型信息素的调谐由一类保守进化的气味受体分支完成，也被称为典型的信息素受体分支（Classic PR clade）（Wanner *et al*., 2007）。然而，最近的研究表明，PR 分支之外的偏性别表达 OR 也参与信息素感受，例如 *Lampronia capitella* 中偏雄表达的 OR6 和 OR8 分别调控信息素 *Z*9，*E*11-十四碳烯醛（*Z*9，*E*11-14：Ald）和 *Z*9，*E*11-十四碳烯醇（*Z*9，*E*11-14：OH），而后进一步发现在高等蛾类如夜蛾中也存在典型 PR 分支外的新 PR 分支（Yuvaraj *et al*., 2018; Bastin-Héline *et al*., 2019）。

鳞翅目的典型 PRs 主要用于识别种内性信息素组分，具有专一性，单个氨基酸残基改变即足以影响配体的识别（Leary *et al*., 2012; Yang *et al*., 2018; Cao *et al*., 2021），同时具有相似调谐谱的多个直系同源 PR 亦可通过靶向 MGC 区不同的神经纤维球，调控夜蛾种间化学交流，强化合子前生殖隔离，平衡同域发生物种的生态位竞争（Jiang *et al*., 2020）。蛾类中典型 PR 分支的扩张和出现是昆虫化学感受系统对环境适应性演化的重要事件，但这一过程目前仍不清楚。通过组学技术研究气味受体结构和功能的演化，可为解析典型 PR 的起源提供参考（程李莉等, 2023）。利用原始的鳞翅目物种如蝙蝠蛾基因组，分析发现在染色体上物理串联的基因可通过非对称演化产生新的功能基因（Holland *et al*., 2017）。我们在鳞翅目 OR 的演化中观察到了类似的现象，比较基因组分析显示最早具备典型 PR 序列结构域的蛋白可以追溯到比鳞翅目更早的毛翅目类群，之后蛾类的典型 PR 在各物种中可能通过非对称演化模式进行平行分化（Tang *et al*., 2024），与 Zhang 等（2024）推测的新 PR 分支的平行分化起源类似。同时，由于 PR 的配体-受体保守性，同科或同属内 PR 的进化更倾向于线性进化，通过核苷酸位点突变产生新的功能（Li *et al*., 2023），这一现象在对植物源气味感受的 OR 中也存在（Guo *et al*., 2021），可推测昆虫 ORs 的功能演化存在一些通用模式。

3　昆虫嗅觉调控的部位扩展

对昆虫来说，除了触角这一主要嗅觉器官之外，已证实多个器官都高度参与嗅觉调控。黑腹果蝇的头部化学感受器官下颚须中，每对含有 120 个感觉神经元，这些神经元储存在 60 个基底感器中，并表达 7 种不同的气味受体（de Bruyne *et al*., 1999; Dweck *et al*., 2016）。进一步研究表明，果蝇的下颚须对某些特定气味非常敏

感，这些气味在短距离和长距离上都可介导行为趋向，调控模式并非接触型的味觉（Singh and Nayak, 1985; de Bruyne *et al*., 1999; Hallem *et al*., 2006; Dweck *et al*., 2016）。蛾类和蚊子的下唇须/下颚须与 CO_2 检测有关，而果蝇则利用触角的 ab1C 神经元来检测这一物质（Kent *et al*., 1986; Thom *et al*., 2004; Kwon *et al*., 2007; Lu *et al*., 2007; Turner and Ray, 2009; de Bruyne *et al*., 2010; Ning *et al*., 2016）。在沙漠蝗中，下唇须和下颚须表达 SNMP1，表明两者都可能参与对信息素的感受（Lemke *et al*., 2020）。可见下唇须/下颚须的化学感受功能在昆虫物种中分化较大（刘金香等, 2005; 汤清波等, 2011）。

嗅觉反应也存在于一种味觉器官——喙。烟草天蛾 *Manduca sexta* 利用喙来检测苯乙酮，以提高适应性（Haverkamp *et al*., 2016）。然而，通过喙感受的气味对烟草天蛾无法形成学习行为，表明喙和触角的嗅觉感受在信号通路上具有差别（Adam *et al*., 2021）。类似的现象也发现在冈比亚按蚊 *Anopheles gambiae* 中，其喙上的 OSN 共表达 AgOR6 和 AgORco，对人体皮肤气味物质产生反应，并将信号投射到咽下神经节（Subesophageal ganglion, SOG）或触角叶（Pitts *et al*., 2004; Kwon *et al*., 2006; Riabinina *et al*., 2016）。此外，埃及伊蚊的喙表达 OR8、OR49 和 ORco，对血液挥发物进行调谐，分别投射到 2 个神经纤维球（Jung *et al*., 2015）。

研究报道，产卵器对于识别和辨认产卵地的挥发性信号起到重要作用。烟草天蛾的产卵器上有数个感器具有多孔结构，并且表达了 MsOR9、MsOR26 和 MsOrco 受体（Klinner *et al*., 2016），通过单感器记录（Single sensillum recording, SSR）进一步发现此类感器对 *γ*-己内酯、甲基-1-戊醇和其他气味具有敏感性（Klinner *et al*., 2016）。另外发现烟青虫 *Helicoverpa assulta* 产卵器上表达了 HassOr31 和 HassOrco 受体，用于调控在寄主植物上精确选择产卵位置（Li *et al*., 2020）。此外，缩腹榕小蜂属的 *Apocrypta westwoodi* 其产卵器在封闭的微环境下可感受挥发性化合物信号（Yadav and Borges, 2017）。然而，昆虫产卵器中 OSN 的中枢投射模式目前仍不清楚。

4　多基因家族对昆虫嗅觉的功能扩展

OR/ORco 是昆虫嗅觉感知过程最关键的功能单元。第一个昆虫 OR 通过果蝇基因组测序而被发现，归类为 G 蛋白偶联受体（G protein-coupled receptors, GPCRs）家族的成员（Clyne *et al*., 1999; Gao and Chess, 1999; Vosshall *et al*., 1999; Adams *et al*., 2000; Galizia *et al*., 2010）。与高度保守的 ORco 不同，不同物种的 OR 之间序列相似性较小（Larsson *et al*., 2004; Benton *et al*., 2006; 巩中军等, 2008; Touhara and Vosshall, 2009）。在 OR 进化方面，目前存在不同的观点。有学者认为 OR 和 ORco 的起源是从味觉受体（Gustatory receptor, GR）家族进化而来，实现从水生到陆生生活方式的适应（Robertson *et al*., 2003; Krång *et al*., 2012）。但通过对早期昆虫物种的触角转录组测序发现，石蛃目 Archaeognatha 昆虫 *Lepismachilis y-signata* 缺乏 OR 和 ORco；衣鱼目 Zygentoma 的斑衣鱼 *Thermobia domestica* 缺乏 OR，但存在 3 个 ORco 的同源基因；而竹节虫目 Phasmatodea 的东方叶䗛 *Phyllium siccifolium* 存在 OR/ORco 系统（Missbach *et al*., 2014）。这些结果表明，OR 并非为应对陆生生活方式的适应而产生，而是在昆虫纲进化的较晚阶段产生的功能演化，且共受体 ORco 在 OR 之前出现（Missbach *et al*., 2014）。通过对弹尾目 Collembola、双尾目 Diplura、石蛃目、衣鱼目、蜻蛉目 Odonata 和蜉蝣目 Ephemeroptera 的基因组进行分析，发现 ORco 仅在原始无翅昆虫石蛃目中缺失，而在斑衣鱼中发现了完整的 OR/ORco 系统（Brand *et al*., 2018）。这些结果证实了 OR 在昆虫有翅飞行之前就进化产生，可能作为对陆地环境的适应（Brand *et al*., 2018）。对斑衣鱼中 OR 数量不同报道的原因可能是：首先，这些 OR 在组织、生命周期和测序深度上可能具有不同的表达模式（Brand *et al*., 2018）；其次，基于当前大量新翅下纲 Neoptera 物种的 OR 进行注释和分析可能存在偏差，因为早期昆虫中的“原始 OR”与现代昆虫的 OR 不同（Thoma *et al*., 2019）。最近，石蛃目物种 *Machilis hrabei* 的

OR5 被发现可组成具有广泛化学调谐谱的四聚体气味门控离子通道，与昆虫 GR 的功能单元类似（del Mármol *et al*., 2021; Ma *et al*., 2024），表明在原始昆虫物种中 OR 无需 ORco 存在而可单独行使嗅觉功能，因此 OR 可能比 ORco 更早出现。为了了解昆虫中 OR 的演化，需要对更加关键的物种如衣鱼目等的 OR 或 OR/ORco 进行功能研究。

除 ORs 以外，GRs、离子通道型受体（Ionotropic receptor, IRs）和瞬时受体电位（Transient receptor potential, TRPs）通道也参与昆虫嗅觉感受。其中，GRs 和 ORs 都起源于真核祖先中的“味觉受体样受体”（杜立啸等, 2016; Benton *et al*., 2020）。昆虫的 GR 最早也是从果蝇基因组中发现的（Clyne *et al*., 2000），它们被分为 4 个分支：CO_2、GR43a-like、糖类和苦味 GR 分支（Slone *et al*., 2007; Wanner and Robertson, 2008; Kent and Robertson, 2009; Robertson and Kent, 2009; Sato *et al*., 2011）。其中，编码 CO_2 的 GR 分支与 ORs 相似，都具有 7 次跨膜结构（Jones *et al*., 2007）。在果蝇中，GR21a 与 GR63a 共同表达，用于 CO_2 嗅觉感受（Suh *et al*., 2004; Kwon *et al*., 2006; Jones *et al*., 2007）。蛾类的 HarmGr1、HarmGr3 和蚊子的 AgGR22、AgGR24 受体同样被报道用于对 CO_2 的嗅觉探测（Hill *et al*., 2002; Lu *et al*., 2007; McMeniman *et al*., 2014; Ning *et al*., 2016; Xu, 2020）。

此外，通过生物信息学分析和基因表达筛选，在果蝇中发现了一种与保守的离子型谷氨酸受体（Ionotropic glutamate receptors, iGluRs）高度分化的新受体家族，命名为离子通道型受体 IRs（Benton *et al*., 2009）。IRs 很可能存在于原口动物（Protostomia）的共同祖先中（Croset *et al*., 2010）。其中 IR8a、IR25a、IR93a 和 IR76b 被认为是 IRs 的共受体（Benton *et al*., 2009; Abuin *et al*., 2011; Silbering *et al*., 2011; Ai *et al*., 2013; Hussain *et al*., 2018; 莫建初等, 2019; Ni, 2021）。通过对腔锥感器进行神经电生理记录研究，确定了表达 IR 的 OSNs，并且发现了这类 OSNs 的配体几乎都是胺类、羧酸或醛类（表 1）（Yao *et al*., 2005; Silbering *et al*., 2011）。利用 Cas9 介导 *T2A-QF2* 的新遗传敲入（Knock-in）策略，与 *UAS-GFP* 品系杂交定位果蝇中的 4 个共受体（*ORco*、*IR8a*、*IR25a*、*IR76b*），发现 *IR25a* 广泛表达于 OSNs 中，包括下颚须中的所有神经元类别（Task *et al*., 2022），同时 *ORco*、*IR8a* 和 *IR76b* 的表达模式也有所扩展（Task *et al*., 2022）。IRs 家族的发现颠覆了对昆虫嗅觉系统的一贯认识，早期在果蝇触角中以多色荧光原位杂交方法观察到 *ORco* 和 *IR76b* 共受体可能在同一 OSN 中表达，但后续研究显示果蝇表达 *OR* 和 *IR* 的 OSNs 在触角叶中神经纤维球的投射严格分离，仍然遵循已知的昆虫嗅觉模式（Benton *et al*., 2009; Grabe *et al*., 2016）。最新研究发现埃及伊蚊使用完全不同的组织原理来构建其嗅觉系统，许多神经元共同表达至少 2 个化学感受受体家族的成员，并且其 *OR* 和 *IR* 所在 OSNs 在触角叶中的神经纤维球投射互相重叠（Herre *et al*., 2022）。同一时期，对疟蚊 *Anopheles coluzzii* 的研究发现了 *IR25a* 和 *ORco*、*IR76b* 和 *ORco* 共表达的情况，而黑腹果蝇和果蝇 *D. sechellia* 中的研究也表明 *IR25a* 和 *ORco* 共表达，Raji 和 Potter（2022）及 Task 等（2022）认为在昆虫的嗅觉神经元中不同化感受体的共表达可能是常见现象。然而，由于昆虫的 IRs 共受体同时具备温度、湿度、味觉等多种调控功能，仅通过其广泛的表达情况尚不足以判断除埃及伊蚊外其他物种的嗅觉模式（Chen *et al*., 2015; Rimal and Lee, 2018）。总之，上述发现对昆虫嗅觉中经典的“一个 OR-一个 OSN-一个神经纤维球”模式提出了挑战，ORs 和 IRs 在相同神经元共表达绘制了昆虫嗅觉的新蓝图。

另外，瞬时受体电位通道家族的部分蛋白也在昆虫嗅觉中发挥作用。TRP 通道具有 6 个跨膜结构域，分为 TRPC、TRPA、TRPM、TRPML、TRPV、TRPN 和 TRPP（Montell *et al*., 2002a, 2002b; Montell, 2005）。其中，TRPA 亚家族主要对热（或疼痛）和味觉物质作出反应（Montell, 2005; Joseph and Carlson, 2015），但一些昆虫的 TRPA 被发现参与嗅觉感受。例如，果蝇和蚊子的 TRPA1 被报道对猫薄荷 *Nepeta cataria* 植物中的气味物质荆芥内酯进行感受（Melo *et al*.,

表 1 黑腹果蝇的外周嗅觉系统功能编码

Table 1 Organization of peripheral olfactory system in *Drosophila melanogaster*

感器 Sensillum	神经元类型 OSN	受体 Receptor	共受体 Co-receptor	神经纤维球 Glomerulus	最佳配体 Best ligand
ab1	ab1A	OR42b	ORco	DM1	乙酸乙酯 Ethyl acetate（Kreher *et al*., 2008; Marshall *et al*., 2010; Münch and Galizia, 2016）
	ab1B	OR92a	ORco	VA2	乳酸乙酯 Ethyl lactate（Marshall *et al*., 2010）
	ab1C	GR21a, GR63a	NA NA	V 未知 Unknown	二氧化碳 Carbon dioxide（Marshall *et al*., 2010）
	ab1D	OR10a, GR10a	ORco NA	DL1 未知 Unknown	水杨酸甲酯 Methyl salicylate（Hallem *et al*., 2004; Marshall *et al*., 2010）
ab2	ab2A	OR59b	ORco	DM4	乙酸甲酯 Methyl acetate（Hallem *et al*., 2004; Marshall *et al*., 2010）
	ab2B	OR33b, OR85a	ORco ORco	DM5/DM5	2-乙基吡嗪 2-Ethylpyrazine/丙酸乙酯 Ethyl propionate（Kreher *et al*., 2008; Marshall *et al*., 2010; Montague *et al*., 2011） 3-羟基丁酸乙酯 Ethyl 3-hyroxybutyrate（Hallem *et al*., 2004）
ab3	ab3A	OR22a, OR22b	ORco	DM2 未知 Unknown	己酸甲酯 Methyl hexanoate（Dobritsa *et al*., 2003; Hallem *et al*., 2004; Pelz *et al*., 2006; Marshall *et al*., 2010）
	ab3B	OR85b	ORco	VM5d	2-庚酮 2-Heptanone（Hallem *et al*., 2004; Marshall *et al*., 2010）
ab4	ab4A	OR7a	ORco	DL5	反-2-己烯醛 E2-Hexenal（Hallem *et al*., 2004; Kreher *et al*., 2008; Marshall *et al*., 2010）
	ab4B	OR33a, OR56a	ORco	DA2/DA2 未知 Unknown	土臭素 Geosmin（Marshall *et al*., 2010; Stensmyr et al., 2012）
ab5	ab5A	OR82a	ORco	VA6	乙酸香叶酯 Geranyl acetate（Hallem *et al*., 2004; Kreher *et al*., 2008; Marshall *et al*., 2010）
	ab5B	OR33b, OR47a	ORco	DM3/DM3	2-乙基吡嗪 2-Ethylpyrazine/丙酸乙酯 Ethyl propionate（Marshall *et al*., 2010; Koerte *et al*., 2018） 乙酸戊酯 Pentyl acetate（Dobritsa *et al*., 2003; Hallem *et al*., 2004; Kreher *et al*., 2008）
ab6	ab6A	OR13a	ORco	DC2	1-辛烯-3-醇 1-Octen-3-ol（Kreher *et al*., 2008）
	ab6B	OR49b	ORco	VA5	2-甲基苯酚 2-Methyl phenol/愈创木酚 Guaiacol （Hallem *et al*., 2004; Marshall *et al*., 2010）
ab7	ab7A	OR98a	ORco	VM5v	苯甲酸乙酯 Ethyl benzoate（Hallem *et al*., 2004; Marshall *et al*., 2010）
	ab7B	OR67c	ORco	VC4	乳酸乙酯 Ethyl lactate（Marshall *et al*., 2010; Gabler *et al*., 2013）
ab8	ab8A	OR43b	ORco	VM2	反式-2-丁烯酸乙酯 Aethyl trans-2-butenoatus/丁酸乙酯 Ethyl butyrate（Hallem *et al*., 2004; Marshall *et al*., 2010; Gabler *et al*., 2013）
	ab8B	OR9a	ORco	VM3	2, 3-丁二醇 2,3-Butanediol（Marshall *et al*., 2010）

续表 1 (Table 1 continued)

感器 Sensillum	神经元类型 OSN	受体 Receptor	共受体 Co-receptor	神经纤维球 Glomerulus	最佳配体 Best ligand
ab9	ab9A	OR69aA, OR69aB	ORco	D	α-松油醇 α-Terpineol/香芹酮 Carvone/*Z*4-十一碳烯醛 *Z*4-11Ald（Lebreton *et al*., 2017）
	ab9B	OR67b	ORco	VA3	苯乙酮 Acetophenone（Kreher *et al*., 2005; Kreher *et al*., 2008）
ab10	ab10A	OR67a	ORco	DM6	6-甲基-5-庚烯-2-酮 6-Methyl-5-hepten-2-one/丁酸苄酯 Benzyl butyrate/丙酸丁酯 Butyl propanoate（Münch and Galizia, 2016）
	ab10B	OR49a, OR85f	ORco	DL4	伊蚁内酯 Iridomyrmecin/猕猴桃碱 Actinidine/荆芥醇 Nepetalactol（Kreher *et al*., 2005; Kreher *et al*., 2008; Ebrahim *et al*., 2015）
at1	at1A	OR67d	ORco	DA1	顺-11-十八烯酸乙酸酯 *cis*-11-Vaccenyl acetate（Kurtovic *et al*., 2007）
at4	at4A	OR47b	ORco	VA1v	月桂酸甲酯 Methyl laurate/棕榈油酸 Palmitoleic acid（Hallem *et al*., 2004; Lin *et al*., 2016）
	at4B	OR65a, OR65b, OR65c	ORco	DL3	顺-11-十八烯酸乙酸酯 *cis*-11-Vaccenyl acetate（van der Goes van Naters and Calson, 2007）
	at4C	OR88a	ORco	VA1d	棕榈酸甲酯 Methyl palmitate（van der Goes van Naters and Calson, 2007）
ai2	ai2A (at2A)	OR83c	ORco	DC3	法尼醇 Farnesol（Ronderos *et al*., 2014）
	ai2B (at2B)	OR23a	ORco	DA3	未知 Unknown（Münch and Galizia, 2016）
ai3	ai3A (at3A)	OR19a, OR19b	ORco	DC1	巴伦西亚橘烯 Valencene（Dweck *et al*., 2013）
	ai3B (at3B)	OR2a	ORco	DA4m	未知 Unknown（Kreher *et al*., 2008）
	ai3C (at3C)	OR43a	ORco	DA4l	1-己醇 1-Hexanol（Hallem *et al*., 2006）
ac1	ac1A	IR31a	IR8a	VL2p	2-氧代戊酸 2-Oxovaleric acid/2-戊酮酸 2-Oxopentanoic acid（Marshall *et al*., 2010; Silbering *et al*., 2011; Koerte *et al*., 2018）
	ac1B	IR75d	IR25a	VL1	吡咯烷 Pyrrolidine（Silbering *et al*., 2011）
	ac1C	IR92a	IR25a, IR76b	VL2p	二甲胺 Dimethylamine/氨 Ammonia（Silbering *et al*., 2011）
ac2	ac2A	IR75a	IR8a	DP1l	乙酸 Acetic acid/丙酸 Propionic acid（Marshall *et al*., 2010）
	ac2B	IR75d	IR25a	VL1	吡咯烷 Pyrrolidine（Silbering *et al*., 2011）
	ac2C	IR41a	IR25a, IR76b	VC5	腐胺 Putrescine（Silbering *et al*., 2011）
ac3	ac3A	IR75a, IR75b, IR75c	IR8a	DL2d/v	乙酸 Acetic acid/丁酸 Butyric acid（Silbering *et al*., 2011）
	ac3B	OR35a	ORco, IR76b	VC3	1-己醇 1-Hexanol/环己酮 Cyclohexanone（Hallem *et al*., 2004; Kreher *et al*., 2008; Marshall *et al*., 2010）

续表 1 (Table 1 continued)

感器 Sensillum	神经元类型 OSN	受体 Receptor	共受体 Co-receptor	神经纤维球 Glomerulus	最佳配体 Best ligand
ac4	ac4A	IR84a	IR8a	VL2a	苯乙醛 Phenylacetaldehyde/苯乙酸 Phenylacetic acid（Silbering *et al*., 2011）
	ac4B	IR75d	IR25a	VL1	吡咯烷 Pyrrolidine（Silbering *et al*., 2011）
	ac4C	IR76a	IR25a, IR76b	VM4	苯乙胺 Phenylethylamine/氨水 Ammonium hydroxide（Silbering *et al*., 2011）
	Sac Ⅰ + Ⅱ	IR40a	IR25a	VP1	氨 Ammonia（Münch and Galizia, 2016）
	Sac Ⅰ + Ⅱ	IR40a	IR25a	VP4	氨 Ammonia（Münch and Galizia, 2016）
	Sac Ⅲ	IR64a	IR8a	DC4	乙酸 Acetic acid（Silbering *et al*., 2011）
	Sac Ⅲ	IR64a	IR8a	DP1m	2,3-丁二醇 2,3-Butanediol（Silbering *et al*., 2011）
pb1	pb1A	OR42a	ORco	VM7d	乙酸丙酯 Propyl acetate/丙酸乙酯 Ethyl propionate/5-己烯-3-酮 5-Hexen-3-one（Kreher *et al*., 2005, 2008; Marshall *et al*., 2010; Dweck *et al*., 2016）
	pb1B	OR71a	ORco	VC2	4-乙基愈创木酚 4-Ethylguaiacol/甲基丁香酚 Methyleugenol/对甲酚 4-Methylphenol（de Bruyne *et al*., 1999; Marshall *et al*., 2010; Dweck *et al*., 2015, 2016）
pb2	pb2A	OR33c, OR85e	ORco	VC1	(-)-葑酮(-)-Fenchone/呋喃酮甲基醚 Furaneolmethylether（Marshall *et al*., 2010; Dweck *et al*., 2016）
	pb2B	OR46a	ORco	VA7l	对甲酚 4-Methylphenol/苯酚 Phenol（de Bruyne *et al*., 1999; Marshall *et al*., 2010; Dweck *et al*., 2016）
pb3	pb3A	OR59c	ORco	VM7v	3-羟基丁酸丁酯 Butyl 3-hydroxy butyrate/乙酸丁酯 Butyl acetate（Marshall *et al*., 2010; Dweck *et al*., 2016）
	pb3B	OR85D	ORco	VA4	2-乙酸苯乙酯 2-Phenethyl acetate/丙酸苯乙酯 Phenethyl propionate（Marshall *et al*., 2010; Dweck *et al*., 2016）

2021），而盲蝽 *Lygus hesperus* 和赤拟谷盗 *Tribolium castaneum* 中 TRPA1 被发现用于介导对香茅醛的嗅觉趋避反应（Hull *et al*., 2020; Shimomura *et al*., 2022）。目前 TRPA1 参与昆虫嗅觉的发现集中于对于刺激性气味的回避，因此其行为决定模式被认为是由于 TRPA 介导疼痛神经通路，从而引发了昆虫的驱避反应（Melo *et al*., 2021）。由于 TRP 家族的功能多样，对于其参与昆虫嗅觉调控的分子和神经机制尚待进一步探索。

5 昆虫在人类世（Anthropocene）的嗅觉适应性

在人类世中，空气污染物如 CO、NOx、SO_2 和地面 O_3 改变了自然环境中的气味，从而影响昆虫的嗅觉感受以及相应的行为。地面 O_3 通过 3 种方式影响气味介导的昆虫行为：（1）通过强氧化作用，将寄主挥发性有机化合物（Volatile organic compounds, VOCs）转化为未知的反应产物，从而干扰昆虫对寄主的定向；（2）改变昆虫的气味，从而干扰种内和种间的化学通讯；（3）对昆虫具有直接毒性，导致嗅觉障碍（Guenther *et al*., 1997; Pinto *et al*., 2007, 2010; McFrederick *et al*., 2008; Li and Blande, 2015; Dötterl *et al*., 2016; Giron-Calva *et al*., 2017; Agathokleous *et al*., 2020; Vanderplanck *et al*., 2021）。

昆虫如何在空气污染物浓度升高的环境中进行嗅觉适应是一个有趣的问题。昆虫适应寄主 VOCs 改变的可能策略之一是通过非嗅觉感知新的线索，通过联想、记忆和学习掌握新的行为模式。例如，花烟草 *Nicotiana alata* 的 VOCs 可以被 O_3 氧化，导致对烟草天蛾的吸引力降低或无

法被识别（Cook *et al*., 2020）。结合视觉导航和学习，烟草天蛾可重获对 O_3 改变的花香气味的识别能力，使它们能够再次与这种协同进化的植物保持化学通讯（Cook *et al*., 2020）。其他城市空气污染物同样影响烟草天蛾的嗅觉，如甲苯和二甲苯介导强触角电生理活性，并且在触角叶激活与花朵气味苯甲醛一致的区域，从而影响成虫对寄主植物曼陀罗 *Datura wrightii* 的定位（Riffell *et al*., 2014）。类似地，夜间空气中的 NOx 浓度升高会显著降低烟草天蛾通过花香定位其寄主苍白月见草 *Oenothera pallida* 的嗅觉能力（Chan *et al*., 2024）。除了寄主 VOCs，O_3 还影响昆虫的信息素通讯（Arndt, 1995; Savage *et al*., 2021）。而昆虫可以通过识别信息素氧化产物来适应信息素的变化，例如黑腹果蝇雌性信息素 *Z*7,*Z*11-十七碳二烯（7,11-HD）可以被氧化为 *Z*4-十一烯醛（*Z*4-11:Ald）和庚醛（Lebreton *et al*., 2017）。在 ab9A 神经元中表达的 OR69aB 编码对 *Z*4-11Ald 的感受，并在果蝇中介导飞行趋向（Lebreton *et al*., 2017）。最近以 9 个不同果蝇物种进行的研究也显示，人类世的 O_3 水平可以氧化多种昆虫信息素中的双键，导致雄性成虫对异性趋向降低，甚至被同种雄虫吸引（Jiang *et al*., 2023）。昆虫与人类的关系也有互利的一面，较为典型的研究方向包括法医昆虫学、食品科学、资源昆虫研究等领域。其中城市媒介昆虫和人工气味的化学通讯机制也是一个有趣的方向，例如 Chen 等（2024）发现传统调味品中添加剂的使用会显著影响媒介昆虫的趋向性，结果可用于工厂化食品生产中的质量控制。昆虫释放的报警信息素等物质，可以用于开发更安全有效的靶向害虫驱避剂（任炳忠等, 2017; Zhong *et al*., 2018）。这些研究为一个新问题提供了视角——昆虫在人类世的嗅觉适应如何进行。为了回答这个问题，有必要通过行为学、分析化学、分子生物学和神经学等一系列综合方法对昆虫嗅觉系统的功能和演化模式进行研究。

6 展望

昆虫嗅觉的研究当前需解决的一些问题包括：（1）关键嗅觉和生态学表型的功能产生和演化机制；（2）嗅觉蛋白编码化学物质信号的一般规律；（3）非模式物种高级神经中枢的信号编码模式及行为决定机制；（4）昆虫嗅觉行为在人类世的策略变化。到目前为止，黑腹果蝇的嗅觉编码已经得到了很好的了解，因为它具有明确的遗传背景。然而，在昆虫中，果蝇的感受模式在生态学上的意义有限。对于大多数非模式昆虫，它们的编码机制和行为的生态学意义仍需进一步探索。基于 CRISPR/Cas9 的研究方法为昆虫的嗅觉神经回路提供了新的研究途径（Trible *et al*., 2017; Yan *et al*., 2017）。同时，单细胞测序可能为感觉神经元研究提供更精确的视角（McLaughlin *et al*., 2021; Task *et al*., 2022）。此外，结构生物学和相关算法的发展也为阐述受体-配体结合机制提供了更多信息（Butterwick *et al*., 2018; del Mármol *et al*., 2021; Abramson *et al*., 2024）。随着新技术的应用和发展，越来越多昆虫物种的嗅觉编码模式已经被揭示，这些成果不仅能为害虫防控提供新的手段，也可为资源昆虫保护提供新的思路。

致谢：感谢马普化学生态研究所江南纪博士对论文撰写过程中的帮助。

参考文献 (References)

Abramson J, Adler J, Dunger J, Evans R, Green T, Pritzel A, Ronneberger O, Willmore L, Ballard AJ, Bambrick J, Bodenstein SW, Evans DA, Hung CC, O'Neill M, Reiman D, Tunyasuvunakool K, Wu Z, Žemgulytė A, Arvaniti E, Beattie C, Bertolli O, Bridgland A, Cherepanov A, Congreve M, Cowen-Rivers AI, Cowie A, Figurnov M, Fuchs FB, Gladman H, Jain R, Khan YA, Low CMR, Perlin K, Potapenko A, Savy P, Singh S, Stecula A, Thillaisundaram A, Tong C, Yakneen S, Zhong ED, Zielinski M, Žídek A, Bapst V, Kohli P, Jaderberg M, Hassabis D, Jumper JM, 2024. Accurate structure prediction of biomolecular interactions with AlphaFold 3. *Nature*, https://doi.org/10.1038/s41586-024-07487-w.

Abuin L, Bargeton B, Ulbrich MH, Isacoff EY, Kellenberger S, Benton R, 2011. Functional architecture of olfactory ionotropic glutamate receptors. *Neuron*, 69(1): 44–60.

Adam E, Hansson BS, Knaden M, 2021. Moths sense but do not learn flower odors with their proboscis during flower investigation. *Journal of Experimental Biology*, 224(17): jeb242780.

Adams MD, Celniker SE, Holt RA, Evans CA, Gocayne JD, Amanatides PG, Scherer SE, Li PW, Hoskins RA, Galle RF, George RA, Lewis SE, Richards S, Ashburner M, Henderson SN, Sutton GG, Wortman JR, Yandell MD, Zhang Q, Chen LX, Brandon RC, Rogers YH, Blazej RG, Champe M, Pfeiffer BD, Wan KH, Doyle C, Baxter EG, Helt G, Nelson CR, Gabor GL, Abril JF, Agbayani A, An HJ, Andrews-Pfannkoch C, Baldwin D, Ballew RM, Basu A, Baxendale J, Bayraktaroglu L, Beasley EM, Beeson KY, Benos PV, Berman BP, Bhandari D, Bolshakov S, Borkova D, Botchan MR, Bouck J, Brokstein P, Brottier P, Burtis KC, Busam DA, Butler H, Cadieu E, Center A, Chandra I, Cherry JM, Cawley S, Dahlke C, Davenport LB, Davies P, de Pablos B, Delcher A, Deng Z, Mays AD, Dew I, Dietz SM, Dodson K, Doup LE, Downes M, Dugan-Rocha S, Dunkov BC, Dunn P, Durbin KJ, Evangelista CC, Ferraz C, Ferriera S, Fleischmann W, Fosler C, Gabrielian AE, Garg NS, Gelbart WM, Glasser K, Glodek A, Gong F, Gorrell JH, Gu Z, Guan P, Harris M, Harris NL, Harvey D, Heiman TJ, Hernandez JR, Houck J, Hostin D, Houston KA, Howland TJ, Wei MH, Ibegwam C, Jalali M, Kalush F, Karpen GH, Ke Z, Kennison JA, Ketchum KA, Kimmel BE, Kodira CD, Kraft C, Kravitz S, Kulp D, Lai Z, Lasko P, Lei Y, Levitsky AA, Li J, Li Z, Liang Y, Lin X, Liu X, Mattei B, McIntosh TC, McLeod MP, McPherson D, Merkulov G, Milshina NV, Mobarry C, Morris J, Moshrefi A, Mount SM, Moy M, Murphy B, Murphy L, Muzny DM, Nelson DL, Nelson DR, Nelson KA, Nixon K, Nusskern DR, Pacleb JM, Palazzolo M, Pittman GS, Pan S, Pollard J, Puri V, Reese MG, Reinert K, Remington K, Saunders RD, Scheeler F, Shen H, Shue BC, Sidén-Kiamos I, Simpson M, Skupski MP, Smith T, Spier E, Spradling AC, Stapleton M, Strong R, Sun E, Svirskas R, Tector C, Turner R, Venter E, Wang AH, Wang X, Wang ZY, Wassarman DA, Weinstock GM, Weissenbach J, Williams SM, WoodageT, Worley KC, Wu D, Yang S, Yao QA, Ye J, Yeh RF, Zaveri JS, Zhan M, Zhang G, Zhao Q, Zheng L, Zheng XH, Zhong FN, Zhong W, Zhou X, Zhu S, Zhu X, Smith HO, Gibbs RA, Myers EW, Rubin GM, Venter JC, 2000. The genome sequence of *Drosophila melanogaster*. *Science*, 287(5461): 2185–2195.

Agathokleous E, Feng ZZ, Oksanen E, Sicard P, Wang Q, Saitanis CJ, Araminiene V, Blande JD, Hayes F, Calatayud V, Domingos M, Veresoglou SD, Peñuelas J, Wardle DA, De Marco A, Li ZZ, Harmens H, Yuan XY, Vitale M, Paoletti E, 2020. Ozone affects plant, insect, and soil microbial communities: A threat to terrestrial ecosystems and biodiversity. *Science Advances*, 6(33): eabc1176.

Ai MR, Blais S, Park JY, Min S, Neubert TA, Suh GSB, 2013. Ionotropic glutamate receptors IR64a and IR8a form a functional odorant receptor complex *in vivo* in *Drosophila*. *Journal of Neuroscience*, 33(26): 10741–10749.

Ando T, Inomata S, Yamamoto M, 2004. Lepidopteran sex pheromones. *Topics in Current Chemistry*, 239: 51–96.

Anton S, Ignell R, Hansson BS, 2002. Developmental changes in the structure and function of the central olfactory system in gregarious and solitary desert locusts. *Microscopy Research and Technique*, 56(4): 281–291.

Arndt U, 1995. Air pollutants and pheromones-a problem? *Chemosphere*, 30(6): 1023–1031.

Bastin-Héline L, de Fouchier A, Cao S, Koutroumpa F, Caballero-Vidal G, Robakiewicz S, Monsempes C, François MC, Ribeyre T, Maria A, Chertemps T, de Cian A, Walker WB 3rd, Wang GR, Jacquin-Joly E, Montagné N, 2019. A novel lineage of candidate pheromone receptors for sex communication in moths. *eLife*, 8: e49826.

Benton R, Dessimoz C, Moi D, 2020. A putative origin of the insect chemosensory receptor superfamily in the last common eukaryotic ancestor. *eLife*, 9: e62507.

Benton R, Sachse S, Michnick SW, Vosshall LB, 2006. Atypical membrane topology and heteromeric function of *Drosophila* odorant receptors *in vivo*. *PLoS Biology*, 4(2): e20.

Benton R, Vannice KS, Gomez-Diaz C, Vosshall LB, 2009. Variant ionotropic glutamate receptors as chemosensory receptors in *Drosophila*. *Cell*, 136(1): 149–162.

Benton R, Vannice KS, Vosshall LB, 2007. An essential role for a CD36-related receptor in pheromone detection in *Drosophila*. *Nature*, 450(7167): 289–293.

Boeckh J, Boeckh V, 1979. Threshold and odor specificity of pheromone-sensitive neurons in the deutocerebrum of *Antheraea pernyi* and *A. polyphemus* (Saturnidae). *Journal of Comparative Physiology A-neuroethology Sensory Neural and Behavioral*, 132(3): 235–242.

Brand P, Robertson HM, Lin W, Pothula R, Klingeman WE, Jurat-Fuentes JL, Johnson BR, 2018. The origin of the odorant receptor gene family in insects. *eLife*, 7: e38340.

Butenandt A, Beckmann R, Hecker E, 1961. Über den sexuallockstoff des seidenspinners, i. der biologische test und die isolierung des reinen sexuallockstoffes bombykol. *Biological Chemistry*, 324: 71–83.

Butterwick JA, Del Mármol J, Kim KH, Kahlson MA, Rogow JA, Walz T, Ruta V, 2018. Cryo-EM structure of the insect olfactory receptor Orco. *Nature*, 560(7719): 447–452.

Cao S, Liu Y, Wang B, Wang GR, 2021. A single point mutation causes one-way alteration of pheromone receptor function in two *Heliothis* species. *iScience*, 24(9): 102981.

Chang H, Unni AP, Tom MT, Cao Q, Liu Y, Wang G, Llorca LC, Brase S, Bucks S, Weniger K, Bisch-Knaden S, Hansson BS, Knaden, M, 2023. Odorant detection in a locust exhibits unusually low redundancy. *Current Biology*, 33(24): 5427–5438.

Chan JK, Parasurama S, Atlas R, Xu R, Jongebloed UA, Alexander B, Langenhan JM, Thornton JA, Riffell JA, 2024. Olfaction in the Anthropocene: NO_3 negatively affects floral scent and nocturnal pollination. *Science*, 383(6683): 607–611.

Chen CH, Buhl E, Xu M, Croset V, Rees JS, Lilley KS, Benton R, Hodge JJL, Stanewsky R, 2015. *Drosophila* ionotropic receptor 25a mediates circadian clock resetting by temperature. *Nature*, 527(7579): 516–520.

Cheng LL, Kang L, Guo XJ, 2023. Coding principles of insect olfactory system. *Nature Magazine*, 45(4): 239–246. [程李莉, 康乐, 郭晓娇, 2023. 昆虫嗅觉系统编码规律. 自然杂志, 45(4): 239–246.]

Chen JH, Peng H, Wei S, Huang MJ, Tang R, 2024. An olfactory model for evaluating the larviposition preference of a vector fly. *Insect Science*. doi: 10.1111/1744-7917.13426.

Clyne PJ, Warr CG, Carlson JR, 2000. Candidate taste receptors in *Drosophila*. *Science*, 287(5459): 1830–1834.

Clyne PJ, Warr CG, Freeman MR, Lessing D, Kim J, Carlson JR, 1999. A novel family of divergent seven-transmembrane proteins: Candidate odorant receptors in *Drosophila*. *Neuron*, 22(2): 327–338.

Cook B, Haverkamp A, Hansson BS, Roulston T, Lerdau M, Knaden M, 2020. Pollination in the anthropocene: A moth can learn ozone-altered floral blends. *Journal of Chemical Ecology*, 46(10): 987–996.

Croset V, Rytz R, Cummins SF, Budd A, Brawand D, Kaessmann H, Gibson TJ, Benton R, 2010. Ancient protostome origin of chemosensory ionotropic glutamate receptors and the evolution of insect taste and olfaction. *PLoS Genetics*, 6(8): e1001064.

de Bruyne M, Clyne PJ, Carlson JR, 1999. Odor coding in a model olfactory organ: The *Drosophila* maxillary palp. *Journal of Neuroscience*, 19(11): 4520–4532.

de Bruyne M, Baker TC, 2008. Odor detection in insects: Volatile codes. *Journal of Chemical Ecology*, 34(7): 882–897.

de Bruyne M, Smart R, Zammit E, Warr CG, 2010. Functional and molecular evolution of olfactory neurons and receptors for aliphatic esters across the *Drosophila* genus. *Journal of Comparative Physiology A Sensory Neural & Behavioral Physiology*, 196(2): 97–109.

de Fouchier A, Walker WB 3rd, Montagné N, Steiner C, Binyameen M, Schlyter F, Chertemps T, Maria A, François MC, Monsempes C, Anderson P, Hansson BS, Larsson MC, Jacquin-Joly E, 2017. Functional evolution of Lepidoptera olfactory receptors revealed by deorphanization of a moth repertoire. *Nature Communications*, 8: 15709.

del Mármol J, Yedlin MA, Ruta V, 2021. The structural basis of odorant recognition in insect olfactory receptors. *Nature*, 597(7874): 126–131.

Dethier VG, 1982. Mechanism of host-plant recognition. *Entomologia Experimentalis et Applicata*, 31(1): 49–56.

Di C, Ning C, Huang LQ, Wang CZ, 2017. Design of larval chemical attractants based on odorant response spectra of odorant receptors in the cotton bollworm. *Insect Biochemistry and Molecular Biology*, 84: 48–62.

Dobritsa AA, van der Goes van Naters W, Warr CG, Steinbrecht RA, Carlson JR, 2003. Integrating the molecular and cellular basis of odor coding in the *Drosophila* antenna. *Neuron*, 37(5): 827–841.

Dötterl S, Vater M, Rupp T, Held A, 2016. Ozone differentially affects perception of plant volatiles in western honey bees. *Journal of Chemical Ecology*, 42(6): 486–489.

Du LX, Liu Y, Wang GR, 2016. Research progress on signal transduction mechanisms of the insect peripheral olfactory system. *Science China*: *Life Sciences*, 46(5): 573–583. [杜立啸, 刘杨, 王桂荣, 2016. 昆虫外周嗅觉系统信号转导机制研究进展. 中国科学: 生命科学, 46(5): 573–583.]

Dweck HKM, Ebrahim SAM, Khallaf MA, Koenig C, Farhan A, Stieber R, Weißflog J, Svatoš A, Grosse-Wilde E, Knaden M, Hansson BS, 2016. Olfactory channels associated with the *Drosophila* maxillary palp mediate short- and long-range attraction. *eLife*, 5: e14925.

Dweck HKM, Ebrahim SAM, Kromann S, Bown D, Hillbur Y, Sachse S, Hansson BS, Stensmyr MC, 2013. Olfactory preference for egg laying on citrus substrates in *Drosophila*. *Current Biology*, 23(24): 2472–2480.

Dweck HKM, Ebrahim SAM, Thoma M, Mohamed AAM, Keesey IW, Trona F, Lavista-Llanos S, Svatoš A, Sachse S, Knaden M, Hansson BS, 2015. Pheromones mediating copulation and attraction in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 112(21): E2829–E2835.

Du BJ, Chen R, Tao WT, Shi HL, Bu WJ, Liu Y, Ma S, Ni MY, Kong FL, Xiao JH, Huang DW, 2020. A Cretaceous bug with exaggerated antennae might be a double-edged sword in evolution. *iScience*, 24(1): 101932.

Ebrahim SAM, Dweck HKM, Stökl J, Hofferberth JE, Trona F, Weniger K, Rybak J, Seki Y, Stensmyr MC, Sachse S, Hansson BS, Knaden M, 2015. *Drosophila* avoids parasitoids by sensing their semiochemicals via a dedicated olfactory circuit. *PLoS Biology*, 13(12): e1002318.

Elmore T, Ignell R, Carlson JR, Smith DP, 2003. Targeted mutation of a *Drosophila* odor receptor defines receptor requirement in a novel class of sensillum. *Journal of Neuroscience*, 23(30): 9906–9912.

Fleischer J, Pregitzer P, Breer H, Krieger J, 2018. Access to the odor world: Olfactory receptors and their role for signal transduction in insects. *Cellular and Molecular Life Sciences*, 75(3): 485–508.

Gabler S, Soelter J, Hussain T, Sachse S, Schmuker M, 2013. Physicochemical vs. vibrational descriptors for prediction of odor receptor responses. *Molecular Informatics*, 32(9/10): 855–865.

Galizia CG, Münch D, Strauch M, Nissler A, Ma SW, 2010. Integrating heterogeneous odor response data into a common response model: A DoOR to the complete olfactome. *Chemical Senses*, 35(7): 551–563.

Gao Q, Chess A, 1999. Identification of candidate *Drosophila* olfactory receptors from genomic DNA sequence. *Genomics*, 60(1): 31–39.

Giron-Calva PS, Li T, Blande JD, 2017. Volatile mediated interactions between cabbage plants in the field and the impact of ozone pollution. *Journal of Chemical Ecology*, 43(4): 339–350.

Grabe V, Baschwitz A, Dweck HKM, Lavista-Llanos S, Hansson BS, Sachse S, 2016. Elucidating the neuronal architecture of olfactory glomeruli in the *Drosophila* antennal lobe. *Cell Reports*, 16(12): 3401–3413.

Gomez-Diaz C, Bargeton B, Abuin L, Bukar N, Reina JH, Bartoi T, Graf M, Ong H, Ulbrich MH, Masson JF, Benton R, 2016. A CD36 ectodomain mediates insect pheromone detection via a putative tunnelling mechanism. *Nature Communications*, 7: 11866.

Gong ZJ, Zhou WW, Zhu ZR, Cheng JA, 2008. Research progress on insect olfactory receptors. *Acta Entomologica Sinica*, 51(7): 761–768. [巩中军, 周文武, 祝增荣, 程家安, 2008. 昆虫嗅觉受体的研究进展. 昆虫学报, 51(7): 761–768.]

Guenther A, 1997. Seasonal and spatial variations in natural volatile organic compound emissions. *Ecological Applications*, 7(1): 34–45.

Guo MB, Du LX, Chen QY, Feng YL, Zhang J, Zhang XX, Tian K, Cao S, Huang TY, Jacquin-Joly E, Wang GR, Liu Y, 2021. Odorant receptors for detecting flowering plant cues are functionally conserved across moths and butterflies. *Molecular Biology and Evolution*, 38(4): 1413–1427.

Hallem EA, Carlson JR, 2006. Coding of odors by a receptor repertoire. *Cell*, 125(1): 143–160.

Hallem EA, Dahanukar A, Carlson JR, 2006. Insect odor and taste receptors. *Annual Review of Entomology*, 51: 113–135.

Hallem EA, Ho MG, Carlson JR, 2004. The molecular basis of odor coding in the *Drosophila* antenna. *Cell*, 117(7): 965–979.

Hansson BS, Ljungberg H, Hallberg E, Löfstedt C, 1992. Functional specialization of olfactory glomeruli in a moth. *Science*, 256(5061): 1313–1315.

Hansson BS, Ochieng SA, Grosmaitre X, Anton S, Njagi PGN, 1996. Physiological responses and central nervous projections of antennal olfactory receptor neurons in the adult desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *Journal of Comparative Physiology A-neuroethology Sensory Neural and Behavioral*, 179: 157–167.

Hansson BS, Stensmyr MC, 2011. Evolution of insect olfaction. *Neuron*, 72(5): 698–711.

Haverkamp A, Hansson BS, Knaden M, 2018. Combinatorial codes and labeled lines: How insects use olfactory cues to find and judge food, mates, and oviposition sites in complex environments. *Frontiers in Physiology*, 9: 49.

Haverkamp A, Yon F, Keesey IW, Mißbach C, Koenig C, Hansson BS, Baldwin IT, Knaden M, Kessler D, 2016. Hawkmoths evaluate scenting flowers with the tip of their proboscis. *eLife*, 5: e15039.

Herre M, Goldman OV, Lu TC, Caballero-Vidal G, Qi YY, Gilbert ZN, Gong ZY, Morita T, Rahiel S, Ghaninia M, Ignell R, Matthews BJ, Li HJ, Vosshall LB, Younger MA, 2022. Non-canonical odor coding in the mosquito. *Cell*, 185(17): 3104–3123.

Hildebrand JG, Shepherd GM, 1997. Mechanisms of olfactory discrimination: Converging evidence for common principles across phyla. *Annual Review of Neuroscience*, 20: 595–631.

Hill CA, Fox AN, Pitts RJ, Kent LB, Tan PL, Chrystal MA, Cravchik A, Collins FH, Robertson HM, Zwiebel LJ, 2002. G protein-coupled receptors in *Anopheles gambiae*. *Science*, 298(5591): 176–178.

Holland PWH, Marlétaz F, Maeso I, Dunwell TL, Paps J, 2017. New genes from old: Asymmetric divergence of gene duplicates and the evolution of development. *Philosophical Transactions of The Royal Society B-Biological Sciences*, 372(1713): 20150480.

Hou XQ, Yuvaraj JK, Roberts RE, Zhang DD, Unelius CR, Löfstedt C, Andersson MN, 2021. Functional evolution of a bark beetle odorant receptor clade detecting monoterpenoids of different ecological origins. *Molecular Biology and Evolution*, 38(11): 4934–4947.

Hoyle G, 1984. The scope of neuroethology. *Behavioral and Brain Sciences*, 7(3): 367–381.

Hull JJ, Yang YW, Miyasaki K, Brent CS, 2020. TRPA1 modulates noxious odor responses in *Lygus hesperus*. *Journal of Insect Physiology*, 122: 104038.

Hussain A, Zhang M, Üçpunar HK, Svensson T, Quillery E, Gompel N, Ignell R, Grunwald Kadow IC, 2018. Correction: Ionotropic chemosensory receptors mediate the taste and smell of polyamines. *PLoS Biology*, 16(3): e1002624.

Hu YY, Xu SF, Wubie AJ, Li W, Guo ZB, Zho T, 2013. Overview of research on insect olfactory-related proteins and olfactory recognition mechanisms. *Genomics and Applied Biology*. 32(5): 667–676. [胡颖颖, 徐书法, Wubie Abebe Jenberie, 李薇, 国占宝, 周婷, 2013. 昆虫嗅觉相关蛋白及嗅觉识别机理研究概述.

基因组学与应用生物学, 32(5): 667–676.]

Ignell R, Anton S, Hansson BS, 1998. Central nervous processing of behaviourally relevant odours in solitary and gregarious fifth instar locusts, *Schistocerca gregaria. Journal of Comparative Physiology A-neuroethology Sensory Neural and Behavioral*, 183(4): 453–465.

Ishida Y, Leal WS, 2005. Rapid inactivation of a moth pheromone. *Proceedings of the National Academy of Sciences of the United States of America*, 102(39): 14075–14079.

Jiang NJ, Chang HT, Weißflog J, Eberl F, Veit D, Weniger K, Hansson BS, Knaden M, 2023. Ozone exposure disrupts insect sexual communication. *Nature Communications*, 14(1): 1186.

Jiang NJ, Tang R, Guo H, Ning C, Li JC, Wu H, Huang LQ, Wang CZ, 2020. Olfactory coding of intra- and interspecific pheromonal messages by the male *Mythimna separata* in North China. *Insect Biochemistry and Molecular Biology*, 125: 103439.

Jones WD, Cayirlioglu P, Kadow IG, Vosshall LB, 2007. Two chemosensory receptors together mediate carbon dioxide detection in *Drosophila*. *Nature*, 445(7123): 86–90.

Joseph RM, Carlson JR, 2015. *Drosophila* chemoreceptors: A molecular interface between the chemical world and the brain. *Trends in Genetics*, 31(12): 683–695.

Jung JW, Baeck SJ, Perumalsamy H, Hansson BS, Ahn YJ, Kwon HW, 2015. A novel olfactory pathway is essential for fast and efficient blood-feeding in mosquitoes. *Scientific Reports*, 5: 13444.

Kaissling KE, 1986. Chemo-electrical transduction in insect olfactory receptors. *Annual Review of Neuroscience*, 9: 121–145.

Keil TA, 1999. Morphology and development of the peripheral olfactory organ// Hansson BS (ed.). Insect Olfaction. Berlin, Heidelberg: Springer. 5–47.

Kent KS, Harrow ID, Quartararo P, Hildebrand JG, 1986. An accessory olfactory pathway in Lepidoptera: The labial pit organ and its central projections in *Manduca sexta* and certain other sphinx moths and silk moths. *Cell and Tissue Research*, 245(2): 237–245.

Kent LB, Robertson HM, 2009. Evolution of the sugar receptors in insects. *BMC Evolutionary Biology*, 9: 41.

Klinner CF, König C, Missbach C, Werckenthin A, Daly KC, Bisch-Knaden S, Stengl M, Hansson BS, Große-Wilde E, 2016. Functional olfactory sensory neurons housed in olfactory sensilla on the ovipositor of the hawkmoth *Manduca sexta*. *Frontiers in Ecology and Evolution*, 4: 130.

Koerte S, Keesey IW, Khallaf MA, Cortés Llorca L, Grosse-Wilde E, Hansson BS, Knaden M, 2018. Evaluation of the DREAM technique for a high-throughput deorphanization of chemosensory receptors in *Drosophila*. *Frontiers in Molecular Neuroscience*, 11: 366.

Koontz MA, Schneider D, 1987. Sexual dimorphism in neuronal projections from the antennae of silk moths (*Bombyx mori*, *Antheraea polyphemus*) and the gypsy moth (*Lymantria dispar*). *Cell and Tissue Research*, 249(1): 39–50.

Krång AS, Knaden M, Steck K, Hansson BS, 2012. Transition from sea to land: Olfactory function and constraints in the terrestrial hermit crab *Coenobita clypeatus*. *Proceedings of The Royal Society B-Biological Sciences*, 279: 3510–3519.

Kreher SA, Kwon JY, Carlson JR, 2005. The molecular basis of odor coding in the *Drosophila* larva. *Neuron*, 46(3): 445–456.

Kreher SA, Mathew D, Kim J, Carlson JR, 2008. Translation of sensory input into behavioral output via an olfactory system. *Neuron*, 59(1): 110–124.

Krieger J, Klink O, Mohl C, Raming K, Breer H, 2003. A candidate olfactory receptor subtype highly conserved across different insect orders. *Journal of Comparative Physiology*, 189(7): 519–526.

Kurtovic A, Widmer A, Dickson BJ, 2007. A single class of olfactory neurons mediates behavioural responses to a *Drosophila* sex pheromone. *Nature*, 446(7135): 542–546.

Kwon HW, Lu T, Rützler M, Zwiebel LJ, 2006. Olfactory responses in a gustatory organ of the malaria vector mosquito *Anopheles gambiae*. *Proceedings of the National Academy of Sciences of the United States of America*, 103(36): 13526–13531.

Kwon JY, Dahanukar A, Weiss LA, Carlson JR, 2007. The molecular basis of CO_2 reception in Drosophila. *Proceedings of the National Academy of Sciences of the United States of America*, 104(9): 3574–3578.

Larsson MC, Domingos AI, Jones WD, Chiappe ME, Amrein H, Vosshall LB, 2004. Or83b encodes a broadly expressed odorant receptor essential for *Drosophila* olfaction. *Neuron,* 43(5): 703–714.

Leal WS, 2013. Odorant reception in insects: Roles of receptors, binding proteins, and degrading enzymes. *Annual Review of Entomology*, 58: 373–391.

Leary GP, Allen JE, Bunger PL, Luginbill JB, Linn CE Jr, MacAllister IE, Kavanaugh MP, Wanner KW, 2012. Single mutation to a sex pheromone receptor provides adaptive specificity between closely related moth species. *Proceedings of the National Academy of Sciences of the United States of America*, 109(35): 14081–14086.

Lebreton S, Borrero-Echeverry F, Gonzalez F, Solum M, Wallin EA, Hedenström E, Hansson BS, Gustavsson AL, Bengtsson M, Birgersson G, Walker WB 3rd, Dweck HKM, Becher PG, Witzgall P, 2017. A *Drosophila* female pheromone elicits species-specific long-range attraction via an olfactory channel with dual specificity for sex and food. *BMC Biology*, 15(1): 88.

Lemke RS, Pregitzer P, Eichhorn AS, Breer H, Krieger J, Fleischer J,

2020. SNMP1 and odorant receptors are co-expressed in olfactory neurons of the labial and maxillary palps from the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). *Cell and Tissue Research*, 379(2): 275–289.

Liu JX, Zhong GH, Xie JJ, Guan S, Hu MY, 2005. Recent advances in chemosensory proteins of insects. *Acta Entomologica Sinica*, 48(3): 418–426. [刘金香, 钟国华, 谢建军, 官珊, 胡美英, 2005. 昆虫化学感受蛋白研究进展. 昆虫学报, 48(3): 418–426.]

Li RT, Huang LQ, Dong JF, Wang CZ, 2020. A moth odorant receptor highly expressed in the ovipositor is involved in detecting host-plant volatiles. *eLife*, 9: e53706.

Li T, Blande JD, 2015. Associational susceptibility in broccoli: Mediated by plant volatiles, impeded by ozone. *Global Change Biology*, 21(5): 1993–2004.

Li ZB, Capoduro R, Bastin-Héline L, Zhang S, Sun DD, Lucas P, Dabir-Moghaddam D, François MC, Liu Y, Wang GR, Jacquin-Joly E, Montagné N, Meslin C, 2023. A tale of two copies: Evolutionary trajectories of moth pheromone receptors. *Proceedings of the National Academy of Sciences of the United States of America*, 120(20): e2221166120.

Lin HH, Cao DS, Sethi S, Zeng Z, Chin JSR, Chakraborty TS, Shepherd AK, Nguyen CA, Yew JY, Su CY, Wang JW, 2016. Hormonal modulation of pheromone detection enhances male courtship success. *Neuron*, 90(6): 1272–1285.

Löfstedt C, Wahlberg N, Millar JG, 2016. Evolutionary patterns of pheromone diversity in Lepidoptera// Allison JD, Carde RT (eds.). Pheromone Communication in Moths: Evolution, Behavior, and Application. California: University of California Press. 43–78.

Lu T, Qiu YT, Wang GR, Kwon JY, Rutzler M, Kwon HW, Pitts RJ, van Loon JJA, Takken W, Carlson JR, Zwiebel LJ, 2007. Odor coding in the maxillary palp of the malaria vector mosquito *Anopheles gambiae*. *Current Biology*, 17(18): 1533–1544.

Ma DM, Hu MQ, Yang XT, Liu Q, Ye F, Cai WJ, Wang Y, Xu XM, Chang SH, Wang RY, Yang W, Ye S, Su NN, Fan MR, Xu HX, Guo JT, 2024. Structural basis for sugar perception by *Drosophila* gustatory receptors. *Science*, 383(6685): eadj2609.

Malnic B, Hirono J, Sato T, Buck LB, 1999. Combinatorial receptor codes for odors. *Cell*, 96(5): 713–723.

Marshall B, Warr CG, de Bruyne M, 2010. Detection of volatile indicators of illicit substances by the olfactory receptors of *Drosophila melanogaster*. *Chemical Senses*, 35(7): 613–625.

McFrederick QS, Kathilankal JC, Fuentes JD, 2008. Air pollution modifies floral scent trails. *Atmospheric Environment*, 42(10): 2336–2348.

McLaughlin CN, Brbić M, Xie QJ, Li TC, Horns F, Kolluru SS, Kebschull JM, Vacek D, Xie A, Li JF, Jones RC, Leskovec J, Quake SR, Luo LQ, Li HJ, 2021. Single-cell transcriptomes of developing and adult olfactory receptor neurons in *Drosophila*. *eLife*, 10: e63856.

McMeniman CJ, Corfas RA, Matthews BJ, Ritchie SA, Vosshall LB, 2014. Multimodal integration of carbon dioxide and other sensory cues drives mosquito attraction to humans. *Cell*, 156(5): 1060–1071.

Melo N, Capek M, Arenas OM, Afify A, Yilmaz A, Potter CJ, Laminette PJ, Para A, Gallio M, Stensmyr MC, 2021. The irritant receptor TRPA1 mediates the mosquito repellent effect of catnip. *Current Biology*, 31(9): 1988–1994.

Missbach C, Dweck HK, Vogel H, Vilcinskas A, Stensmyr MC, Hansson BS, Grosse-Wilde E, 2014. Evolution of insect olfactory receptors. *eLife*, 3: e02115.

Mo JC, Wang CP, Wei JQ, 2019. Research progress on the insect peripheral olfactory system. *Journal of Jiangxi Agricultural University*, 41(1): 50–57. [莫建初, 王成盼, 尉吉乾, 2019. 昆虫外周嗅觉系统研究进展. 江西农业大学学报, 41(1): 50–57.]

Montague SA, Mathew D, Carlson JR, 2011. Similar odorants elicit different behavioral and physiological responses, some supersustained. *Journal of Neuroscience*, 31(21): 7891–7899.

Montell C, 2005. The TRP superfamily of cation channels. *Science*'*s STKE*, 2005(272): re3.

Montell C, Birnbaumer L, Flockerzi V, 2002a. The TRP channels, a remarkably functional family. *Cell*, 108(5): 595–598.

Montell C, Birnbaumer L, Flockerzi V, Bindels RJ, Bruford EA, Caterina MJ, Clapham DE, Harteneck C, Heller S, Julius D, Kojima I, Mori YS, Penner R, Prawitt D, Scharenberg AM, Schultz G, Shimizu N, Zhu MX, 2002b. A unified nomenclature for the superfamily of TRP cation channels. *Molecules and Cells*, 9(2): 229–231.

Münch D, Galizia CG, 2016. DoOR 2.0 Comprehensive mapping of *Drosophila melanogaster* odorant responses. *Scientific Reports*, 6: 21841.

Ni LN, 2021. The structure and function of ionotropic receptors in *Drosophila*. *Frontiers in Molecular Neuroscience*, 13: 638839.

Ning C, Yang K, Xu M, Huang LQ, Wang CZ, 2016. Functional validation of the carbon dioxide receptor in labial palps of *Helicoverpa armigera* moths. *Insect Biochemistry and Molecular Biology*, 73: 12–19.

Ochieng SA, Hallberg E, Hansson BS, 1998. Fine structure and distribution of antennal sensilla of the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *Cell and Tissue Research*, 291(3): 525–536.

Pelz D, Roeske T, Syed Z, de Bruyne M, Galizia CG, 2006. The molecular receptive range of an olfactory receptor *in vivo* (*Drosophila melanogaster* Or22a). *Journal of Neurobiology*, 66(14): 1544–1563.

Pinto DM, Blande JD, Nykänen R, Dong WX, Nerg AM, Holopainen JK, 2007. Ozone degrades common herbivore-induced plant volatiles: Does this affect herbivore prey location by predators and parasitoids? *Journal of Chemical Ecology*, 33(4): 683–694.

Pinto DM, Blande JD, Souza SR, Nerg AM, Holopainen JK, 2010. Plant volatile organic compounds (VOCs) in ozone (O_3) polluted atmospheres: The ecological effects. *Journal of Chemical Ecology*, 36(1): 22–34.

Pitts RJ, Fox AN, Zwiebel LJ, 2004. A highly conserved candidate chemoreceptor expressed in both olfactory and gustatory tissues in the malaria vector *Anopheles gambiae*. *Proceedings of the National Academy of Sciences of the United States of America*, 101(14): 5058–5063.

Raji JI, Potter CJ, 2022. Chemosensory ionotropic receptors in human host-seeking mosquitoes. *Current Opinion in Insect Science*, 54: 100967.

Ren BZ, Luo WQ, Zhang X, Wang YL, 2017. Overview and prospects of research on insect olfactory communication. *Journal of Jilin Agricultural University*, 39(3): 253–261. [任炳忠, 雒雯琦, 张雪, 王寅亮, 2017. 昆虫嗅觉通讯研究概述与展望. 吉林农业大学学报, 39(3): 253–261.]

Riabinina O, Task D, Marr E, Lin CC, Alford R, O'Brochta DA, Potter CJ, 2016. Organization of olfactory centres in the malaria mosquito *Anopheles gambiae*. *Nature Communications*, 7: 13010.

Riffell JA, Shlizerman E, Sanders E, Abrell L, Medina B, Hinterwirth AJ, Kutz JN, 2014. Flower discrimination by pollinators in a dynamic chemical environment. *Science*, 344(6191): 1515–1518.

Rimal S, Lee Y, 2018. The multidimensional ionotropic receptors of *Drosophila melanogaster*. *Insect Molecular Biology*, 27(1): 1–7.

Robertson HM, Kent LB, 2009. Evolution of the gene lineage encoding the carbon dioxide receptor in insects. *Journal of Insect Science*, 9: 19.

Robertson HM, Warr CG, Carlson JR, 2003. Molecular evolution of the insect chemoreceptor gene superfamily in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America*, 100(Suppl. 2): 14537–14542.

Ronderos DS, Lin CC, Potter CJ, Smith DP, 2014. Farnesol-detecting olfactory neurons in *Drosophila*. *Journal of Neuroscience*, 34(11): 3959–3968.

Sato K, Pellegrino M, Nakagawa T, Nakagawa T, Vosshall LB, Touhara K, 2008. Insect olfactory receptors are heteromeric ligand-gated ion channels. *Nature*, 452(7190): 1002–1006.

Sato K, Tanaka K, Touhara K, 2011. Sugar-regulated cation channel formed by an insect gustatory receptor. *Proceedings of the National Academy of Sciences of the United States of America*, 108(28): 11680–11685.

Savage B, Wang ZN, Chung H, Masten S, Grieshop M, 2021. An ozonolysis based method and applications for the non-lethal modification of insect cuticular hydrocarbons. *Journal of Chemical Ecology*, 47(7): 628–641.

Shanbhag SR, Müller B, Steinbrecht RA, 1999. Atlas of olfactory organs of *Drosophila melanogaster* 1. Types, external organization, innervation and distribution of olfactory sensilla. *International Journal of Insect Morphology and Embryology*, 28(4): 377–397.

Shimomura K, Ino S, Tamura K, Terajima T, Tomizawa M, 2022. TRPA1-mediated repellency behavior in the red flour beetle *Tribolium castaneum*. *Scientific Reports*, 12(1): 15270.

Silbering AF, Rytz R, Grosjean Y, Abuin L, Ramdya P, Jefferis GSXE, Benton R, 2011. Complementary function and integrated wiring of the evolutionarily distinct *Drosophila* olfactory subsystems. *Journal of Neuroscience*, 31(38): 13357–13375.

Singh RN, Nayak SV, 1985. Fine structure and primary sensory projections of sensilla on the maxillary palp of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). *International Journal of Insect Morphology and Embryology*, 14(5): 291–306.

Slone J, Daniels J, Amrein H, 2007. Sugar receptors in *Drosophila*. *Current Biology*, 17(20): 1809–1816.

Steinbrecht RA, 1997. Pore structures in insect olfactory sensilla: A review of data and concepts. *International Journal of Insect Morphology and Embryology*, 26(3/4): 229–245.

Stensmyr MC, Dweck HKM, Farhan A, Ibba I, Strutz A, Mukunda L, Linz J, Grabe V, Steck K, Lavista-Llanos S, Wicher D, Sachse S, Knaden M, Becher PG, Seki Y, Hansson BS, 2012. A conserved dedicated olfactory circuit for detecting harmful microbes in *Drosophila*. *Cell*, 151(6): 1345–1357.

Stocker RF, 1994. The organization of the chemosensory system in *Drosophila melanogaster*: Areview. *Cell and Tissue Research*, 275(1): 3–26.

Suh GSB, Wong AM, Hergarden AC, Wang JW, Simon AF, Benzer S, Axel R, Anderson DJ, 2004. A single population of olfactory sensory neurons mediates an innate avoidance behaviour in *Drosophila*. *Nature*, 431(7010): 854–859.

Tang QB, Ma Y, Huang LQ, Wang SZ, 2011. Research progress on insect gustatory sensory mechanisms. *Acta Entomologica Sinica*, 54(12): 1433–1444. [汤清波, 马英, 黄玲巧, 王琛柱, 2011. 昆虫味觉感受机制研究进展. 昆虫学报, 54(12): 1433–1444.]

Tang R, Huang C, Yang J, Rao ZC, Cao L, Bai PH, Zhao XC, Dong JF, Yan XZ, Wan FH, Jiang NJ, Han RC, 2024. A ghost moth olfactory prototype of the lepidopteran sex communication, *GigaScience*, 13: giae044.

Task D, Lin CC, Vulpe A, Afify A, Ballou S, Brbic M, Schlegel P, Raji J, Jefferis GSXE, Li HJ, Menuz K, Potter CJ, 2022. Chemoreceptor co-expression in *Drosophila melanogaster* olfactory neurons. *eLife*, 11: e72599.

Thom C, Guerenstein PG, Mechaber WL, Hildebrand JG, 2004. Floral CO_2 reveals flower profitability to moths. *Journal of Chemical Ecology*, 30(6): 1285–1288.

Thoma M, Missbach C, Jordan MD, Grosse-Wilde E, Newcomb RD, Hansson BS, 2019. Transcriptome surveys in silverfish suggest a multistep origin of the insect odorant receptor gene family. *Frontiers in Ecology and Evolution*, 7: 281.

Touhara K, Vosshall LB, 2009. Sensing odorants and pheromones with chemosensory receptors. *Annual Review of Physiology*, 71: 307–332.

Trible W, Olivos-Cisneros L, McKenzie SK, Saragosti J, Chang NC, Matthews BJ, Oxley PR, Kronauer DJC, 2017. Orco mutagenesis causes loss of antennal lobe glomeruli and impaired social behavior in ants. *Cell*, 170(4): 727–735.

Turner SL, Ray A, 2009. Modification of CO_2 avoidance behaviour in *Drosophila* by inhibitory odorants. *Nature*, 461: 277–281.

van der Goes van Naters W, Carlson JR, 2007. Receptors and neurons for fly odors in *Drosophila*. *Current Biology*, 17(7): 606–612.

Vanderplanck M, Lapeyre B, Brondani M, Opsommer M, Dufay M, Hossaert-McKey M, Proffit M, 2021. Ozone pollution alters olfaction and behavior of pollinators. *Antioxidants* (*Basel*), 10(5): 636.

Vosshall LB, 2000. Olfaction in *Drosophila*. *Current Opinion in Neurobiology*, 10(4): 498–503.

Vosshall LB, Amrein H, Morozov PS, Rzhetsky A, Axel R, 1999. A spatial map of olfactory receptor expression in the *Drosophila* antenna. *Cell*, 96(5): 725–736.

Vosshall LB, Wong AM, Axel R, 2000. An olfactory sensory map in the fly brain. *Cell*, 102(2): 147–159.

Wanner KW, Anderson AR, Trowell SC, Theilmann DA, Robertson HM, Newcomb RD, 2007. Female-biased expression of odourant receptor genes in the adult antennae of the silkworm, *Bombyx mori*. *Insect Molecular Biology*, 16(1): 107–119.

Wanner KW, Robertson HM, 2008. The gustatory receptor family in the silkworm moth *Bombyx mori* is characterized by a large expansion of a single lineage of putative bitter receptors. *Insect Molecular Biology*, 17(6): 621–629.

Wicher D, Schäfer R, Bauernfeind R, Stensmyr MC, Heller R, Heinemann SH, Hansson BS, 2008. *Drosophila* odorant receptors are both ligand-gated and cyclic-nucleotide-activated cation channels. *Nature*, 452(7190): 1007–1011.

Xu W, 2020. How do moth and butterfly taste? -Molecular basis of gustatory receptors in Lepidoptera. *Insect Science*, 27(6): 1148–1157.

Yadav P, Borges RM, 2017. The insect ovipositor as a volatile sensor within a closed microcosm. *Journal of Experimental Biology*, 220(Pt 9): 1554–1557.

Yan H, Opachaloemphan C, Mancini G, Yang H, Gallitto M, Mlejnek J, Leibholz A, Haight K, Ghaninia M, Huo L, Perry M, Slone J, Zhou X, Traficante M, Penick CA, Dolezal K, Gokhale K, Stevens K, Fetter-Pruneda I, Bonasio R, Zwiebel LJ, Berger SL, Liebig J, Reinberg D, Desplan C, 2017. An engineered orco mutation produces aberrant social behavior and defective neural development in ants. *Cell*, 170(4): 736–747.

Yang B, Liu Y, Wang B, Wang GR, 2020. The current status, opportunities, and challenges of research on pest olfactory behavior regulation technology. *China National Natural Science Foundation*, 34(4): 441–446. [杨斌, 刘杨, 王冰, 王桂荣, 2020. 害虫嗅觉行为调控技术的研究现状、机遇与挑战. 中国科学基金, 34(4): 441–446.]

Yang K, Huang LQ, Ning C, Wang CZ, 2018. Correction: Two single-point mutations shift the ligand selectivity of a pheromone receptor between two closely related moth species. *eLife*, 7: e42513.

Yao CA, Ignell R, Carlson JR, 2005. Chemosensory coding by neurons in the coeloconic sensilla of the *Drosophila* antenna. *Journal of Neuroscience*, 25(37): 8359–8367.

Yuvaraj JK, Andersson MN, Corcoran JA, Anderbrant O, Löfstedt C, 2018. Functional characterization of odorant receptors from *Lampronia capitella* suggests a non-ditrysian origin of the lepidopteran pheromone receptor clade. *Insect Biochemistry and Molecular Biology*, 100: 39–47.

Zacharuk RY, 1980. Ultrastructure and function of insect chemosensilla. *Annual Review of Entomology*, 25: 27–47.

Zhang S, Jacquin-Joly E, Montagné N, Liu F, Liu Y, Wang GR, 2024. Identification of an odorant receptor responding to sex pheromones in *Spodoptera frugiperda* extends the novel type-I PR lineage in moths. *Insect Science*, 31(2): 489–502.

Zhang Y, Zhang SN, Zhang YY, Liu ZT, Sun ZH, Wen XJ, 2016. Advances in insect olfactory mechanism. *Fujian Journal of Agricultural Sciences*, 31(5): 538–544. [张瑜, 张胜男, 张媛媛, 刘志韬, 孙朝辉, 温秀军, 2016. 昆虫嗅觉机制的研究进展. 福建农业学报, 31(5): 538–544.]

Zhong YZ, Tang R, Zhang JP, Yang SY, Chen GH, He KL, Wang ZY, Zhang F, 2018. Behavioral evidence and olfactory reception of a single alarm pheromone component in *Halyomorpha halys*. *Frontiers in Physiology*, 9: 1610.