Chemical Ecology of Arachnids - Morphology, Behaviour, and Semiochemicals

Andreas Fischer[1], N. Kirk Hillier[2], Lise Roy[3], and Nicoletta Faraone[4]
[1]General and Systematic Zoology, University of Greifswald; Greifswald, 17489, MV, Germany
[2]Department of Biology, Acadia University, 33 Westwood Avenue, B4P2R6 Wolfville, Nova Scotia, Canada
[3] CEFE, University of Montpellier, CNRS, EPHE, IRD, Université Paul-Valéry Montpellier 3, Montpellier, France
[4]Department of Chemistry, Acadia University, 6 University Avenue, B4P2R6 Wolfville, Nova Scotia, Canada

ABSTRACT

Arachnids represent a diverse and ecologically influential paraphyletic assemblage of chelicerate arthropods that has colonized virtually every terrestrial habitat. Arachnids contribute to ecosystems as predators, parasites and decomposers. Yet, the chemical mechanisms that allow arachnids to interact with the environment remain strikingly understudied relative to their taxonomic breadth. Much of what is known for insect chemical communications has yet to be investigated for arachnids. Compared to insects, arachnids lack antennae and only share two out of three chemo-receptor families which mediate chemoreception across Insecta. The sophisticated and structural diversity with which arachnids taste and smell recently gained appreciation. Here, we compare the diverse modified appendages that enable gustation and olfaction of arachnids: from pectines of scorpions and malleoli of solifuges to the Haller's organ of ticks and the antenniform legs of amblypygids. The detected chemical information mediates basic behaviours including mate recognition and choice, social interactions, prey or host detection and predator avoidance.

Our review provides a comprehensive synthesis of arachnid chemical ecology, from sensory detection to behavioural response. We provide an overview of the diversity of arachnid behaviours in response to semiochemicals, from pheromones through cuticular hydrocarbons to kairomones. The few identified semiochemicals produced by arachnids are likewise discussed and compared against those of the better studied insects. We catalogue the underlying morpho-anatomy of chemosensory organs across Arachnida and discuss where investigations could yet reveal chemosensory structures. We record the electrophysiological evidence linking sense organs to specific semiochemicals as well as sense organs to behavioural responses, highlighting the technical challenges and recent methodological advancements.

Yet critical questions persist for the chemical ecology of Arachnida: Which chemoreceptor families detect pheromones, kairomones, and other semiochemicals? Where are the chemosensory organs located on the body, apart from the few that have been identified? Recent advances in genomics, transcriptomics, electrophysiology, and metabolomics now offer unprecedented opportunities to bridge knowledge gaps. Comparative analyses of chemoreceptor gene candidates amongst transcript profiles, coupled with computer tracked behavioural assays, are beginning to reveal the molecular and neural mechanisms that shape arachnid chemical communication. We identify the ongoing challenges that can now be addressed with improved methodology. Particularly the scarcity of identified pheromones across most Arachnida or the near absence of integrative studies in smaller, historically neglected orders. By integrating perspectives from evolutionary biology, chemical ecology at different spatial scales, neurology and metabolomics, we outline priority directions for future research to uncover the breadth, complexity, and evolutionary origins of chemical communication across Arachnida.

Key words: ticks, spiders, mites, sensory morphology, electrophysiology, Chelicerata, metabolomics, sensory ecology, chemical communication, Arachnida

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I Introduction

Arachnids are a remarkably diverse and ecologically significant group of arthropods encompassing spiders, scorpions, ticks, mites, and several lesser-known groups (**Fig. 1**). Over 120,000 species of arachnids have been described (World Arachnid Catalog, 2026), with estimates suggesting that the true number could be two to three times higher due to under-sampling and cryptic diversity (Zhang, 2013). This highlights the exceptional evolutionary success of arachnids across ecosystems.

Arachnids occupy virtually every terrestrial and many aquatic environments. Across ecosystems, they function as predators regulating arthropod populations, parasites of animals and plants, detritivores contributing to nutrient cycling, and prey supporting higher trophic levels. Collectively, these roles position arachnids as central drivers of food web structure, ecosystem stability, and, in some cases, disease dynamics (Moro, Chauve & Zenner, 2005; Pekár & Raspotnig, 2022; Foelix, 2025).

Survival and reproductive success of arachnids rely on a suite of finely tuned sensory modalities. Mechanoreception and vision contribute for some species to prey capture and navigation; however, chemosensation plays the pivotal role in mediating interactions with conspecifics, predators, hosts and the environment, especially in the many blind species. Chemical information, whether airborne (i.e., olfaction) or substrate-bound (i.e., gustation), are integral for mate location, aggregation, prey detection, and predator avoidance (Uhl, 2013; Fischer, 2019). Acknowledging the ecological significance of chemosensation for arachnids, fundamental questions remain unanswered: How do different chemosensory organs function in tandem or in isolation? What molecular receptors underlie the detection of specific semiochemicals? Which semiochemicals are used to transfer information and how do the biosynthetic pathways of chemical signals relate with phylogeny? To what extent is chemosensory behaviour shaped by context, phylogenetic constraints, or convergent evolution?

Chemical communication in arachnid is facilitated by a diverse array of chemosensory organs, including specialized sensilla on unique appendages, such as the pectines of scorpions (Wolf, 2017), or specific organs such as the Haller's organ of ticks (Faraone, 2022). The diversity of these sensory systems and their behavioural outputs mirror the ecological niches and evolutionary histories of each arachnid lineage. However, detailed knowledge of chemosensory function is limited to a few model taxa—particularly araneomorph spiders and parasitiform ticks—leaving most arachnid lineages comparatively unexplored. In this review, we synthesize current knowledge of chemosensory systems and chemical communication across major arachnid lineages, highlighting both established findings and critical gaps.

(1) Biodiversity of Arachnids

"Arachnids" are considered paraphyletic within the Chelicerata (Sharma & Gavish-Regev, 2024). Modern phylogenetic hypotheses of Chelicerata nest the horseshoe crabs and seaspiders among the Arachnida. "Arachnida" thus comprises eleven extant orders (**Table 1**), together representing a wide spectrum of life histories and sensory adaptations relevant to chemical ecology.

Table 1: "Arachnid" orders based on the phylogeny presented in Sharma & Gavish-Regev, 2024

Order	Common name	Accepted species	Reference
Araneae	Spiders	53,644	World Spider Catalog, 2026
Acariformes	Mites	42,096	Zhang, 2013
Parasitiformes	Mites and Ticks	12,377	Zhang, 2013
Opiliones	Harvestmen	6,686	Kury *et al.*, 2026
Pseudoscorpiones	Pseudoscorpions	4,208	World Pseudoscopriones Catalog, 2026
Scorpiones	Scorpions	2,750	Santibáñez-López *et al.*, 2023
Pycnogonida	Seaspiders	1,591	Bamber *et al.*, 2026
Solifugae	Camel spiders	1,221	World Solifugae Catalog, 2026
Schizomida	Short-tailed whip-scorpion	376	World Schizomida Catalog, 2026
Amblypygi	Whip spiders	279	World Amblypygi Catalog, 2026
Palpigradi	Microwhip scorpion	139	World Palpigradi Catalog, 2026
Uropygi	Whip scorpions	128	World Uropygi Catalog, 2026
Ricinulei	Hooded tickspiders	103	World Ricinulei Catalog, 2026
Xiphosura	Horseshoe crabs	4	Lamsdell, 2020

Each arachnid order possesses unique morphological and behavioural adaptations that influence their modes of chemical communication. The following sections summarize general features of these groups and provide insights into their known or potential roles in chemosensation. Chemical ecology provides a powerful lens for examining behavioural and evolutionary processes in arachnids. Olfactory-mediated behaviours influence prey capture strategies, predator avoidance, mate selection, and social structuring (Uhl & Elias, 2011; Foelix, 2025).

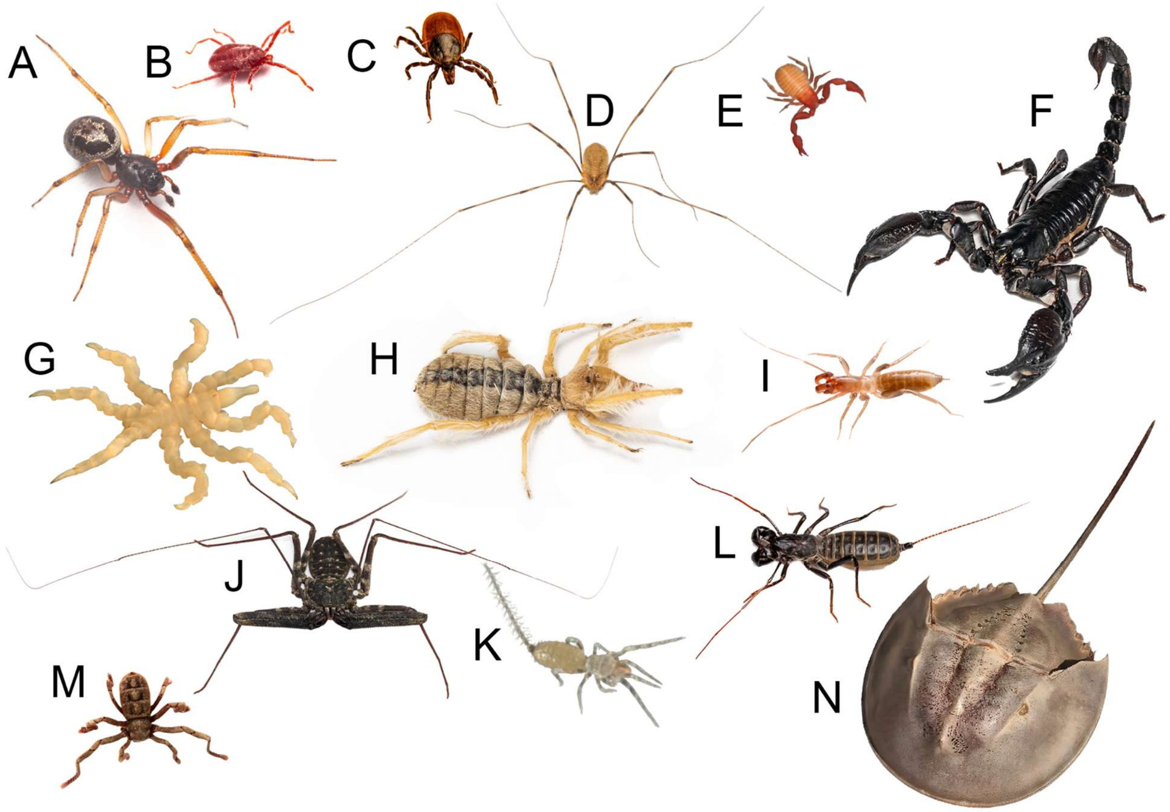

Fig. 1: Photographs of selected arachnids. (A) *Steatoda nobilis* (Araneae: Theridiidae, photo: AF), (B) *Trombidium holosericeum* (Acariformes: Trombidiidae, photo: AF), (C) *Ixodes scapularis* (Parasitiformes: Ixodidae, photo: AF), (D) *Opilio canestrinii* (Opiliones: Phalangiidae, photo: AF), (E) *Lamprochernes nodosus* (Pseudoscorpiones: Chernetidae, photo LR), (F) *Heterometrus laoticus* (Scorpiones: Scorpionidae, photo: AF), (G) *Pycnogonum litorale* (Pycnogonida: Pycnogonidae, photo: Jesús Ballesteros), (H) *Galeodes* sp. (Solifugae: Galeodes, photo: AF), (I) Hubbardia sp. (Schizomida: Hubbardiidae, photo: Dr. Marshal Hedin), (J) *Damon medius* (Amblypygi: Phrynichidae, photo: AF), (K) unidentified Palpigradi (photo: Jillian Cowles), (L) *Mastigoproctus giganteus* (Uropygi: Thelyphonidae, photo: AF), (M) *Cryptocellus narino* (Ricinulei: Ricinoididae, photo: Dr. Giovanni Talarico), (N) *Limulus polyphemus* (Xiphosura: Limulidae, photo: AF).

(2) General Introduction on each Order

Spiders (Araneae)

Spiders (**Fig. 1A**) are the most speciose arachnid with over 53,500 species categorized within 120 families (World Spider Catalog, 2026). Spiders are unwarrantly perceived as infamous (Mammola *et al.*, 2025) given that arachnophobia is the most commonly reported biophobia (Zeller *et al.*, 2025). However, spiders are generally (99.5% of them) harmless for humans (Hauke & Herzig, 2017). While mostly safe for humans, spiders are important predators of arthropods, contributing to ecosystem functions by limiting insect populations and indirectly shaping plant communities and diversity (Nyffeler & Birkhofer, 2017; Cardoso *et al.*, 2025). The ecological niches of spiders are as diverse as spiders themselves, some spiders are sessile on webs, or in silk-lined crevices, while others hunt cursorily (Foelix, 2025). Spiders are divided into three suborders: Mesothelae, the tarantula containing Mygalomorphae, and the hyperdiverse Araneomorphae (Wheeler *et al.*, 2017). Chemical communication has been observed in the Mygalomorphae

(Dor *et al.*, 2008) and is relatively best studied in the Araneomorphae (Schulz, 2004, 2013; Gaskett, 2007; Uhl & Elias, 2011; Uhl, 2013; Fischer, 2019; Foelix, 2025). No experimental investigation of chemical communication of Mesothelae spiders is known to us with rare reports suggesting chemosensation by Mygalomorphs (Dor *et al.*, 2008). Spiders taste substrate-bound molecules via tip-pore sensilla primarily located on their legs, pedipalps and mouthparts (Foelix, 1985a; Tichy *et al.*, 2001; Ganske & Uhl, 2018; Müller, Ganske & Uhl, 2020; Talukder *et al.*, 2025a). Olfactory perception (i.e., smelling) of sex pheromones has been attributed to wall-pore sensilla that are likewise located on the spider's leg (Talukder *et al.*, 2025b). Sex pheromones facilitate mate choice of male and female spiders by mediating attraction and courtship and providing fitness information. Interestingly, the biosynthetic pathways of the few identified pheromones differ widely across spider phylogeny. Spiders use pheromones to communicate among males and among females (Scott *et al.*, 2015a; Fischer *et al.*, 2023a). Prey is detected chemically (Jackson & Cross, 2015), while in specialized spiders even attracted by scent (Haynes *et al.*, 2002). Danger, such as predators, may be detected and avoided via chemical information (Shannon, Kutz & Persons, 2022; Narimanov *et al.*, 2024).

The Acariformes (Fig. 1B) and Parasitiformes (Fig. 1C) groups comprise over 54,617 described arachnid species (Zhang, 2013). They may be found in nearly all terrestrial and freshwater habitats and display a wide range of diets—predatory, parasitic, saprophagous, and phytophagous. Most lack visual organs and instead rely heavily on chemosensation for intra- and interspecific communication. The common distinction between mites and ticks is not taxonomically accurate. Mites (Fig. 1B) are paraphyletic and encompass much of Parasitiformes (e.g., Mesostigmata, Opilioacarida) and all of Acariformes (Trombidiformes, Sarcoptiformes). While ticks (Fig. 1C) belong to the order Ixodida within the superorder Parasitiformes. Ticks are obligate ectoparasites feeding on mammals, birds, reptiles, and amphibians. Ticks locate hosts via chemical cues like CO_2, heat, and host odours using Haller's organ (Carr *et al.*, 2017; Josek, Allan & Alleyne, 2018; Faraone, 2022). Ticks also use pheromones for aggregation and mating, which are critical for survival and potential targets for control strategies (Carr & Roe, 2016).

Mesostigmata includes mites with diverse life histories in soil, litter, nests, and on plants. Parasitism has evolved independently multiple times and constitute a small part of clades grouping predatory and saprophagous species (Dowling & OConnor, 2010). Families like Dermanyssidae and Macronyssidae affect poultry, while Varroidae and Laelapidae impact beekeeping. These mites use volatile kairomones to detect hosts (Light *et al.*, 2020; Auffray *et al.*, 2022). Predatory Phytoseiidae respond to herbivore-induced plant volatiles (Maeda & Takabayashi, 2001), and aggregation pheromones are known in several groups (e.g. Entrekin & Oliver, 1982), though sex pheromones remain largely unstudied. Acariformes show even greater ecological and feeding diversity, including terrestrial, aquatic, and marine forms and may be predatory, parasitic, saprophagous, or phytophagous (Lindquist, 1999). Sarcoptiformes include dust mites, cheese mites, scabies mites (Astigmata), and soil-dwelling Oribatida. Trombidiformes are highly diverse, with predators (e.g., Trombidiidae), plant pests (e.g., Tetranychidae), and vertebrate parasites (e.g., Trombiculidae). Some species show stage-specific behaviour, such as parasitic larvae (e.g., chigger mites) and predatory adults.

Opiliones (**Fig. 1D**), commonly known as harvestmen, constitute the third largest arachnid order with over 6,600 described species (Kury *et al.*, 2026), which lack venom or silk glands. Harvestmen occur across terrestrial ecosystems and function as generalist predators and scavengers. Contact chemoreception is used to find food (Willemart *et al.*, 2007) and they utilize their second pair of legs as specialized antenniform organs to perceive the environment (Gainett *et al.*, 2017). Chemical defenses are particularly well described which are secreted via ozopores (Hara, Cavalheiro & Gnaspini, 2005). Pheromones have not yet been identified, whereas ethological evidence suggests chemical communication to mediate mate choice and aggregation behaviour (Donaldson & Grether, 2007; Fernandes *et al.*, 2017).

With over 4,000 species, pseudoscorpions (**Fig. 1E**) are small predators commonly found in leaf litter, under bark, and in soil habitats. Despite their ubiquity and potential role in soil ecosystems, chemosensory studies remain sparse (Stemme & Pfeffer, 2022).

Scorpions (**Fig. 1F**) represent a major extant lineage within Arachnida, with roughly 2,750 described species. Their chemosensory systems include specialized ventral comb-like appendages called pectines (Wolf, 2017), which are thought to play a role in both substrate-borne and airborne chemical detection. Scorpions use chemosensory information for mate location, prey tracking, and territorial marking according to behavioural reports and the semiochemicals involved are yet to be identified. Although less extensively studied than in spiders or ticks, recent research has begun to elucidate the molecular basis of scorpion olfaction and its behavioural relevance (Wolf, 2008, 2017; Oviedo-Diego *et al.*, 2021).

Pycnogonida (**Fig. 1G**), Solifuges (**Fig. 1H**), Schizomida (**Fig. 1I**), Amblypygi (**Fig. 1J**) Palpigradi (**Fig. 1K**), Uropygi (**Fig. 1L**) Ricinulei (**Fig. 1M**) and Xiphosura (**Fig. 1N**) are less specious arachnid orders, often referred to as lower or the “neglected arachnids” (Harvey, 2002). These arachnids exhibit an array of behaviours which suggest chemosensory adaptations – but studies to substantiate are few (Botton, Loveland & Jacobsen, 1988; Talarico, Palacios-Vargas & Alberti, 2007, 2008; Chapin & Hebets, 2016; Hebets *et al.*, 2024).

II Semiochemicals and Behavioural Evidence of Chemosensation in “Arachnida”

Semiochemicals play a pivotal role in mediating both intra- and interspecific behaviours among chelicerates, encompassing a vast array of ecological contexts including mate choice, aggregation, alarm signaling, host and prey detection and defense. Chemical information can be broadly categorized into pheromones, which facilitate communication between conspecifics, and allelochemicals, which mediate interactions between different species. Allelochemicals are further subdivided into kairomones (i.e., benefiting the receiver), allomones (i.e., benefiting the emitter), and synomones (i.e., benefiting both parties) (Wyatt, 2014). Insects have been best studied for their chemical ecology, while research on arachnids remains comparatively underdeveloped. Here we accumulate evidence that highlights the essential role of chemical signals across chelicerate taxa.

(1) Pheromones and Reproductive Semiochemistry

Pheromonal communication is vital to reproductive success in chelicerates, orchestrating a series of behaviours including mate location, species recognition, assessment of partner quality, and mating itself (Johansson & Jones, 2007). Chemical signals mediate a hierarchical sequence of mate choice decisions to narrow the pool of potential partners (Andersson & Simmons, 2006). The primary level is mate recognition, encompassing both species and sex identification (Ptacek, 2000). For many arachnids, volatile long range pheromones, or upon contact, cuticular (or silk borne) inform the receiver that the sender is a fertile conspecific of the opposite sex.

Once a potential mate is recognized it is favourable to assess their quality. Pheromones vary among individuals and may reflect their quality when dependent on the condition of the signaller (Laidre & Johnstone, 2013). Pheromones that are metabolically costly to produce or depend on the nutritional status can serve as 'honest signals' of phenotypic condition, revealing information about the signaler's body size or weight, parasite load and by proxy, their reproductive value (Hamilton & Zuk, 1982; Johnstone & Grafen, 1993). Consequently, variations in pheromone composition or quantity enable the choosing sex to discriminate among potential mates, driving the evolution of elaborate and diverse chemical courtships via sexual selection.

Spiders exhibit an impressive array of pheromone-mediated reproductive strategies. Of over 53,500 species, sex pheromonal structures have been identified in only 19 species so far (**Figs. 2 A+B**), work that has been pioneered by Stefan Schulz (reviewed in Schulz, 2013). Female spider pheromones serve to attract mates or release courtship, or both (**Figs. 2 B+C**) (Uhl, 2013; Fischer, 2019). In the widow spiders (Theridiidae: Latrodectinae), nitrogenous pheromones (**Fig. 2C**) are produced in greater quantities during peak mating season (Fischer *et al.*, 2025a) and are constrained under conditions of starvation (Fischer *et al.*, 2024) or aging (Waner *et al.*, 2018), suggesting significant metabolic investment. The male courtship investment was observed to be dose dependent of female pheromone (Fischer *et al.*, 2022, 2024), indicating potential honest signaling. The production cost of pheromone likely varies across taxa, species like *Argiope bruennichi* (Araneae: Araneidae) and *Cupiennius salei* (Araneae: Trechaleidae) employ citric acid-derived pheromones (**Fig. 2C**) (Papke *et al.*, 2000; Chinta *et al.*, 2010), which are presumably less costly to produce than amino-acid derived pheromones (**Fig. 2C**). Differing constraints in pheromone production could be investigated in spiders, as pheromones evolved from metabolic pathways with apparent different production costs.

Across investigated species, immature male spiders accelerate their maturity in response to female sex pheromone, a tactic that results in smaller males that aim to secure available mates (Kasumovic & Andrade, 2006; Cory & Schneider, 2017; Fischer *et al.*, 2020). Males may also change their reproductive strategy depending on their experience of female scent (Nessler, Uhl & Schneider, 2009). Male spiders may emit pheromones to manipulate female receptivity, such as the only identified male spider pheromone, (*Z*)-9-tricosene of *Pholcus beijingensis* (Araneae: Pholcidae) that acts as an aphrodisiac (Xiao, Zhang & Li, 2010). Other male pheromones are suggested by behavioural studies such as the induction of female quiescence (Becker, Riechert & Singer, 2005; Cargnelutti *et al.*, 2023; Kralj-Fišer *et al.*, 2025). Further, males of various black widow spiders suppress rival attraction with pheromone on their courtship silk (Scott *et al.*, 2015a) either by inhibiting the female mate call, or by repelling rival males directly. The courtship silk of these males likely also contains aphrodisiac pheromones which increases the likelihood of mating (DiRienzo *et al.*, 2019; Golobinek, Gregorič & Kralj-Fišer, 2021).

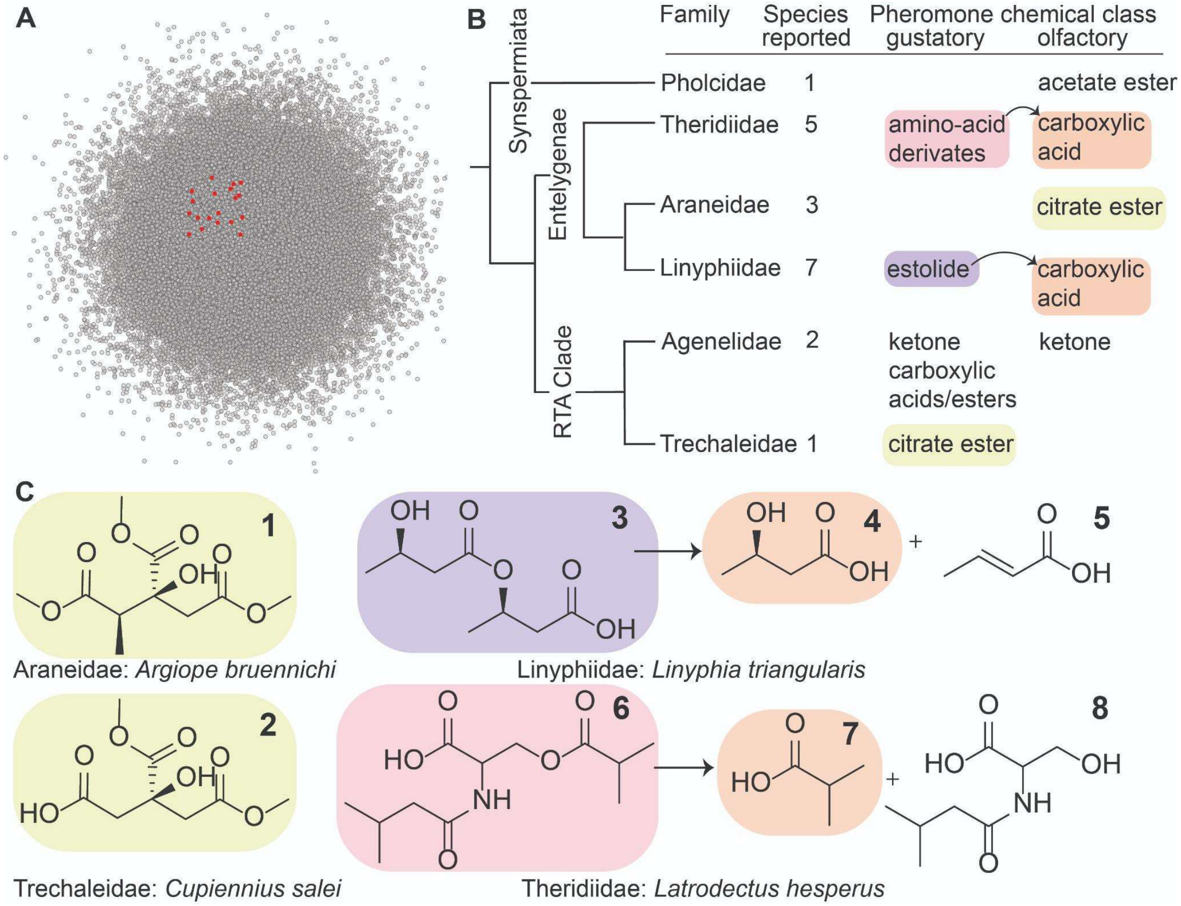

Fig. 2 Overview of female spider pheromones. (A) Representation of ~53,500 spider species (dots) of which 19 (red dots) have a chemical structure identified based on bioassay of synthetic pheromone. (B) Phylogeny of spider families (after (Kulkarni, Wood & Hormiga, 2023) and number of species thereof to which pheromonal structures were assigned. The chemical class of the identified pheromones as well as the modality of their perception were assigned. (C) Examples of spider pheromone structures. *Argiope bruennichi* (Araneidae): (**1**) trimethyl (2*R*,3*S*)-methylcitrate which attracts males (Chinta *et al.*, 2010); *Cupiennius salei* (Trechaleidae): (**2**) *S*-dimethyl citrate which elicits courtship (Papke *et al.*, 2000); *Linyphia triangularis* (Linyphiidae): (**3**) (*R*,*R*)-3-(3-hydroxybutyroloxy)butyric acid which elicits courtship and autocatalytically forms 3-hydroxybutyric acid (**4**) which attracts males, whereas the resulting crotonic acid (**5**) could not be linked to any behavior (Schulz & Toft, 1993)*; Latrodectus hesperus* (Theridiidae): (**6**) *N*-3-methylbutanoyl-*O*-methylpropanoyl-L-serine which elicits male courtship and slowly hydrolyzes to release the mate-attractant isobutyric acid (**7**), while *N*-3-methylbutanoyl-serine (**8**) accumulates on the web with unknown biological function (Fischer *et al.*, 2025a). Colors link selected chemical classes in (B) to structures in (C). The arrows in (B) refer to the functional transition of gustatory to olfactory pheromone components.

In ixodid ticks, a particularly well-characterized sex pheromone is 2,6-dichlorophenol. This phenol is synthesized by partially engorged females and detected by conspecific males using the Haller's organ. The pheromone induces anemotaxis and initiates courtship behaviours in species such as *Dermacentor variabilis*, *Rhipicephalus appendiculatus*, and *Amblyomma variegatum* (Parasitiformes: Ixodidae; Sonenshine *et al.*, 1976; Waladde, 1982). Volatile signals are especially important in environments where ticks are sparse and direct encounters between potential mates are rare. Electrophysiological responses to the phenol have been documented, affirming its strong excitatory effect on male sensory neurons (de Bruyne & Guerin, 1998; Josek *et al.*, 2021).

The parasitiform mite *Varroa destructor* (Parasitiformes: Varroidae) evolved a complex semiochemical system. Females produce a multi-component sex pheromone composed of fatty acids and esters, including palmitic acid and ethyl oleate, which attracts males inside sealed brood cells during mating (Ziegelmann *et al.*, 2013; Häußermann *et al.*, 2015). These signals are tightly integrated with host-derived kairomones that guide mites to suitable brood cells, exemplifying how reproductive and foraging information can be interlinked. In some predatory parasitiform mites, not only has the emission of uncharacterized sex pheromones by females been demonstrated (Rock, Monroe & Yeargan, 1976), but also by immature females (Hoy & Smilanick, 1979), which males track and guard before adult emergence as part of sexual competition.

In Acariformes, males of at least two *Tetranychus* (Acariformes: Tetranychidae) species are attracted by a sex pheromone emitted by quiescent female deutonymphs (Cone *et al.*, 1971), then engage in precopulatory guarding until adult females emerge. In case a female emerges unguarded, these virgin females continue to emit mate-attracting pheromone until they are mated (Oku *et al.*, 2005). To our knowledge, none of these pheromones has been chemically characterized to date.

Among harvestmen, males are known to respond to female-derived information —either from the cuticle or secreted onto substrates—by initiating courtship, including penis exposure and stroking behaviours (Fernandes *et al.*, 2017). Though specific chemical identities remain unknown, evidence strongly supports pheromonal mediation of these behaviours. Males of many harvestment species present a nuptial gift secretions on their pensises which are transferred orally to the female, seemingly to convey chemical aphrodisiacs that influence her receptivity (Kahn *et al.*, 2018; Brown, Marinko & Burns, 2025).

In pseudoscorpions, reproductive semiochemistry is multifaceted. Males deposit spermatophores on the substrate, marking the stalk with droplets containing chemical cues that guide females to the sperm packet. These droplets may persist for up to 24 hours and include amino acids and proteinaceous substances likely involved in detection by the female's chemosensory structures (Legg, 1973; Stemme & Pfeffer, 2022). Males of *Cordylochernes scorpioides* (Pseudoscorpiones: Chernetidae) transfer anti-aphrodisiac pheromone onto mated females, reducing subsequent male interest and sperm competition (Bonilla *et al.*, 2011). These behaviours highlight a complex interplay between sexual communication and mate manipulation, while the active semiochemicals remain to be identified.

Scorpions provide further examples of chemically guided reproduction. In *Hadrurus arizonensis* (Scorpiones: Hadruridae), males detect and follow pheromonal trails deposited by females, which are believed to contain contact-based cues that provide information on receptivity (Melville, Tallarovic & Brownell, 2003). In *Urophonius brachycentrus* (Scorpiones: Bothriuridae), males exhibit olfactory attraction to females in the absence of trails, indicating possible airborne signals. The temporary loss of attractiveness in mated *U. brachycentrus* females fitted with mating plugs—reversed upon plug removal—implies a possible male-derived deterrent pheromone affecting female signaling (Romero-Lebrón *et al.*, 2019). Males of the scorpion *Tityus pusillus* (Scorpiones: Buthidae) seemingly respond with courtship-behaviour to female chemical signals and the existence of an unknown polar pheromone was postulated as the non-polar cuticular components did not elicit male courtship (Barbosa-da-Silva *et al.*, 2025).

In horseshoe crabs no reproductive pheromone has been chemically characterized, although experimental studies demonstrate female-associated chemical cues that attract males and prolong satellite male association during spawning (Schwab & Brockmann, 2007; Saunders *et al.*, 2010).

Chelicerate taxa demonstrate the diverse evolution of pheromone-mediated mating strategies. Despite taxon-specific nuances in signal production and reception, the underlying selective pressures—sparse mate availability, the need for accurate species recognition, and minimization of energetic costs—appear to shape a shared reliance on semiochemicals to regulate reproductive success (Johansson & Jones, 2007).

Social Semiochemistry and Behaviour

In many chelicerates, semiochemicals play a central role in organizing and maintaining non-sexual intraspecific communication structures, coordinating aggregations, mediating territory, and alarm signaling. Chemical signals provide a flexible and efficient mechanism to manage intra-species interactions, particularly in gregarious or aggregation-prone species. In spiders, female sex pheromones extend beyond sexual communication to mediate conspecific attraction. Female widow spiders such as *Steatoda grossa* (Araneae: Theridiidae) emits short chained carboxylic acids from their webs that serve dual purposes—attracting mates and informing other females about potential competition for mates and resources, as well as predation risk (Fischer *et al.*, 2022, 2023a). Such response to the sex pheromone of the same sex is has been termed 'autodetection' (reviewed in Holdcraft, Rodriguez-Saona & Stelinski, 2016). Clustering within pockets of suitable habitats has been documented in orb-weaving spiders and other sedentary web-builders (Kasumovic & Jordan, 2013; Fischer, Hung & Gries, 2019), suggesting that autodetection-mediated clustering may be a common strategy in taxa with high web construction costs (Salomon, 2009; Fischer *et al.*, 2023a). Field experiments further suggest that sex pheromones could mediate site fidelity, as female widow spiders are less likely to relocate when conspecifics are present (Salomon, 2007).

Among Acariformes, especially within the Astigmata and Oribatida, both aggregation and alarm behaviours are well-documented and chemically mediated. Aggregation pheromones such as lardolure (1,3,4,7-tetramethyldecyl formate) in *Lardoglyphus konoi* (Sarcoptiformes: Lardoglyphidae) promote conspecific clustering, enhancing collective thermoregulation, increasing mating opportunities, and reducing predation risk through the dilution effect (Kuwahara, 2004; Raspotnig, 2006). Alarm pheromones like neral and geranial are produced by astigmatid and oribatid mites to trigger rapid dispersal in response to environmental stress or predation threats. The same compounds can function in opposite directions depending on their concentration, with low doses promoting aggregation and high doses triggering dispersal, as demonstrated in *Halotydeus destructor* (Trombidiformes: Penthaleidae) (Jiang, Ridsdill-Smith & Ghisalberti, 1997; Heethoff & Raspotnig, 2012).

In Parasitiformes, the existence of aggregation pheromones has been demonstrated both from individuals and from their feces, with likely complementary effects: in the blood-feeding mite *Dermanyssus gallinae* (Parasitiformes: Dermanyssidae), the existence of a chemically uncharacterized aggregation pheromone emitted by individuals has been unambiguously demonstrated, with individuals freshly fed on blood showing the maximum attractive effect for conspecifics (Entrekin & Oliver, 1982; Koenraadt & Dicke, 2010; Masier *et al.*, 2023). Two compounds in mite feces have been shown to have an arresting effect on the same species (Qi *et al.*, 2023), namely guanine and hematin. In the tick *Argas walkera* (Parasitiformes: Argasidae), uncharacterized aggregation pheromones have been shown to originate from females, and guanine has also been shown to be strongly attractive to fed and unfed individuals at various life stages (Neitz & Gothe, 1984).

Harvestmen (Opiliones) also show evidence of chemically mediated non-sexual communication. Some species are solitary and defend individual territories, others form mixed-species aggregations in shared refuges. Chemical recruitment signals are hypothesized to underlie these behaviours, although the specific compounds and source glands remain unidentified (Donaldson & Grether, 2007; Escalante *et al.*, 2022). Male *Mischonyx cuspidatus* (Opiliones: Gonyleptidae) are attracted to scent of conspecific males, while not of females supporting the idea of scent mediated aggregations (Dias, Segovia & Willemart, 2020). Learning of chemical cues associated with favorable shelter conditions has been demonstrated in *Discocyrtus invalidus* (Opiliones: Gonyleptidae), suggesting a capacity for associative learning involving semiochemicals (Dos Santos, Hogan & Willemart, 2013). In some species, males may secrete territorial markers from sexually dimorphic glands to maintain individual spacing, further supporting the importance of semiochemical communication in non-reproductive contexts (Fernandes & Willemart, 2014).

Territorial marking using chemical signals has been observed in pseudoscorpions, where males rub their ventral surfaces along substrates to mark spatial boundaries (Weygoldt, 1966). These behaviours, likely mediated by pheromones, may serve to deter rivals and communicate dominance or reproductive status. Male-male chemical signaling remains underexplored but is suspected to play a role in maintaining spacing and reducing conflict.

In whip spiders (*Amblypygi*), evidence for social communication remains limited, but homing behaviour provides strong indirect evidence (Chapin & Hebets, 2016; Casto *et al.*, 2019). The species *Phrynus marginemaculatus* (Amblybygi: Phrynidae) shows a significant preference for filter paper previously touched by itself over that touched by a conspecific or untouched paper, suggesting the use of self-referential chemical cues in orientation and site fidelity (Casto *et al.*, 2019). The variety of chemical strategies employed across chelicerate taxa to mediate social interactions—ranging from aggregation and alarm to territory marking and individual recognition—demonstrates the broad utility of semiochemicals in social organization. While detailed chemical analyses are still lacking for many groups, especially in the lesser-studied orders, the behavioural evidence suggests that semiochemical communication is a conserved and evolutionarily flexible solution to the challenges of intra-specific coordination in these largely solitary but occasionally gregarious animals.

Host or Prey Detection and Feeding (Kairomonal Cues)

Kairomonal cues—semiochemicals emitted by one species and exploited by another for its benefit—play a critical role in host location, prey detection, and foraging strategies across a range of chelicerate taxa. These cues are particularly important for hematophagous groups such as ticks and poultry red mites, but also guide predatory behaviours in spiders, scorpions, harvestmen, parasitiform predatory mites and others (Ratz *et al.*, 2023).

Ticks, particularly those in the family Ixodidae, are archetypal examples of kairomone-driven host-seeking. These ectoparasites rely on complex blends of volatile organic compounds (VOCs) to detect and locate hosts in their environment. The Haller’s organ, located on the first pair of legs, is a specialized sensory apparatus that detects CO_2, lactic acid, ammonia, and other host-derived carboxylic acids, which are critical components of vertebrate body odor (Leonovich, 2004; Carr & Roe, 2016; Faraone, 2022). For instance, lactic acid and ammonia elicit significant questing behaviour in *Ixodes scapularis* (Parasitiformes: Ixodidae) and *A. americanum*, while blends of butyric acid and other skin-emitted volatiles improve host-tracking precision (Soares & Borges, 2012). Studies using Y-tube olfactometers and electrophysiology have confirmed that ticks not only detect but can discriminate between host species based on odor profiles (López-López *et al.*, 2023; Bezerra-Santos *et al.*, 2024). Beyond host-seeking, tick kairomonal sensitivity also plays a role in microhabitat selection. Volatiles emitted from vegetation or associated with host bedding materials may guide ticks to optimal questing sites. Certain odors, such as those from donkey sweat containing *E*2-octenal, act as repellents, illustrating how odors can also serve to signal less suitable hosts (Ferreira *et al.*, 2019).

Amongst other Parasitiformes, *Varroa destructor*, a parasitic mite of honeybees, uses kairomones such as methyl linoleate, ethyl palmitate, and brood food volatiles to locate appropriate developmental stages of bee larvae for invasion and reproduction (Calderone & Lin, 2001; Nganso *et al.*, 2020; Light *et al.*, 2020). In addition, adults preferentially seek out nurses during their phoretic phase rather than foragers, thanks to an uncharacterized kairomone that differs between castes (Eliash *et al.*, 2014). These kairomones are detected by a foreleg sense organ that integrates olfactory and gustatory signals. In poultry red mites, host-derived odorants influence movement only at close range and vary in effectiveness among populations, suggesting limited reliance on long-distance chemical guidance in high-host environments (Roy *et al.*, 2017; Auffray *et al.*, 2022; Masier *et al.*, 2023). Responses to CO_2 are similarly conditional, with attraction in darkness but freezing under bright light, reflecting modulation by predation risk (Kilpinen, 2005). Contact kairomones can act as feeding stimulants once the host is reached (Zeman, 1988). In contrast, predatory phytoseiid mites exploit herbivore-induced plant volatiles to locate prey (Maeda & Takabayashi, 2001; Bao *et al.*, 2026), while macrochelid mites use kairomones from flying insects to select phoretic carriers, facilitating dispersal rather than foraging (Niogret, Lumaret & Bertrand, 2006).

In spiders, kairomonal cues from prey are used in both active hunting and habitat selection (Fischer, 2019). Web-building spiders like *Latrodectus* spp. (Araneae: Theriidae) may choose web sites based on prey availability inferred from environmental residues (Johnson, Revis & Johnson, 2011), while active hunters such as the jumping spider *Evarcha culicivora* (Araneae: Salticidae) detects and prefers the scent of blood-fed mosquito, as well as the scent of potential mates that recently fed on a blood-fed mosquito (Jackson & Cross, 2015). Notably, aggressive mimicry—where predators exploit prey pheromones to lure them into range—is exemplified by *Mastophora* (Araneae: Araneidae) bolas spiders (Haynes *et al.*, 2002). Individual *Mastophora* mimic the sex pheromones of multiple moth species, *M. cornigera* for example attracts up to 19 different prey species (Stowe *et al.*, 1995). Similarly, *Habronestes bradleyi* (Zodariidae), mimics the alarm pheromone 6-methyl-5-hepten-2-one of its ant prey *Iridomyrmex purpureus* (Hymenoptera: Formicidae) (Allan, Elgar & Capon, 1996). Conversely, obligate kleptoparasites Argyrodinae (Araneae: Therídiidae) detect the resource quality and parasite load of their host spiders, while the underlying cues remain to be investigated (Gregorič *et al.*, 2024).

Other chelicerates illustrate a continuum of chemically guided behaviors that vary with sensory modality, ecological context, and phylogenetic history. Scorpions and pseudoscorpions also rely on kairomones for prey localization. Contact chemoreception plays a major role in *Androctonus australis* (Buthidae) and *Buthus occitanus* (Buthidae), which initiate grasping behaviours upon detecting prey cuticular compounds or extracts (Krapf, 1986). In scorpions, contact chemoreception is central to prey localization, with species such as *Androctonus australis* and *Buthus occitanus* initiating grasping behaviors upon detecting prey cuticular compounds or extracts (Krapf, 1986), while in pseudoscorpions like *Chelifer cancroides*, chemically guided prey capture is reinforced by venom peptides that ensure rapid immobilization (Krämer et al., 2022). Harvestmen further demonstrate variability in kairomonal sensitivity, as some species respond to odors from live or freshly killed prey whereas others do not, highlighting interspecific and phylogenetic differences in chemical cue use (Willemart et al., 2007; Costa & Willemart, 2013). Finally, comparative evidence from horseshoe crabs locate buried prey using chemical cues detected by chelae and gnathobase spines, providing a functional analogue to kairomone-mediated prey detection in predatory arachnids (Smith, 1953).

Collectively, these findings reveal a sophisticated chemosensory ecology in chelicerates, in which kairomones inform both partners engaged in antagonistic interactions (predator /parasite and prey). The evolution of this system highlights the selective pressures imposed by foraging efficiency, host specificity, and predator avoidance, emphasizing the centrality of kairomonal cues in ecological interactions across Arachnida.

Avoiding Danger (Allelochemicals)

In the ongoing evolutionary arms race between predator and prey, arachnids have evolved diverse chemical defenses—known as allomones—that benefit the emitter by deterring, confusing, or repelling predators (Pekár & Raspotnig, 2022). These compounds range from volatile deterrents to long-lasting cuticular secretions and serve as crucial components of the animal's anti-predator strategy. Conversely, arachnids eavesdrop on chemical cues (kairomones) of their predators and respond with life-extending behaviour, suggesting the existence of a chemically mediated "landscape of fear" that influences distribution and behaviour (Gooding *et al.*, 2024).

Opiliones (i.e., harvestmen) have long been recognized for their use of benzoquinones and other reactive chemicals in defense (Dettner, 2010). These compounds are produced in paired scent glands called ozopores, which open on the sides of the prosoma. Upon mechanical disturbance, species such as *P. calcariferus* release benzoquinone-rich secretions, sometimes in sex-specific patterns, with females more frequently deploying these defenses (Moore & Townsend, 2019). Such secretions serve a dual purpose: deterring invertebrate and vertebrate predators and alerting conspecifics to danger, functioning in both defense and alarm signaling (Machado, Bonato & Oliveira, 2002; Hara *et al.*, 2005; Föttinger *et al.*, 2010).

Among Parasitiformes several allomonal defenses have been described. In ticks, long-chain hydrocarbons and terpenes such as squalene, secreted by ixodid ticks, have been shown to repel predatory ants and deter attack (Yoder, Pollack & Spielman, 1993). More recently, *I. scapularis* has been found to avoid areas contaminated with secretions from the Dufour's gland of *Formica oreas* (Hymenoptera: Formicidae), suggesting sensitivity to ant-produced alarm and trail pheromones (Gooding *et al.*, 2024). This behaviour likely serves to reduce encounters with aggressive, chemically defended predators in shared environments. The parasitic mite *V. destructor* also employs chemical avoidance strategies. Non-host volatiles such as octanoic acid and (*Z*)-8-heptadecene—compounds found in pollen and royal jelly—act as natural repellents, reducing mite colonization of certain brood types. Such chemical sensitivity not only facilitates host choice but also underlies potential avenues for integrated pest management using repellent cues.

Acariformes Hydrachnidia water mites release potent fish repellents from their pyriform glands (Pekár & Raspotnig, 2022). The oil glands of most Oribatida and Astigmata likewise release potent predator repellents alongside alarm pheromones that induce dispersal of conspecifics. *Collohmannia gigantea* (Acariformes: Oribatida) for example releases the monoterpenes neryl formate, neral, geranial, the aromatic 2-hydroxy-6-methyl-benzaldehyde and the hydrocarbons tridecane and pentadecane, with each semiochemical deterring the potential predator *Euconnus oblongus* (Coleoptera: Scydmaenidae) (Raspotnig, 2006). The poison hydrogen cyanide is released by *Oribatula tibialis* (Acariformes: Oribatulidae). The highly volatile cyanide is stored in the form of mendelonitrile-hexanoate which degrades upon release into the lethal gas (Brückner *et al.*, 2017).

Spiders, so far we know, do not release predator repelling volatiles but are equipped with detection systems to avoid predators. For example, certain wolf spiders avoid areas contaminated with chemical cues of larger or older cannibalistic spiders (Schonewolf *et al.*, 2006; Shannon *et al.*, 2022). Likewise, many spiders exhibit avoidance of ant-derived chemical cues. Generalist predators such as ants leave behind chemical cues that spiders use to identify and avoid risky microhabitats (Mestre *et al.*, 2020; Fischer *et al.*, 2021a). Some spider species even display chemical mimicry to become cryptic, and thus survive within ant colonies (Cushing *et al.*, 2022). Interestingly, spiders do not seem to detect danger associated with mud-dauber wasps, a group of spider specialist predators (Obin, 1982). Spiders of potential prey taxa indiscriminately build webs in direct vicinity to their potential hymenopteran predators that locate their spider-prey based on olfactory cues (Uma & Weiss, 2010, 2012). Distasteful prey are also chemically recognized and avoided by spiders (Bristowe, 1941). The terrestrial crustacean isopod *Porcellio scaber* (Isopoda: Porcellionidae) secretes defensive quinolines that protect them from the predation by generalist spiders such as *S. grossa* (Fischer *et al.*, 2025b). On the other hand, red devil spiders (Araneae: Dysderidae) specialize on isopods and overcome their defenses, likely driving the diversification within this spider family (Bellvert *et al.*, 2023, 2025b, 2025a). It remains to be investigated whether the elongated chelicerae of some dysderids also aid in avoiding gustatory contact with the defensive metabolites of their isopod prey (Fischer *et al.*, 2025b). The use of venom as defense has been difficult to disentangle from their offensive use (Lüddecke *et al.*, 2022). At least in the case of male funnel-web spider venom there is convincing evidence that δ-hexatoxins have evolved primarily for defense against vertebrate predators (Herzig *et al.*, 2020).

Scorpions, while famous for their venomous sting, also display olfactory-based avoidance behaviours that suggest chemical cue detection of predatory threats. In experimental settings, prey species such as *Paruroctonus marksi* (Scorpiones: Vaejovidae) have been shown to avoid chemical traces left by predatory conspecifics like *Hadrurus arizonensis*, indicating kairomonal sensitivity and intraspecific risk management (Nisani *et al.*, 2018).

Sea spiders (Pycnogonida), though less studied behaviourally, also exhibit chemical defenses. *Pycnogonum litorale* (Pycnogonida: Pycnogonidae), for instance, produces an ecdysteroid known as exogenous 55, which deters marine crustacean predators such as the green crab *Carcinus maenas* (Decapoda: Portunidae) (Brown, Sieglaff & Rees, 2009).

Though no known defensive substances are known from Xiphosura, juvenile horseshoe crabs respond to predator-associated chemical cues and integrate this information with visual signals, indicating that chemically mediated risk assessment is conserved across Chelicerata (Medina & Tankersley, 2010).

Uropygi (whipscorpions) and Schizomida (short-tailed whip-scorpions) possess one of the most dramatic examples of chemical defense among arachnids (Pekár & Raspotnig, 2022). When threatened, they emit an acetic acid-rich spray from their pygidial glands. This secretion contains short-chain carboxylic acids, including acetic and formic acids, and is projected in a directed stream towards the predator (Schmidt *et al.*, 2000). The giant whipscorpion, *Mastigoproctus giganteus* (Uropygi: Thelyphonidae), may spray up to 84% concentrated acetic acid as far as 80 cm onto potential predators (Eisner *et al.*, 1961). The spray is highly effective against both invertebrate and vertebrate predators and is not employed during intraspecific competition, indicating a strict predator-specific function (Watari & Komine, 2016).

An anecdote suggests potential chemical defense for ricinuleids: *Ricinoides afzelii* (Ricinoididae) larvae release a fine spray from their anus when disturbed (Pollock, 1967). Pollock assumed the spraying represents defecation with chemical analyses yet to be conducted.

Although many chelicerate taxa exhibit strong chemical defenses, some remain poorly characterized in this regard. For example, Solifugae have no confirmed reports of chemical defenses despite their exposure to predation. However, morphological and behavioural observations suggest that at least some chemosensory-based predator detection may be present.

Altogether, these examples underscore the adaptive value of allomones and predator-detection cues across chelicerates. Defensive semiochemistry enhances survivorship in diverse habitats, allowing chelicerates to avoid predation proactively and in real time. Expanding our understanding of these cues may lead to novel biocontrol agents or repellents that exploit natural predator-prey communication systems

Production and Release of Semiochemicals

Semiochemical production in chelicerates is functionally diverse and context-dependent. Spiders commonly deposit their pheromone with their silk (Fischer, 2019). Whether pheromone is emitted from the spider's body remains to be investigated. *Argiope* spider females emit their volatile mate-attractant from their orb webs (Chinta *et al.*, 2010; Weiss & Schneider, 2022). While mate attractant pheromone of female widow spiders (Theridiidae: Latrodectinae) is gradually, over the course of weeks, emitted via the hydrolysis of the web-borne courtship-inducing sex pheromone (Fischer *et al.*, 2025a). This web-borne pheromone of female widow spiders has been linked to the posterior aggregate gland responsible for sticky glue production (Fischer *et al.*, 2022). If glue-producing glands of other spiders also produce the sex pheromone remains to be investigated.

Direct release of volatiles is known in ixodid ticks metathoracic glands that produce pheromones dispersed into the air or deposited onto substrates (Sonenshine, 2004). *Amblyomma* (Ixodidae) species release aggregation pheromones from their coxal gland complex, which exhibit conserved structural traits across individuals (Dusbabek, Zahradniékovaz & Simekz, 1998; Sonenshine, 2004).

Contact-based semiochemicals are involved in courtship, aggregation, and territorial behaviours. Pseudoscorpions deposit a pheromone-laden droplet on the spermatophore stalk, aiding females in locating sperm for uptake (Legg, 1973). These chemicals include amino acids and fibroin-like proteins (Stemme & Pfeffer, 2022). Female scorpions deposit contact pheromone onto the substrate that triggers male courtship behaviour (Taylor, Cosper & Gaffin, 2012; Pordeus, Lira & Albuquerque, 2019; Barbosa-da-Silva *et al.*, 2025). *Hadrurus arizonensis* (Scorpiones: Hadruridae) evidently uses a contact-trail pheromone that males follow to their potential mate while courting along the way (Melville *et al.*, 2003).

Defensive compounds such as benzoquinones in Opiliones or ecdysteroids in sea spiders are synthesized and stored in specialized reservoirs and released when threatened.

In *Pycnogonum litorale* (Pantopoda: Pycnogonidae), an ecdysteroid deters crustacean predators (Brown *et al.*, 2009), while harvestmen, such as *Phareicranaus calcariferus* (Opiliones: Cranaidae), release defensive secretions from ozopores, paired glands on the prosoma, in a sex-specific manner (Moore & Townsend, 2019).

Known Semiochemicals

Chelicerates produce and respond to a wide array of chemical compounds, many of which are conserved across different taxa. Short-chain carboxylic acids, such as acetic acid and butyric acid, are ubiquitous in vertebrate odors and decomposing matter, and play a key role in the host-seeking behaviour of parasitic ticks and mites. For instance, *A. americanum* and *I. scapularis* ticks exhibit heightened questing behaviour in response to lactic acid and other carboxylic acid derivatives found in human sweat, sensed through the Haller's organ (Leonovich, 2004; Carr & Roe, 2016).

Convergently, short-chain carboxylic acids are the male attractant sex pheromone of various *Linyphia* (Aranaea: Linyphiidae) species (Schulz & Toft, 1993; Schulz, 2013) and the widow spiders (Theridiidae: Latrodectinae) *Latrodectus* (Bryan *et al.*, 2018; Fischer *et al.*, 2025a) and *Steatoda* (Fischer *et al.*, 2022, 2023b). Methyl-esters are frequently found as sex pheromones of spiders (**Fig. 2C**) (Schulz, 2013; Fischer, 2019). Trimethyl methyl citrates act as volatile mate-attractant sex pheromones in *Argiope* (Araneidae) wasp spiders (Chinta *et al.*, 2010). Similarly, asymmetric dimethyl citrate acts as courtship-inducing sex pheromone of *C. salei* wandering spider (Papke *et al.*, 2000). Methyl-serine derivatives are contact sex pheromone components of black widow, *Latrodectus*, spiders (Jerhot *et al.*, 2010; Scott *et al.*, 2015b), while the corresponding acid were found to be the main courtship-inducing component (Fischer *et al.*, 2025a) (**Fig. 2C**).

Aldehydes, such as trans-2-hexenal, nonanal, and benzaldehyde, function as volatiles that can either attract or repel depending on context and concentration. In the mite *Halotydeus destructor* (Acariformes: Penthaleidae), low concentrations of 2-(*E*)-hexenal promote aggregation, while higher doses cause dispersal and increased mortality, illustrating the dual functionality of these compounds (Jiang *et al.*, 1997; Kuwahara, 2004). Terpenoids, including geraniol, neral, and citronellol, are commonly employed by oribatid and astigmatid mites as repellent or alarm substances, and many have a repellent activity against parasitiform hematophagous mites which do not produce them but often meet astigmatic mites on farms (Roy *et al.*, 2020). These compounds are often released in response to physical disturbance or perceived predation threats, and are detected through specialized sensilla (Leal & Mochizuki, 1990; Skelton *et al.*, 2010). Phenolic compounds, particularly 2,6-dichlorophenol, are key sex pheromones in ixodid ticks. This compound is released by engorged females and serves to attract conspecific males, as shown in *D. variabilis*, *R. appendiculatus*, and *A. variegatum* (Sonenshine *et al.*, 1976; Waladde, 1982). The pheromone elicits strong olfactory receptor responses of male ticks, highlighting its role in mate localization.

Cuticular hydrocarbons (CHCs) also play multiple roles across arachnids. The primary role of CHCs is to retain water and protect against desiccation. The CHC of insects consists mainly of alkanes and alkenes. Curiously, the CHC profiles of spiders and scorpions are structurally more diverse than those of insects (Chinta *et al.*, 2016; Fischer *et al.*, 2021b; Gerbaulet *et al.*, 2022; Adams *et al.*, 2024; Barbosa-da-Silva *et al.*, 2025). Arachnids feature proportionally more methyl-branched long chain methyl ethers, fatty acids, aliphatic alcohols and esters. These diverse CHCs can also be found on the silk of spiders with a similar component profile as the respective cuticle (Fischer *et al.*, 2021b).

Communication via CHCs has been reported in diverse contexts. Species recognition among co-occurring *Tetragnatha* spiders (Araneae: Tetragnathidae) was correlated to unique blends of long chain alkyl methyl ethers on the silk (Adams *et al.*, 2024). Kin recognition in the solitary orb spider *A. bruennichi* has been attributed to CHC profiles (Weiss & Schneider, 2021). Likewise, in the subsocial spider *Stegodyphus lineatus* (Araneae: Eresidae), siblings are seemingly identified by similar CHC profiles (Grinsted, Bilde & d'Ettorre, 2011). Changing CHC profiles of developing *Pardosa saltans* (Araneae: Lycosidae) embryos seem to inform mothers of the imminent emergence of offspring (Ruhland *et al.*, 2019). Similarly, developing *P. paludicola* experiences an ongoing decrease and increase of CHC components from egg over embryo to spiderling (Suprunowicz *et al.*, 2025). CHC profiles of *L. geometricus* spiderlings are similar to their mother and become increasingly unique with growth, while the chemical similarity is thought to suppress maternal cannibalism

(Guimarães *et al.*, 2016). Thus, CHCs are important signals during the development of spiders. Myrmecophile spiders have more diverse CHC profiles compared to their ant-host, resulting in many spider unique cues the ants do not respond to (von Beeren *et al.*, 2021). It seems that chemical mimicry is facilitated by the components which these spiders share with the ant-host, mainly *n*-alkanes (Cushing *et al.*, 2022). Nest-specific chemical mimicry seems acquired by the spiders, either by consumption or physical contact with the ants (Elgar & Allan, 2004).
CHCs of *Varroa destructor* closely match those of their honey bee hosts and shift quantitatively with host developmental stage, supporting a well-documented role in chemical camouflage that reduces host detection and facilitates parasitism and host switching (Kather *et al.*, 2015b; Kather, Drijfhout & Martin, 2015a; Le Conte *et al.*, 2015). In ticks (Ixodida), CHCs have been experimentally demonstrated to inhibit entomopathogenic fungi (Ribeiro-Silva *et al.*, 2022). Tick CHCs vary among populations and host-associated lineages, making them useful chemotaxonomic and population-structuring markers (Dupraz *et al.*, 2022). In *Parachernes melanopygus* (Pseudoscorpiones: Chernetidae), a pseudoscorpion, CHCs are similarly adjusted to match the chemical signatures of their congeneric hosts over 48 hours, promoting social integration (Tizo-Pedroso & Del-Claro, 2014). Collectively these studies indicate a wide array of potential social cues being detected by chelicerates.

III Morphology and anatomy of chemosensation across Arachnida

Understanding chemosensory systems relies on identifying links between behavioural responses to semiochemical compounds and morpho-anatomy at different scales. Chemosensory systems are well understood in mammals and insects (Meyerhof & Korsching, 2009). In all these animals, chemical compounds are perceived by receptor proteins located in sense-organs on the body surface (nose, antenna cuticle, etc.). The local perception signal is transferred to the central nervous system (CNS), where it is integrated and processed, resulting in a motor response (**Fig. 3**). Insects carry a majority of their olfactory organs on paired specialized appendages, the antennae, although some olfactory sensilla and receptors have been discovered on the legs (Yang *et al.*, 2020; Wu *et al.*, 2022). The organs of contact chemosensation (i.e., gustation) in insects are distributed on the palps, mouthparts, legs, wings and the ovipositor (Stocker, 1994; Wang *et al.*, 2004; Agnel, Da Rocha & Robichon, 2017; Seada *et al.*, 2018; Sevarika, Rossi Stacconi & Romani, 2021). Across arachnids, behavioural responses to chemosensation have been well documented. However, knowledge of their chemosensory systems relies largely on inferences by analogy with insects' morpho-anatomy (Hallberg & Hansson, 1999). In this section, we will discuss the integrative scales: chemosensory circuits throughout the body and receptor molecules. Further, we will provide an overview of the current state of knowledge and knowledge gaps of the morpho-anatomy of chemo-sensing organs among arachnids.

At the body level, many gaps of knowledge prevent us from providing a robust description of the arachnids' chemosensory circuits. Most neuronal-level knowledge in arachnids comes from a few focus species (Hayes, 1971; Brownell, 1998; Steinhoff, Harzsch & Uhl, 2024), while the pathway from chemosensory detection to motor output is still inferred from analogies with insects or other arthropods. Despite the high degree of compression of the central nervous system (CNS) in arachnids, the homologies established between insect neuromeres and regions of the arachnid synganglion (Smarandache-Wellmann, 2016) allows for some rough organizational comparisons. Studies using histoimmunochemical techniques, anterograde tracing and transmission electron microscopy (**Table 2**) revealed major differences compared to insects without allowing chemosensory circuits to be drawn. Therefore, we will rely on the best-described chemosensory circuits of insects (**Fig. 3**) and simply highlight below the areas of disagreement between the two taxa. Figure **3** provides a simplified overview of the current state of knowledge regarding insect chemosensory circuits, based on (Edgecomb & Murdock, 1992; Stocker, 1994; Wang *et al.*, 2004; Kim, Kirkhart & Scott, 2017; Zhao & McBride, 2020; Lucas, Montagne & Jacquin-Joly, 2022; Walker, Peña-Garcia & Devineni, 2025). It should be noted that much less is known about insects' gustatory processing (steps 2 and 3 in **Fig. 3**) than about their olfactory processing. Regarding the nerve transmission of the signal detected in the periphery (step 1), insects generally have no synapses between the olfactory sense organs and the first neuropile. In contrast, arachnids - at least spiders, whip spiders, harvestmen and scorpions - have numerous synapses in peripheral sensory nerves, indicating a more distributed organization of the chemosensory circuits (Foelix, 1975, 1985b; Fabian-Fine, Meinertzhagen & Seyfarth, 2000; Gaffin, 2002; Zhang, Wang & Uhl, 2026). In arachnids, given the absence of antennae, the neuropiles where primary processing takes place (step 2) are located in fairly diverse lobes of the synganglion, corresponding to the location of the sense-organs [e.g., pecten lobes in scorpions (Drozd, Wolf & Stemme, 2020); first leg neuromere in a tick (Borges *et al.*, 2016) and in a parasitiform predator (van Wijk, Wadman & Sabelis, 2006)]. These lobes contain presumable glomeruli of various shapes, sometimes similar to those described in the antennal lobes of insects' supraoesophageal ganglia (spheroidal), sometimes elongated, spindle-shaped, or laminar (Drozd *et al.*, 2020; Gronenberg, 2026). Interestingly, Amblypygi's mushroom bodies are exceptionally large and elaborated as compared to insects' and apparently receive massive olfactory information via a prominent tract originating from the "olfactory glomeruli" (Wiegmann *et al.*, 2016). Furthermore, the mapping logic of signal integration (**Fig. 3C**) differs greatly between the olfactory and the gustatory systems in insects (Wang *et al.*, 2004; Lucas *et al.*, 2022). The insect olfactory system follows a chemotopic logic, i.e. all neurons expressing the same olfactory receptor converge on a single glomerulus, so olfactory projections are separated exclusively by the molecule (odor) detected . The gustatory system follows an organotopic logic, i.e. the appendage at the origin of the signal is mapped onto the neuropile, so gustatory projections are separated first by their peripheral location. In arachnids, available studies demonstrate the recurrent presence of an organotopic logic (e.g. Obenchain, 1974, in a tick). In most cases, organotopy is reinforced in the arachnids studied: projections not only allow to locate which appendage the perception occurred in, but also to locate the precise location within that appendage (somatotopy; Anton & Barth, 1993 in a spider; Wolf, 2008 and Drozd, 2024 in scorpions). At the body level, the olfactory and gustatory systems of arachnids seem to share more similarities with the gustatory system of insects than with their olfactory system. This could well be the result of a common ancestral origin, since most of chemosensory organs in arachnids are located on body parts homologous to those that carry the gustatory organs in insects (palps or legs).

At the molecule level, (Missbach *et al.*, 2014) showed that among the three gene families containing olfactory receptors (OR, IR, GR), ORs (concentrated in the antennae) were an innovation in insects. Indeed, arachnid genes sequenced since then confirm the absence of ORs and the presence of at least IRs and often GRs (e.g., in Parasitiformes, Carr *et al.*, 2017; Eliash *et al.*, 2019; Bhowmick *et al.*, 2020; Zhang *et al.*, 2026). However, to date, we do not know the role of IRs and GRs in the chemosensation of arachnids. Many other proteins have been proposed as potential candidates for contributing to chemosensation in several Parasitiformes (Carr *et al.*, 2017; Eliash *et al.*, 2019; Bhowmick *et al.*, 2020). The role in *Varroa* olfaction of a protein homologous to pheromone receptor transcription factor (PRTF) has been demonstrated by combining behavioral bioassays and gene silencing (Singh *et al.*, 2016), and the role of Niemann-Pick type C2 genes in olfaction of a parasitiform predatory mite has been demonstrated by combining behavioral bioassays (including tarsal amputation) and differential transcriptomics on tarsi (Bao *et al.*, 2026). Interestingly, through heterologous expression of spider ionotropic glutamate receptors (iGluRs, conserved across animals and beyond, of which IRs are variants), Zhang *et al.*, (2026) recorded key differences in their properties with respect to two ligands compared to related iGlurs studied in *Drosophila*.

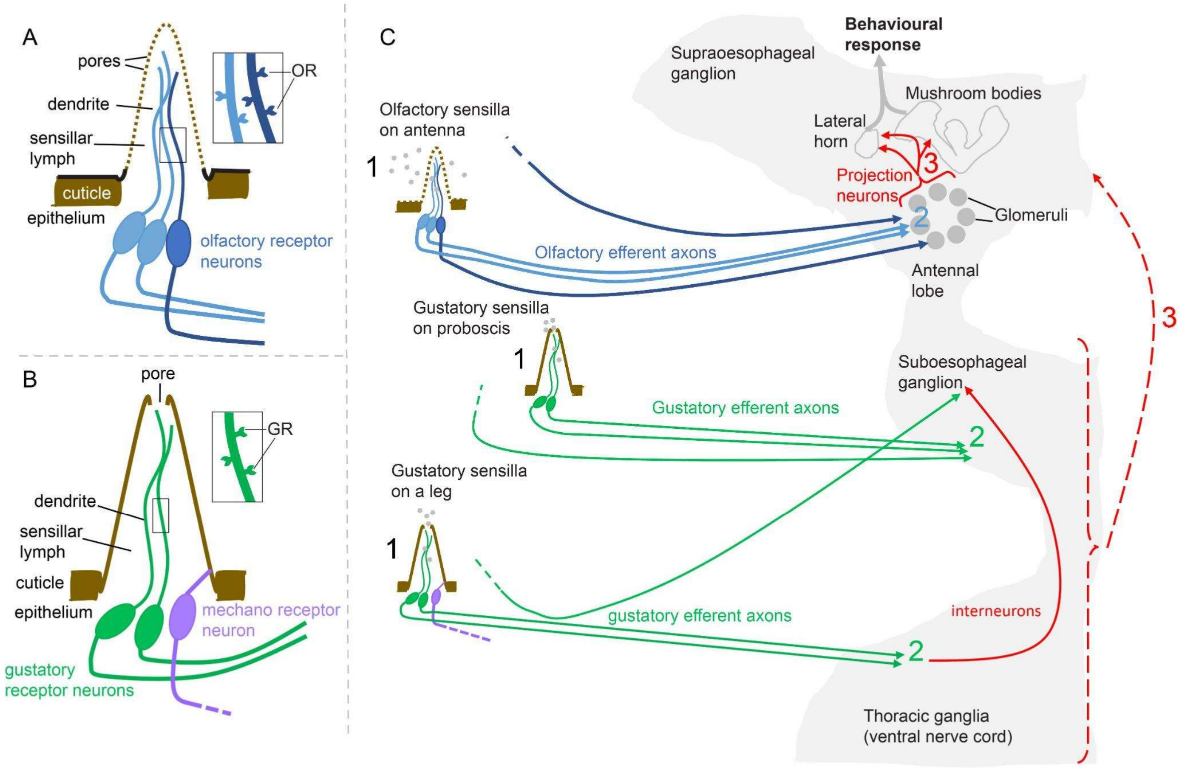

Fig. 3. Simplified schematic of the chemosensory system in insects. The chemosensory differences between insects and arachnids are discussed in the text. Olfactory pathways are displayed in blue, while gustatory pathways in green. A. Diagram of a wall-pore type olfactory sensillum. B. Diagram of a tip-pore type gustatory sensillum. We show a bimodal sensillum, integrated with a mechano-perceiving neuron (purple), which is common in insects. Molecules enter the sensilla through cuticular pores and interact with ORs or GRs, receptor proteins located in the dendritic membrane of olfactory (ORN) or gustatory receptor neurons (GRN) (boxes). C. Diagram summarizing the olfactory and gustatory circuits from peripheral detection of molecules (1) to the integration of signals into the CNS ganglia (grey). In the olfactory circuit, the signal transmitted directly by the ORN axons is integrated by the antennal lobe (2), a neuropile located in the supraesophageal ganglion (brain) containing glomeruli (grey circles) and a network of interneurons and projection neurons (not shown here). All ORNs of the same type (expressing the same OR) located in different sensilla project to the same glomerulus (chemotopy). The projection neurons project in one or more nerve bundles to the mushroom bodies and lateral horns (3). The gustatory circuit has similarities with the olfactory circuit in terms of peripheral detection (1) and signal transmission by GRN axons (2), but the first stage of signal integration takes place in the subesophageal ganglion (SOG), which does not contain a discrete glomerular structure. Most of leg GRN terminate into the corresponding thoracic ganglion where second order interneurones are sent into SOG. Nevertheless, a small number of leg GRN are directly sent to SOG. In addition, GRN projections are segregated in the SOG according to the organ from which they originate (proboscis, mouthparts, legs, etc.), regardless of the receptor protein (organotopy). Higher-order processing steps for insect gustation is less understood than for olfaction (3).

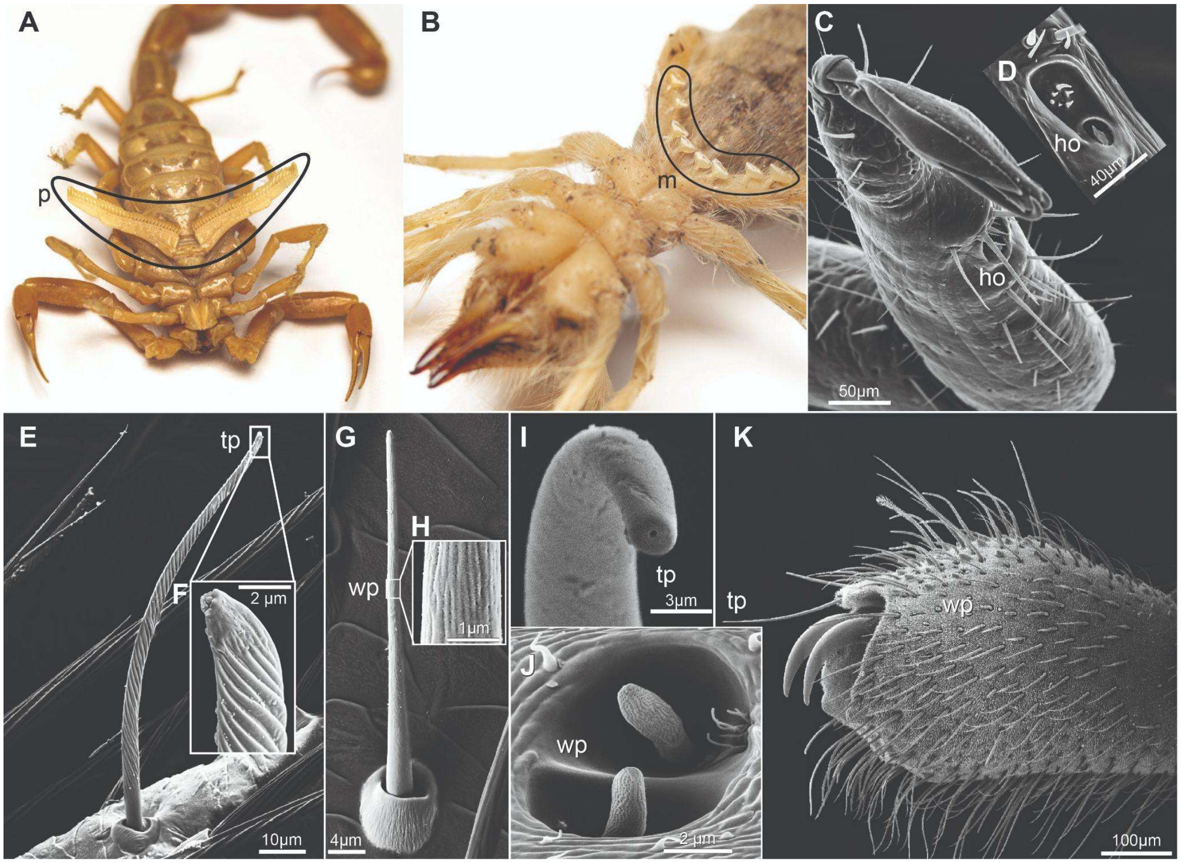

Fig. 4: External view of chemosensory organs of selected arachnids. (A): Ventral view of pectines (p) positioned on the ventral side of the mesosoma in proximity to the first walking legs of a scorpion. (B) Ventral view of a *Galeodes* sp. (Solifugidae: Galeodidae) showing malleoli (m) positioned on the 4th leg. c-k are scanning electron microscope images. (C) Distal foreleg of *Ixodes scapularis* (Parasitiformes: Ixodidae) with Haller's organ (ho) and (D) the closeup of the Haller's organ (ho) with sensilla array. (E) Tip-pore sensillum on the metatarsus of the 1st leg of a male *Argiope bruennichi* (Araneae: Araneidae) with (F) closeup of the tip pore. (G) Wall-pore sensillum on the femur of the 1st leg of a male *A. bruennichi* (Araneae: Araneidae) with (H) closeup of the wall pores. (I) Tip-pore sensillum of the distal tarsomere I of *Cryptocellus narino* (Ricinulei: Ricinoididae) (J) two short wall-pore sensilla from the distal tarsomere II of *C. narino* (Ricinulei: Ricinoididae). (K) Distal tarsomere I of *C. narino* (Ricinulei: Ricinoididae) with tip-pore and wall pore sensilla. p = pectines; m = malleoli, ho = Haller's organ; tp = tip pore sensillum; wp = wall pore sensillum. Photo credit: AF: a, b; NF: c,d; M. Belal Talukder: e, f, g, h; Giovanni Talarico: i, j and k.

The organs of olfactory or gustatory chemosensation of arachnids are mostly carried by appendages as in insects, but with highly contrasting levels of specialization depending on the taxa studied. Scorpions possess feather-like pectines (Wolf, 2017) located on the ventral mesosoma that are capable of chemo- and mechanosensation (**Fig. 4A**), while Solifuges possess malleoli (**Fig. 4B**), contrasting the antenniform legs of e.g. Ricinulei, Uropygi and Amblypygi (**Fig. 1**) used for chemosensation. Like in insects, the presence of specialized chemosensory appendages does not exclude the existence of other sensory organs located on other parts of the body in arachnids. In scorpions, additional chemosensory organs appear to be present on the pedipalp chelae (Fet *et al.*, 2006; Nisani *et al.*, 2018), and structures that may be chemosensory organs have also been reported on the metasoma and telson (Fet *et al.*, 2003). In other arachnids, many organs of olfactory or gustatory chemosensation are carried by appendages whose primary function is non-sensory such as the four pairs of walking legs in spiders (Talukder *et al.*, 2025a, 2025b), the IVth pair of walking legs in Solifugae (Sombke *et al.*, 2019), all pairs of walking legs and chilariae (1-segment paired appendages ventrally located on the vestigial first abdominal segment) in horseshoe crabs (Hayes, 1971; Hassler & Brockmann, 2001), the tarsus of the first pair of walking legs and the chelicerae in Parasitiformes (Sonenshine, Taylor & Carson, 1986; Dillier, Fluri & Imdorf, 2006; Leonovich & Stanyukovich, 2011; Bao *et al.*, 2026). It should be noted that studies on Acariformes and Parasitiformes have largely focused on the tarsi of legs I, mainly because their location is similar to that of insect antennae, and because mites themselves use them to explore their environment. However, this does not exclude the possibility that sensory organs are present elsewhere in these taxa.

Chemosensory appendages of arachnids bear different types of sensilla, some of which resemble those found in insects (i.e., hair sensilla or chaetica; e.g. **Fig. 4E-K**) (Dillier *et al.*, 2006) while others are specific to an arachnid order (e.g. malleoli of Solifugae, peg sensilla of scorpions; Wolf, 2017; Sombke *et al.*, 2019; **Fig. 4A-B**) (see **Table 2**). Sensilla are organs whose external part consists of a modification of the cuticle, forming either a protrusion, a groove, pit or just a pore. These different types of sensilla are distributed either sparsely or in dense groups, some of which are considered as distinct organs. The "Haller's organ" of ticks for example (**Fig. 4C-D**) are cuticular depressions on the apex of the first tarsus that feature groups of heterogeneous and highly specific sensilla (Sonenshine *et al.*, 1986). Similarly, groups of hair sensilla on the fixed finger of the pedipalps of scorpions form the "constellation arrays" (Fet *et al.*, 2006; Nisani *et al.*, 2018) (**Table 2**). Within and beneath the cuticular structures of the sensilla are sensory receptor neurons. Based on insect knowledge, transmembrane receptors are expressed on the dendritic membrane of sensory neurons housed inside or beneath the sensillum-modified cuticle (**Fig. 3**). In **Table 2**, we present a summary of current knowledge regarding the external shapes of chemosensory sensilla in arachnids, and the state of knowledge regarding their functions. The general shapes of hair sensilla are extremely varied, as in insects (with many similarities), resulting from various protuberances, with one or more lumens, pointed, blunt, spatulate, or bifid tips, and straight, curved, or club-shaped bodies. For the sake of brevity, we will not detail categories based on general shape and will only distinguish between hair sensilla with wall pores (wp) and those with a tip pore (tp).

To establish whether a cuticular structure is the external part of a sensory organ, it is necessary to demonstrate that there is a functional link between it and at least one of the steps of a sensory circuit (**Fig. 3**). The description of a neural system located beneath the cuticular modification (step 1 in **Fig. 3**), sometimes even nerve connections to the neuropiles (step 2), using histoimmunochemical approaches and/or transmission electron microscopy (**Table 2**, "Histology/ultrastructure") has confirmed the existence of a sensory function in various sensilla in 10 orders of arachnids, without identifying their specific function with certainty. To determine whether a sensillum had a chemosensory or another sensory function (e.g. mechanosensory), a few studies used sensillum-level electrophysiological approaches (see below). Thus, it was demonstrated that neurons of a specific sensillum detect semiochemicals (step 1 of the chemosensory circuit in **Fig. 3**): for a spider (Tichy *et al.*, 2001), scorpion (Gaffin & Brownell, 1997), or tick (Leonovich, 2004). However, characterizing the behavioural response is necessary to accurately determine the biological activity of semiochemicals perceived by the organ under study. A link between chemodetection by a given sensillum and a behavioural response (step 3 in **Fig. 3**) may be demonstrated by inactivation of the sensillum by ablation, painting or gene slicing. For example, this was performed in a parasitiform mite (Bao *et al.*, 2026), tick (Hess & Vlimant, 1986), Leal & Mochizuk (1990) in an acariform mite (Leal & Mochizuki, 1990), or scorpions (Nisani *et al.*, 2018; Drozd, 2024). In addition, (Talukder *et al.*, 2025a)) provided strong support for such a dependence by observing the positioning of the body parts carrying the sensilla studied during the target behaviours.

In most studies, authors rely on analogies to deduce the precise sensory functions of sensilla. Sensilla are considered to have olfactory, gustatory, or mechanoreceptive function depending on their external morphology, by analogy with insect's sensilla (Moraza, 2004; Judson, 2007; Leonovich & Stanyukovich, 2011; Wiegmann *et al.*, 2016). The similarities in the general organization of the nervous system of arthropods are supported by demonstrated homologies (Smarandache-Wellmann, 2016), with highly probable functional similarities. However, similarities between individual sensilla should be considered with caution. Functional inferences based on local analogies are more uncertain, especially since morphological similarity alone may mislead attributions of chemosensory function even in insects (King & Gunathunga, 2023). Interestingly, demonstrating a mechanosensory function has recurrently resulted in the exclusion of any chemosensory function from various arachnids' sensilla. Yet, amongst the very few sensilla whose chemosensory function has been specifically studied to date, several have been demonstrated to be bimodal (see **Table 2)**. Bimodal gustatory and mechanosensory sensilla are well known from the legs of flies (Stocker, 1994), with neuronal organization similar to arachnids' (Haupt, 1982; Müller *et al.*, 2020; Drozd *et al.*, 2020). Such bimodality of single sensilla should open up the field of study on the potential chemosensory role of various arachnid sensilla across the body. Further, bimodal sensilla are another argument supporting comparability between arachnid chemosensory systems and insect gustatory systems, rather than with olfactory systems of insects. Ganske & Uhl (2018) and Talukder *et al*. (2025a and 2025b) conducted an in-depth study of hair sensilla on all segments of all four legs in two spider species. Talukder et al. (2025b) revealed that wall pore setae distributed across all four pairs of legs do indeed have an olfactory function at least in males, while females seemingly lack wall pore setae on legs. A more comprehensive view of arachnid chemosensory organization may be gained by investigating sensory structures throughout the body. In addition to these arguments for broadening the scope of investigation of chemosensory sensilla in arachnids, technical difficulties may limit the exploration of the morphology of the sensillum wall. For chemo-dectection to occur, semiochemicals must come in contact with chemosensory dendrites. Thus, many scientists considered only those sensilla with visible openings in their cuticular wall (wall pore or tip pore sensilla) as candidates for chemosensation. On the one hand, openings can be overlooked even under SEM microscopy: for example, compare Ganske & Uhl (2018) versus Talukder *et al.*, (2025b). Therefore, a distal pore of mesostigmatic chemosensory setae not directly visible under SEM microscopy was only assumed by Bhowmick *et al.* (2020). Furthermore, it is not certain that pores visible under microscopy are necessary, since many molecules are much smaller than the pores detectable under microscopy. Electrophysiological signals of equivalent amplitude have been measured on legs I, II, III, and IV excised from dozens of adult females of *Dermanyssus gallinae* (Parasitiformes: Dermanyssidae)*, Stratiolaelaps scimitus* (Parasitiformes: Mesostigmata: Laelapidae) and *Ornithodoros maritimus* (Parasitiformes: Ixodida: Argasidae) in response to ammonia puffs (LR, unpublished data). The strong attractive response to volatile ammonia in *D. gallinae* measured by (Auffray *et al.*, 2022) may well come from detection by the four locomotive appendages. However, in the three Parasitiformes examined, wall pore or tip pore setae were detected exclusively on the tarsi of the first leg pair. All other leg segments possessed only setae without visible pores, as well as slit sensilla (LR, unpublished data).

A more complete characterization of arachnid chemosensory systems will likely emerge from integrative studies of chemosensory pathways starting from the various sensilla described to date and limiting preconceptions about their sensory functions.

Table 2. Summary overview of the current state of knowledge regarding the links between morpho-anatomy and chemosensory function in Arachnida. Only sensilla considered to be chemosensory are presented here (other sensilla may also have this type of function without this having been noticed yet). **Behaviour**: here are mentioned studies that have demonstrated a behavioral response in the presence of semiochemicals (whether or not they have demonstrated the specific role of any sensillum in this response). See the text concerning studies that specifically investigated the effect of specific sensilla inactivation. **Histology/ultrastructure:** studies that have examined the cellular organization located under and within the sensilla, either by dissection and staining or by transmission electron microscopy (TEM). Studies that have examined the external ultrastructure (cuticle) of the sensilla are mentioned in **Type of sensilla (external morphology)**. **Multimodal sensilla**: some single sensilla have been shown to possess other sensory functions at the same time (e.g., sensilla that are both chemosensory and mechanosensory, sensilla that are chemo-, hygro-, and thermosensory). Bibliographic references corresponding to the header are listed using 2-letters and 1 or 2 digits (correspondences listed below).

Taxon	Type of sensilla (external morphology)	Appendage	Methods			Multimodal sensilla
			Behaviour	Electrophysiology	Histology /ultrastructure	
Araneae	wp hair sensilla [ar1, ar6]	walking legs I, II, III, IV (femur, patella, tibia, metatarsus)	ar6	ar6	ar1, ar6	
	tp hair sensilla [ar2,ar3,ar7]	pedipalps, walking legs I, II, III, IV (several segments)			ar2, ar3	ar3
	tarsal organ [ar4,ar5]	pedipalp, walking legs I, II, III, IV (tarsus)		ar4	ar4	ar4
Acariformes	(undefined)	(undefined)	ac1	ac1		
	hair sensilla ("external scapular seta") [ac2]	proterosoma (dorsal position)	ac2			
Parasitiformes	wp hair sensilla (incl. within the Haller's organ) [pa2,pa5,pa6,pa9]	walking leg I (tarsus)	pa1, pa3, pa4, pa7, pa9, pa10, pa11	pa1, pa3, pa4, pa7, pa14	pa8, pa12, pa13, pa14	
		pedipalps		pa1	pa1	pa1
	tp hair sensilla (incl. within the Haller's organ) [pa8]	walking leg I (tarsus)			pa8, pa12, pa13	
	pore sensilla ("cheliceral digit sensilla") [pa1]	chelicerae		pa1	pa1	pa1
Opiliones	wp hair sensilla [op1]	walking legs I, II,(distal tarsomeres)	op1	op2	op2	
	tp hair sensilla [op1]	walking legs I, II, III, IV (distal tarsomeres)		op2	op2	
Pseudoscorpiones	(undefined)	pedipalp chela (fixed and movable fingers)	ps1		ps2	
	peg-sensilla [sc5]	pectines	sc4, sc5, sc6	sc1, sc3, sc7	sc5,sc7	sc5

Scorpiones	hair sensilla (mixed) [sc5]	pectines				
	hair sensilla (mixed) [sc2]	pedipalp chela (fixed fingers)				
	hair sensilla (tp) [sc7]	all walking legs			sc8	
	tarsal organ [sc7]	all walking legs			sc8	
Pycnogonida						
Solifugae	malleoli [so2]	walking legs IV			so3	
	hair sensilla ("sensilla ampullacea") [so1]	pedipalps			so1	
	hair sensilla (unknown type)	walking legs II and III			so4	so4
Schizomida						
Amblypigi	tp and wp hair sensilla [am1,am3]	antenniform legs I	am1	am2	am3, am4	
Palpigradi						
Uropygi						
Ricinulei	tp and wp hair sensilla (incl. into tarsal organ) [ri1]	antenniform legs I and II, pedipalps			ri1, ri2	
Xiphosura	pore sensilla (= “channel sensilla”) xi1,xi2	all pairs of walking legs (on coxal gnathobases and on chelae), walking legs V (on flabella), chilariae	xi3	xi2, xi4, xi5	xi1	xi2

[am1] (Casto *et al.*, 2019); [am2] (Hebets & Chapman, 2000); [am2] (Foelix & Hebets, 2001); [am3] (Foelix, Chu-Wang & Beck, 1975); [ar1] (Foelix, 1985a); [ar2] (Foelix, 1970); [ar3] (Müller *et al.*, 2020); [ar4] (Ehn & Tichy, 1994); [ar5] (Platnick *et al.*, 2012); [ar6] (Talukder *et al.*, 2025a, 2025b); [ar7] (Ganske & Uhl, 2018); [ac1] (Gaudet, Faraone & Hillier, 2023); [ac2] (Leal & Mochizuki, 1990); [op1] (Fernandes *et al.*, 2017); [op2] (Gainett *et al.*, 2017) ; [pa1] (Sonenshine *et al.*, 1986); [pa2] (Leonovich & Stanyukovich, 2011); [pa3] (Eliash *et al.*, 2014); [pa4] (Faraone *et al.*, 2020); [pa5] (Leonovich, 2007); [pa6] (Bhowmick *et al.*, 2020); [pa7] (Gaudet *et al.*, 2024); [pa8] (Foelix & Axtell, 1971); [pa9] (Su, Zhang & Xu, 2021); [pa10] (Nganso *et al.*, 2020); [pa11] (Bao *et al.*, 2026); [pa12] (Hess & Vlimant, 1986); [pa13] (Chu-Wang & Axtell,

1974); [pa14] (Leonovich, 2004); [ps1] (Weygoldt, 1966); [ps2] (Stemme & Pfeffer, 2022); [ri1] (Talarico *et al.*, 2006); [ri2] (Talarico *et al.*, 2008); [sc1] (Gaffin & Brownell, 1997); [sc2] (Fet *et al.*, 2006); [sc3] (Knowlton & Gaffin, 2011); [sc4] (Nisani *et al.*, 2018); [sc5] (Drozd, 2024); [sc6] (Abushama, 1964); [sc7] (Gaffin, 2002); [sc8] (Foelix & Schabronath, 1983); [so1] (Bauchhenss, 1983); [so2] (Yiğit *et al.*, 2012); [so3] (Sombke *et al.*, 2019); [so4] (Haupt, 1982); [xi1] (Hayes, 1971); [xi2] (Wyse, 1971); [xi3] (Hassler & Brockmann, 2001); [xi4] (Barber, 1956); [xi5] (Hayes, 1965).

III Electrophysiological evidence

Electrophysiological studies have been carried out to record the action potentials induced by semiochemicals (Olsson & Hansson, 2013). The action potential exerted by individual compounds have been measured in different ways based on the morphological structures of the arthropod olfactory appendages or sensilla and can be broadly divided into appendage-level and sensillum-level recordings, reflecting hierarchical organization of arthropod chemosensory systems.

At appendage-level, electroantennography (EAG) and electropalpography (EPG) record summed action potentials from the entire appendage. The average output of the arthropod chemosensory appendage to its CNS (in adapted-EAG) is thus integrated as a proxy of the global neural response of a chemosensory appendage to chemical stimulation. Because appendages typically contain multiple sensillum types, each housing variable numbers of receptor neurons with distinct tuning properties, appendage-level recordings do not quantify discrete neural output as single sensillum recordings (SSR) and may not directly reflect stimulus-specific information transmitted to the central nervous system. Indeed, standard EAG amplitudes do not consistently covariate with behavioural responses, a limitation that has prompted methodological refinements such as the triple-EAG approach proposed by Ramiaranjatovo, Reynaud & Jacob, 2023 to improve the interpretability of appendage-level electrophysiological measurements. In contrast, sensillum-level electrophysiology, most commonly performed using SSR, targets individual chemosensory units. In SSR, an electrode is inserted close to the neurons under just one sensillum and the recording is performed from only the receptor neurons that are contained within that sensillum.

Electrophysiological techniques have been successfully used for insects providing valuable information on the sensitivity to the studied species towards specific semiochemicals (Pickett *et al.*, 2012; Olsson & Hansson, 2013). However, more challenges have been encountered with arachnids because of the lack of antennae (traditional EAG not possible), the knowledge on the location and role of sensilla, the different morphological organization of their chemosensory organs and the sometimes very small structures (especially hard with SSR in mites), slowing down the advancement in this field of research.

Electrophysiology across arachnids

Electrophysiological investigations of chemosensory responses in arachnid orders other than Parasitiformes and Acariformes remain comparatively limited, and only a small number of studies have directly examined responses to chemical stimuli in these groups. In spiders and scorpions, most electrophysiological evidence derives from appendages-level recordings, with comparatively few studies achieving sensillum- or neuron-level resolution. Spiders possess the ability to smell and detect chemical volatiles and, similarly to mites and ticks, are equipped with wall-pore sensilla that have shown olfactory function (Talukder *et al.*, 2025a, 2025b) and can be compared to the olfactory sensilla in insects. An adaptation to the insect electroantennography (called ‘electrolegogram’) was used to record the olfactory response of the whip spider *Phrynus parvulus* (Amblypygi: Phrynidae) towards a series of chemicals (Hebets & Chapman, 2000). Among the tested compounds, some induced excitatory responses (e.g., monocarboxylic acids); however, others produced no signal (e.g., alpha-pinene) or gave an inhibitory response (e.g., citral). These volatile compounds are typically linked to repellent-induced behaviour, and some have not been reported to trigger electrophysiological responses in other parasitiform species (Faraone, MacPherson & Hillier, 2019; Gaudet *et al.*, 2023, 2024). Finally, in horseshoe crabs, electrophysiological recordings from parts of legs (coxal gnathobase and chela) reveal broadly tuned responses to amino acids and food extracts, providing a functional contrast to the more ligand-specific pheromone-sensitive sensilla characterized in other groups (Wyse, 1971).

The identification of sex pheromone receptive gustatory cells in the cursorial spider *C. salei* has been successfully achieved through electrophysiological recordings performed on the tip pore sensilla (Tichy *et al.*, 2001). Electrophysiological single-sensillum recording has been used to demonstrate the olfactory role of the wall-pore sensilla located on walking legs of *A. bruennichi* spider in pheromone detection (Talukder *et al.*, 2025b) being specific only to males and involved in detecting signaling females. Electrograms that integrate the sum-potential of the sensilla of spider appendages were involved in the identification of pheromone candidates of *P. bejingensis* (Xiao *et al.*, 2010) and *A. diadematus* (Fischer *et al.*, 2021b).
Extracellular electrophysiological studies conducted on eleven solifugae species provided interesting insight on arthropod mechanoreceptors (Cushing *et al.*, 2014). These camel spiders are equipped with specialized conical setae called papillae located on the pedipalps and they have been found to function as mechanoreceptors, and potentially as chemoreceptors as well.
Scorpions offer an accessible system for investigating chemosensory organs using electrophysiological techniques. They are equipped with unique chemo-tactile appendages called pectines (**Fig. 4A**) involved in mating and food-seeking behaviours (Wolf, 2017). Because of their structures and accessibility, pectines are well suitable for electrophysiological screenings, providing stable connection with tungsten electrodes and long-lasting recordings (Gaffin, 2002). The peg sensilla on scorpion pectines have been shown, through electrophysiological studies, to detect a wide range of semiochemicals (Gaffin & Brownell, 1997; Hughes & Gaffin, 2019), and respond to mechanosensory stimuli through peg deflection (Peeples & Gaffin, 2024).

Tick and mite electrophysiology

Electrophysiological studies of chemosensation in ticks and mites have relied on a range of approaches that vary in spatial resolution and technical complexity. These include sensillum-level recordings (e.g., SSR and tip recording), appendage-level recordings adapted for the tarsi or palps (e.g., electrotarsography, tip-recording technique) and whole-appendage or body-region recordings designed to overcome the extreme miniaturization and structural complexity of parasitiform and acariform sensory organs. While sensillum-level approaches offer higher specificity, they are technically challenging in ticks and especially in mites, resulting in a predominance of adapted appendage-level and multi-unit electriophysiological methods in these taxa.

SSR in ticks and even worse in mites has been shown to be technically challenging and time-consuming, resulting in only occasional reports on the activity of tick chemosensory sensilla with limited compound panels (Leonovich, 2004; Josek *et al.*, 2021). Previous studies have reported electrophysiological recordings from individual sensilla in various tick species targeting the olfactory sensilla in all four parts of the Haller's organ (capsule, anterior pit, posterior sensillum group, distal knoll, **Fig. 4D)**. These sensilla responded to sex pheromone components, exhale breath and CO_2, and host body odors (including fatty acids, aldehydes, lactones, and phenolic compounds) (Leonovich, 2004; Faraone *et al.*, 2020; Josek *et al.*, 2021). The procedure, used to measure the extracellular action potentials from neurons associated with tick tarsal sensilla, has been adapted to simplify the technical challenges presented by SSR. In Ixodidae and Tetranychidae electrophysiological recordings have been successfully performed by using a fork electrode, and electrotarsal detection showed sensitivity of two-spotted spider mites, *Tetranychus urticae* to many terpenoids commonly found in plant essential oils, such as eucalyptol, thymol, and linalool, and to carboxylic acids and aldehydes, which are known to be detected by ionotropic receptors (Gaudet *et al.*, 2023). Similarly, tick electrophysiological response towards butyric acid has been recorded from the foretarsi using a similar mounting technique called 'electrotarsography' based on the use of a fork-electrode set-up (Gaudet *et al.*, 2024; Amiro, Plazas & Faraone, 2026; Dhunna, Hobbs & Hillier, under review). Another adaptation of the SSR technique was based on using sharpened tungsten electrodes inserted below the apotele of either the left or right foretarsi in parasitiform mites, *Varroa destructor* to measure changes in electrical potential (Light *et al.*, 2021) after exposure to essential oil components.

To overcome the limitations of sensillum-level recordings in ticks, a novel body-region–level electrophysiological approach, termed electroscutumography, was developed (Faraone *et al.*, 2020). In this method, a sharpened tungsten electrode is inserted into the soft tissue beneath the scutum, in proximity to the synganglion, allowing the recording of integrated neural responses to chemical stimulation. Using electroscutumography, electrophysiological responses to attractants (e.g., aldehydes and carboxylic acids) and other volatile organic compounds were successfully recorded in *Ixodes scapularis*. This approach has proven particularly informative for assessing inhibitory interactions between attractants and repellents, revealing reduced neural responsiveness following repellent exposure (Faraone *et al.*, 2020; Gaudet *et al.*, 2024). The use of a glass electrode connected to the cut tip of the distal knoll sensilla provided interesting data on the characterization of phenol and lactone receptors in the distal sensilla located in the Haller's organ in *Ixodes* ticks (Leonovich, 2004). A similar setup was used to record the electrophysiological response of *Varroa* mites to bee volatiles, either alone or in combination with repellents. The foreleg - where the sensory organ is located - was dissected and mounted between two glass electrodes, both filled with KCl solution and containing a silver recording electrode (Eliash *et al.*, 2014; Singh *et al.*, 2015). A similar set-up made it possible to detect an unambiguous electrophysiological response in each leg pair to volatile ammonia (attractant) in three parasitiform species (LR, unpublished data). The lack of electrophysiological response of ticks towards individual repellents (Faraone *et al.*, 2020; Gaudet *et al.*, 2024) and the induced reduction in electrophysiological response to attractant after repellent exposure (Gaudet *et al.*, 2024; Amiro *et al.*, 2026) has inspired more research in trying to explain the mechanism behind repellent detection. Perhaps, the absence of receptors in the OR protein family ('olfactory receptors'; Gulia-Nuss *et al.*, 2016; Bhowmick *et al.*, 2020) might explain the recurring trend. In a previous study, electrophysiological assays have revealed that the inhibitory response of *V. destructor* to honeybee headspace volatiles significantly decreases in the presence of certain compounds, such as DEET, and is dose-dependent and long-lasting. However, the exposure of DEET alone to *V. destructor* foreleg did not elicit a significant and consistent electrophysiological response (Singh *et al.*, 2015). A similar trend was observed in *I. scapularis* ticks where electrophysiological response to butyric acid was significantly reduced when delivered together with repellents (Faraone *et al.*, 2020) or after exposure to repellents (Gaudet *et al.*, 2024; Amiro *et al.*, 2026). Gustatory sensilla have been identified on the pedipalps of male *R. microplus* , which come into contact with the female cuticle during mating. Electrophysiological recordings have provided evidence for contact chemoreceptors in these sensilla. Taste receptors have been shown to be present in the distal segment of the palps and chelicerae, as well as the tip of tarsus of this tick and *Amblyomma cajennense* (de Bruyne & Guerin, 1998; Soares & Borges, 2012). Cheliceral pit sensilla of female *R. microplus* have also been studied using taste electrophysiological experiments. On the other hand, cheliceral sensilla of *R. sanguineu*s have been found to present only one pore sensillum (Soares *et al.*, 2012). In terms of olfaction, chemosensory sensilla have been identified in the Haller's organ of adult male *A.americanum, A. cajennense, A. variegatum, D. variabilis*, and *Rhipicephalus appendiculatus* (Parasitiformes: Ixodidae) that are responsible for detecting 2,6-dichlorophenol, although only mature males respond to it. The tip-recording technique has been used to study olfactory sensilla located on tarsi in *R. appendiculatus* and *A. variegatum* (Haggart & Davis, 1981; Waladde, 1982; Leonovich, 2004; Soares & Borges, 2012). Interestingly, very few studies have been published reporting electrophysiological response of tick and mites towards repellent compounds found in essential oils (Josek *et al.*, 2021; Gaudet *et al.*, 2023). In addition, no examples assessing repellents through electrophysiology in a dose-response fashion are available, emphasizing the lack of knowledge on chemosensory system-repellent compound interaction at neurological and molecular level. Despite significant advancements in tick neurobiology over the past two decades, further research is needed to clarify the mechanisms underlying repellent detection.

Analytical Tools to Identify Arachnid Semiochemicals

The identification of chemical messengers presents a set of challenges that chemical ecologists must overcome. This process involves several key stages: the semiochemicals must be i) sampled, ii) separated, iii) detected, and iv) structurally characterized. Finally, one must v) select the few behaviourally active components out of the vast number of detected ones (Fischer, 2019).

Behavioural assays guide the i) sampling of the unknown semiochemicals. For example, once the presence of volatile attractants or deterrents has been demonstrated in bioassays, the semiochemicals can be captured in the headspace using filters (e.g., activated charcoal, Tenax®, or Poropak®) (Sahm *et al.*, 2024; Dössel, Weiss & Schneider, 2026). For subsequent analysis, the adsorbed compounds can be released via thermal desorption (TD) or extracted with a solvent (Brodie *et al.*, 2016; von Hoermann *et al.*, 2022). Solid-phase microextraction (SPME) is another valuable technique, where a coated fiber is exposed to the sample (either headspace or liquid) to adsorb analytes, which are then thermally desorbed directly in the instrument's injection port (El Adouzi *et al.*, 2020; Gries *et al.*, 2022). Low-volatile components, on the other hand, can be sampled using solvent washes of relevant substrates such as silk, the cuticle, or dissected glands (Fischer *et al.*, 2021b, 2022). The choice of solvent is critical and should be guided by bioassays; non-polar solvents, like hexane, are commonly chosen to acquire CHCs (Bey *et al.*, 2025). More polar solvents, such as methanol or acetonitrile, are used to extract polar compounds (Fischer *et al.*, 2023b). Before proceeding with chemical analysis, it is crucial that behavioural assays with the initial headspace or solvent extracts confirm the successful capture of the active semiochemicals. The resulting behaviourally active sample typically consists of a complex mixture of semiochemicals that require separation to allow for the identification of individual compounds (Millar & Haynes, 1998).

Gas chromatography (GC) is the standard tool to ii) separate complex samples (Millar & Haynes, 1998). Upon injection, the mixture is vaporized at a high temperature, and carried by an inert gas through a heated column. This column is lined with a stationary phase that retains semiochemicals based on their properties, primarily polarity and volatility. Stronger interactions with the column or lower volatility delay the passage of a compound, resulting in a characteristic retention time that effectively separates the components of the mixture (Harris, 2016). However, only an estimated 10% of known organic compounds are detectable for GC analysis; heat-labile, very polar, or high molecular weight compounds (>500 Da) tend to be unsuitable for GC-analysis (Rood, 2007).

For compounds not amenable to GC, liquid chromatography (LC) has become increasingly popular, a trend driven by recent developments of powerful detectors (Siuzdak, 2025). In LC, the sample is injected into a liquid mobile phase (solvent) that carries the analytes through a column lined with a stationary phase. Differences in solubility with the mobile phase and interactions with the stationary phase cause characteristic differential retention of compounds, leading to their separation (Harris, 2016).

Once separated, the compounds must be iii) detected. The mass spectrometer (MS) is arguably the most informative detector, as it ionizes and fragments molecules, and the resulting fragment masses provide crucial structural information and require minute quantities (Siuzdak, 2025). When coupled with GC, the MS generates characteristic fragmentation patterns for each separated compound through electron ionization (EI) ("hard" ionization technique) (Harris, 2016). These patterns can be compared against extensive libraries of reference standards to aid in structural identification (Siuzdak, 2025). In contrast, the electrospray ionization (ESI) typically used in LC-MS is a "soft" ionization technique that often results in less informative fragmentation; to overcome this, tandem mass spectrometry (MS-MS) is employed. Tandem-MS isolates and further fragments the initial ions, yielding additional structural data. Reference libraries for LC-MS/MS are rapidly emerging, further establishing this method for the structural elucidation of unknown metabolites (Siuzdak, 2025). Other detectors are also commonly employed; for instance, GC coupled with a flame ionization detector (GC-FID) is frequently used to identify or quantify known compounds based on their characteristic retention times and chemical standards (Fischer *et al.*, 2021b).

The iv) structural characterization of detected compounds is typically based on MS or MS/MS data combined with chromatographic retention times. However, mass spectra alone are sometimes insufficient to definitively determine a chemical structure. Nuclear Magnetic Resonance (NMR) spectroscopy is a powerful tool for elucidating the exact structure of unknown compounds, but this technique requires microgram quantities of the purified metabolite (Harris, 2016). Individual metabolites are commonly isolated for NMR by collecting fractions as they elute from an LC column at their respective retention times (Fischer *et al.*, 2022).

After compounds are separated, detected, and characterized, the few behaviourally active ones must be v) selected. The most direct selection method involves using the animal itself as a bio-detector via electrophysiology (see above). Here, an electrode records the neural response of the animal's primary olfactory organ when exposed to compounds eluting from a gas chromatograph. Synchronous peaks from the bio-detector and a chemical detector (e.g., FID or MS) indicate that a specific semiochemical is detected by the animal. For insects, electroantennography (GC-EAD) is well-established (Moorhouse *et al.*, 1969; Gries *et al.*, 2021). When electrophysiological methods are not feasible, comparative metabolomics can be employed to select candidate semiochemicals (Fischer *et al.*, 2023b). In comparative metabolomics, samples from signaling and non-signaling individuals are collected, analyzed, and statistically compared. Compounds that are unique to or significantly more abundant in the signaling group are considered potential candidates. While, traditionally this involved targeted analysis of well-separated chromatogram peaks, co-eluting compounds introduce difficulties, particularly when the target compound is detected in trace amounts. Non-targeted metabolomics has demonstrated to be a powerful tool for selecting candidates detected by MS detectors (Fischer *et al.*, 2023b; Covington & Seyedsayamdost, 2025). Instead of comparing integrated peaks, this method considers individual fragment-masses across the entire dataset, effectively deconvoluting candidate compounds from co-eluents, even at trace quantities (Fischer *et al.*, 2023b).

As a final step, any candidate compounds that have been separated, detected, characterized, and selected need to be synthesized and tested in behavioural assays to test their biological activity.

Future directions

Studies on the chemical ecology of Arachnida have revealed ubiquitous use of chemical information that is detected by diverse chemoreception organs, some of which are unique to their order. Patchy knowledge is based on few well characterized groups, with most of the diversity of arachnids to be investigated. The next frontier of chemical ecology of Arachnida requires comparative and mechanistic approaches that integrate advanced chemical analysis with neuroethology, additionally to ongoing behavioural descriptions. By continuing the identification of arachnid semiochemicals and pheromones, particularly of non-model lineages, we will be able to distinguish unique evolutionary innovations from conserved traits. We propose to systematically address the identified knowledge gaps within each order:

Spiders are the most speciose arachnid order and abundant predators in nearly every terrestrial ecosystem. Spiders are also the most studied group for chemoreception, yet we still have a poor understanding of their chemical communication (Fischer, 2019; Talukder *et al.*, 2025a). Our knowledge is concentrated on a handful of species within the hyperdiverse Araneomorphae, leaving vast branches of the spider tree of life to be investigated. We have anecdotal evidence of chemosensation in tarantulas (Mygalomorphae) (Dor *et al.*, 2008), leaving the more basely branching segmented Mesothelae in the unknown. An exciting frontier is to explore these phylogenetic gaps to build a more complete picture of how chemical signaling evolved within the Araneae. Even within the best-studied groups, fundamental questions remain. We have identified sex pheromone components for nineteen of over 53,500 species, we know little about how spiders produce pheromones and how the biosynthetic pathways evolved. How conserved are production pathways within a family? Diversity in biosynthesis of pheromones opens another intriguing frontier: does pheromone production costs render spider pheromones ‘honest signals’ of quality (Fischer *et al.*, 2024). Further, most research has focused on female-to-male signals, it became evident that spiders have much more complex chemical conversations rather than female biased monologues (Xiao *et al.*, 2010; Fischer *et al.*, 2023a). Male anti-aphrodisiacs fend off rivals (Watson, 1986; Malouines, 2017) while their aphrodisiacs represent underinvestigated chemical courtship (Xiao *et al.*, 2010; DiRienzo *et al.*, 2019). Research should explore beyond a simple mate-attraction model to disentangle the web of spider chemical ecology.

The sensory world of the Parasitiformes and Acariformes is primarily chemical, as most species lack eyes entirely. Our research efforts have been narrowly focused on a few dozen species of ticks and mites that are of medical or agricultural importance, leaving the chemical ecology of over 48,000 species as a scientific frontier. We have a good understanding of the kairomonal cues, like CO_2 and carboxylic acids, that parasitic ticks and mites use to find their hosts (Light *et al.*, 2020; Auffray *et al.*, 2022; Faraone, 2022), or like herbivore-induced plant volatile, that phytophilous predatory mites use to find their prey (Maeda & Takabayashi, 2001). But how does a predatory mite find its prey through the granular soil material? How does a free-living mite find a mate in heterogenous environments? Similarly, how does a tick find a suitable blood meal or a mate relying mainly on chemical cues? Outstanding and exciting questions of arachnid chemical ecology lie within this vast, unstudied majority. We know that some mites use compounds like neral and geranial as alarm pheromones (Jiang *et al.*, 1997; Heethoff & Raspotnig, 2012), and others use aggregation pheromones (Entrekin & Oliver, 1982), sex pheromones remain almost entirely unknown outside of a few pest species (Ziegelmann *et al.*, 2013; Häußermann *et al.*, 2015). Sex pheromones have been well characterized in metastriate ticks (*Dermacentor* and *Amblyomma* spp.) (Sonenshine *et al.*, 1976; Waladde, 1982), but the pheromones involved in mating among prostriate ticks, such as those in the genus *Ixodes*, remain poorly understood. Another important question concerns the mechanism by which ticks process semiochemicals. Uncovering how they detect these signals and respond behaviourally could lead to the development of effective repellents or attractants). What are the specific chemical attractants that mediate reproduction in the thousands of non-parasitic species? Furthermore, how do the chemical signals used by a plant-feeding spider mite compare to those of a soil-dwelling Oribatid or a marine Halacarid? The Parasitiformes and Acariformes provide ideal systems in which to study how extreme ecological diversification—from obligate parasitism to predation and detritivory—has shaped the evolution of chemical communication systems. Answering these questions will not only fill a significant gap in our basic biological knowledge but could also provide novel avenues for the biocontrol of pest species by exploiting their own chemical languages.

Pseudoscorpions exhibit a complex, chemically mediated social life. Males deposit pheromones on spermatophores (Legg, 1973), mark their mates with anti-aphrodisiacs (Bonilla *et al.*, 2011), and even alter their own chemical signature to mimic their hosts (Tizo-Pedroso & Del-Claro, 2014). The frontier here is to move beyond behavioural descriptions to identify the specific molecules driving these interactions. What are the compounds that guide females to sperm, deter rival males, or grant a parasite safe passage into a host colony?

Scorpions present a promising model group. We have decades of behavioural reports describing pheromonal communication for mating and chemical trail-following (Melville *et al.*, 2003; Taylor *et al.*, 2012; Pordeus *et al.*, 2019; Barbosa-da-Silva *et al.*, 2025), yet not a single compound has been structurally identified. A primary frontier is the chemical identification of these elusive signals. With pheromone structures at hand we may be able to ask: what is the precise function of the pectines? Do they detect airborne molecules, substrate-bound chemicals, or both? Are they pheromone-specific (Gaffin & Brownell, 1997; Hughes & Gaffin, 2019)?

Solifugae have long been considered to be animals that perceive the world primarily through vibrations (Kundu *et al.*, 2025), emerging evidence suggests that chemosensation is a critical, underexplored modality for solifuges (Hebets *et al.*, 2024; Simian *et al.*, 2025). The malleoli are covered in chemoreceptive sensilla and appear crucial for detecting contact sex pheromones during mating. It remains unclear whether these fast predators use volatile cues for longer-range detection of prey or mates? Likewise, linking the function of the malleoli to identified chemical structures represents a central frontier of chemical ecology of arachnids.

For the relatively neglected groups such as Amblypygi, Uropygi, Schizomida, Palpigradi, seaspiders and horseshoe crabs we are in the infancy of discovery. The defensive spray of whip scorpions is unlikely to be their sole chemical communication (Schmidt *et al.*, 2000). For whip spiders there is strong evidence for chemically-guided homing (Casto *et al.*, 2019), but what are their self-referential semiochemicals?

Advances in morphological technology will benefit arachnid investigations by visualizing in greater detail the structure of chemosensory organs and their associated neural pathways. Emerging techniques such as high-resolution electron microscopy, confocal laser scanning microscopy, and three-dimensional reconstruction from serial sections (Zhao *et al.*, 2024; Ruan *et al.*, 2025; Schindler *et al.*, 2025) now allow for novel insights into the fine architecture and spatial organization of sensory structures. Combining these tools with molecular labeling and connectomics approaches will help link morphology with function, deepening our understanding of how chemical cues are detected and processed. Future studies integrating these technologies are expected to reveal novel sensory adaptations across parasitiform and acariform taxa and refine our interpretation of the evolution and diversification of arachnid chemosensory systems.

The rise of ‘omics technologies offers unprecedented opportunities to connect genes to behaviour (Li, Wang & Zhou, 2025). A major frontier will be to integrate genomic and transcriptomic data with chemical ecology, allowing the characterization of arachnid chemoreceptor toolkits. We should be able to identify the specific receptors tuned to sex pheromones or prey kairomones, linking genes directly to function. Fascinatingly, the distantly related spiders and ticks both use short carboxylic acids to solve different ecological problems - one for mating and the other for host finding (Faraone *et al.*, 2020; Fischer *et al.*, 2025a), the underlying receptors should shed light on the nature of this convergent evolution.

The identification of semiochemicals likewise requires adjustment from solely GC-MS based approaches that worked well for insects (Fischer *et al.*, 2025b). Many spider, and seemingly scorpion pheromones remained undetected via GC-MS analyses (Fischer *et al.*, 2025a; Barbosa-da-Silva *et al.*, 2025). A key frontier lies in the recent advancements of LC-MS/MS and non-targeted metabolomics to capture a more complete picture of an animal's communication metabolome (Fischer *et al.*, 2023b; Siuzdak, 2025). Additionally, targeted spatial metabolomics can provide a direct link between the morphological tissues and the behaviourally active semiochemicals (Chen *et al.*, 2025; Redureau *et al.*, 2025). The rise of machine learning and rapidly growing MS-spectral libraries provide promising outlook on rapid structural annotation that could fasttrack chemical ecology of arachnids and beyond (Covington & Seyedsayamdost, 2025; Siuzdak, 2025).

Even with more traditional methods, it is possible to make significant advances in understanding the chemosensory systems of arachnids by considering two key aspects: interpopulation variation and the scale of individual functioning. At least among Parasitiformes, significant variations between populations in behavioral responses to semiochemicals (Auffray *et al.*, 2022; Masier *et al.*, 2023) and in CHC profiles (Dupraz *et al.*, 2022) have been demonstrated. We recommend, where possible, comparing distant populations within each species of arachnid studied, in order to consolidate conclusions on chemosensory interactions as much as possible. Similarly, despite the real attractant activity of an odorant kairomone, a significant portion of chance in the foraging process has been demonstrated in the Poultry Red Mite based on behavioral experiments at different scales (from in vitro to the field to laboratory; Auffray *et al.*, 2022). While it is certain that kairomones exist and are detected by various arachnids, in many cases we do not really know the role they effectively play in the search for hosts in ticks, prey in the predators studied to date, or even carriers in phorionts, at the scale of arachnid functioning. This can be of considerable importance when it comes to developing pest management tools. We therefore strongly recommend considering the implementation of multi-scale experiments to effectively advance the production of new knowledge on chemosensory interactions in arachnids.

CONCLUSIONS

1. Arachnids exhibit exceptional diversity, exceeding mammals in species richness and ecological roles, with chemosensation serving as the foundation for essential behaviours such as prey detection, mate choice, habitat selection and predator avoidance.
2. Viewed across Chelicerata, arachnid chemosensory systems offer a powerful window into how ancestral, appendage-based chemical detection has been repeatedly modified, elaborated, or repurposed in response to ecological diversification.
3. Integrating data from arachnids with that of extant marine chelicerates will allow explicit tests of homology versus convergence in sensory organs, receptor repertoires, and semiochemical use.
4. Current understanding of arachnid chemosensation is largely restricted to a few model taxa such as spiders, mites and ticks.
5. Sensory biology in scorpions, pseudoscorpions, solifuges, and other arachnid orders is in its infancy, despite clear evidence of chemical sensitivity in these groups.
6. The adaptation of electrophysiological techniques from insect models has yielded functional insights into chemosensilla, though technical constraints remain due to the morphological diversity and small size of organs.

7. Research on arachnid semiochemistry (pheromones, kairomones, allomones and synomones) is neglected compared to insect chemical ecology.
8. The integration of modern analytical approaches, including GC-MS, LC-MS/MS based metabolomics, differential transcriptomics, and three-dimensional imaging with behavioural and electrophysiological assays, offers promising avenues for characterizing behaviourally active semiochemicals.
9. Expanding interdisciplinary research to underrepresented taxa is essential for constructing a comprehensive framework of arachnid chemosensory evolution and addressing fundamental questions in neuroethology and evolutionary biology.
10. Advancing the study of arachnid chemical communication systems has practical implications for pest management, biodiversity conservation, and biomimetic design.

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VII Author contributions:

All authors conceptualized, investigated, wrote the original draft and edited it.

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