前沿与综述

# 昆虫嗅觉编码的分子功能研究进展*

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**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

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**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

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

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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<br>Sensillum | 神经元类型<br>OSN | 受体<br>Receptor | 共受体<br>Co-receptor | 神经纤维球<br>Glomerulus | 最佳配体<br>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,<br>GR63a | NA<br>NA | V 未知<br>Unknown | 二氧化碳 Carbon dioxide（Marshall *et al*., 2010） |
| | ab1D | OR10a,<br>GR10a | ORco<br>NA | DL1<br>未知<br>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,<br>OR85a | ORco<br>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）<br>3-羟基丁酸乙酯 Ethyl 3-hyroxybutyrate（Hallem *et al*., 2004） |
| ab3 | ab3A | OR22a,<br>OR22b | ORco | DM2<br>未知<br>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,<br>OR56a | ORco | DA2/DA2<br>未知<br>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,<br>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）<br>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。

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