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1 **Chemical communication in springtails: a review of facts and perspectives**

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17 **Abstract**

18 The present knowledge on chemical communication in springtails (Collembola), one of the two most
19 abundant invertebrate groups living in soil and environments in tight contact with soil (e.g. plant litter,
20 moss), is reviewed here. Chemical communication in an environment where light is absent or dimmed
21 becomes a prominent driver of trophic and non-trophic interactions between soil organisms at a time
22 when better knowledge on the biological determinants of soil communities is required. Like insects
23 and many other arthropods, collembolan individuals of the same population intercommunicate by

24 pheromones, which allow them to signal a risk or to cluster in places favourable for feeding, mating,
25 moulting and ovipositing. Olfaction is also used to select preferred food and mates. Researches so far
26 conducted allowed to discern common trends in the role and chemical composition of odour blends
27 used by Collembola. However, much more needs to be done before reaching straightforward
28 conclusions about chemical communication issues at evolutionary and community levels, making this
29 domain even more rewarding.

30 **Keywords:** Chemical communication, Collembola, Pheromones, Aggregation, Phylogeny,
31 Community

32

33 **Introduction**

34 Chemical communication among soil organisms is a still poorly explored scientific domain, despite
35 recent focus on the functional importance of chemical signalling in plant-microbial (Peters and Verma
36 1990; Sanon et al. 2009; Combès et al. 2012), plant-faunal (Blouin et al. 2005; Rosenstiel et al. 2012;
37 Leach et al. 2017) and plant-faunal-microbial interactions (Bonkowski 2004; Bais et al. 2006; Jousset
38 et al. 2008). However, better knowledge of these interactions might illuminate our still imperfect
39 knowledge of soil food webs (DeAngelis 2016). Ignored for a long time, positive interactions
40 (Bertness and Callaway 1994; Leigh and Rowell 1995; Stachowicz 2001) are now recognized as a key
41 process in the building and stability of communities, involving plants, microbes and animals (Wall and
42 Moore 1999; Callaway et al. 2002; Wisz et al. 2013). Positive interactions are also acknowledged as a
43 driving force of evolution (Laland and Boogert 2010; Rosenberg and Zilber-Rosenberg 2016; Prinzing
44 et al. 2017). Negative and positive interactions among species are at least partly governed by chemical
45 signals (Callaway 2002; Taga and Bassler 2003). This makes chemical communication a key factor of
46 species coexistence (Vet 1999; Austin et al. 2014).

47 Chemical signals, based on volatile (olfactory) or contact molecules (O'Connell 1986), are
48 known to play a prominent role in positive as well as negative interactions between soil organisms
49 (Wenke et al. 2010; Lavelle et al. 2016). In soil invertebrates, they play a direct role in mating (Zizzari
50 et al. 2017), search for food (Brückner et al. 2018), search of safe sites for growth and reproduction
51 (Kuenen and Nooteboom 1963), aggregation (Benoit et al. 2009), avoidance of death risk (Nilsson and
52 Bengtsson 2004a), prey location and catching (Huber 1978) and deterrence of predators (Smolanoff et
53 al. 1975). Some chemical compounds excreted by soil animals have hormonal properties which
54 stimulate the growth of plants and their resistance against stress factors and pathogens (Puga-Freitas
55 and Blouin 2015). All these chemical signals are known as semiochemicals and are classified into two
56 broad classes depending on their intra- or interspecific action. Pheromones are intraspecific
57 compounds capable of acting outside the body of the secreting individual to impact the behaviour of a
58 receiving individual of the same species (Karlson and Lüscher 1959). These chemical signals allow

59 individuals of the same species to interact between them in the course of aggregation (aggregation
60 pheromones), mating (sex pheromones) or by signalling a risk (alarm pheromones) (Wilson and
61 Bossert 1963; Shorey 1973). Conversely, allelochemicals are interspecific molecules that are grouped
62 according to the benefits they provide to both producer and receiver. Allomones, kairomones and
63 synomones are produced by a given species and act on another species (Sbarbati and Osculati 2006).
64 They are favourable either to the producer (allomones, e.g. repulsive odours) or to the receiver
65 (kairomones, e.g. fungal odours), or to both of them (synomones).

66 Springtails (Collembola) are among the most widespread and abundant groups of soil
67 arthropods (20,000 to 400,000 individuals.m²), and as such they impact ecosystem functioning
68 (Seastedt 1984; Hopkin 1997). They have long been considered as insects, but now belong to a
69 separate taxonomic class. Collembola are phylogenetically sisters of other hexapods, which comprise
70 mainly the insects. They are divided into four orders: Entomobryomorpha (~4000 known species),
71 Poduromorpha (~3300 species), Symphypleona (~1200 species) and Neelipleona (~50 species). These
72 microarthropods (0.25–3 mm in length) live mainly, but not exclusively, in soil and litter. The main
73 role of Collembola is the decomposition of organic matter and the recycling of nutrients that can
74 subsequently be taken up by plants (De Vries et al. 2013). They exert a direct action on organic matter
75 decomposition and recycling of nutrients through the consumption of litter. Indirect effects occur
76 through the regulation and dispersion of microorganisms (fungi and bacteria on which they feed),
77 which are responsible for the mineralization of organic matter. As the role of Collembola varies
78 according to species, the chemical communication regulating the interactions between Collembola
79 species indirectly impacts soil functioning (Bardgett and Van der Putten 2014).

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

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

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

96 **The use of pheromones, allomones and kairomones by Collembola**

97 Collembola are endowed with a strong sensitivity to olfactory signals. Receptors are mostly localized
98 on the antenna, in particular the two apical segments. This has been demonstrated directly by
99 anatomical investigations (Keil 1999; Kollmann et al. 2011), total and partial antennal amputations
100 (Waldorf 1976; Verhoef et al. 1977b), and indirectly by checking antennal cleaning behaviour
101 (Waldorf 1974b). However, the chemosensitivity of other cephalic organs like postantennal organs
102 cannot be excluded (Karuhize 1971; Altner and Thies 1976). Although this has not been demonstrated
103 as yet on these tiny arthropods, it can be postulated that the double nature of the antennae allows them
104 not only to detect chemical signals at distance, but also to evaluate the direction of the odour source
105 like in insects (Bell and Tobin 1982). This might explain directional movements towards preferred
106 food (Auclerc et al. 2010), as it has been observed in aboveground invertebrates (Schooley and Wiens
107 2003). Furthermore, pheromones produced by collembolans can also be diverted from their purpose
108 and used as kairomones by predators to detect their prey (Kielty et al. 1996).

109 **Aggregation pheromones**

110 Pheromones play a key role in the aggregation process of Collembola, such as in numerous other
111 arthropods (Ishii and Kuwahara 1967; Wertheim et al. 2005). They have been first evidenced by their
112 effects, e.g. the fact that a place previously conditioned by the presence of one or more individuals
113 becomes attractive to conspecifics (Mertens and Bourgoignie 1977; Verhoef et al. 1977a, b; Mertens et
114 al. 1979; Joosse and Koelman 1979). When extracted from a conditioned substrate with an appropriate
115 solvent, pheromones were able to reproduce the same phenomenon (Manica et al. 2001). However,
116 these experiments did not demonstrate that the molecules were remotely detected. In fact, erratic
117 movements of an animal may favour random encounters with conditioned places, upon which the
118 animal ceases to move: only contact (non-volatile) molecules are required in this type of chemical
119 signalling. Other experiments showed that individuals attracted and induced the aggregation of
120 conspecifics without any contact or visual signal, suggesting a volatile signal (Leonard and Bradbury
121 1984; Krool and Bauer 1987). Motility decreased then ceased totally at high concentration, i.e. at short
122 distance from conspecifics (Shorey 1973; Mertens and Bourgoignie 1977).

123 Aggregation pheromones have been evidenced in a large number of collembolan species
124 (Table 1), encompassing Poduromorpha and Entomobryomorpha living above or below ground in
125 various environments. Surprisingly, Neelipleona and Symphypleona are absent from this list, when
126 excluding short courtships displayed between sexual partners (Betsch-Pinot 1977; Kozłowski and Shi
127 2006).

128 Aggregation pheromones allow encounters between individuals of the same species in places
129 favourable for feeding (Barra and Christiansen 1975; Benoit et al. 2009), mating (Joosse 1970;
130 Verhoef and Nagelkerke 1977), moulting (Joosse and Verhoef 1974; Verhoef and Nagelkerke 1977)
131 and ovipositing (Verhoef and Nagelkerke 1977; Benoit et al. 2009). Aggregation in favourable micro-
132 niches is of paramount importance to limit water losses (Joosse 1970; Benoit et al. 2009). Limiting
133 water loss is more particularly required during moulting periods which happen repetitively all along
134 the life of Collembola (Verhoef and Nagelkerke 1977). Synchronized moulting controlled by chemical
135 communication has been demonstrated in group-living hypogastrurids (Leinaas 1983). It also appears

136 that species that are most sensitive to desiccation would be also most prone to aggregation (Joosse
137 1970, 1971). Awaiting further confirmation on a larger array of species, parthenogenetic species are
138 less prone to aggregation than sexual species (Chernova et al. 2010). Although aggregations
139 comprising different species are commonplace in Collembola (Poole 1961; Hale 1966; Benoit et al.
140 2009; Joosse 1970), only two cross-species attractions by pheromones have been demonstrated
141 (*Tomocerus minor* attracted to *Orchesella villosa* and *O. cincta*) out of the three interactions tested in
142 two independent studies (Verhoef et al. 1977a, Benoit et al. 2009).

143 Aggregation pheromones are produced by adults of both sexes (Verhoef et al. 1977a; Krool
144 and Bauer 1987), even during starvation (Verhoef 1984) and moulting periods (Verhoef and
145 Nagelkerke 1977; Verhoef et al. 1977a). Their production is negatively abundance-dependent
146 (Verhoef 1984). They are deposited on the substrate (Mertens and Bourgoignie 1977) and some of
147 them are seemingly volatile, being attractive at distance (Verhoef et al. 1977a; Leonard and Bradbury
148 1984; Krool and Bauer 1987; Manica et al. 2001; Nilsson and Bengtsson 2004b). They are emitted
149 through the intestine, as being found in the faeces (Verhoef 1984), but probably also through the
150 cuticle, as they were detected in extracts from entire uncrushed individuals (Benoit et al. 2009).

151 **Sex pheromones**

152 Sex pheromones can be produced by females, conditioning the deposition of spermatophores by males
153 (Waldorf 1974a). They can be also produced by males, attracting females directly (Porco et al. 2009)
154 or indirectly through their spermatophores (Zizzari et al. 2017). They are present in the cuticle (Porco
155 et al. 2004, 2009) and in spermatophores (Zizzari et al. 2017). Sex pheromones are thought to mediate
156 sexual selection (Hedlund et al. 1990; Stam et al. 2002; Zizzari et al. 2009). Although still largely
157 speculative in the studied group, the idea of an evolutionary role of sex pheromones has been
158 considered by entomologists (Greenfield 1981; Symonds and Elgar 2008), but deeper research in this
159 direction is needed before clear hypotheses could emerge.

160 **Alarm pheromones and allomones**

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

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

174 **Kairomones**

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

184 Microcosm experiments demonstrated that fungal strains are preferred or avoided when their
185 odour is attractive or repellent, respectively (Bengtsson et al. 1988; Hedlund et al. 1995; Sadaka-
186 Laulan et al. 1998). They also demonstrated that discrimination between preferred and discarded

187 fungal colonies is mediated by secondary metabolites (Staadén et al. 2011). Preferred fungal strains
188 maximize fitness parameters, with the exception of a few erroneous choices (Sadaka-Laulan et al.
189 1998; Heděnc et al. 2013). The volatile compounds present in the odour of preferred fungal strains
190 were isolated and tested. An attractive effect of some specific compounds was demonstrated on the
191 onychiurid *Protaphorura armata* (Bengtsson et al. 1991). A strong influence of fungal defence
192 chemicals on the aggregative behaviour of the fungus-feeding *Folsomia candida* has also been shown
193 by using wild-type fungi and modified strains lacking the ability to secrete secondary metabolites
194 (Stötefeld et al. 2012).

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

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

214 Swaisgood 2007).

215 **Composition of collembolan semiochemicals**

216 Most insect pheromones are made of mixtures of various molecules, the proportion of which varies
 217 among species and within and among populations of the same species (Wertheim et al. 2005; Symonds
 218 and Elgar 2008). In various species, aggregation and sex pheromones are alcohols, esters, amino acids,
 219 fatty acids, aldehydes and ketones commonly linked to a hydrophobic alkyl chain. They are often
 220 derived from fatty acids, or from phenol (O'Connell 1986; Leal 1997; Tillman et al. 1999).

221 Recognition mechanisms based on insect pheromones are highly species-specific (Roelofs and Brown
 222 1982; De Bruyne and Baker 2008; Kaissling 2014). This suggests that in collembolan too, the ratio of
 223 chemical compounds found in pheromones allows a fine tuning between emitters and receptors (Bruce
 224 et al. 2005; Lei et al. 2013).

225 In Collembola, various compounds have been isolated among alarm pheromones and
 226 necromones (chemicals arising from dead individuals). Most of them are aromatic compounds and
 227 fatty acids (Purrington et al. 1991; Messer et al. 1999; Nilsson and Bengtsson 2004b). Some
 228 compounds commonly isolated from collembolan alarm pheromones, such as linoleic acid, have a
 229 wide spectrum of action, being accordingly repulsive to ants, aphids, beetles and woodlice (Greenway
 230 et al. 1978; Nijholt 1980; Howard and Blomquist 1982; Rollo et al. 1994). Three compounds have
 231 been isolated from collembolan repulsive allomones (Table 3). The onychiurids *T. bielensis*,
 232 *Deuteraphorura scotaria* and *Onychiurus circulans* were shown to excrete 2,3-dimethoxy-pyrido[2,3-
 233 b] pyrazine, a heterocyclic aromatic compound. However, the repellent effect of this molecule has
 234 only been observed in *T. bielensis*. Furthermore, all onychiurids do not produce this molecule, since
 235 it has not been found in *P. armata* (Dettner et al. 1996; Nilsson and Bengtsson 2004b). These
 236 compounds were identified in fluids excreted by secretory organs (pseudocella) and were not found in
 237 food and faeces (Dettner et al. 1996). The hypogastrurid *Ceratophysella denticulata* was shown to
 238 excrete 3-hydroxy-4,5-dimethoxybenzoic acid (DmHbA) and 4-hydroxy-3,5-dimethoxybenzoic acid,
 239 better known as syringic acid (Bitzer et al. 2004). These phenolic acids are known for their strongly

240 irritating properties (Hayashi et al. 1999). The strong resemblance between repellent substances
241 emitted by arthropods and allelochemicals produced by plants against herbivores (and other plants, i.e.
242 allelopathy) has been highlighted a long time ago (Smolanoff et al. 1975). It can be explained by the
243 use of plant semiochemicals as precursors of insect pheromones (Reddy and Guerrero 2004; Stökl and
244 Steiger 2017; Blomquist et al. 2010). Nevertheless, Malcicka et al. (2017, 2018) showed that, similar
245 to some other soil invertebrates, some collembolan species were able to synthesize de novo linoleic
246 acid, a common component of alarm pheromones, while other arthropods needed to get it from their
247 food. The attraction of males of *T. bielanensis* by the odour of females was shown to be mediated by
248 the polar fraction of cuticular extracts, e.g. fatty acids, ketones, alcohols and esters (Porco et al. 2009).
249 The (Z)-14-tricosenol hydrocarbon was shown to be the main volatile compound emitted by
250 spermatophores (spermatid capsules deposited on the substrate) of the entomobryid *Orchesella cincta*
251 (Zizzari et al. 2017). We did not find any study describing unambiguously the identification and
252 biological activity of aggregation pheromones isolated from collembolan extracts. The only exception
253 is a recent study in which potentially attractive cuticular extracts were isolated and fatty acids
254 proposed as the pheromones (Liu and Wu 2017). However, the authors neither demonstrated
255 unambiguously the role of the extracts in aggregation nor the emission or excretion of the compounds
256 in the environment. Hence in the conducted experiments, the extracted fatty acids could have been
257 dissolved from the animal body (Malcicka et al. 2017), making the results questionable. In the search
258 of necromones (repellent molecules), synthetic palmitic acid was shown to be attractive to *P. armata*
259 and was present in *P. armata*, *Folsomia candida*, *D. scotaria* and *O. circulans* (Nilsson and Bengtsson
260 2004a, b). However, these authors could not demonstrate that *P. armata* was attractive to *O. circulans*
261 and *D. scotaria*. It suggests that the sensitivity to a given concentration of palmitic acid can vary
262 according to species. Furthermore, fatty acids and fatty acid-related compounds (e.g. n-alkanes, n-
263 alcohols) are well-known as persistent components of soil organic matter (Marseille et al. 1999).
264 Consequently, distinguishing their potential role in aggregation phenomena is very challenging
265 (Baldock and Nelson 2000, Reiffarth et al. 2016).

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

284 **Ecological and evolutionary perspectives in chemical communication**

285 **among Collembola**

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

292 microorganisms they host.

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

303 Contrary to sex pheromones, variegated results were obtained with insect aggregation
304 pheromones. Despite preferences for conspecifics, cross-attraction between species belonging to
305 various families is known as an adaptive mechanism thought to enhance species coexistence (Vet
306 1999; Wertheim et al. 2005). Working with phylogenetic distances, Symonds and Elgar (2004)
307 showed that no links between morphologically- and chemically-based scolytid phylogenies could be
308 evidenced. On the contrary, a close relationship between both phylogenies was shown in drosophilids
309 (Symonds and Wertheim 2005). In the former case, random saltational shifts in chemical
310 communication systems, a typical case of punctuated equilibrium (Gould and Eldredge 1993), are
311 expected to favour sympatric speciation. In this case, like geographical or ecological isolation,
312 aggregation pheromones create behavioural barriers against gene flow (Baker 2002; Wertheim et al.
313 2005; Mendelson et al. 2014). In the latter case, phyletic gradualism is expected because of the
314 absence of selection pressure on aggregation pheromones, non-chemical cues being used in mate
315 assortment (Symonds and Wertheim 2005).

316 Despite the lack of large datasets allowing discerning evolutionary trends in Collembola, some
317 multi-species experiments deserve our attention. Positive as well as negative results of cross-repulsion

318 by necromones of another species were obtained (Purrington et al. 1991; Nilsson and Bengtsson
319 2004b). These results are not in favour of the existence of a phylogenetic signal related to necromones.
320 Thus, further research is needed on this question, especially on sex or aggregation pheromones, before
321 drawing straightforward conclusions. Multi-species attraction experiments in the order
322 Entomobryomorpha showed that *Tomocerus minor* (family Tomoceridae) was attracted by aggregation
323 pheromones of two species of *Orchesella* (family Entomobryidae), while *Orchesella* species were
324 only attracted by their conspecifics (Verhoef et al. 1977a). On the contrary, two co-occurring Antarctic
325 species, *Cryptopygus antarcticus* (Entomobryomorpha, family Isotomidae) and *Friesea grisea*
326 (Poduromorpha, family Neanuridae) did not reveal any cross-attraction (Benoit et al. 2009). The same
327 was observed for *P. armata* versus *O. circulans* and *D. scotaria*, all belonging to the same
328 Onychiuridae family in Poduromorpha (Nilsson and Bengtsson 2004b). To date, no research of cross-
329 attraction has been reported in Symphypleona and Neelipleona, the former displaying elaborate mating
330 courtships in many species. Clearly, all these results are insufficient to discern a pattern of attraction as
331 a function of the phylogenetic distance between species, since only one cross-attraction was observed
332 between species belonging to different families. Consequently inferring a general trend in the role of
333 chemical communication in collembolan species assembly rules and speciation is premature.
334 Nevertheless, the partial results so far obtained point to the existence of asymmetrical effects of
335 semiochemicals across species. Some species repel or attract other species, while the reverse does not
336 apply (species “1” repels or attracts species “2”, but species “2” does not repel or attract species “1”).
337 This might contribute to explain dominance effects in multi-species laboratory cultures (Christiansen
338 1967; Culver 1974; Christiansen et al. 1992; Walsh and Bolger 1993). Such mechanisms might also
339 explain the field co-occurrence (Benoit et al. 2009) or on the contrary segregation (Ponge 1973; Ponge
340 and Salmon 2013) of species sharing similar ecological requirements.

341 Some aspects of chemical communication, so far unquestioned within soil ecosystems, should
342 now deserve the attention of researchers. When several species are attracted to the same food or
343 habitat (Maraun et al. 2003; Staaden et al. 2011; Boulay et al. 2019), several events can occur
344 following the encounter instar. Both species can compete by using the same resource (exploitative

345 competition), or be expelled from each other (interference competition), or even one of them may kill
346 the other (egg predation, cannibalism). The sign (negative, positive, or nil) of pheromone interactions
347 between species might determine the fate of their encounters. Indifference, avoidance or attraction
348 might possibly act in advance of any contact or agonistic behaviour. Such a phenomenon cannot be
349 revealed in laboratory culture conditions where species are constrained to cohabit in a restricted space.
350 Positive or nil chemical interactions (between-species attraction or indifference, respectively) will
351 result in multi-species aggregations around the same food or habitat, in the former case with a
352 stabilizing mechanism according to Barot and Gignoux (2004). Conversely, negative interactions,
353 whether symmetrical or asymmetrical, will result in either niche shifts or checkerboard distributions,
354 according to different or similar ecological species requirements, respectively. A better knowledge of
355 chemical communication systems might thus contribute to explain fine-scale niche segregation
356 (Anderson 1978; Zhao et al. 2013) and competition-mediated over-dispersion of functional traits
357 (Widenfalk et al. 2016), as observed in soil samples, and then to finally resolve the famous “enigma of
358 soil animal species diversity” (Anderson 1975; Maraun et al. 2003; Wehner et al. 2016).

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

365 Undoubtedly, the role of the Collembola-associated microbiota in intra- and interspecies
366 communication should be a major research field in the next decade. Until now, this role has been
367 scarcely explored in insect communication since the 1970’s, and more actively since 2000 (Dillon and
368 Charnley 2002; Sharon et al. 2013). Gut microbiota appears as the most important insect-associated
369 microbial community, contributing to the production of sex or aggregation pheromones, or to the
370 insect defence. As an example, the gut microbiota of the desert locust *Schistocerca gregaria* was

371 shown to produce guaiacol and phenols having both antimicrobial and aggregation pheromone
372 functions (Dillon and Charnley 2002). Molecular defence in insects through their associated
373 microorganisms has been largely explored (for a review, see Van Arnam et al. 2018). On another side,
374 chemical studies point to the production of pyrazines as common communication molecules in many
375 organisms, including Collembola (Dettner et al. 1996; Nilsson and Bengtsson 2004b). This suggests
376 the possible involvement of the microbial compartment in animal chemical communication because
377 pyrazine molecules are synthesized by several bacterial species (Dickschat et al. 2005).

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

384 **Conclusions and future research needs**

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

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

410 We also opened avenues in the evolutionary and functional importance of collembolan
411 chemical communication. More research on multi-species aggregation (versus segregation) might
412 throw light on the reasons why so many species contribute to similar or complementary functions in
413 the same soil sample (Bardgett 2002) while repeated sampling shows so much unexplained micro-
414 scale variation (Ims et al. 2004). Moreover, the roles that the associated microbial communities could
415 play in the production of collembolan semiochemicals may explain several discrepancies observed in
416 the results acquired until now, such as variations in the chemical nature of the main pheromone
417 components identified according to the location of collected individuals or their number (Benoit et al.
418 2009). It also appears that many of the results accumulated for the last 40 years would need being re-
419 examined in the light of analysing the composition and metabolic potential of the endo- and global
420 associated microbiota, using metagenomics and metabolomics. In this context it is clear that, taking
421 into-account the current methodological advances in analytical chemistry, massively parallel
422 sequencing technology (NGS) and the potential applications of signalling molecules in various

423 domains and particularly in agricultural ecology to reduce pest incidence (Beck et al 2018),
424 deciphering springtail communication strategies offers an extraordinary opportunity for future
425 multidisciplinary research.

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803 **Table 1.** Observations of aggregation pheromones in collembolan species.

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

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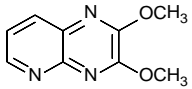
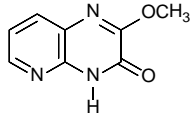
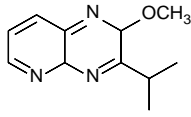
806 **Table 2.** Observations of alarm pheromones in collembolan species

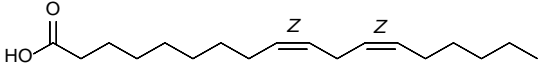
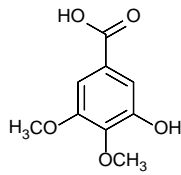
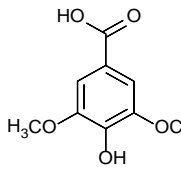
Order	Superfamily	Species name	Literature source
Poduromorpha	Hypogastruridae	<i>Ceratophysella sigillata</i>	Pfander and Zettel (2004)
	Hypogastruridae	<i>Hypogastrura pannosa</i>	Purrington et al. (1991)
	Neanuridae	<i>Neanura muscorum</i>	Messer et al. (1999), Purrington et al. (1991)
	Onychiuridae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

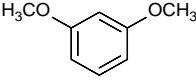
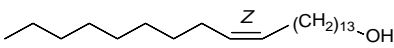
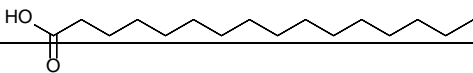
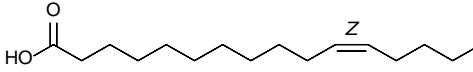
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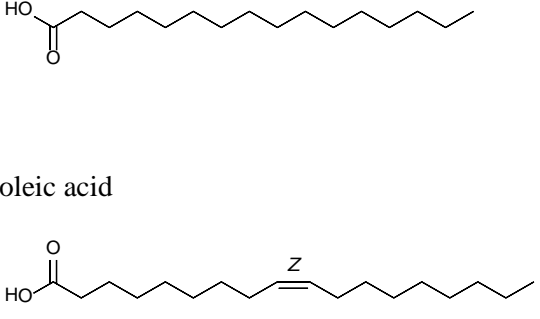
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809 Table 3. Communication molecules in springtails, localization and proposed functions

Collembola species (super-family)	Localization/ Organ	Function	Communication type	Molecule	Class of Molecule	Reference
<i>Tetradotonphora bielensis</i> (Onychiuridae)	Pseudocells	Defense	Repulsive allomones	2,3-dimethoxy-pyrido[2,3-b]pyrazine 	Pyridopyrazine alkaloids	Dettner et al. (1996)
				2-methoxy-4 <i>H</i> -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) 		

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

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

				 <p>oleic acid</p>		
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*Repellent and attractant effects of linoleic and palmitic acid, respectively have been demonstrated only against *Protaphorura armata*

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