

# A novel set of traits to describe Collembola mouthparts: taking a bite out of the broad chewing mandible classification

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## ABSTRACT

The use of functional traits in arthropod ecology has gained in popularity and could be a valuable tool to predict consumer-resource interactions among soil invertebrates. Currently, Collembola feeding strategies are categorized very broadly with either piercing-sucking or chewing mouthparts, despite the diversity of resources they consume. This study described and measured a new set of Collembola mandibular traits in order to better discriminate chewing species based on their mouthpart morphology. Then, we evaluated whether these consumer traits covaried with various litter quality resource traits (physical, chemical or microbial). Out of our 50 studied species, 42 clustered significantly in seven new chewing mandible functional groups. Neither body length, nor phylogeny, were adequate proxies for this set of mandibular traits given tremendous variation across closely related species. Furthermore, when covariation with litter traits occurred, Collembola mandibular traits explained just as much covariation as species composition. These novel traits describing Collembola mouthparts could be a promising venue for predicting feeding interactions of Collembola and their resources.

## 1. Introduction

Soils are a major hub of biological diversity that contribute to the functioning of terrestrial ecosystems through determinant processes such as litter decomposition and nutrient cycling (Bardgett and van der Putten, 2014; Handa et al., 2014). However, such functions are often simplified as a “black box”, despite the underlying complex interactions among soil biota and their abiotic environment. Soil food webs remain poorly understood and improving our understanding of interactions has been identified as a top research priority (Eisenhauer et al., 2017). Major knowledge gaps result in part from a remarkably poor description of soil biodiversity (e.g. an estimated 17% of Collembola species are described worldwide; Orgiazzi et al., 2016), as well as a tendency for community ecologists to neglect multi-trophic studies (Seibold et al., 2018). Interactions among soil organisms are often challenging to observe given their small size, extreme diversity and opaque soil habitat. Common methods used to determine soil invertebrate diets (e.g. gut content and stable isotope analyses) have provided important advances in documenting interactions across trophic levels (Chahartaghi et al., 2005; Maraun et al., 2011; Pollierer et al., 2009; Potapov et al., 2019; Scheu, 2002), but have not revealed clear mechanisms driving

consumer-resource interactions. It is imperative to understand such mechanisms in order to better understand and predict relationships between soil diversity, ecosystem stability and ecosystem functioning (Seibold et al., 2018).

The functional trait-based approach could accelerate the development of better predictive tools for soil trophic networks as results observed for a given species can be generalized to other species once mechanisms associated to selected traits are understood (Brousseau et al., 2018a). This capacity for generalization is more limited when documenting trophic interactions from a purely taxonomic perspective. The first condition of the trait-based approach suggests that the trophic interaction is the result of a match between traits of interacting species (Bartomeus et al., 2016; Gravel et al., 2016). Therefore, a species' diet is constrained by its own feeding traits, which include morphological and behavioral characteristics (Moretti et al., 2017), as well as the traits of its resource (Bartomeus et al., 2016; Gravel et al., 2016). For example, ground beetles need to bear mouthparts that are strong enough to bite through the cuticle of their prey (Brousseau et al., 2018b). The second condition is that consumer and resource species need to co-occur in space and time in order for trait-matching to be realized (Bartomeus et al., 2016; Gravel et al., 2016). For this reason, extrapolation of

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laboratory feeding experiments to *in situ* scenarios is tricky, as species might not encounter each other in natural environments despite having matching traits. Based on these two principles, abundant species in a given locality will more likely encounter each other than rare species, and thus have more possibilities to interact if their traits allow for it (Bartomeus et al., 2016). Therefore, studying co-occurrence of consumer and resource traits (covariation of trait values weighted by the abundance) is a useful first step towards understanding potential mechanisms driving community assembly (Gravel et al., 2018). Recent work has demonstrated that the traits of interacting trophic levels (litter-detritivore, prey-predator, plant-herbivore) covary in space, such as leaf litter toughness and detritivore biting force, suggesting the potential for trophic interactions to occur, even if not directly observed (Brousseau et al., 2019; Le Provost et al., 2017). However, if feeding traits are too broadly or finely described to really influence a trophic niche (e.g. fine structure of Diplopoda mandibles; Semenyuk et al., 2011), they might not match with resource traits and be irrelevant for studying trait covariation between consumers and their resources.

Collembola, ubiquitous hexapods across the planet with an estimated abundance up to 40 000 individuals per m<sup>2</sup> in terrestrial habitats (Orgiazzi et al., 2016), are a good case in point of such mismatch between the documented feeding traits and the actual trophic niche. Traditionally considered as fungivorous feeders, their diet has proven to be much more diverse (Hopkin, 1997; Ponge, 2000; Potapov et al., 2016; Rusek, 1998) and more context-dependent than previously thought (Endlweber et al., 2009; Gillet and Ponge, 2003; Filser, 2002). Regarding potential resource use, Potapov et al. (2016) used stable isotope composition of 82 Collembola species from temperate forest ecosystems to show how trophic niches can differ considerably. Their work suggests that some species feed selectively on microbes that colonize leaf litter, while others consume leaf litter with its microbes or resources that are non-litter related such as animals, mycorrhizal fungi and roots (Potapov et al., 2016). This evidence is concurrent with the diversity of Collembola feeding habits on leaf litter suggested by Rusek (1998); shredding, skeletonizing leaves in between veins and consuming partly degraded pieces. However, the two mouthpart types currently recognized for Collembola, i.e. “chewing” mouthparts with a molar plate and “piercing-sucking” a.k.a “scratching-piercing” mouthparts without a molar plate, poorly explain this diversity of diets observed across and within taxonomic families (Malcicka et al., 2017; Potapov et al., 2016). In fact, the majority of Collembola families are considered to bear chewing mouthparts (79% of known species; Bellinger et al. 1996–2019), while other families have either no mandibles (Brachystomellidae) or piercing-sucking mouthparts (Neauridae and Odontellidae; Hopkin, 1997). Not only this classification poorly discriminates species, but numerous diets are common to both mouthpart categories (e.g. detritivore, fungivore, predator; Fiera, 2014; Hoskins et al., 2015; Malcicka et al., 2017; Potapov et al., 2016; Rusek, 1998), suggesting that mouthpart morphology is too broadly described to be related to the consumed resource traits. As the mechanisms allowing and constraining resource consumption by Collembola species are not fully understood, it remains uncertain whether their diet is only determined by behavioral traits (e.g. feeding strategies suggested by Potapov et al., 2016) or also by mouthpart morphology such as demonstrated for ground beetles and mites (Brousseau et al., 2018b; Perdomo et al., 2012).

Surprisingly, beyond the two classic feeding groups, attempts to better understand functionality of Collembola mouthpart morphology remain rare (Adams and Salmon, 1972; Chen et al., 1997; Christian, 1989; Goto, 1972; Manton, 1964; Santorufu et al., 2014; Wetton, 1988). This is likely because of their entognathous character, i.e. mouthparts located inside the head capsule. Even more startling is that maxillae are generally much more detailed in the literature than mandibles (Fjellberg, 1998, 2007; Malcicka et al., 2017), despite being harder to observe on a microscope, especially on chewing species. As a result, the taxonomic potential of mandibles for Collembola is often overlooked (Wetton, 1988). Although Goto (1972) concluded that mandibles were

unlikely to be a useful trait for *Folsomia* species recognition, Wetton (1988) demonstrated, in contrast, that mandibular apical morphology varied greatly among *Folsomia* species, differentiated taxonomically otherwise only by a setal character. This suggests that developing new mandibular traits could be key to overcome this mismatch between the trophic niche and the feeding traits of Collembola species. Yet, different mandibles within a taxonomic family could still be more similar than across families. To date, it is unknown if detailed mandibular morphology has been conserved through evolution of the clade. Malcicka et al. (2017) demonstrated no phylogenetic signal for the shape of Collembola maxillae (length/width ratio) suggesting that even close species can have different mouthparts. Determining the correlation between species' mandibular traits and other characteristics commonly used to infer trophic position (such as taxonomic identity and body size) is essential to assess the usefulness of working with mandibular traits. If no correlations are found, detailed study of mandibles (as for beetles; Brousseau et al., 2018b; Wheeler and Evans, 1989) could bring novel insight on consumer-resource relations and allow us to better infer Collembola species trophic position in the soil network.

Our aim with this study was to use a new set of mandibular functional traits to redefine the broad Collembola chewing mouthpart category and to explore the relevance of these traits to better predict trophic interactions based on mouthpart morphology. Based on 50 species of litter or soil-dwelling forest Collembola, we propose a measurement protocol for seven morphological traits and hypothesized related functions (Table 1). These mandibular traits were either scarcely mentioned in the literature (mandible length, mouth opening), newly associated to Collembola (mechanical advantage, mandible/head ratio), revisited (molar plate length) or newly developed (deployment capacity, apical development). First, we verified whether measuring these traits was a worthwhile investment by determining if they were correlated to body length and phylogenetic position. Then, we assessed if the traits could allow us to better discriminate chewing species by grouping them in new functional groups based on detailed mandibular morphology. Finally, we explored the potential of using these traits rather than old mouthpart categories to better understand the mechanisms implied in Collembola trophic interactions. To do so, we determined if there was a spatial covariation between traits of Collembola chewing consumers and of a potential direct or indirect resource, leaf litter.

## 2. Material and methods

### 2.1. Sampling sites

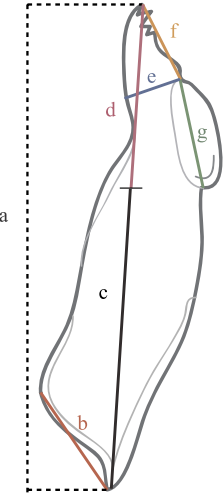
Litter and Collembola were sampled in two sites from the International Diversity Experiment Network with Trees (IDENT), a network of Biodiversity – Ecosystem Function experiments: one near Auclair, Québec, Canada (47.7° N, 68.6° W) and the other in Cloquet, Minnesota, USA (46.7° N, 92.5° W; Tobner et al., 2014). Twelve single-species tree communities of high density (i.e. 49 trees of the same species in 10 m<sup>2</sup>), each replicated four times in each site, were sampled for a total of 96 plots: *Acer saccharum*, *A. platanoides*, *Betula papyrifera*, *B. pendula*, *Larix decidua*, *L. laricina*, *Quercus robur*, *Q. rubra*, *Picea abies*, *P. glauca*, *Pinus strobus* and *P. sylvestris*. We presumed that the dominant litter resource in single-species tree communities can be reasonably expected to be derived from the tree species composing the community.

### 2.2. Leaf litter sampling

In 2015, senescent leaves were shaken from at least twenty trees per species that were randomly selected in each site. This was realized in October for the deciduous species (*Acer*, *Betula*, *Larix* and *Quercus*) and throughout the field season in June, July and August for the coniferous evergreen species (*Picea* and *Pinus* species). All leaves per tree species were then pooled together by site and mixed homogeneously before trait measurement. Senescent leaves were favored over leaf litter of unknown

**Table 1**

Details on Collembola mandibular trait measurements and hypothesized functions associated to each trait.

Schematic illustration	Trait	Measurement	Hypothesized function	References
	Mandible length	= a	Related to mechanical advantage, deployment capacity, size and type of ingested particles.	Chen et al., 1997
	Mandible/Head ratio	= a/head length		Perdomo et al., 2012 (mites)
	Mechanical advantage	= b/a	If low, mandibles make short and fast movements (e.g. predator) but if high, mandibles make big and slow movements (e.g. litter consumers). Could also be a proxy for mandibular strength.	Perdomo et al., 2012 (mites)
	Deployment capacity	= d/c	If high, bigger portion of the mandible can be protruded from the head capsule to collect resources (e.g. scraping scavengers). Also, the higher it is, the more the mandibles are conceived to transform their food (cut, grind, tear, etc.), and therefore should be adapted to eat more recalcitrant resources. Could be also related to scraping (if high) or cutting movement (if low).	Wheater and Evans, 1989 (beetles) No reference
	Mouth opening	= labrum width – 2* (e)	Determines the size of the particles that can be manipulated and ingested.	Chen et al., 1997
	Apical development	= f/g, then classed in categories; 1 – < 0.75 2 – [0.75–0.95] 3 – [0.95–1.05] 4 – [1.05–1.25] 5 – > 1.25	If high (4–5) to cutting, grinding or scraping mouthparts. If low (1–2), rather related to consumption of fungi.	Chen et al., 1997 Christian, 1989 Goto, 1972
	Molar plate length	= g	Associated with consumption of fungi (brushing of hyphae), but probably not to grinding or chewing activity.	Chen et al., 1997 Hopkin, 1997 Goto, 1972
a) Mandible length b) Mandible width c) Proximal portion length d) Distal portion length e) Distal portion width f) Toothed region length g) Molar plate length				

age from the soil surface to standardize trait measurements at the same decomposition stage. Despite being less representative of the actual resource available on the soil surface as litter traits change inevitably as leaves decompose, characterizing initial litter quality is indicative of its subsequent quality for consumers (e.g. microbial communities; Bray et al., 2012). Additionally, decomposed litter was manually collected directly on the forest floor at five random positions per plot during Collembola sampling and air-dried until homogeneous humidification for MicroResp analyses (Campbell et al., 2003).

### 2.3. Collembola sampling

Collembola were sampled in late July (Auclair) and early August (Cloquet) 2015 in each plot. For each plot, two subsamples were randomly collected at its center to minimize any edge effect. For each subsample, litter was collected manually in a 15 × 15 cm quadrat. Then, at the center of the quadrats, soil was extracted with a split core soil sampler (diameter 5.08 cm x depth 5 cm). Both the litter and the superficial layer of the soil were sampled in order to capture Collembola potentially interacting with the litter layer. Litter and soil were transferred in hermetic containers and kept at 4 °C for transport to the laboratory within 48 h. Litter and soil subsamples were pooled prior to Tullgren (Auclair) and Kempson (Cloquet) extraction during which the temperature was gradually increased during 7 days (20 °C to 50 °C). Fauna was collected in 70% ethanol. Kempson extraction differs slightly from Tullgren's by having a cooling system to keep the lower surface of the sample moist while heating the upper surface (Edwards, 1991). Collembola were cleared in lactic acid at 60 °C to better see identification criteria and mandibular structures. Identification to the species level was done using the key of Christiansen and Bellinger (1998) and the taxonomy updated according to the recent version of Bellinger et al. (1996–2018). Cleared specimens were all slide-mounted in Hoyer's medium (50 ml distilled water – 30 g gum arabic – 200 g chloral hydrate – 20 ml glycerol). A few damaged specimens were identified only to the family or genus level (<3% of total Collembola abundance) and therefore excluded from further analyses.

### 2.4. Justification of trait selection and measurement of litter and collembola traits

Collembola and litter traits were chosen to explore possible feeding interactions between these two trophic levels. In general, we reasoned that the more mandibular structures were developed (e.g. apical toothed region, mouth opening, size of mandible, size of molar plate), the more species should be able to consume recalcitrant resources, thus should be more abundant in recalcitrant single-species tree communities than species with weakly developed mandibles (Table 1). Diverse traits were selected to characterize litter resource quality, including one biological trait (microbial basal respiration), three physical traits (thickness, resistance and water saturation capacity) and six chemical traits (C/N, lignin/N, N, lignin, hemicellulose, cellulose) that were each measured on the 12 studied tree litter species. For all litter traits, mean values were determined for each species per site. Litter trait measurements are described in detail in Raymond-Léonard et al. (2018).

For mandibular traits, a morphometric approach was chosen to discriminate species and to understand the potential function of different structures (Table 1). Once Collembola were mounted, we measured traits with Leica LAS live measurement software (to the nearest nm) on a Leica DM1000 LED phase contrast microscope with a maximum magnification of 800x and equipped with a Leica ICC50 W camera. *Heteromurus nitidus* was excluded from the analyses because sampled individuals were damaged, making the mandibles difficult to observe. Resulting richness of chewing Collembola species for which mandibular traits were measured included 50 species: 28 species at the Cloquet site (n = 554) and 33 species at the Auclair site (n = 947), with 11 species common to both sites. For each Collembola species per site, the seven mandibular traits described in Table 1 were measured on at least six individuals along with body length (from the end of the abdomen to the top of the head, appendices excluded). For rare species, the number of individuals was as high as possible (Appendix S1). In total, 2079 trait measurements were taken among 308 individuals. A mean trait value was then calculated for each trait per species (see Appendix S1 for associated variances). Only well-mounted specimens in

dorsal position were considered to avoid biases due to mandible position on the slide. Given the unknown extent of Collembola intraspecific mandibular trait variation, measurements were done strictly on left mandibles of female adults to avoid potential sexual, life stage (Chen et al., 1997) and mandibular side dimorphism (Goto, 1972). However, as sex was difficult to confirm on some Entomobryidae (genital plate hidden by furcula), we may have taken measurements on males or juveniles in this family. In order to compensate for this possible bias, more replicates were measured ( $n \geq 10$ ; Appendix S1) and marginally small individuals were not considered. As the collected Symphypleona in the samples were mostly juveniles in very low abundance, traits were measured on all possible individuals irrespective of their sex and life stage. Further detail on mandibular trait measurements is provided in Appendix S2.

## 2.5. Statistical analyses

Correlations between mean mandibular traits of Collembola species and body length as well as phylogenetic signal were measured to assess if these characteristics could be used to infer mandibular morphology. Non-parametric Spearman rank correlations between body length and mandibular traits were used as mean trait data for Collembola species were not normally distributed for 4 out of the 7 traits (Shapiro-Wilk test;  $P < 0.0001$ ). Three complementary indices were computed to determine the strength of the phylogenetic signal for each trait (Blomberg's K, Pagel's  $\lambda$  and Abouheif's  $C_{\text{mean}}$ ), which refers to the tendency of related species to have more similar traits than randomly picked species (Münkemüller et al., 2012). Significance of results was tested respectively with a randomization test, likelihood ratio test (null hypothesis  $\lambda = 0$ ) and Monte Carlo simulation (for all indices, randomization = 9999; Münkemüller et al., 2012). Topology of the phylogeny was determined with a species distance matrix based on taxonomy for which each taxonomic level was given the same weight (order, superfamily, family, subfamily, tribe, genus and species; Appendix S3).

Cluster analysis was performed to identify potential mandible functional groups based on mandibular traits. Clustering was done with Ward's method on standardized mandibular trait Euclidean distance (Legendre and Legendre, 2012). Clustering significance was assessed with approximately unbiased p-value via multiscale bootstrap resampling (bootstrap = 9999; Suzuki and Shimodaira, 2006). For the species grouped in significant trait clusters ( $n = 42$ ), mandibular trait variation was visualized with principal component analysis ordinations (PCA) after trait data standardization (Legendre and Legendre, 2012) in order to determine which traits are characterizing clustered groups. In order to explore how correcting body length variation would have affected species mandible discrimination, PCA was also done using body length ratios instead of absolute values of body length-related traits. Similarity between species mandibular trait and species phylogeny was assessed by cluster comparison with Adjusted Rand Index (ARI; Hubert and Arabie, 1985). Additionally, five samples for which Collembola total abundance equaled zero were also excluded.

Procrustes analyses were subsequently performed to quantify the association of standardized litter traits with Collembola communities (Peres-Neto and Jackson, 2001). We considered three different data tables to represent communities: species, feeding traits and chewing mandible functional groups identified in clustering analysis. Collembola species and mandibular group abundances were Hellinger transformed for the species and group matrices (Legendre and Legendre, 2012). A community weighted mean (CWM) for each trait was calculated for the trait matrix (Lavorel et al., 2008). Five plots for which total Collembola abundance equaled zero were excluded from procrustes analyses.

All statistical analyses were performed with R (R Core Team, 2017) and RStudio environment (RStudio Team, 2016). Vegan package functions v. 2.4-0 (Oksanen et al., 2016) were used for various procedures including Hellinger transformation (decostand/vegdist), trait standardization (decostand), PCAs (rda), cluster (hclust) and procrustes analyses

(protest). FD package v. 1.0–12 (Laliberté et al., 2015) was used to compute CWM matrices (dbFD). Clustering uncertainty was tested with the pvclust package v. 2.0-0 (Suzuki and Shimodaira, 2015). The phylogenetic distance matrix was transformed as a “phylo” object (as.phylo) with the ape package v. 5.0 (Paradis et al., 2017). The phytools package v. 0.6–44 (Revell, 2017) was used to compute and test Pagel's  $\lambda$  and Blomberg's K (phylosig) and the adephylo package v. 1.1–11 (Jombart et al., 2017) was used to compute a “phylo4d” object for Abouheif's Cmean analyses with the phylobase package v. 0.8.4 (Hackathon et al. 2017; abouheif.moran). ARI was determined with the “fossil” package v. 0.3.7 (adj.rand.index/rclust; Vavrek, 2015).

## 3. Results

### 3.1. Relationship of mandibular traits with body length and phylogeny

Mean mandibular trait values and associated standard deviation for each Collembola species per site are shown in Appendix S1. Three out of seven mandibular traits (mandible length, molar plate length and mouth opening) correlated significantly with body length (Spearman's  $r = 0.7$  to  $0.8$ ; Table 2) indicating that the bigger the chewing species, the bigger the mouthparts. Depending on the indices, weak or no phylogenetic signal was detected for mandible/head ratio, molar plate length and mouth opening (Table 2). In contrast, a stronger phylogenetic signal was consistently detected across indices for apical development, deployment capacity and mechanical advantage, suggesting that the variance for these traits is more similar between closely related species than for the other traits (Table 2). Results using the three different indices were coherent, except for mandible length which showed a strong Pagel's  $\lambda$  ( $> 0.9$ ) in contrast to a null Blomberg's K (no signal) and weak Abouheif's  $C_{\text{mean}}$  (0.15), despite the latter being more likely to detect a signal for other traits (Table 2). It is noteworthy that the observed trait correlations with body length were not mirrored by phylogenetic signals and vice versa (e.g. apical development, molar plate length and mechanical advantage).

### 3.2. Clustered chewing mandible functional groups and the traits describing them

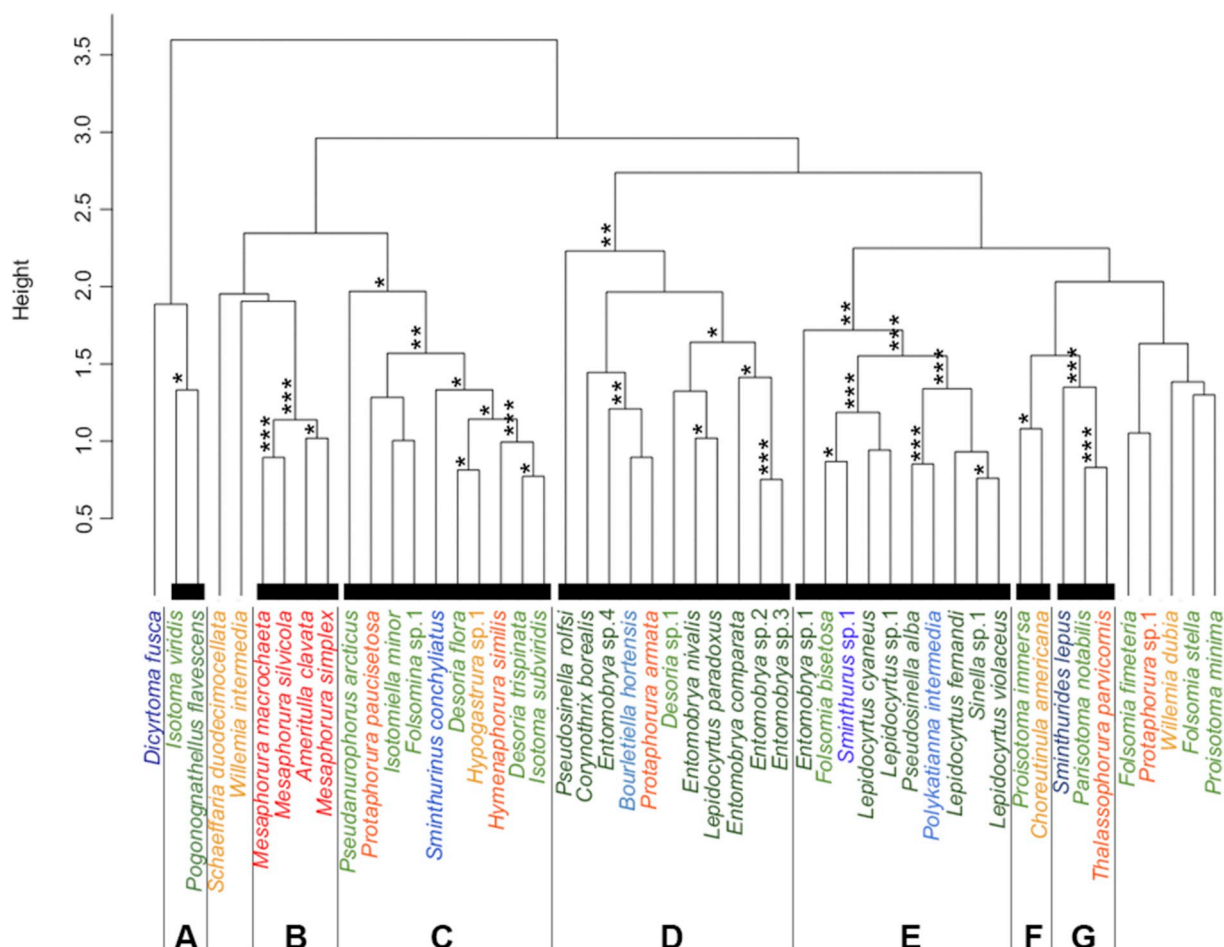
Based on mandibular traits, most of the species (42/50) were clustered within seven distinct groups (Fig. 1). Despite the observed phylogenetic signal for some traits (Table 2), variation of all mandible traits among genera and families was generally substantial, particularly for Isotomidae which were represented in 86% of the significant clusters

**Table 2**

Correlation of body length and phylogenetic position with mandibular traits for 50 chewing Collembola species from Auclair and Cloquet. For each mandibular trait, Spearman rank correlations with body length ( $r_s$ ) and three indices of phylogenetic signal (Blomberg's K, Pagel's  $\lambda$ , Abouheif's  $C_{\text{mean}}$ ) were assessed. Significance levels (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , ns = not significant) in parentheses were determined after 9999 simulations.

Mandibular trait	Body length	Phylogeny		
	$r_s$	K	$\lambda$	Abouheif's $C_{\text{mean}}$
Apical development	−0.10 (ns)	0.50 (**)	1.00 (***)	0.29 (***)
Deployment capacity	−0.08 (ns)	0.40 (*)	0.40 (*)	0.31 (***)
Mandible length	0.81 (***)	0.35 (ns)	0.94 (*)	0.15 (***)
Mechanical advantage	0.20 (ns)	0.54 (***)	0.47 (**)	0.31 (***)
Mandible/head ratio	0.06 (ns)	0.31 (ns)	0.20 (ns)	0.13 (***)
Molar plate length	0.79 (***)	0.34 (ns)	0.91 (ns)	0.15 (ns)
Mouth opening	0.70 (***)	0.30 (ns)	0.33 (ns)	0.09 (***)





**Fig. 1.** Clustering of 50 chewing species from Auclair and Cloquet sites according to the seven standardized mandibular traits (Ward's method, Euclidean distance) and colored by family. Blues, greens and warm colours show the Symphypleona, Entomobryomorpha and Poduromorpha respectively. Significant clusters (black rectangles and letters) were determined by multiscale bootstrap resampling (bootstrap = 9999). Approximately unbiased p-value: \* $p < 0.05$  \*\* $p < 0.01$  \*\*\* $p < 0.001$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

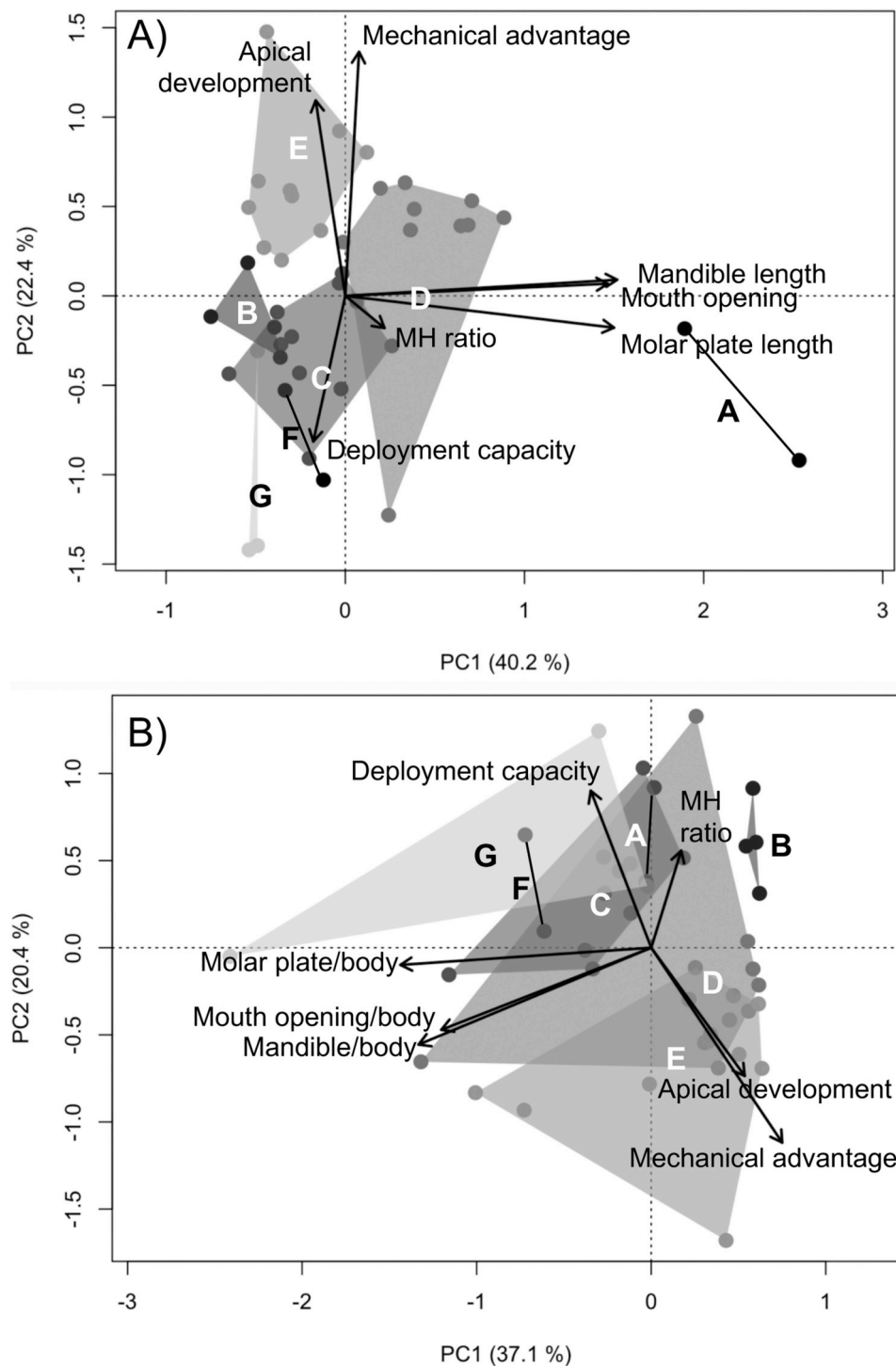
(light green in Fig. 1). Only Tullbergiidae (*Mesaphorura* and *Ameritulla*) species were all grouped together (red in Fig. 1). In short, phylogeny was a poor proxy for mandibular traits; taxonomically close species often showed dissimilar mandibles and distant species showed similar mandibles (Fig. 1). This result is concordant with the near zero ARI value (0.03) that suggests independence of clustering between trait and phylogenetic matrices. Collembola species within the seven clustered groups (Fig. 1) were well defined by their functional traits: the first two PCA axes explained 63% of the variation in Collembola mandibular trait scores (Fig. 2a). Body length-correlated mandibular traits (i.e. mouth opening, mandible length and molar plate length; Table 2) explained most variation of the first axis (40.2%) and were positively correlated with each other (Fig. 2a). Based on that, the observed mandibular groups could be put in three categories along a body size gradient: very large (A), large to intermediate (D) and intermediate to small (B, C, E, F, G; Fig. 2a). Variation on the second axis (22.4%) was rather explained by apical development, deployment capacity and mechanical advantage (Fig. 2a). Deployment capacity was inversely correlated with mechanical advantage and apical development (Fig. 2a), suggesting that mandibles able to protrude further out of the head capsule are not only having a more developed toothed region but could potentially make smaller and faster movements than mandibles with limited deployment capacity (e.g. group B; Fig. 2a). When converting body length-related traits (Table 2) in body length ratios, the same correlations were observed between mandibular traits but the first axis (37.1%) explained differently variation among species, resulting in mandibular groups

being differently distributed in space (Fig. 2b). For example, conversion to ratios allowed to better discriminate group B and G on the first axis (Fig. 2b), despite being similar in body size (Fig. 2a).

### 3.3. Litter as a potential resource for collembola consumers

Leaf litter from deciduous tree species (*Acer*, *Betula* and *Quercus* species) was characterized by labile characteristics such as high basal respiration, water saturation capacity, N and hemicellulose concentrations (Appendix S4; Raymond-Léonard et al., 2018). In contrast, litter from coniferous evergreen species (*Picea* and *Pinus* species) was rather recalcitrant and described by high foliar resistance, thickness, lignin and cellulose concentrations, lignin/N and C/N ratios (Appendix S4; Raymond-Léonard et al., 2018). However, litter from *Larix* species, which are both coniferous and deciduous, was characterized by intermediate trait values (Appendix S4; Raymond-Léonard et al., 2018). Mean litter trait values and associated standard deviation and total Collembola richness and abundance for each litter species per site are shown in Appendix S4.

Procrustes analyses demonstrated a significant trait-trait correlation at Cloquet (0.36), but not Auclair (Table 3). Furthermore, we found that all approaches (Collembola taxonomy, functional traits and functional groups) gave similar results with comparable correlations with litter traits (Table 3) with no correlation at Auclair and a consistent 0.4 correlation in Cloquet (Table 3). Fig. 3 illustrates in detail the significant litter trait – mandibular trait and chewing mandible functional group



**Fig. 2.** In a), principal component analysis (PCA) ordination of Collembola mandibular traits arranged by the seven mandibular groups identified through clustering analysis (42 species from Auclair and Cloquet). In b), body length-related traits were transformed in body length ratios. Letters position represents weighted group centroid. Data were standardized before analyses.

correlations observed at Cloquet. Traits correlated to body length (Table 1) and mechanical advantage were associated with chemically recalcitrant litters but molar plate length was more strongly associated with water saturation capacity (Fig. 3a). Apical development was rather correlated to physical recalcitrance (Fig. 3a). Deployment capacity along with mandible/head ratio correlated with labile litters (Fig. 3a). Mandibular functional groups (A to G; Figs. 1 and 2) also covaried with litter resource traits: A was correlated to both physical recalcitrance (resistance) and chemical palatability (N) with high microbial activity, B

and G to chemical palatability (N, hemicellulose) with high microbial activity, C to physical recalcitrance (resistance) with high microbial activity, D to chemical recalcitrance (C/N, lignin/N), E to both physical and chemical recalcitrance (lignin, cellulose, thickness) and F to physical palatability (water saturation capacity).

**Table 3**

Procrustes correlation analysis between litter traits and Collembola community composition (species, traits and mandibular groups) for each site. Only Collembola species clustered in the seven mandibular groups were considered in this analysis (28 for Auclair and 24 for Cloquet). Here “species” refers to Hellinger-transformed species abundances, “traits” to CWMs matrix of the seven mandibular traits and “mandibular groups” to Hellinger-transformed group abundances. \*\*\*P < 0.001, \*\*P < 0.01, \*P < 0.05, ns not significant.

Site	Species	Traits	Mandibular groups
Auclair	0.31 (ns)	0.29 (ns)	0.29 (ns)
Cloquet	0.39 (**)	0.36 (**)	0.41 (***)

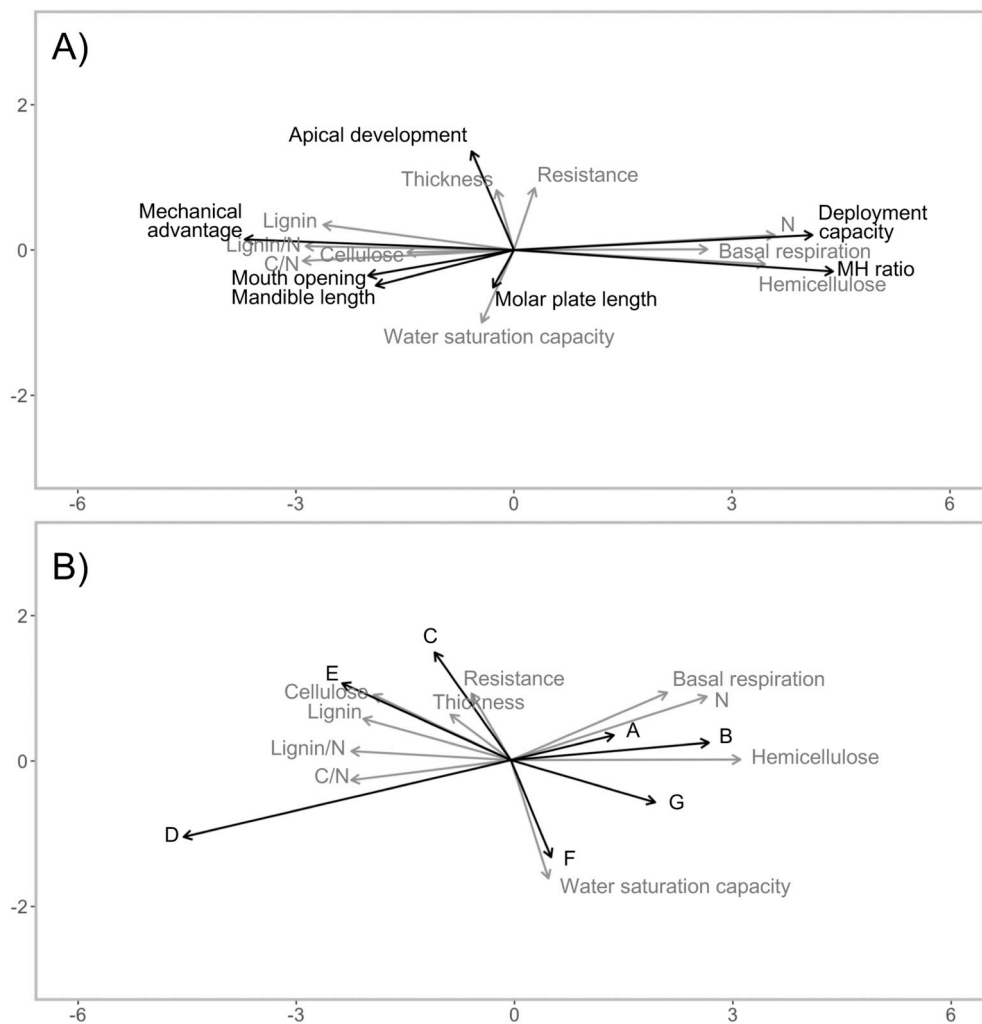
Sum of squares values → Species-CI = 0.85/Traits-CI = 0.87/Groups-CI = 0.83/  
Species-Au = 0.90/Traits Au = 0.92/Groups-Au = 0.92.

#### 4. Discussion

##### 4.1. Can we infer the set of mandibular traits from other characteristics such as body length and phylogeny?

Concordant with [Chen et al. \(1997\)](#), our results demonstrate that mouth opening and mandible length are correlated to body length based on 50 chewing species. Moreover, we bring new evidence that molar plate length also correlates with body length. While this evidence suggests that these three mandibular traits could be inferred by body length

itself, it remains challenging to associate body length with mandibular functionality. On one hand, it can be assumed that species with larger mouthparts can consume larger food particles ([Chen et al., 1997](#)). However, mandibular groups characterized by similar body lengths e.g. C and F are associated with different litter resources. Therefore, focusing only on body length-related traits could lead to a wrong prediction of a species diet and/or oversimplify mandible functionality to mouthpart size. As for phylogeny, while it was associated with some trait variation (i.e. mechanical advantage, apical development), mandibular traits had a weak phylogenetic signal overall. In line with [Malczicka et al. \(2017\)](#) who demonstrated no phylogenetic signal for Collembola maxillae length to width ratio, mandibular morphology can vary greatly between taxonomically close species within a genus (e.g. *Desoria*, *Isotoma*, *Folsomia* and *Protaphorura*) as observed by [Wetton \(1988\)](#) on *Folsomia* (through apical morphometry). It was previously suggested that family affiliation can be useful to roughly estimate species trophic niche, but variation of diets within a given family can still be extensive, e.g. Onychiuridae, making it challenging to predict trophic interactions that are shaping soil networks ([Potapov et al., 2016](#)). Our results suggest that mandibular morphology variation within families could be key to explain this diet variation between close species. Interestingly, mandibular traits correlated differently with body length and phylogeny. This finding highlights the risk of using one of those two characteristics to infer Collembola mandibular global morphology (i.e. set of



**Fig. 3.** Procrustes correlation of Collembola mandibular (a) traits and (b) groups (black) with litter traits (grey) of Cloquet communities (9999 permutations, correlation = 0.4,  $p < 0.05$ ). All traits values were standardized. In (a), CWMs were calculated for mandibular traits and MH ratio is the Mandible/Head ratio. In (b), mandibular group abundances were Hellinger-transformed.

traits) as it can hardly describe all traits, misleading our interpretation of mandibular mechanisms and their subsequent functional implications.

#### 4.2. Is it possible to discriminate collembola chewing species based on these mandibular traits?

More than 80% of the studied species clustered significantly within seven more refined groups (A to G) based on their mandibular traits. This result highlights that it is indeed possible to go beyond the chewing/piercing-sucking mouthpart dichotomy using a quantitative functional approach, i.e. measurements of mandibular characteristics rather than presence/absence of structures. Observing such clustering on a small number of species and on closely related species suggests that mandibular traits could be useful to discriminate mouthparts of chewing Collembola species worldwide. Still, determining new mouthpart categories based on these traits could be tricky as the choice of traits influence species grouping such as demonstrated here (e.g. ratios vs absolute values for body length-related traits). As such, our clustering of 42 species in groups A to G should be used with caution in further studies. We encourage the use of multiple traits rather than groups to describe Collembola species. Further steps will also be necessary to verify the extent of intra-specific variation (e.g. > 50 individuals by species as proposed by Griffiths et al., 2016) to confirm that we can discriminate species based on mandibular traits. For example, comparing trait values within species (instead of mean values across species) could help to determine if there are different mandibular morphologies, and thus ecological functions, among development stages, sexes (beyond body length-induced variation) and environmental contexts (trait plasticity).

#### 4.3. Could collembola trophic interactions be potentially inferred by such mandibular traits?

While exciting, such new mandibular groups are only useful to understand Collembola trophic interactions if correlated with the consumed resources (trait-matching and co-occurrence). As a first step, we demonstrated that when leaf litter traits covaried with taxonomic composition of Collembola communities, they equally covaried with the seven mandibular groups suggesting that the observed correlations are associated with resource availability rather than habitat preference. Litter traits could influence microhabitat properties for Collembola (litter and humus layers; Trap et al., 2013) and consequently Collembola community composition (Cassagne et al., 2003). However, observed correlation of mandibular traits with litter traits emphasizes that these consumer traits could indeed respond directly to resource quality (Brousseau et al., 2019). We acknowledge that our observations imply only co-occurrence, and thus, only the possibility of interaction and not an actual interaction. For example, the covariation of eudaphic Collembola species (e.g. living in deeper soil layers) with leaf litter traits might indicate an association with other resources than litter itself such as typical microbial or prey communities. Nonetheless, one can still assume that from a bottom-up perspective, a resource will be more likely consumed by its potential consumers (i.e. covarying in time and space). In this sense, the observed correlation of 0.4 at Cloquet is rather high considering that we did not select exclusively litter consumers, nor consider other filters often shaping communities that include both trophic or non-trophic biotic interactions and environmental abiotic conditions (Brousseau et al., 2018a).

The presence of a relationship between Collembola and litter at the Cloquet but not at the Auclair site likely reflects different use of resources between sites. Indeed, omnivorous Collembola can switch diet depending on the environmental context such as soil moisture, resource availability and soil contamination (Endlweber et al., 2009; Filser, 2002; Gillet and Ponge, 2003). Moist soil conditions at Auclair might have strengthened the influence of belowground resources in contrast to Cloquet (Raymond-Léonard et al., 2018). We recognize that a set of mandibular traits should allow a species to consume a given range of

resources. In short, the mandibular traits associated to litter traits in this study could be associated to other resource traits such as root traits, given that Collembola diet could be more root-than litter-driven in favorable conditions (Pollierer et al., 2009; Endlweber et al., 2009). Knowing how diet depends on the environmental context and to which resources a set of mandibular traits is associated will be key to predict Collembola trophic interactions.

#### 4.4. Can we deepen our understanding of collembola feeding mechanisms based on our results?

Arguably, mandibular traits that correlate with each other, but also with the same resource are probably involved in the same feeding mechanisms. Four such examples emerge from our study. First, deployment capacity and mandible/head ratio strongly covaried with chemically labile litters that had a high microbial activity. As bacteria are considered to consume only labile C contrary to fungi (de Vries and Caruso, 2016), we could presume that these traits are associated with bacterial consumption by “scraping” (induced by longer amplitude of movement). Such a strategy could represent a more efficient method to forage bacteria than cutting, as bacteria probably need less transformation before ingestion than fungi. Secondly, body length-related traits might constrain the size of the consumed resource: observing larger species with bigger mouthparts in chemically recalcitrant litters and smaller species in labile litters might tip us off on potentially dominant microbial resources available as their diet could be respectively fungi- and bacteria-centered given their body size (Chen et al., 1997). Thirdly, the covariation of mechanical advantage with recalcitrant litters might indicate that it is related to mandibular strength such as for ground beetles (Wheater and Evans, 1989) thus consumption of the recalcitrant litter itself (Brousseau et al., 2018b; Ibanez et al., 2013; Le Provost et al., 2017; Perdomo et al., 2012). Finally, apical development was likely implied in other feeding mechanisms as it was related to physical traits. In chewing species, the distal portion of the mandible consists of the molar plate and the apical teeth, the latter being likely useful in food transformation before ingestion (e.g. recalcitrant and/or complex resources; Goto, 1972; Chen et al., 1997). Our results showed that apical teeth development correlated with physical recalcitrance, while a more-developed molar plate was related to litters with high water saturation capacity. One interpretation is that Collembola having more developed teeth than the molar plate may be able to break down litter particles prior to ingestion.

If such generalizations can be made at the trait level, they are harder to apply to the mandibular groups as they are described by multiple traits. For example, the group with the largest species (A) covaried with labile litters which contradicts any generalization on the correlation between body length-related traits and litter recalcitrance. Moreover, some groups covaried differently with litter traits despite having similar mandibular morphology (e.g. C and F), suggesting that other traits (e.g. behavioural) may be relevant in trophic interactions. Inversely, groups with different mandibular morphology covarying with similar litter resources (e.g. C and E) could suggest that they feed on different resources associated with recalcitrant litters (e.g. litter vs microbes). Moreover, trait variation related to body length could also hide species-specific morphological features that are determinant to understand feeding mechanisms. Such variation among species could be corrected by transforming trait values into body length ratios. On the other hand, body size is a determinant factor in trophic interactions (Brousseau et al., 2018b) and should not be completely disregarded to further understand mechanisms inducing such interactions. Depending on the research questions, absolute and/or ratio values could be used for body length-related traits. In order to really understand the mechanisms explaining specific diet, a mandibular multi-trait approach should be combined to other approaches such as enzymatic activity (Berg et al., 2004) and isotopic composition to confirm the diet (Potapov et al., 2016). Such evidence would allow us to better determine which types of



mandibular morphology are more or less constraining for consumption of the different resources.

## 5. Conclusion

The following recommendations for future studies emerge from our new categorization of chewing Collembola species. Firstly, using a complementary subset of four of the seven mandibular traits (mandible length, deployment capacity, apical development and mechanical advantage) will better describe mouthpart functionality, while avoiding trait redundancy. Secondly, our results suggest that Collembola diet not only results from food preference and/or availability, but is likely limited by mouthpart biomechanics. Further efforts will be needed to assess covariation and matching of mandibular traits with a broader range of resource traits (e.g. roots, fungi, bacteria, litter decomposed at different stages) and environmental contexts. Thirdly, intraspecific variation of traits should be assessed on a larger number of individuals per species to confirm that it is less than interspecific variation. Finally, such an approach could also be developed for piercing-sucking species with their distinct mandibular morphology. Our hope is that revisiting mouthpart classification based on functional traits will contribute to demystifying trophic interactions and improve our ability to predict soil food webs.

## Data accessibility

Mean mandibular trait values can be found in S1, but the full dataset is available in the Canadian Repository for Invertebrate Traits and Trait-like Ecological Records (CRITTER). Mean litter trait values and spring-tail abundances used in this study can be found in S4. Species taxonomy used to determine topology of the phylogeny can be found in S3.

## Author's contributions

LJRL and ITH conceived the study, interpreted results and led the writing of the manuscript. LJRL developed the methodology, collected the data and performed analyses. DG contributed through critical review of the manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107608>.

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