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The neuroecology of olfaction in bees

Wendy Carolina Gomez Ramirez, Nyasha KT Thomas,
Iman J Muktar and Olena Riabinina

The focus of bee neuroscience has for a long time been on only a handful of social honeybee and bumblebee species, out of thousands of bees species that have been described. On the other hand, information about the chemical ecology of bees is much more abundant. Here we attempted to compile the scarce information about olfactory systems of bees across species. We also review the major categories of intra- and inter-specific olfactory behaviors of bees, with specific focus on recent literature. We finish by discussing the most promising avenues for bee olfactory research in the near future.

Address
Department of Biosciences, Durham University, Durham, UK

Corresponding authors: Gomez Ramirez, W. Carolina
(wendy.c.gomez-ramirez@durham.ac.uk),
Riabinina, Olena (olena.riabinina@durham.ac.uk)

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Introduction

Bees comprise 20 000 described species [1], most distant of which are separated by over 120 mln years [2,3]. The exchange of chemical messages is crucial for bees to carry out their day-to-day tasks [4–6]. Important chemical signals are also produced by plants that bees forage on [7], and by other insects [8]. However, little or nothing is known about the neuroscience of olfaction in most bee species. Olfactory systems of honeybees (*Apis mellifera*) and, to some extent, bumblebees (*Bombus terrestris* and *Bombus impatiens*) have been studied in the laboratory due to easy logistics: a single bee hive may supply hundreds of workers for experiments, and colonies of the two bumblebee species are commercially available and are easy to maintain in-house. Most of other bee species are not commonly bred, and need to be collected in the field, which hampered our understanding of their sensory systems. Below we attempted to summarize the scarce findings about olfactory receptors and brain organization of bees.

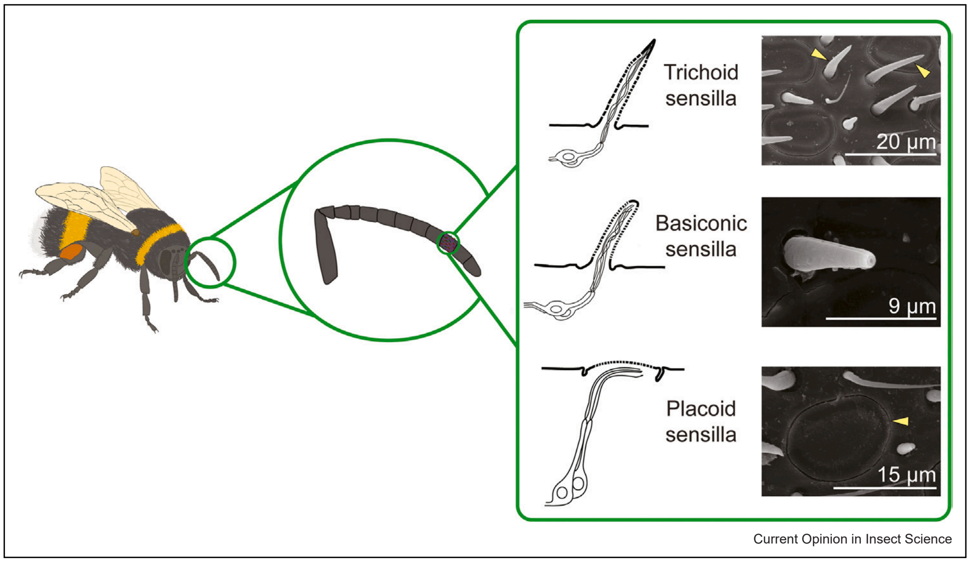
Olfactory behaviors of bees, on the other hand, are much better studied, although our understanding of them is by no means complete. As technology progressed, the focus of researchers shifted from purely behavioral studies to interdisciplinary ones, where attempts were made to identify specific chemical compounds of natural bouquets or the neuronal and genetic basis of olfactory behaviors. Below we focus on the most recent findings about intra- and inter-specific olfactory behaviors of bees, and discuss the underlying molecular mechanisms whenever possible. We review studies on chemical nest marks, threat, alarm and queen pheromones, nestmate recognition and parasitism, and plant-derived olfactory cues that bees use during foraging. The section on olfaction-mediated interactions mostly focusses on the latest advances in the field; a comprehensive review of these topics was not our aim. Finally, we attempted to give the reader a feel of where the field of bee chemical ecology and neuroethology is heading in the nearest future.

Bee olfactory systems

Olfactory receptors

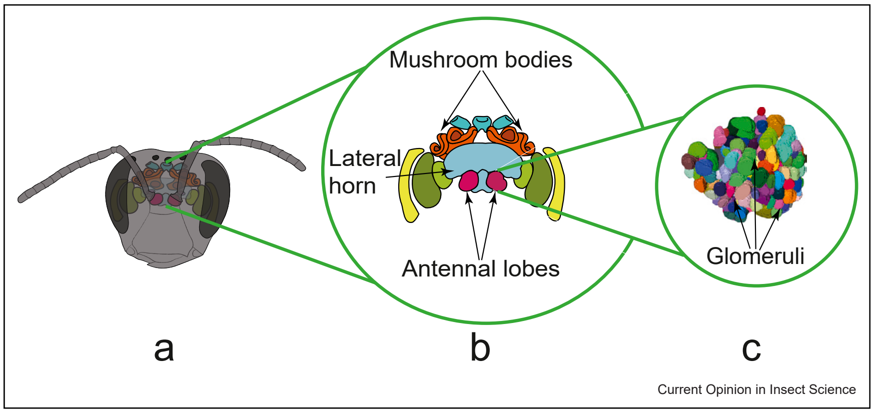
Airborne chemical compounds bind olfactory receptors located inside thin hairs, called sensilla, on the bee antennae (Figure 1). Three classes of olfactory and gustatory sensilla were identified in bees: trichoid, basiconic and placoid [9–12] (Figure 1). The number, length, and distribution of olfactory sensilla are sexually dimorphic in nonparasitic bees [13] and may be plastic, for example, in facultatively social sweat bees *Halictus rubicundus* it depends on climatic conditions [14]. Olfactory receptor genes of bees, as well as other insects, come from two distinct families: odorant receptors (ORs) and ionotropic receptors (IRs). The number of receptor genes varies between bee species — for example, there are 96 in the genome of orchid bees *Euglossa dilemma* and *Euglossa viridissima* [15], 129 in asian honeybees *Apis cerana* [16], 186 in bumblebees *Bombus terrestris* [17] and 187 in european honeybees *Apis mellifera* [18,19]. In some species, only ORs were identified: 112 ORs in thesolitary bee *Dufourea novaeangliae*, 151 ORs in

Figure 1



Anatomy of the peripheral olfactory system of bees. Peripheral olfactory organs of bees, antennae, consist of 10 flagellomeres in females (as shown) and 11 in males. Antennae are covered by chemosensory sensilla of 3 types: trichoid (top panel, yellow arrowheads), basiconic (middle panel) and placoid (bottom panel, yellow arrowhead). SEM images are from *Lasioglossum malachurum* (worker) by Carlo Polidori.

Figure 2



Anatomy of the central olfactory system of bees. **(a)** An outline of *Bombus pascuorum* head with its brain**. (b)** An outline of *B. pascuorum* brain, showing AL (magenta), MB (orange), and LH (purple), as well as nonolfactory brains regions. **(c)** 3D reconstruction of *B. pascuorum* AL. Each glomerulus is colored randomly, with a color distinct from that of its neighbors (IJM, unpublished data).

another solitary species, *Habropoda laboriosa* [20], and 180 ORs in the honeybee *Apis florea* [21]. Similarly to the number of sensilla, expression of olfactory receptor genes is also sexually dimorphic — for example, 67 ORs are upregulated in *A.mellifera* workers, compared to 21 ORs upregulated in drones [22]. OR expression may change depending on bee experiences [23]. Gene expression studies also provide useful information about the receptor repertoire for bee species whose genome has not been sequenced yet (e.g. *Osmia cornuta* [24]). Olfactory receptors are located in the membranes of olfactory receptor neurons (ORNs). Until recently, it has been assumed in insects that each ORN expresses either one OR with common coreceptor ORCO, or one IR with its coreceptor(s). However, this model turned out to be incorrect in *Drosophila melanogaster* [25] and *Aedes aegypti* mosquitoes [26], and it remains to be seen whether it still holds up in bees.

Anatomy of olfactory brain centers

Most of the information about the brain anatomy of bees currently comes from studies on social honeybee *Apis mellifera* (e.g. [27–29]) and bumblebees (e.g. [30–32]), although information about the brain anatomy of facultatively eusocial/solitary sweat bee *Megalopta genalis* [33,34], and solitary bees *Andrena vaga* [35], *Eucera berlandi* [36] and *Euglossa dilemma* [37] is also available (see https://www.bcp.fu-berlin.de/en/biologie/arbeitsgruppen/neurobiologie/ag_menzel/beebrain/index.html, http://neuro.uni-konstanz.de/, https://www.insectbraindb.org/app/ for interactive brain atlases). Specifically, ORNs send their axons from antennae to the first olfactory center in the brain, the antennal lobe (AL). The AL consists of a number of separate spherical structures, glomeruli (Figure 2). Each glomerulus is thought to be innervated by ORNs that express the same receptors. Drones of honeybees *Apis mellifera* and long-horned solitary bees *Eucera berlandi* have larger antennae with higher number of olfactory sensilla than female workers. However, the workers possess higher number of olfactory glomeruli in the AL [36]. This organization suggests that drones are able to detect fewer stimuli than workers, but are sensitive to a broader range of concentrations of their detectable stimuli. Second-order olfactory neurons, called projection neurons, receive information from the AL and deliver it to Mushroom Bodies (MB) and Lateral Horn (LH) (Figure 2). The AL is also innervated by local interneurons. Functional studies of AL, LH, and MB responses to odorants have so far been conducted on *Apis mellifera* [38–41], *Bombus terrestris* [42,43] and *Andrena vaga* [35,44] using electrophysiology and live imaging methods. Responses of ORNs have also been studied via electrophysiological recordings from olfactory sensilla in a number of bee species [9,45–50].

While the overall organization of olfactory system is similar across insects [51–53], many important differences exist even in species of the same insect order, as was recently exemplified by studies on flies and mosquitoes [54–58]. The chemical ecology and behavioral repertoire of a particular bee species are thus likely to determine its responses to odorants and details of its olfactory anatomy. Below we focus on selected intra- and inter-specific olfactory behaviors of bees and discuss specific chemical compounds that mediate these behaviors.

Intraspecific interactions

Chemical nest marks as cues to self and conspecifics

Solitary bees often nest in large aggregates of conspecifics, but forage and collect provisions to repeatedly return to their individual nests [59,60]. Living in large aggregates presents the challenge of distinguishing an individual's nest amongst many visually identical ones, as well as within a complex landscape [61–64]. Solitary bees must therefore be able to use a variety of environmental cues, such as spatial, visual, and chemosensory identifiers to locate their nests [65–71].

Both social bees (*Bombus*) and solitary bees (e.g. *Xylocopa*, *Osmia*, *Megachile* spp) deposit scent marks at nesting sites [4,66,68–74]. Previous investigations into the origin of scent marks utilized analytical methods such as gas chromatography–mass spectrometry (GC-MS) to identify the chemical composition of samples collected from the nest entrances and inner nest walls, comparing them with the chemical composition of cuticular and mandibular secretions [75–77]. Comparisons revealed that the chemical composition of nest samples of the alfalfa leafcutting bee *Megachile rotundata*, the orchard mason bee *Osmia lignaria*, and other species were highly consistent with the composition of their cuticular hydrocarbons (CHCs), mandibular and abdominal secretions [76–78]. Behavioral observations revealed that bees deposit the secretion by dragging their mandibles and abdomens along nest [66,69,70,79,80], scraping of inner nest wall with mandibles, and dabbing with the tips of abdomens prior to brood cell construction [61,70,76,81,82]. Extracts originating from nest cavities were dominated by alkanes and mono-alkenes, largely corresponding to secretions from the exocrine gland, Dufour's gland, for example, alkenes, esters, and primary alcohols [76,77,82,83]. The origin of other compounds identified from nest entrances, including primarily alkenes and some alkanes, have been attributed to the cuticle of studied bees, suggesting that they also contribute to the tag [75,77,82,83]. Recently, Frahnert and Seidelmann [82] additionally identified compounds that could not be attributed to cuticular or glandular secretions and suggested that they likely come from the local environment (i.e. floral volatiles). The composition of marks changed over time, suggesting a plasticity of the marks in response to time and the environment [76,82]. This, along with previous observations suggest that nest scent marks originate from a dynamic mixture of glandular secretions, CHC passive transfers, as well as local environmental factors.

Olfactory perception of nest mark compounds — alkanes, alkenes, esters, and alcohols — is likely to be mediated via OR family of receptors. Although ligands for ORs of *Osmia*, *Xylocopa*, and *Megachile* spp. have not been investigated yet, *Apis mellifera* OR151 and OR152 responded to a mixture of floral volatiles in an *in vitro* assay [36]. In addition, ORs of the ant *Harpegnathos saltator* were shown to bind CHCs (alkanes) [84], and Dipteran ORs are known to bind hydrocarbons, esters, and alcohols [85–87]. Responses to primary alcohols were also observed in the AL of *Bombus terrestris* [42] and *Apis mellifera* [88], although it is not known which receptors mediate these responses.

Threat and alarm pheromones

Pheromone-based communication enables bees to broadcast information widely to all colony members [89–92]. Aside from extensively studied sex pheromones, bees that live in large colonies also use threat and alarm pheromones to coordinate a colony's response in an emergency [8]. Alarm pheromones are usually released from mandibular or sting glands, and contain alcohols, ketones and esters [8]. In the honeybee *Apis mellifera*, for example, the alarm pheromone contains more than 40 compounds, the most prominent of which is isoamyl acetate with its characteristic banana smell [93,94]. Alarm pheromone compounds of stingless bees *Trigona spp*, *Scaptotrigona depilis*, *Oxytrigona mediorufa*, and *Melipona beecheii* were also characterized (reviewed in [50]). A recent study found that the stingless bee *Melipona solani* produces (S)-2-heptanol as a single alarm pheromone compound in its mandibular gland and releases it when threatened [50]. Electroantennograms have demonstrated that *M.solani* antennae respond to this compound, providing further evidence for its role as a pheromone. In contrast to other species of stingless bees who exhibit aggressive behavior in response to their alarm pheromones (*Scaptotrigona spp.*) [95], *M. solani* shows a docile response by retreating into the colony and closing the nest entrance with wax [50].

Defensive behavior may be elicited not only by conspecific alarm pheromones, but also by kairomones from a predator. For example, citral is produced by robber bees *Lestrimellita limao* and acts as alarm kairomone for the stingless bee *Tetragonisca angustula*, triggering their defensive behavior [96,97]. A recent paper investigated neuronal responses to citral in *T. angustula* and found that antennal responses are higher in guards than in foragers, which might be due to the higher number of placoid sensilla in guards [45]. Similarly, in *Tetragonisca fiebrigi*, guard bees have longer olfactory sensilla than foragers, which could be associated with the guards' defense tasks in the colony [13].

Olfactory receptors that bind bee alarm compounds, and the neuronal substrates that process these signals, have not been identified yet.

Nestmate recognition

Kin recognition is an important ability that allows bees to protect brood, food, and nesting resources [98–100]. Discrimination between resident and nonresident odors has been largely studied in eusocial bees such as *Lasioglossum zephyrum*, in which early experiments showed that guard bees can learn the odor of their nestmates, and use the odors to accept or reject bees entering in the colony [98,101]. CHC profiles are the odor signatures that bees use to distinguish nestmates from alien conspecifics [70,99,102]. These signatures are so specific that a change in one alkene can trigger aggressive behavior towards a forager and even the expulsion from the colony in honey bees [99]. A recent study revealed that the use of biocides in crops affects the composition of CHCs in honeybee foragers, leading to less aggressive behavior by guards and an increased acceptance of non-nestmates to the colony, which can dramatically affect the colony survival [103]. In addition to honeybees, studies of several species of neotropical stingless bees of the genus *Melipona* demonstrated that each species produces a unique content of alkene isomers in their CHCs profiles, which is crucial for nestmate recognition [102]. Research conducted on African stingless bees (*Meliponula ferruginea*, *Plebeina hildebrandti*, *Hypotrigona gribodoi* and *Hypotrigona ruspoli*) indicated that nest materials (nest entrance and involucrum sheaths) have CHCs profiles similar to foragers, which makes them an additional channel of nestmate recognition cues [104]. Despite the high number of studies on the topic, there is a lack of knowledge on non-eusocial bees. A recent paper described and characterized the composition of CHCs in the sub-social species *Ceratina calcarata*, which is capable of kin recognition. However, the researchers argue that the chemical basis of that behaviors is not verified and needs further studies [105].

The understanding of nestmate recognition in bees still presents many gaps in terms of plasticity of CHCs (how can this be affected by the environment conditions and pollutants), detection of these signals at the neuronal level (ORs, IRs and Odorant binding protein, OBPs involved), and relevance to the evolution of sociality (how this works for primitively social and solitary bees).

Queen pheromones and division of labor

Instead of direct aggression, queen bees use a pheromone to subordinate their workers and, in some cases (e.g. honeybees, stingless bees), suppress the workers' reproduction [89,90,92,106]. Queen pheromones have been extensively studied in highly eusocial bees [107]. In *Apis mellifera*, the queen pheromone consists of multiple components, with 4 being key to suppress worker reproduction: 9-hydroxy- and 9-keto-2(*E*)-decenoic acids (9-ODA), methyl p-hydroxybenzoate (HOB), and 4-hydroxy-3-methoxyphenyl-ethanol (HVA) [92,108]. In *Apis cerana*, the HVA is not present in the queen pheromone, but the other three components effect worker suppression [107]. The pheromone of *Apis florea*, *Apis dorsata* and *Apis andreniformis* lack both HVA and HOB [107]. Interestingly, in bumblebees *Bombus terrestris* queen pheromone consists of a single hydrocarbon, pentacosane [109]. In *Bombus impatiens*, the chemical identity of the pheromone is unclear but seems to also consist of CHCs [110]. However, this pheromone alone is insufficient to suppress the reproduction of workers, and must be supplemented by other sources of information, such as the presence of brood and a dominant female to elicit effective suppression [111,112]. Recent studies on primitively eusocial halictid bees *Megalopta genalis*, *Lasioglossum pauxillum*, *Lasioglossum malachurum* and *Halictus rubicundus* established that an additional chemical class of compounds, macrocyclic lactones, may contribute to the queen pheromone in these bees and elicit antennal and behavioral responses in workers [83,113–115]. Macrocyclic lactones were previously found in the Dufour's gland secretion of 18 species of halictid bees, suggesting their possible involvement in the division of labor in these species [116].

The *A.mellifera* receptor AmOR11 is activated by the queen pheromone component 9-ODA *in vitro* [27], and is upregulated in drones. It is unclear what receptors are responsible for queen pheromone detection in workers. In *Apis cerana*, the odorant binding protein AcerOBP11, found only in basiconic sensilla of workers' antenna (see Figure 1), has a strong binding affinity for HOB and 9-ODA [117]. Receptors or OBPs that bind pheromone components in halictid bees are not known, while hydrocarbon detection is likely to be mediated by an OR, as discussed above (see *Chemical nest marks as cues to self and conspecifics*).

Sex pheromones

In bees, the detection of the partner's smell has driven an evident sexual dimorphism in peripheral olfactory organs and the AL. Males possess larger antennae (11 flagellomeres) that house a higher number of olfactory sensilla (placoid sensilla) than females (10 flagellomeres) (see Figure 1) [22,118,119]. Honeybee males also possess macroglomeruli (large glomeruli) in their AL, specialized for the processing of pheromone signals [120,121]. However, this dimorphism goes further than just the morphological traits. Recent studies in honeybees have identified differences in the OR expression in drones and females, both workers and queens, showing higher expression of AmOR11, involved in the detection of 9-ODA, and AmOR18 and AmOR170 in males [22,119]. 9-ODA thus plays a role not only in worker suppression, but also in drone attraction to a queen. *In situ* hybridization experiments indicated that AmOR11 are expressed in placoid sensilla of drones [119]. Interestingly, in bumblebees queen sex pheromone has not been as widely studied and tested as male sex pheromones [122]. Chemical components of the male pheromone are numerous and species specific, with key active components not yet identified. Male-derived sex pheromones have also been reported in *Andrena*, *Centris*, *Xylocopa*, and *Collettes* bees (reviewed in [122]).

Males of orchid bees *Euglossini* do not produce a pheromone inside their bodies, but instead cover themselves with a specific chemical blend that they collect from fungi, flowers, and vegetation [123]. This perfume functions as their sexual pheromone. A recent study compared two species, *Euglossa dilemma* and *Euglossa viridissima*, and established that the perfume components are distinct in these two species [124]. 2-hydroxy-6-nona-1,3-dienyl-benzaldehyde (HNDB) is the major compound in perfume blend of *E.dilemma* and is absent in *E.viridissima*, while the opposite is true for linoleic acid lactone-derivative (L97). Genome sequencing and analysis of selective sweeps narrowed down on one olfactory receptor gene, OR41, that is present in both species, but has acquired nonsynonymous substitutions in *E.dilemma*. When both receptor variants were expressed in *Drosophila* empty neuron, only *E.dilemma* variant responded to HNDB, thus demonstrating the likely signal-receptor (HNDB-OR41) coevolution in this species [124].

Inter-specific interactions

Parasitism

Chemical signaling, such as chemical mimicry and chemical insignificance, among others, is important for communication between species (e.g. [5,125,126]). As discussed before, recognition of cuticular chemical profiles allows bees and other Hymenopterans to discriminate between nestmates and intruders [125] (see also, *Nestmate recognition*). Cleptoparasitic bees, however, have developed strategies to sneak into host nests, avoiding aggression from nest natives by copying their CHC profiles or by reducing their own signal. Recent work investigated chemical mimicry between two sympatric cleptobiotic bees of *Lestrimelitta sp.* and their hosts. By copying the alkene profiles of the preferred host species, *Lestrimelitta niitkib* and another *Lestrimelitta sp.* (unidentified) go unnoticed into their hosts nest (*Nannotrigona perilampoides* and *Scaptotrigona pectoralis*, respectively) [127]. Interestingly, the CHC profile of *L.niitkib* is dramatically different from its nonhost *S.pectoralis*, and the profile of other *Lestrimelitta* sp. is distinct from its nonhost *N. perilampoides* [127]. This finding implies that CHC composition of *Lestrimelitta* and their hosts coevolved — a phenomenon previously described for wasps [128], ants [129], and bumblebees [130].

Cuckoo wasps and a cuckoo bee use a related strategy, whereby they exhibit a CHC profile that copies that of their hosts, but with a much lower number of compounds [131–133]. This strategy, called chemical insignificance, makes the cuckoo species undetectable to their hosts. For example, cuckoo bees *Sphecodes monilicornis* have a CHC profile that contains only 9 linear alkanes and no other compounds. These CHCs constitute 30–50% of CHCs found in their host, the social bees *Lasioglossum*. As a result, *Lasioglossum* do not react aggressively towards *S.monilicornis* when the latter invade their nest [133].

Plant-derived olfactory cues

There is a large compendium of literature aimed at understanding the chemical communication between plants and bees, mostly focussed on specialist foragers. The role of flower volatiles began to be studied in the 1960s with the work on interactions between orchids and euglossine bees [134–136]. Since then, many studies addressed different aspects of the floral scent as a signal, from the plant physiology perspective to the attraction, detection, and ecological relevance for bees [137–139].

Nowadays, it is clear that olfactory cues are used by bees when foraging (e.g. [139–141]), thereby, recent studies have focused primarily on identification of specific volatile compounds to which bees respond [35,44,141–145]. For instance, a GC-MS analysis found 108 organic volatile compounds in the European pear (*Pyrus communis* L.), of which 17 elicited responses in honeybee neurons when assayed by electroantennography [146]. Some of these compounds were previously identified in other floral scents [147], and one of the most abundant compounds, linalool, elicited both neuronal and behavioral [148] responses in honeybees. Specialist bees require a fine-tuned sense of smell to find their host plants; this is the case of *Andrena vaga*, who shows strong responses in the AL glomeruli to 4-Oxoisophorone, a common constituent in the scent of its host plant *Salix spp*. The honeybee *Apis mellifera*, who is a generalist, does not respond to this compound [44]. Interestingly, the specialist bee *Chelostoma rapunculi* shows attraction to other plants apart from its hosts; however, this could be explained by a small fraction of spiroacetals (compounds mainly produced by *Campanula spp.*) in the nonhost plant *Geranium sanguineum* [149]. The studies mentioned support the idea of high degree of specialization on the detection of flower volatiles in oligolectic bees.

Nocturnal bees also rely on the detection of plant volatiles to make their foraging choices. *Ptiloglossa latecalcarata* (female bees only), *Megalopta aegis*, and *Megalopta amoena* (both males and females) mostly collect pollen from a common fruit crop *Caryocar brasiliense*, amongst other flowers, but, interestingly, do not contribute to its pollination [150]. *C. brasiliense* flower volatiles contain aliphatic hydrocarbons and sulfurous compounds [151] that are absent in the headspace of other melittophilous flowers. It is unclear however whether these volatiles are attractive to the nocturnal bees. Another recent study used a different set of synthetic compounds as odor baits to identify aromatic compounds that are present in floral smells and are attractive to nocturnal bees *Ptiloglossa*, *Megalopta*, and *Megommation* [145]. 2-phenyletanol, eugenol, methyl salicylate, and eucalyptol were the most effective attractants. Electroantennography on *Megommation insigne* bees indicated that a 6-component *s*ynthetic scent mixture based on the floral smell of the cambuci plant *Campomanesia phaea* and 2-phenylethanol elicit neuronal responses in *M.insigne* [145].

Conclusions and outlook

Deorphanisation of olfactory receptors and establishment of olfactory coding in bees is lagging well behind that of Diptera, possibly due to the strikingly diverse behaviors of bees, unavailability of sequenced genomes, difficulty of keeping lab colonies, producing transgenics, and the high number of receptors to be tested (although see [152] for most recent efforts). It is also likely that many species of bees are not yet identified. Large-scale efforts are required to sequence bee genomes [153] and establish libraries of basic tools, for example, for heterologous receptor expression and gene knockout or knockdown. It is also important to thoroughly characterize electrophysiological responses of chemosensory sensilla across bee species. We suggest that, apart from the agriculturally important pollinators, these efforts should also include species with interesting and unusual behaviors.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data were used for the research described in the article.

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Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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