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To cite this version:

Sandrine Salmon, Sylvie Rebuffat, Soizic Prado, Michel Sablier, Cyrille d'Haese, et al.. Chemical communication in springtails: a review of facts and perspectives. Biology and Fertility of Soils, 2019, 55 (5), pp.425-438. 10.1007/s00374-019-01365-8 . hal-02152310v2

HAL Id: hal-02152310
https://hal.science/hal-02152310v2

Submitted on 28 Apr 2020

Chemical communication in springtails: a review of facts and perspectives

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Abstract

The present knowledge on chemical communication in springtails (Collembola), one of the two most abundant invertebrate groups living in soil and environments in tight contact with soil (e.g. plant litter, moss), is reviewed here. Chemical communication in an environment where light is absent or dimmed becomes a prominent driver of trophic and non-trophic interactions between soil organisms at a time when better knowledge on the biological determinants of soil communities is required. Like insects and many other arthropods, collembolan individuals of the same population intercommunicate by pheromones, which allow them to signal a risk or to cluster in places favourable for feeding, mating, moulting and ovipositing. Olfaction is also used to select preferred food and mates. Researches so far conducted allowed to discern common trends in the role and chemical composition of odour blends used by Collembola. However, much more needs to be done before reaching straightforward conclusions about chemical communication issues at evolutionary and community levels, making this domain even more rewarding.

Keywords: Chemical communication, Collembola, Pheromones, Aggregation, Phylogeny, Community

Introduction

Chemical communication among soil organisms is a still poorly explored scientific domain, despite recent focus on the functional importance of chemical signalling in plant-microbial (Peters and Verma 1990; Sanon et al. 2009; Combès et al. 2012), plant-faunal (Blouin et al. 2005; Rosenstiel et al. 2012; Leach et al. 2017) and plant-faunal-microbial interactions (Bonkowski 2004; Bais et al. 2006; Jousset et al. 2008). However, better knowledge of these interactions might illuminate our still imperfect knowledge of soil food webs (DeAngelis 2016). Ignored for a long time, positive interactions (Bertness and Callaway 1994; Leigh and Rowell 1995; Stachowicz 2001) are now recognized as a key process in the building and stability of communities, involving plants, microbes and animals (Wall and Moore 1999; Callaway et al. 2002; Wisz et al. 2013). Positive interactions are also acknowledged as a driving force of evolution (Laland and Boogert 2010; Rosenberg and Zilber-Rosenberg 2016; Prinzing et al. 2017). Negative and positive interactions among species are at least partly governed by chemical signals (Callaway 2002; Taga and Bassler 2003). This makes chemical communication a key factor of species coexistence (Vet 1999; Austin et al. 2014).

Chemical signals, based on volatile (olfactory) or contact molecules (O’Connell 1986), are known to play a prominent role in positive as well as negative interactions between soil organisms (Wenke et al. 2010; Lavelle et al. 2016). In soil invertebrates, they play a direct role in mating (Zizzari et al. 2017), search for food (Brückner et al. 2018), search of safe sites for growth and reproduction (Kuenen and Nooteboom 1963), aggregation (Benoit et al. 2009), avoidance of death risk (Nilsson and Bengtsson 2004a), prey location and catching (Huber 1978) and deterrence of predators (Smolanoff et al. 1975). Some chemical compounds excreted by soil animals have hormonal properties which stimulate the growth of plants and their resistance against stress factors and pathogens (Puga-Freitas and Blouin 2015). All these chemical signals are known as semiochemicals and are classified into two broad classes depending on their intra- or interspecific action. Pheromones are intraspecific compounds capable of acting outside the body of the secreting individual to impact the behaviour of a receiving individual of the same species (Karlson and Lüscher 1959). These chemical signals allow individuals of the same species to interact between them in the course of aggregation (aggregation pheromones), mating (sex pheromones) or by signalling a risk (alarm pheromones) (Wilson and Bossert 1963; Shorey 1973). Conversely, allelochemicals are interspecific molecules that are grouped according to the benefits they provide to both producer and receiver. Allomones, kairomones and synomones are produced by a given species and act on another species (Sbarbati and Osculati 2006). They are favourable either to the producer (allomones, e.g. repulsive odours) or to the receiver (kairomones, e.g. fungal odours), or to both of them (synomones).

Springtails (Collembola) are among the most widespread and abundant groups of soil arthropods (20,000 to 400,000 individuals.m^{-2}), and as such they impact ecosystem functioning (Seastedt 1984; Hopkin 1997). They have long been considered as insects, but now belong to a separate taxonomic class. Collembola are phylogenetically sisters of other hexapods, which comprise mainly the insects. They are divided into four orders: Entomobryomorpha (~4000 known species), Poduromorpha (~3300 species), Symphypleona (~1200 species) and Neelipleona (~50 species). These microarthropods (0.25‒3 mm in length) live mainly, but not exclusively, in soil and litter. The main role of Collembola is the decomposition of organic matter and the recycling of nutrients that can subsequently be taken up by plants (De Vries et al. 2013). They exert a direct action on organic matter decomposition and recycling of nutrients through the consumption of litter. Indirect effects occur through the regulation and dispersion of microorganisms (fungi and bacteria on which they feed), which are responsible for the mineralization of organic matter. As the role of Collembola varies according to species, the chemical communication regulating the interactions between Collembola species indirectly impacts soil functioning (Bardgett and Van der Putten 2014).

Collembola are known for a long time for their aggregative behaviour (Glasgow 1939). Aggregation is mediated by environmental heterogeneity (Poole 1961; Usher 1969), mass dispersal (Lyford 1975), selection of proper habitats (Joosse 1970; Verhoef and Nagelkerke 1977; Salmon and Ponge 1999; Auclerc et al. 2009) and food resources (Ponge 2000; Salmon 2004; Chauvat et al. 2014). Evidence for the existence of sex (Waldorf 1974a) and aggregation pheromones (Mertens and

Bourgoignie 1977; Verhoef et al. 1977a, b) stimulated studies on olfactory signals involved in communication between congeners and mates in an environment and a zoological group such as soil-dwelling species where visual systems are rudimentary (Leinaas 1983; Pfander and Zettel 2004; Porco et al. 2009). Remarkable fossils preserved in Early Cretaceous amber allow describing a courtship behaviour in a Symphypleona and an aggregative behaviour in an Entomobryomorpha, thus suggesting the presence of pheromones more than 105 Ma ago (Sánchez-García et al. 2018). However, information on the importance of chemical communication for coexistence or avoidance and the evolution of collembolan species is still scarce (Nilsson and Bengtsson 2004b, Wertheim et al. 2005).

Given the accumulated data it is now time to review the present state of knowledge on chemical communication in Collembola, and make a prospect of ecological and evolutionary perspectives.

The use of pheromones, allomones and kairomones by Collembola

Collembola are endowed with a strong sensitivity to olfactory signals. Receptors are mostly localized on the antenna, in particular the two apical segments. This has been demonstrated directly by anatomical investigations (Keil 1999; Kollmann et al. 2011), total and partial antennal amputations (Waldorf 1976; Verhoef et al. 1977b), and indirectly by checking antennal cleaning behaviour (Waldorf 1974b). However, the chemosensitivity of other cephalic organs like postantennal organs cannot be excluded (Karuhize 1971; Altner and Thies 1976). Although this has not been demonstrated as yet on these tiny arthropods, it can be postulated that the double nature of the antennae allows them not only to detect chemical signals at distance, but also to evaluate the direction of the odour source like in insects (Bell and Tobin 1982). This might explain directional movements towards preferred food (Auclerc et al. 2010), as it has been observed in aboveground invertebrates (Schooley and Wiens 2003). Furthermore, pheromones produced by collembolans can also be diverted from their purpose and used as kairomones by predators to detect their prey (Kielty et al. 1996).

Aggregation pheromones

Pheromones play a key role in the aggregation process of Collembola, such as in numerous other arthropods (Ishii and Kuwahara 1967; Wertheim et al. 2005). They have been first evidenced by their effects, e.g. the fact that a place previously conditioned by the presence of one or more individuals becomes attractive to conspecifics (Mertens and Bourgoignie 1977; Verhoef et al. 1977a, b; Mertens et al. 1979; Joosse and Koelman 1979). When extracted from a conditioned substrate with an appropriate solvent, pheromones were able to reproduce the same phenomenon (Manica et al. 2001). However, these experiments did not demonstrate that the molecules were remotely detected. In fact, erratic movements of an animal may favour random encounters with conditioned places, upon which the animal ceases to move: only contact (non-volatile) molecules are required in this type of chemical signalling. Other experiments showed that individuals attracted and induced the aggregation of conspecifics without any contact or visual signal, suggesting a volatile signal (Leonard and Bradbury 1984; Krool and Bauer 1987). Motility decreased then ceased totally at high concentration, i.e. at short distance from conspecifics (Shorey 1973; Mertens and Bourgoignie 1977).

Aggregation pheromones have been evidenced in a large number of collembolan species (Table 1), encompassing Poduromorpha and Entomobryomorpha living above or below ground in various environments. Surprisingly, Neelipleona and Symphypleona are absent from this list, when excluding short courtships displayed between sexual partners (Betsch-Pinot 1977; Kozlowski and Shi 2006).

Aggregation pheromones allow encounters between individuals of the same species in places favourable for feeding (Barra and Christiansen 1975; Benoit et al. 2009), mating (Joosse 1970; Verhoef and Nagelkerke 1977), moulting (Joosse and Verhoef 1974; Verhoef and Nagelkerke 1977) and ovipositing (Verhoef and Nagelkerke 1977; Benoit et al. 2009). Aggregation in favourable micro-niches is of paramount importance to limit water losses (Joosse 1970; Benoit et al. 2009). Limiting water loss is more particularly required during moulting periods which happen repetitively all along the life of Collembola (Verhoef and Nagelkerke 1977). Synchronized moulting controlled by chemical communication has been demonstrated in group-living hypogastrurids (Leinaas 1983). It also appears that species that are most sensitive to desiccation would be also most prone to aggregation (Joosse 1970, 1971). Awaiting further confirmation on a larger array of species, parthenogenetic species are less prone to aggregation than sexual species (Chernova et al. 2010). Although aggregations comprising different species are commonplace in Collembola (Poole 1961; Hale 1966; Benoit et al. 2009; Joosse 1970), only two cross-species attractions by pheromones have been demonstrated (*Tomocerus minor* attracted to *Orchesella villosa* and *O. cincta*) out of the three interactions tested in two independent studies (Verhoef et al. 1977a, Benoit et al. 2009).

Aggregation pheromones are produced by adults of both sexes (Verhoef et al. 1977a; Krool and Bauer 1987), even during starvation (Verhoef 1984) and moulting periods (Verhoef and Nagelkerke 1977; Verhoef et al. 1977a). Their production is negatively abundance-dependent (Verhoef 1984). They are deposited on the substrate (Mertens and Bourgoignie 1977) and some of them are seemingly volatile, being attractive at distance (Verhoef et al. 1977a; Leonard and Bradbury 1984; Krool and Bauer 1987; Manica et al. 2001; Nilsson and Bengtsson 2004b). They are emitted through the intestine, as being found in the faeces (Verhoef 1984), but probably also through the cuticle, as they were detected in extracts from entire uncrushed individuals (Benoit et al. 2009).

Sex pheromones

Sex pheromones are produced by females, conditioning the deposition of spermatophores by males (Waldorf 1974a) and attracting them (Porco et al. 2009) while spermatophores produced by males are also known to attract females (Zizzari et al. 2017). They are present in the cuticle (Porco et al. 2004, 2009) and in spermatophores (Zizzari et al. 2017). Sex pheromones are thought to mediate sexual selection (Hedlund et al. 1990; Stam et al. 2002; Zizzari et al. 2009). Although still largely speculative in the studied group, the idea of an evolutionary role of sex pheromones has been considered by entomologists (Greenfield 1981; Symonds and Elgar 2008), but deeper research in this direction is needed before clear hypotheses could emerge.

Alarm pheromones and allomones

Alarm pheromones have been recorded in a number of species, belonging to Poduromorpha, Entomobryomorpha and Symphypleona (Table 2). They are emitted after rupture of the cuticle when springtails die (necromones), or in the presence of predators. They elicit a dispersive behaviour of conspecifics (Purrington et al. 1991; Nilsson and Bengtsson 2004a). Defence strategies vary according to the taxonomic group considered. Some collembolan species have an aggregative behaviour in the presence of a predator, while others move away from each other. This suggests various behavioural effects of alarm pheromones (Negri 2004).

Predator-repulsive allomones have been shown to be emitted by podurid species, e.g. *Ceratophysella denticulata* against a rove beetle (Bitzer et al. 2004), or the giant springtail *Tetradotonphora bielanensis* against a ground beetle (Dettner et al. 1996). The emission of predator-repulsive allomones occurs when predatory attack is simulated with a needle as in *Protaphorura lata* (Usher and Balogun 1966). However, the odour of springtails may also be used by some of their predators as a cue to catch them, such as in the ground beetle *Nebria brevicollis* (Kielty et al. 1996).

Kairomones

Preferences for some food items are known for a long time (Knight and Angel 1967). Despite a wide array of food items potentially used by the same species, preferences may differ to a large extent among species (Jørgensen et al. 2005; Ferlian et al. 2015). It has been shown that selection of or attraction to preferred food can be mediated by olfaction. Indeed, it occurs in advance, and even in the absence of tasting (Salmon and Ponge 2001; Staaden et al. 2011; Chauvat et al. 2014). Attraction to preferred food is associated with directional and rapid movements towards the odour source upon detection at a distance varying from 1 to 40 cm (Bengtsson et al. 1994; Salmon and Ponge 2001; Auclerc et al. 2010). Attraction is followed by cessation of movement in the presence of food (Westerberg et al. 2008).

Microcosm experiments demonstrated that fungal strains are preferred or avoided when their odour is attractive or repellent, respectively (Bengtsson et al. 1988; Hedlund et al. 1995; Sadaka-Laulan et al. 1998). They also demonstrated that discrimination between preferred and discarded fungal colonies is mediated by secondary metabolites (Staaden et al. 2011). Preferred fungal strains maximize fitness parameters, with the exception of a few erroneous choices (Sadaka-Laulan et al. 1998; Heděnec et al. 2013). The volatile compounds present in the odour of preferred fungal strains were isolated and tested. An attractive effect of some specific compounds was demonstrated on the onychiurid *Protaphorura armata* (Bengtsson et al. 1991). A strong influence of fungal defence chemicals on the aggregative behaviour of the fungus-feeding *Folsomia candida* has also been shown by using wild-type fungi and modified strains lacking the ability to secrete secondary metabolites (Stötefeld et al. 2012).

Collembolan olfactory cues are also provided by mosses. A win-win process is mediated by moss volatile compounds which act as kairomones. They increase moss fertilization success by favouring collembolan search for preferred habitat (Gerson 1969) and even for preferred food, although it has not been proven that sperm cells can act as a reward (Rosenstiel et al. 2012). Kairomones are also emitted by leaf litter, repellence to the collembolan *Sinella coeca* being induced by isoprene (2-methylbuta-1,3-diene) (Michelozzi et al. 1997). Repellence mediated by the smell of artificial compounds, such as the herbicide 2,4,5-T (2,4,5-trichlorophenoxyacetic acid), has also been demonstrated in *Onychiurus quadriocellatus* (Eijsackers 1978). The odour of soil animals, e.g. earthworm themselves and their excreta, can be perceived at distance and used as a cue to find proper food and habitat, including protection from predators (Salmon and Ponge 2001; Salmon 2001, 2004; Salmon et al. 2005).

All these results point to a fundamental role of chemical communication in the functional relationships between soil organisms (DeAngelis 2016) and co-adaptation experiments even suggest that they could play a key role in the co-evolution between insects and fungi (Biedermann et al. 2019). It is here suggested that attractive, neutral and repellent odours could explain the so-called ‘home-field advantage hypothesis’, i.e. the optimization of litter decomposition when decomposers are processing litter in their own habitat (Perez et al. 2013; Austin et al. 2014; Veen et al. 2015). They could also explain ‘natal habitat preference induction’, i.e. the propensity of animal species to disperse in an environment that contains stimuli similar to those found in their original environment (Stamps and

Swaisgood 2007).

Composition of collembolan semiochemicals

Most insect pheromones are made of mixtures of various molecules, the proportion of which varies among species and within and among populations of the same species (Wertheim et al. 2005; Symonds and Elgar 2008). In various species, aggregation and sex pheromones are alcohols, esters, amino acids, fatty acids, aldehydes and ketones commonly linked to a hydrophobic alkyl chain. They are often derived from fatty acids, or from phenol (O'Connell 1986; Leal 1997; Tillman et al. 1999). Recognition mechanisms based on insect pheromones are highly species-specific (Roelofs and Brown 1982; De Bruyne and Baker 2008; Kaissling 2014). This suggests that in collembolan too, the ratio of chemical compounds found in pheromones allows a fine tuning between emitters and receptors (Bruce et al. 2005; Lei et al. 2013).

In Collembola, various compounds have been isolated among alarm pheromones and necromones (chemicals arising from dead individuals). Most of them are aromatic compounds and fatty acids (Purrington et al. 1991; Messer et al. 1999; Nilsson and Bengtsson 2004b). Some compounds commonly isolated from collembolan alarm pheromones, such as linoleic acid, have a wide spectrum of action, being accordingly repulsive to ants, aphids, beetles and woodlice (Greenway et al. 1978; Nijholt 1980; Howard and Blomquist 1982; Rollo et al. 1994). Three compounds have been isolated from collembolan repulsive allomones (Table 3). The onychiurids *T. bielanensis, Deuteraphorura scotaria* and *Onychiurus circulans* were shown to excrete 2,3-dimethoxy-pyrido[2,3-b] pyrazine, a heterocyclic aromatic compound. However, the repellent effect of this molecule has only been observed in *T. bielanensis*. Furthermore, all onychiurids do not produce this molecule, since it has not been found in *P. armata* (Dettner et al. 1996; Nilsson and Bengtsson 2004b). These compounds were identified in fluids excreted by secretory organs (pseudocella) and were not found in food and faeces (Dettner et al. 1996). The hypogastrurid *Ceratophysella denticulata* was shown to excrete 3-hydroxy-4,5-dimethoxybenzoic acid (DmHbA) and 4-hydroxy-3,5-dimethoxybenzoic acid, better known as syringic acid (Bitzer et al. 2004). These phenolic acids are known for their strongly irritating properties (Hayashi et al. 1999). The strong resemblance between repellent substances emitted by arthropods and allelochemicals produced by plants against herbivores (and other plants, i.e. allelopathy) has been highlighted a long time ago (Smolanoff et al. 1975). It can be explained by the use of plant semiochemicals as precursors of insect pheromones (Reddy and Guerrero 2004; Stökl and Steiger 2017; Blomquist et al. 2010). Nevertheless, Malcicka et al. (2017, 2018) showed that, similar to some other soil invertebrates, some collembolan species were able to synthesize de novo linoleic acid, a common component of alarm pheromones, while other arthropods needed to get it from their food. The attraction of males of *T. bielanensis* by the odour of females was shown to be mediated by the polar fraction of cuticular extracts, e.g. fatty acids, ketones, alcohols and esters (Porco et al. 2009). The (Z)-14-tricosenol hydrocarbon was shown to be the main volatile compound emitted by spermatophores (spermatic capsules deposited on the substrate) of the entomobryid *Orchesella cincta* (Zizzari et al. 2017). We did not find any study describing unambiguously the identification and biological activity of aggregation pheromones isolated from collembolan extracts. The only exception is a recent study in which potentially attractive cuticular extracts were isolated and fatty acids proposed as the pheromones (Liu and Wu 2017). However, the authors neither demonstrated unambiguously the role of the extracts in aggregation nor the emission or excretion of the compounds in the environment. Hence in the conducted experiments, the extracted fatty acids could have been dissolved from the animal body (Malcicka et al. 2017), making the results questionable. In the search of necromones (repellent molecules), synthetic palmitic acid was shown to be attractive to *P. armata* and was present in *P. armata*, *Folsomia candida*, *D. scotaria* and *O. circulans* (Nilsson and Bengtsson 2004a, b). However, these authors could not demonstrate that *P. armata* was attractive to *O. circulans* and *D. scotaria*. It suggests that the sensitivity to a given concentration of palmitic acid can vary according to species. Furthermore, fatty acids and fatty acid-related compounds (e.g. n-alkanes, n-alcohols) are well-known as persistent components of soil organic matter (Marseille et al. 1999). Consequently, distinguishing their potential role in aggregation phenomena is very challenging (Baldock and Nelson 2000, Reiffarth et al. 2016).

Despite their lack of chemical identification, diverse solubility and polarity properties of some collembolan aggregation pheromones have been established as yet. Those produced by *Hypogastrura viatica* and *O. cincta* (Mertens et al. 1979) are soluble in water while those emitted by the semi-aquatic *Anurida maritima* are insoluble in water but soluble in methanol (Manica et al. 2001). Aggregation pheromones extracted from *Cryptopygus antarcticus* and *Friesea grisea* were more soluble in methanol than in water and acetone, and were insoluble in hexane (Benoit et al. 2009). Those extracted from *P. armata* and *F. candida* were soluble in cyclohexane, hexane or dichloromethane (Nilsson and Bengtsson 2004a; Liu and Wu 2017). This wide range of polarities, while pointing to a common poor solubility in water, highlights the diversity of chemical compounds that can play a role as aggregation pheromones among collembolan species, as well as the difficulty to establish an efficient and common protocol for their isolation. The chemical characterization of such pheromones is still also challenging, most probably because there are produced at very low concentration. This implies a high number of individuals necessary for pheromone collection (Benoit et al. 2009). Olfactory attraction tests allowed deducing that aggregation pheromones are at least composed of some volatile molecules, while the effect of non-volatile molecules acting by contact cannot be excluded (Benoit et al. 2009). Given our knowledge of the chemical compositions of insect pheromones, it can be reasonably hypothesized that collembolan pheromones should be also complex mixtures of a broad range of chemical compounds (Wertheim et al. 2005).

Ecological and evolutionary perspectives in chemical communication among Collembola

Given that our knowledge on chemical communication among arthropods is mainly based on insect pheromones, we will present some ‘insect’ facts which should be of interest for future studies of Collembola semiochemicals. Among the most attractive research directions we can identify (i) the evolutionary point of view, and (ii) the roles played by the microbiota associated with springtails. The metabolic potential of endo- and ectomicrobiota opens new tracks. Furthermore, some of the molecules previously identified as springtail pheromones may possibly originate from the microorganisms they host.

First, we question at which phylogenetic level olfactory signals vary, and whether they intervene in speciation mechanisms. It is known that scarab beetles of the same genus share the same sex pheromones (Leal 1997). This suggests that in this zoological group, speciation was allopatric and mediated by natural geographic or temporal discontinuities. Inter-species pheromone interactions even occur between species belonging to distinct insect orders, e.g. male wine flies responding to honey bee queen sex pheromones (Croft et al. 2017). In butterflies there were strong discrepancies between phylogenies based on morphological characters and those based on synthetic pathways of sex pheromones (Dugdale 1997). Most of these data nevertheless suggest a strong phylogenetic conservatism of sexual olfactory signals, as otherwise demonstrated in insect-plant interactions (Futuyma and Mitter 1996).

Contrary to sex pheromones, variegated results were obtained with insect aggregation pheromones. Despite preferences for conspecifics, cross-attraction between species belonging to various families is known as an adaptive mechanism thought to enhance species coexistence (Vet 1999; Wertheim et al. 2005). Working with phylogenetic distances, Symonds and Elgar (2004) showed that no links between morphologically- and chemically-based scolytid phylogenies could be evidenced. On the contrary, a close relationship between both phylogenies was shown in drosophilids (Symonds and Wertheim 2005). In the former case, random saltational shifts in chemical communication systems, a typical case of punctuated equilibrium (Gould and Eldredge 1993), are expected to favour sympatric speciation. In this case, like geographical or ecological isolation, aggregation pheromones create behavioural barriers against gene flow (Baker 2002; Wertheim et al. 2005; Mendelson et al. 2014). In the latter case, phyletic gradualism is expected because of the absence of selection pressure on aggregation pheromones, non-chemical cues being used in mate assortment (Symonds and Wertheim 2005).

Despite the lack of large datasets allowing discerning evolutionary trends in Collembola, some multi-species experiments deserve our attention. Positive as well as negative results of cross-repulsion by necromones of another species were obtained (Purrington et al. 1991; Nilsson and Bengtsson 2004b). These results are not in favour of the existence of a phylogenetic signal related to necromones. Thus, further research is needed on this question, especially on sex or aggregation pheromones, before drawing straightforward conclusions. Multi-species attraction experiments in the order Entomobryomorpha showed that *Tomocerus minor* (family Tomoceridae) was attracted by aggregation pheromones of two species of *Orchesella* (family Entomobryidae), while *Orchesella* species were only attracted by their conspecifics (Verhoef et al. 1977a). On the contrary, two co-occurring Antarctic species, *Cryptopygus antarcticus* (Entomobryomorpha, family Isotomidae) and *Friesea grisea* (Poduromorpha, family Neanuridae) did not reveal any cross-attraction (Benoit et al. 2009). The same was observed for *P. armata* versus *O. circulans* and *D. scotaria*, all belonging to the same Onychiuridae family in Poduromorpha (Nilsson and Bengtsson 2004b). To date, no research of cross-attraction has been reported in Symphypleona and Neelipleona, the former displaying elaborate mating courtships in many species. Clearly, all these results are insufficient to discern a pattern of attraction as a function of the phylogenetic distance between species, since only one cross-attraction was observed between species belonging to different families. Consequently inferring a general trend in the role of chemical communication in collembolan species assembly rules and speciation is premature. Nevertheless, the partial results so far obtained point to the existence of asymmetrical effects of semiochemicals across species. Some species repel or attract other species, while the reverse does not apply (species “1” repels or attracts species “2”, but species “2” does not repel or attract species “1”). This might contribute to explain dominance effects in multi-species laboratory cultures (Christiansen 1967; Culver 1974; Christiansen et al. 1992; Walsh and Bolger 1993). Such mechanisms might also explain the field co-occurrence (Benoit et al. 2009) or on the contrary segregation (Ponge 1973; Ponge and Salmon 2013) of species sharing similar ecological requirements.

Some aspects of chemical communication, so far unquestioned within soil ecosystems, should now deserve the attention of researchers. When several species are attracted to the same food or habitat (Maraun et al. 2003; Staaden et al. 2011; Boulay et al. 2019), several events can occur following the encounter instar. Both species can compete by using the same resource (exploitative competition), or be expelled from each other (interference competition), or even one of them may kill the other (egg predation, cannibalism). The sign (negative, positive, or nil) of pheromone interactions between species might determine the fate of their encounters. Indifference, avoidance or attraction might possibly act in advance of any contact or agonistic behaviour. Such a phenomenon cannot be revealed in laboratory culture conditions where species are constrained to cohabit in a restricted space. Positive or nil chemical interactions (between-species attraction or indifference, respectively) will result in multi-species aggregations around the same food or habitat, in the former case with a stabilizing mechanism according to Barot and Gignoux (2004). Conversely, negative interactions, whether symmetrical or asymmetrical, will result in either niche shifts or checkerboard distributions, according to different or similar ecological species requirements, respectively. A better knowledge of chemical communication systems might thus contribute to explain fine-scale niche segregation (Anderson 1978; Zhao et al. 2013) and competition-mediated over-dispersion of functional traits (Widenfalk et al. 2016), as observed in soil samples, and then to finally resolve the famous “enigma of soil animal species diversity” (Anderson 1975; Maraun et al. 2003; Wehner et al. 2016).

Finally, the development of our knowledge on the roles played by symbiotic and more largely associated microorganisms in the biology, physiology and biochemistry of any organism, from plants to mammals, thanks to metagenomics and metabolomics methods, opens avenues for further research on springtail communication molecules. Furthermore, many of the molecules previously identified as springtail pheromones are possibly originating from the microorganisms they host, rather than from the springtails themselves.

Undoubtedly, the role of the Collembola-associated microbiota in intra- and interspecies communication should be a major research field in the next decade. Until now, this role has been scarcely explored in insect communication since the 1970’s, and more actively since 2000 (Dillon and Charnley 2002; Sharon et al. 2013). Gut microbiota appears as the most important insect-associated microbial community, contributing to the production of sex or aggregation pheromones, or to the insect defence. As an example, the gut microbiota of the desert locust *Schistocerca gregaria* was shown to produce guaiacol and phenols having both antimicrobial and aggregation pheromone functions (Dillon and Charnley 2002). Molecular defence in insects through their associated microorganisms has been largely explored (for a review, see Van Arnam et al. 2018). On another side, chemical studies point to the production of pyrazines as common communication molecules in many organisms, including Collembola (Dettner et al. 1996; Nilsson and Bengtsson 2004b). This suggests the possible involvement of the microbial compartment in animal chemical communication because pyrazine molecules are synthesized by several bacterial species (Dickschat et al. 2005).

However, in springtails, these orientations are still nascent. Bahrndorff et al. (2018) described the composition of the microbial communities associated with *Orchesella cincta* (Entomobryidae). The results supported a functional role of the microbiota in the enzymatic digestion of food, in the metabolism of aromatic amino acids that act as growth factors, and in soil metabolism including decomposition processes and biodegradation. However, the search for a role in communication was not a focus of the study.

Conclusions and future research needs

This review shows that the existence of aggregation, alarm and sex pheromones is unquestionable and verified experimentally. However, the studies suffered from several difficulties in collecting enough material for the identification of the molecules eliciting a signal. The small size of these animals, and difficulties in rearing them, notably but not only for Symphypleona, may explain why collembolan communication science does not make progress as fast as for other insects. Nothing is known on the receptors involved although strong clues indicate that antennal organs would play a role (Kollmann et al. 2011). It appears highly probable that given their phylogenetic position at the base of Hexapoda (Giribet et al. 2004), Collembola would share with bristletails the absence of specialized olfactory receptors (Missbach et al. 2014) to the benefit of generalized ionotropic receptors. Indeed, basal hexapods are proposed to have ionotropic receptors in common with Crustacea (Corey et al. 2013). Studies on antennal transcriptomes might solve this question.

The origin and kind of molecules involved in collembolan chemical communication needs more attention to the methods used to extract them and experimentally reconstruct the processes in play in aggregation, mating, foraging, and other behavioural responses. The origin of extracted molecules should be clearly determined. Especially, it is crucial to know whether they are excreted in the environment by the animal or not, and from which organ or compartment in the animal they arise. The role of extracted and identified molecules should be unambiguously demonstrated. A simple and instantaneous attraction does not mean that a given molecule enters mandatorily in the composition of aggregation pheromones. These molecules have also to induce a decrease in motility and a clustering of individuals in the course of time. As an example, fatty acids extracted from the body of *Folsomia candida* and attracting *F. candida* (Liu and Wu 2017) are known to attract also other microarthropods towards food sources such as bacteria (Brückner et al. 2018). Thus, all attractive molecules are not necessarily pheromone components. Rather than yes/no sensitivity to a single compound, there are clues in favour of the ability of Collembola to react quantitatively to chemical 'fingerprints', like this has been shown to occur in other arthropods (Barata et al. 2002).

We also opened avenues in the evolutionary and functional importance of collembolan chemical communication. More research on multi-species aggregation (versus segregation) might throw light on the reasons why so many species contribute to similar or complementary functions in the same soil sample (Bardgett 2002) while repeated sampling shows so much unexplained micro-scale variation (Ims et al. 2004). Moreover, the roles that the associated microbial communities could play in the production of collembolan semiochemicals may explain several discrepancies observed in the results acquired until now, such as variations in the chemical nature of the main pheromone components identified according to the location of collected individuals or their number (Benoit et al. 2009). It also appears that many of the results accumulated for the last 40 years would need being re-examined in the light of analysing the composition and metabolic potential of the endo- and global associated microbiota, using metagenomics and metabolomics. In this context it is clear that, taking into-account the current methodological advances in analytical chemistry, massively parallel sequencing technology (NGS) and the potential applications of signalling molecules in various domains and particularly in agricultural ecology to reduce pest incidence (Beck et al 2018), deciphering springtail communication strategies offers an extraordinary opportunity for future multidisciplinary research.

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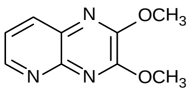
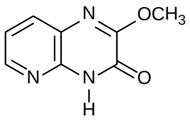
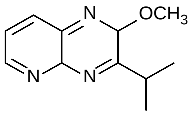
Table 1. Observations of aggregation pheromones in collembolan species.

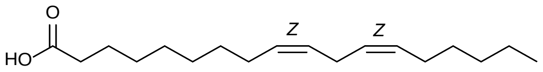
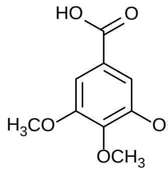
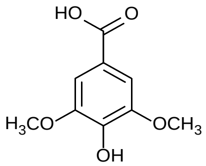
Order	**Superfamily**	**Species name**	**Literature source**
Poduromorpha	*Hypogastruridae*	*Hypogastrura viatica*	Mertens and Bourgoignie (1977)
	Neanuridae	*Anurida maritima*	Manica et al. (2001)
	Neanuridae	*Friesea grisea*	Benoit et al. (2009)
	Onychiuridae	*Protaphorura armata*	Joosse (1970), Joosse and Koelman (1979)
Entomobryomorpha	*Entomobryidae*	*Entomobrya nivalis*	Joosse (1970)
	Entomobryidae	*Heteromurus nitidus*	Krool and Bauer (1987)
	Entomobryidae	*Lepidocyrtus cyaneus*	Joosse (1970)
	Entomobryidae	*Orchesella cincta*	Mertens and Bourgoignie (1977), Verhoef et al. (1977a)
	Entomobryidae	*Orchesella villosa*	Verhoef et al. (1977a)
	Tomoceridae	*Tomocerus minor*	Joosse (1970), Verhoef et al. (1977a)
	Isotomidae	*Cryptopygus antarcticus*	Benoit et al. (2009)
	Isotomidae	*Folsomia candida*	Leonard and Bradbury (1984)
	Isotomidae	*Isotoma viridis*	Joosse (1970)
	Isotomidae	*Isotomurus palustris*	Joosse (1970)

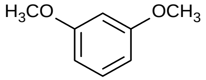
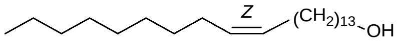
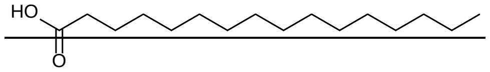
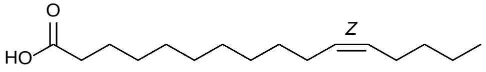
Table 2. Observations of alarm pheromones in collembolan species

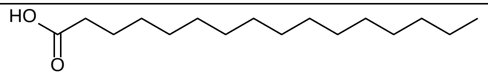
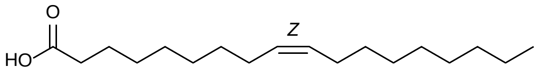
Order	**Superfamily**	**Species name**	**Literature source**
Poduromorpha	Hypogastruridae	*Ceratophysella sigillata*	Pfander and Zettel (2004)
	Hypogastruridae	*Hypogastrura pannosa*	Purrington et al. (1991)
	Neanuridae	*Neanura muscorum*	Messer et al. (1999), Purrington et al. (1991)
	Onychiuridae	*Onychiurus encarpatus*	Purrington et al. (1991)
	Onychiuridae	*Protaphorura armata*	Nilsson and Bengtsson (2004)
Entomobryomorpha	Isotomidae	*Folsomia candida*	Purrington et al. (1991)
	Isotomidae	*Isotomurus bimus*	Purrington et al. (1991)
	Entomobryidae	*Lepidocyrtus pallidus*	Purrington et al. (1991)
Symphypleona	Katiannidae	*Sminthurinus elegans*	Purrington et al. (1991)
Neelipleona	Neelidae	*Megalothorax minimus*	Purrington et al. (1991)

Table 3. Communication molecules in springtails, localization and proposed functions

Collembola species **(super-family)**	**Localization/ Organ**	**Function**	**Communication type**	**Molecule**	**Class of Molecule**	**Reference**
Tetradotonphora bielanensis (Onychiuridae)	Pseudocells	Defense	Repulsive allomones	2,3-dimethoxy-pyrido[2,3-b]pyrazine 	Pyridopyrazine alkaloids	Dettner et al. (1996)
				2-methoxy-4*H*-pyrido[2,3-b]pyrazine-3-one (CAS Name : Pyrido[2,3-b]pyrazin-3(4H)-one, 2-methoxy-) 		
				3-isopropyl-2-methoxypyrido[2,3-b]pyrazine (CAS Name : 2-Methoxy-3-(1-methylethyl)pyrido[2,3-b]pyrazine) 		

Protaphorura armata *Deuteraphorura scotaria* *Onychiurus circulans* (Onychiuridae)	Unknown (whole body extract)	Defense	Necromone *	linoleic acid 	Fatty acids	Nilsson and Bengtsson (2004b)
Ceratophysella denticulata (Hypogastruridae)	Integument	Defense	Deterrent allomone	3-hydroxy-4,5-dimethoxybenzoic acid  4-hydroxy-3,5-dimethoxybenzoic acid (syringic acid) 	Phenolic acids	Bitzer et al. (2004)
Neanura muscorum	Hemolymph, eggs	Defense	Alarm pheromone	1,3-dimethoxybenzene	Phenolic derivative	Messer et al. (1999)

(Neanuridae)						
Orchesella cincta (Entomobryidae)	Male spermatophores	Female attractant	Sex pheromone	(Z)-14-tricosenol 	Polyene	Zizzari et al. (2017)
Protaphorura armata *Onychiurus scotarius* *Onychiurus circulans* (Onychiuridae) *Folsomia candida* (Isotomidae)	Unknown (whole body extract)	Conspecific attractant	Aggregation pheromone*	palmitic acid 	Fatty acid	Nilsson and Bengtsson (2004b)
Folsomia candida (Isotomidae)	Cuticle	Conspecific attractant	Aggregation pheromones*	Blend composed of: (Z)-11-hexadecenoic acid  palmitic acid	Fatty acids	Liu and Wu (2017)

				 oleic acid 		

*Repellent and attractant effects of linoleic and palmitic acid, respectively have been demonstrated only against *Protaphorura armata*