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ECOLOGIA E TAXONOMIA DE COLLEMBOLA (ARTHROPODA: HEXAPODA) NO PAMPA BRASILEIRO

CLÉCIO DANILO DIAS DA SILVA

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NATAL, RN, agosto de 2023

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Tese apresentada ao Programa de Pós-Graduação em Sistemática e Evolução da Universidade Federal do Rio Grande do Norte, como parte dos requisitos para obtenção do título de Doutor em Sistemática e Evolução.

Orientador: Dr. Bruno Cavalcante Bellini
Coorientador: Dr. Rudy Camilo Nunes
Coorientadora: Dra. Bruna Raquel Winck

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Banca examinadora

Dr. Bruno Cavalcante Bellini
Universidade Federal do Rio Grande do Norte (UFRN)
Presidente da banca

Dra. Renata Antonaci Gama
Universidade Federal do Rio Grande do Norte (UFRN)
Examinador interno

Dr. Gabriel Costa Queiroz
Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ)
Examinador externo

Dra. Kauane Maiara Bordin
Universidade Federal do Rio Grande do Sul (UFRGS)
Examinador externo

Dra. Nerivania Nunes Godeiro
Shanghai Natural History Museum (SNHM)
Examinador externo

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RESUMO

Os colêmbolos são microartrópodes amplamente distribuídos por todos os ecossistemas terrestres, e desempenham um papel fundamental no seu funcionamento. Contudo, estudos taxonômicos e ecológicos envolvendo esses animais na América do Sul são limitados e apresentam lacunas em vários domínios fitogeográficos, como é o caso do Pampa. Este domínio é constituído majoritariamente por campos nativos, os quais abrigam uma grande biodiversidade de organismos da fauna e da flora. Os campos nativos estão desaparecendo em ritmo acelerado para dar lugar a espaços para práticas de pecuária extensiva e monoculturas de *Eucalyptus*, gerando preocupação sobre a conservação do domínio na América do Sul, sobretudo no Brasil. Diante disso, esta tese teve como objetivo geral avaliar os efeitos de diferentes usos da terra na composição taxonômica, funcional e propriedades ecológicas das comunidades de Collembola (Arthropoda: Hexapoda) no Pampa brasileiro. Quatro municípios no estado do Rio Grande do Sul com áreas de campos nativos e plantações de *Eucalyptus* foram amostrados: Pinheiro Machado, Jaguarão, Lavras do Sul e São Gabriel. Os colêmbolos foram coletados com armadilhas *pitfall* e funis de Berlese em 10 áreas pareadas com uma transecção de 250 m para cada tipo de uso do solo, divididas em 5 subparcelas. Em laboratório, os espécimes foram triados, quantificados, morfotipados, montados em lâminas para microscopia e identificados com o auxílio de chaves dicotômicas e bibliografias especializadas. A descrição da nova espécie foi realizada com o auxílio de um microscópio óptico acoplado a uma câmara clara, os desenhos foram vetorizados utilizando Corel Draw. As análises ecológicas de diversidade funcional e taxonômica foram realizadas no *software* R. No **Capítulo 1**, avaliamos a composição taxonômica, diversidade alfa e beta de colêmbolos epigéicos após a conversão de campos nativos em plantações de *Eucalyptus*. Utilizamos a análise de *Random Forest* para compreender a influência de fatores ambientais na estrutura e composição das comunidades. Encontramos perdas significativas nas comunidades de colêmbolos em relação à abundância, composição de espécies, riqueza e diversidade taxonômica após a conversão das áreas. A diversidade beta foi explicada principalmente pela substituição de espécies, enquanto a riqueza e dominância de plantas influenciaram a diversidade de colêmbolos. No **Capítulo 2**, avaliamos os efeitos da conversão de campos nativos em cultivos de *Eucalyptus* sobre a diversidade funcional e composição das comunidades de colêmbolos epigéicos e endogéicos. Categorizamos cada morfoespécie por forma de vida usando um índice ecomorfológico. Os resultados indicam que comunidades epigéicas estão mais associadas a áreas campestres, enquanto as endogéicas estão mais associadas aos cultivos de *Eucalyptus*. A conversão de campos para plantações de *Eucalyptus* não afetou os índices funcionais das comunidades epigéicas, mas teve efeitos negativos na riqueza e divergência funcional dos táxons endogéicos, resultando em redução da pigmentação corporal, número de ocelos, tamanho das pernas e apêndices desses animais. No **Capítulo 3,** reavaliamos a identificação e os registros do inventário do primeiro capítulo e realizamos uma revisão de literatura em diferentes bases de dados e artigos. Através do cruzamento dessas informações, fornecemos uma lista das 15 famílias, 35 gêneros e três espécies nominais registrados para o Pampa. Também elaboramos diagnoses e uma chave de identificação para os táxons supragenéricos presentes neste domínio. No **Capítulo 4**, descrevemos e ilustramos a primeira espécie de *Dicranocentrus* Schött para o Rio Grande do Sul e para o domínio do Pampa brasileiro. A nova espécie pertence ao grupo *gracilis sensu* Mari-Mutt. *Dicranocentrus* sp. nov. é única dentro do gênero por apresentar os segmentos antenais Ib e IIb ventralmente com duas cerdas acuminadas lisas cada; lábio com escamas, e cerda M1 ciliada e as demais lisas (m2, r, a1, a2, l1 e l2); *tenent hair* capitado; placa manubrial com 13 cerdas ciliadas e nove pseudoporos, e região ventro-apical do manúbrio com duas cerdas ciliadas. Por fim, apresentamos uma tabela comparativa que abrange todas as espécies de *Dicranocentrus* do grupo *gracilis* em todo o mundo. Os resultados apresentados nesta tese trazem contribuições inéditas para o conhecimento da taxonomia, ecologia e conservação de colêmbolos para o Pampa brasileiro. Eles enfatizam a importância de estudos aprofundados sobre a influência das práticas de uso da terra na biodiversidade dessas comunidades. A conservação dos campos nativos e a adoção de práticas sustentáveis nas plantações de *Eucalyptus* são cruciais para a manutenção da diversidade desses animais, e, consequentemente, para o equilíbrio ecológico do domínio do Pampa.

Palavras-chave: Campos Nativos; Collembola; Diversidade Funcional; Diversidade Taxonômica; Sul do Brasil; Taxonomia.

ABSTRACT

Springtails are microarthropods widely distributed in all terrestrial ecosystems, and they play a fundamental role in ecosystem functioning. However, studies focused in these animals in South America are limited and there are gaps to various phytogeographical domains, such as the Pampa. This domain is mainly composed by native grasslands, which harbor a great biodiversity of fauna and flora. The native grasslands are rapidly disappearing to make way for extensive livestock farming and *Eucalyptus* plantations, raising concerns about conservation in South America, especially in Brazil. In light of this, the main objective of this thesis was to assess the effects of different land uses on the taxonomic composition, functional diversity, and ecological properties of Collembola (Arthropoda: Hexapoda) communities in the Brazilian Pampa. Four municipalities in the state of Rio Grande do Sul (RS) with areas of native grasslands and *Eucalyptus* plantations were sampled: Pinheiro Machado, Jaguarão, Lavras do Sul, and São Gabriel. Springtails were collected using pitfall traps and Berlese funnels in 10 paired areas, each with a 250 m transect for each type of land use, divided into 5 subplots. In the laboratory, the specimens were sorted, quantified, morphotyped, mounted on slides for microscopy and identified with the help of keys and other specialized literature. The description of the new species was performed using an optical microscope with an attached camera and then drawings were vectorized using Corel Draw. Ecological analyses of taxonomic and functional diversity were performed using R software. In **Chapter 1**, we evaluated the taxonomic composition, alpha and beta diversity of springtails after the conversion of native grasslands into *Eucalyptus* plantations. We used Random Forest analysis to understand the influence of environmental factors on the structure and composition of the communities. We found significant losses in the springtail communities concerning abundance, species composition, richness, and taxonomic diversity after the conversion of the areas. Beta diversity was mainly explained by species turnover, while plant richness and dominance influenced springtail diversity. In **Chapter 2**, we assessed the effects of converting native grasslands into *Eucalyptus* plantations on the functional diversity and composition of epigeic and endogeic springtail communities. We categorized each morphospecies by their life form using an ecomorphological index. The results indicate that epigeic communities are more associated with grassland areas, while endogeic communities are more associated with *Eucalyptus* plantations. The conversion of grasslands to *Eucalyptus* plantations did not affect the functional indices of the epigeic communities, but had negative effects on the richness and functional divergence of the endogeic taxa, resulting in a reduction in body pigmentation, number of eyespots, size of the legs, and appendages of these animals. In **Chapter 3**, we reevaluated the identification and inventory records from the first chapter and conducted a literature review using different databases and articles. By cross-referencing these data, we provided a list of 15 families, 35 genera, and three nominal species recorded for the Pampa. We also developed diagnoses and an identification key for the suprageneric taxa present in this domain. In **Chapter 4**, we described and illustrated the first species of *Dicranocentrus* Schött for Rio Grande do Sul and the Brazilian Pampa domain. The new species belongs to the *gracilis*-group *sensu* Mari-Mutt. *Dicranocentrus* sp. nov. is unique within the genus by antennal segments Ib and IIb ventrally with two smooth pointed chaetae each; labium with scales, and chaeta M1 ciliated while the rest are smooth (m2, r, a1, a2, l1, and l2); tenent hair capitate; manubrial plate with 13 ciliated chaetae and nine pseudopores, and ventro-apical region of the manubrium with two ciliated chaetae. Lastly, we present a comparative table that encompasses all *Dicranocentrus* species from the *gracilis*-group worldwide. The results presented in this thesis provide unprecedented contributions to the taxonomy, ecology, and conservation knowledge of springtails in the Brazilian Pampa. They emphasize the importance of in-depth studies on the influence of land-use practices on the biodiversity of these communities. The conservation of native grasslands and the adoption of sustainable practices in *Eucalyptus* plantations are crucial for maintaining the diversity of these animals and, consequently, the ecological balance of the Pampa domain.

Keywords: Native Grasslands; Collembola; Functional Diversity; Taxonomic Diversity; Southern Brazil; Taxonomy.

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INTRODUÇÃO GERAL

1. INTRODUÇÃO GERAL

1.1. COLLEMBOLA: ASPECTOS GERAIS

Collembola representa uma das quatro classes de Hexapoda, juntamente com Protura, Diplura e Insecta (Zhang 2011, Bellinger *et al.* 1996–2023). Sabe-se que os colêmbolos, assemelham-se aos insetos em seu padrão de tagmose (cabeça, tórax e abdome). Contudo, os colêmbolos são ápteros, não possuem asas, assim como os Diplura e Protura, e entognatos, possuem peças bucais ocultas dentro de uma cápsula cefálica, diferindo-os dos insetos (ectognatos) (Zeppelini & Bellini 2004, Cipola *et al.* 2018). Colêmbolos apresentam corpo fusiforme, achatado dorso-ventralmente ou globoso, que podem variar de 0,12 a 17 mm de comprimento (Bellinger *et al.* 1996–2023). Esses organismos apresentam coloração variável ou podem estar desprovidos de pigmentos, a cutícula é hidrofóbica, granulosa ou lisa, revestida por cerdas, escamas, espinhos, sensilas e/ou tricobrótrias (Hopkin 1997, Mendonça *et al.* 2014, Hensel *et al.* 2016, D'Alba *et al.* 2019).

Em sua morfologia externa, os colêmbolos apresentam algumas peculiaridades. Na cabeça, evidencia-se um par de antenas com quatro artículos (alguns gêneros podem apresentar até seis artículos, como *Orchesella* Templeton, Templeton, Westwood, 1836 e *Dicranocentrus* Schött, 1983), e olhos simples, dispostos em uma mancha ocular, variando até um número máximo de oito de cada lado da cabeça, até a sua total ausência (Mendonça *et al.* 2014, Bellinger *et al.* 1996–2023). Ainda na cabeça, encontram-se as peças bucais, um par de maxilas e um par de mandíbulas (este último pode estar ausente), as quais estão inseridas na cápsula cefálica (Mendonça *et al.* 2014). O tórax está dividido em três segmentos geralmente providos de cerdas e com um par de pernas, respectivamente. As pernas são constituídas de sete segmentos: epicoxa, subcoxa, coxa, trocânter, fêmur, tibiotarso e pré-tarso, onde se inserem o unguis e o apêndice empodial chamado de unguículos (Hopkin 1997, Zeppelini & Bellini, 2004, Cipola *et al.* 2018, Bellini *et al.* 2023).

O abdômen desses animais é composto de seis segmentos, distintamente separados e fusiformes. Na superfície ventral do primeiro segmento abdominal está localizado o tubo ventral, também chamado de colóforo, que é a estrutura responsável pela absorção de água, oxigênio, limpeza e por manter o animal aderido ao solo; no terceiro segmento encontra-se o tenáculo, estrutura provida de um par de ganchos, com tamanho e número variável de dentes, cuja função é a sustentação da fúrcula (Hopkin 1997, Mendonça *et al.* 2014, Bellini *et al.* 2023). No quarto segmento está inserido a fúrcula, estrutura saltatória que, quando em repouso, fica presa ao tenáculo e possibilita aos colêmbolos um melhor deslocamento sobre os obstáculos, fuga dos predadores e locomoção (Zeppelini & Bellini 2004, Oliveira 2022, Bellini *et al.* 2023, Bellinger *et al.* 1996–2023). Estas três estruturas são consideradas as principais sinapomorfias da classe Collembola.

Os colêmbolos são classificados como ametábolos, o que significa que não possuem uma fase larval distintiva e as suas formas jovens são relativamente semelhantes aos indivíduos adultos. Durante o desenvolvimento, os colêmbolos passam por mudas periódicas da cutícula corporal, que ocorrem em intervalos variáveis (em menos de uma semana em espécies dos trópicos ou poucas vezes ao ano em parte das espécies de climas temperados) (Hopkin 1997, Chahartaghi *et al.* 2006, Bellini 2016). À medida que crescem, os colêmbolos tornam-se cada vez mais complexos, com cerdas corporais e órgãos sensitivos mais abundantes e bem desenvolvidos. O último estágio importante do desenvolvimento desses organismos é a maturação sexual, transformando os indivíduos jovens em adultos reprodutivos. O número de ovos postos pelos colêmbolos não é fixo, com registros de posturas que variam de dois a mais de cem ovos de uma só vez. Normalmente, os ovos são postos de forma agrupada e eclodem poucos dias após a postura (Bellini 2016).

A Classe Collembola está dividida em quatro ordens e todas têm registro no Brasil: Neelipleona Massoud, 1971, Symphypleona Börner, 1901 *sensu* Massoud, 1971, Poduromorpha Börner, 1913 e Entomobromorpha Börner, 1913 (Soto-Adames *et al.* 2008; Cipola *et al.* 2018). A ordem Poduromorpha (Fig. 1A) abriga indivíduos com um corpo alongado e fusiforme, segmentos corporais nitidamente visíveis, mas com o primeiro segmento torácico plenamente desenvolvido, portando cerdas e/ou vesículas dorsais. Entomobryomorpha (Fig. 1B) também é caracterizado por um corpo alongado, pela presença de um tórax e abdômen bem definidos, no entanto, apresentam redução no primeiro segmento torácico, o qual não apresenta o esclerito dorsal (Hopkin, 1997). Essas duas ordens também podem ser separadas por outras características morfológicas, visto que, os Entomobryomorpha adultos geralmente apresentam cerdas corporais mais abundantes e/ou heterogêneas, especialmente no tronco dorsal e nas pernas, e apêndices mais longos (antenas, pernas, colóforo e fúrcula), contudo, algumas exceções podem ser vistas entre as espécies que vivem no interior do solo (Bellini *et al.* 2023, Bellinger *et al.* 1996–2023).

No que diz respeito a Symphypleona (Fig. 1C) e Neelipleona (Fig. 1D), verifica-se que, ambos possuem um plano corporal mais globoso e arredondado, com os segmentos corporais em grande parte fundidos entre si (Bellini 2016, Cipola *et al.* 2018). Os representantes de Neelipleona são nitidamente diferentes dos Symphypleona uma vez que: apresentam antenas reduzidas, mais curtas que a cabeça; a maior porção de seu tronco formada por segmentos torácicos alargados, e suas coxas são longas e dens subsegmentados. Em contrapartida, os representantes de Symphypleona possuem antenas que são pelo menos mais longas que a cabeça, às vezes até mais longas que o corpo, um tronco majoritariamente constituído por segmentos abdominais, coxas curtas e dens não segmentadas (Bretfeld 1999, Bellini *et al.* 2023).

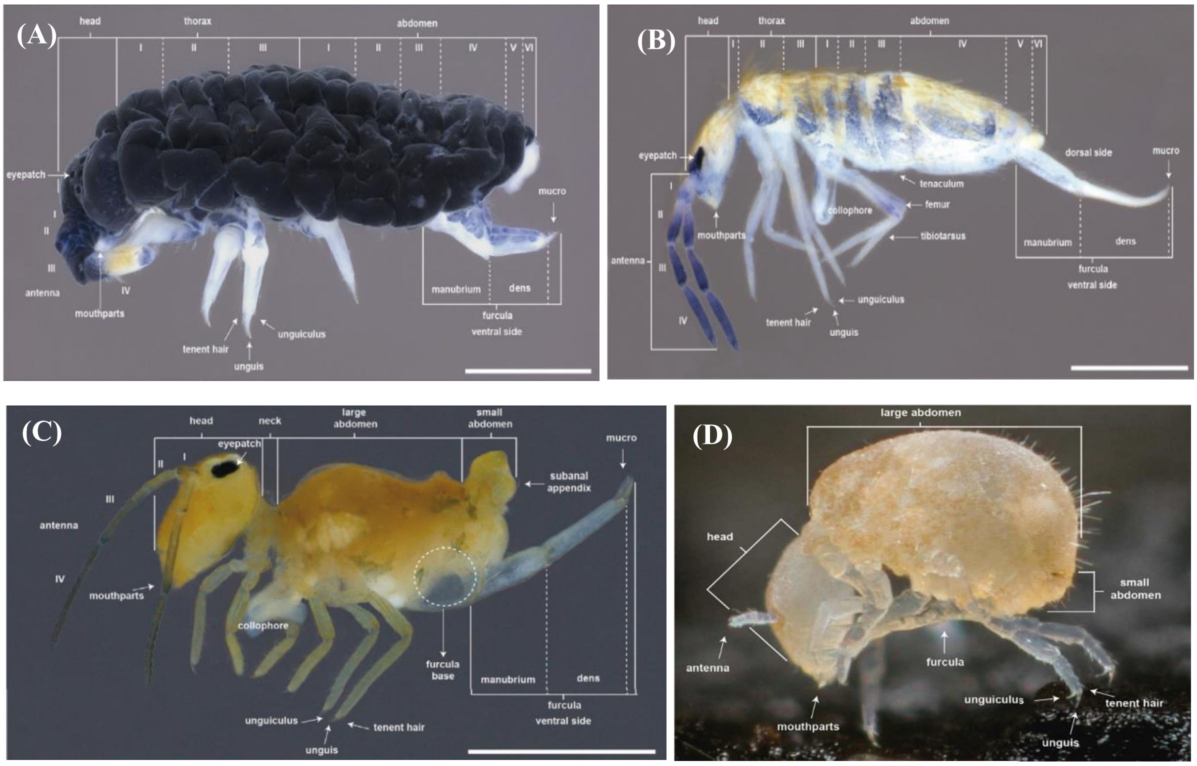

Figura 1: Estrutura corporal das quatro ordens de Collembola. A) Poduromorpha (*Neotropiella carli*), B) Entomobryomorpha (*Seira dowlingi*), C) Symphypleona (*Arlesminthurus* sp.) e D) Neelipleona (*Neelus murinus*).
Fonte: Adaptado de Cipola et al. (2018a).

Atualmente, existem mais de 9.400 espécies nominais de colêmbolos registradas em todo o mundo (Bellinger *et al*. 1996–2023). No entanto, diferentes estimativas sugerem que o número de espécies vivas de Collembola variem de 50.000 a 500.000 (Cicconardi *et al.* 2013), o que significa que a maioria ainda não foi reconhecida pela ciência. Grande parte dos táxons conhecidos foram registrados e descritos nas regiões Paleártica e Neártica, graças aos esforços de muitos pesquisadores europeus e norte-americanos. (Bellinger *et al*. 1996–2023, Bellini *et al.* 2023). Por outro lado, até o momento, mais de 1.300 espécies de colêmbolos foram registradas na Região Neotropical, com 475 dessas espécies ocorrendo no Brasil, das quais 328 são consideradas endêmicas do país (Abrantes *et al.* 2010; 2012; Zeppelini *et al.* 2023). No entanto, o conhecimento taxonômico atual da fauna de Collembola no Brasil ainda apresenta grandes lacunas a serem preenchidas, especialmente considerando que a maioria das espécies conhecidas foram amostradas em áreas com predominância dos domínios fitogeográficos da Mata Atlântica, Amazônia e Caatinga (Zeppelini *et al*. 2023).

1.2. ECOLOGIA DE COLLEMBOLA

Os colêmbolos são encontrados em todos os continentes, dispondo de ampla distribuição geográfica em ambientes terrestres e limitada em ambientes aquáticos. Estes animais são extremamente dependentes de umidade, mas são capazes de habitar cavernas, pequenos corpos aquíferos, rochas, praias, ninhos de animais (aves, mamíferos e insetos sociais), copas de árvores, desertos, regiões glaciares, entre tantos outros locais úmidos (Hopkin 1997, Castaño-Meneses *et al.* 2004, Zeppelini & Bellini 2004). Contudo, sua maior abundância e diversidade está relacionada ao ambiente edáfico e devido ao seu diâmetro corporal, cujo tamanho varia de 0,01 a 2 mm, conseguem se locomover entre os poros do solo e na interface entre a serrapilheira e o solo. Eles são considerados integrantes da mesofauna edáfica, juntamente com os ácaros, sínfilos, proturos, besouros, entre outros organismos (Swift *et al.* 1979).

A riqueza e diversidade de colêmbolos em um determinado ecossistema dependem de diferentes fatores, mas para a maioria das espécies estão intimamente relacionados à: i) temperatura adequada para o desenvolvimento; ii) presença de umidade constante; iii) composição físico-química dos solos; e iv) heterogeneidade da vegetação do local e em seu entorno (Bellini, 2016; Bellini *et al.* 2023).

A temperatura tem um impacto indireto na manutenção da umidade ambiental e corporal, além de afetar diretamente o desenvolvimento desses animais e suas fontes de alimento (Vargas *et al.* 2020). Para muitas espécies, a temperatura desempenha um papel crucial em sua sobrevivência. Por exemplo, os colêmbolos apresentam dificuldades na retenção de água devido à sua cutícula fina e à ausência de escleritos em certas partes do corpo, o que resulta em pontos de desidratação (Nickerl *et al.* 2014, Bellini 2016). Com relação as diferentes composições de solo e vegetação, sabe-se que a associação destas com as variáveis ambientais abióticas geram diversos microambientes passíveis de colonização e especialização pelos colêmbolos (Zardo *et al.*, 2010; Podgaiski e Rodrigues, 2010; Bellini, 2016). Em condições ambientais ótimas, as populações podem se desenvolver ao máximo, chegando até aproximadamente 100.000 indivíduos por m^2 (Chauvat *et al.* 2011, Perez *et al.* 2013).

Os colêmbolos têm um papel fundamental nos ecossistemas devido às funções que desempenham. Por serem organismos de tamanho reduzido e apresentarem populações abundantes, acabam sendo presas para diversos grupos de animais, especialmente outros artrópodes que habitam o solo, como ácaros, coleópteros, pseudoescorpiões e aranhas (Hopkin 1997). Isso resulta na sua integração e sustentação da base de complexas cadeias alimentares que influenciam o desenvolvimento e a manutenção da fauna e flora terrestres conforme as conhecemos (Hopkin 1997, Bellini, 2016). Esses organismos também exercem um controle indireto sobre a fertilidade do solo, uma vez que se alimentam principalmente de detritos de origem vegetal, animal, fungos e bactérias. Ao fazer isso, promovem a particularização da matéria orgânica que nutre o solo, além de dispersar bactérias e fungos benéficos tanto horizontal quanto verticalmente (incluindo camadas mais profundas do solo) e predar parte das bactérias e fungos fitopatogênicos, que são danosos para os organismos vegetais (Cassagne *et al.* 2003, Siddiky *et al.* 2012, Bellini 2016).

É importante destacar que, as mudanças ambientais em diversos níveis, principalmente aquelas causadas por ações antropogênicas, podem afetar a diversidade e distribuição dos colêmbolos nos ecossistemas. Essas mudanças afetam a estrutura e a composição das comunidades dos colêmbolos e, consequentemente, influenciam em todas as funções ecossistêmicas proporcionadas pelas atividades desses organismos. Entre as principais ameaças para a fauna do solo, incluindo Collembola, estão a conversão de habitats nativos em culturas, silvicultura artificial ou pecuária; a expansão urbana e industrial; poluição do solo e da água; e a introdução de espécies exóticas invasoras, dentre outras (Potapov *et al.* 2020). Assim, os colêmbolos são apontados como eficientes bioindicadores em estudos de qualidade de solo, contaminação por substâncias tóxicas e degradação e recuperação de hábitats, particularmente as espécies endêmicas (Lessel *et al.* 2011, Bullinger-Weber *et al*. 2012).

Os colêmbolos exibem diferentes estratégias de vida, classificando-os em distintos grupos funcionais (Petersen & Luxton, 1982). Em relação aos ambientes edáficos, existem indivíduos que vivem dentro do solo (euedáficos), aqueles que habitam a superfície do solo, na serapilheira e/ou em árvores (epiedáficos), e os que apresentam um "comportamento intermediário" (hemiedáficos) (Petersen & Luxton, 1982; Mendonça Jr. *et al*. 2015, Potapov *et al.* 2016, 2020) (Figura 2).

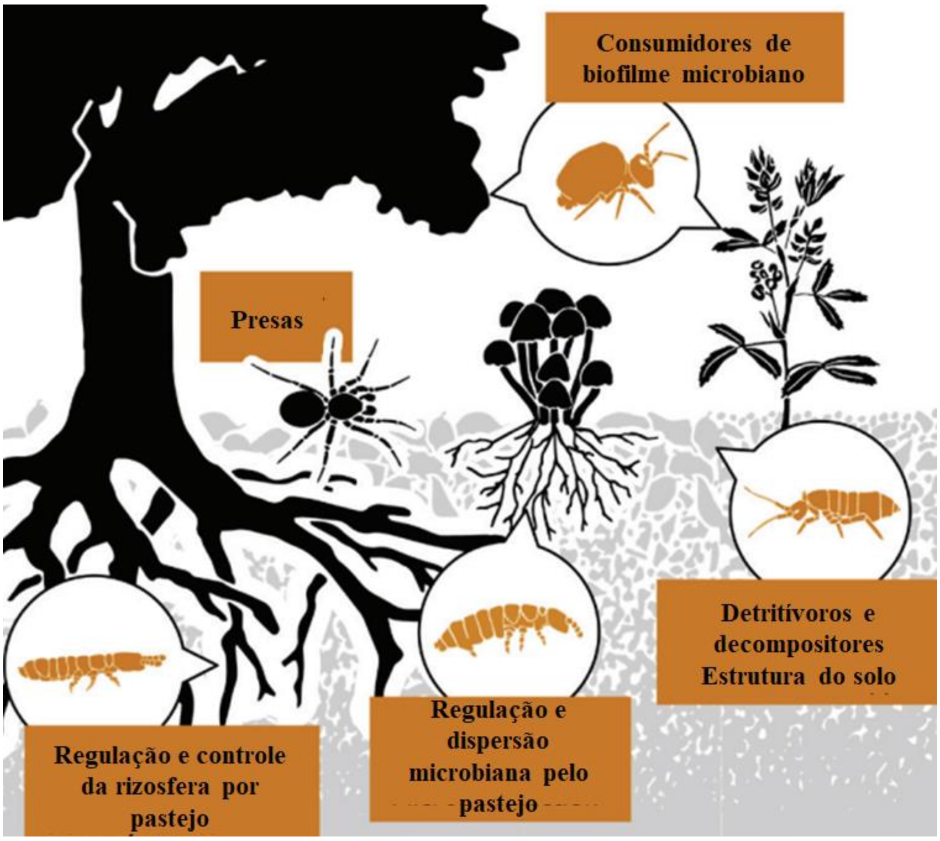

Figura 2: Processos ecossistêmicos que podem ser afetados por diferentes grupos funcionais de Collembola. Fonte: modificado de Potapov *et al.* (2020).

Os colêmbolos epiedáficos habitam a superfície do solo, e são comumente representados pelas ordens Entomobromorpha e Symphypleona. Estes animais possuem maior atividade metabólica e se alimentam de recursos de alta qualidade nutricional (por exemplo, matéria orgânica fresca, microorganismos, detritos vegetais em decomposição, etc.). A reprodução geralmente é sexuada e apresentam menor número de descendentes, apesar da maior quantidade de ovos (Vargas *et al.* 2020). Do ponto de vista morfológico, estes indivíduos são grandes (média de 2 mm), têm apêndices desenvolvidos (antenas, pernas e fúrcula) e possuem de 6 a 8 olhos em cada mancha ocular, os quais são bastante pigmentados. Alguns colêmbolos epiedáficos são providos de escamas (por exemplo, *Seira* spp. e *Lepidocyrtus* ssp.), tricobrótrias e muitas cerdas (Petersen & Luxton, 1982; Martins da Silva *et al.* 2016; Potapov *et al.* 2020).

Os colêmbolos euedáficos são encontrados no interior do solo e são representados especialmente por indivíduos pertencentes às famílias Onychiuridae Börner, 1913, Isotomidae Schäffer, 1896 *sensu* Potapov, 2001, embora haja formas euedáficas de outras linhagens de Collembola. Esses organismos tendem a se alimentar de recursos em menor qualidade, pois sua mobilidade limitada dificulta a busca por fontes alimentares mais nutritivas. Apresentam uma atividade metabólica reduzida e se reproduzem muitas vezes assexuadamente, através de partenogênese, resultando em um maior número de descendentes e menor variabilidade genética. Por habitarem o interior do solo, essas espécies possuem geralmente um tamanho corporal menor, formato cilíndrico e são desprovidas ou apresentam limitada pigmentação, ocelos, tricobótrias e/ou escamas. Fúrcula e tenáculo podem estar reduzidos ou ausentes. No entanto, esses indivíduos possuem órgãos sensoriais bem desenvolvidos, como o órgão pós-antenal, e mecanismos de defesa contra predadores, como os pseudocelos encontrados na família Onychiuridae, que são vesículas que produzem substâncias repugnantes (Petersen & Luxton, 1982; Salmon *et al.* 2014, Martins da Silva *et al.* 2016; Potapov *et al.* 2016).

Com relação aos colêmbolos hemiedáficos, sabe-se que estes vivem na interface solo-serapilheira, apresentando características ecológicas intermediárias entre o grupo epiedáfico e euedáfico. Por meio da movimentação vertical e horizontal, este grupo atua na mistura da matéria orgânica nas primeiras camadas do solo, podendo ter um forte efeito nos processos de mineralização. Este grupo funcional é muito diversificado, pois compreende espécies que pertencem à maioria das famílias de colêmbolos já identificadas (Petersen & Luxton, 1982; Mendonça Jr. *et al.* 2015; Martins da Silva *et al.* 2016; Potapov *et al.* 2016, 2020).

1.3 O DOMÍNIO DO PAMPA NO RIO GRANDE DO SUL, BRASIL

A palavra "Pampa" possui origem quíchua (ou *quechua*), língua indígena da América do Sul, também falada no império Inca, significando "região plana" e está associada à paisagem dominante de extensas planícies cobertas de vegetação rasteira (Suertegaray & Silva 2009, Bencke *et al.* 2016). O Pampa como domínio fitogeográfico é a reunião de formações ecológicas que se intercruzam em uma formação ecopaisagística única, com intenso tráfego de matéria, energia e vida entre os campos, matas ciliares (de galeria), capões de mato e matas de encostas, são suas principais formações.

Este domínio estende-se em uma área de aproximadamente 700.000 km^2, compartilhada entre o Brasil, Uruguai e Argentina (Bilenca & Miñarro 2004, Projeto Mapbiomas 2023)(Figura 3). No Brasil, o domínio é exclusivo da região Sul e abrange cerca de 176.000 km², equivalendo a 63% do território do estado do Rio Grande do Sul (RS) e a 2.1% do território nacional (MMA 2010, Bencke *et al.* 2016). O Pampa brasileiro limita-se a altas latitudes, localizadas entre 30º e 34º latitude Sul e 57° e 63° longitude Oeste, onde o clima de acordo com a classificação de Köppen corresponde ao tipo "CF", temperado, com chuva em todos os meses. Dentro do tipo "CF" ocorrem dois subtipos: "Cfa", subtropical, com temperatura média das máximas superior a 22ºC e a média das mínimas variando entre –3º e 18ºC; "Cfb", subtropical, com a média das máximas inferior a 22ºC e a média das mínimas oscilando entre –3 e 18ºC (Nimer 1977).

Figura 3: Localização do domínio do Pampa brasileiro, dentro da América do Sul.
Fonte: Projeto Mapbiomas (2023).

O Pampa foi oficialmente reconhecido como bioma/domínio no Brasil apenas em 2004, alcançando status equivalente ao da Mata Atlântica, Caatinga, Pantanal, Cerrado e Amazônia. Até então, ele estava vinculado aos chamados Campos Sulinos, como parte da Mata Atlântica (Bencke *et al.* 2016). Essa distinção desencadeou uma identidade pública nacional para uma porção singular do território brasileiro, inserindo-o formalmente na agenda ambiental nacional, contribuindo para a conservação do rico patrimônio natural e cultural da região sul e permitindo destacar, inclusive no âmbito da legislação, a importância, a singularidade e as potencialidades desse ambiente campestre único no mundo (Vélez *et al.* 2009, Bencke *et al.* 2016).

Por trás da aparente uniformidade do Pampa há uma elevada diversidade biológica da fauna e flora, só recentemente revelada graças à intensificação das pesquisas científicas sobre o domínio e ao aumento do interesse pela sua conservação ao longo dos últimos anos (Bencke, 2016). Por exemplo, um estudo recente liderado por Andrade *et al.* (2023) aponta que existem mais de 12.503 espécies conhecidas e registradas no Pampa brasileiro, incluindo plantas, fungos, bactérias e animais. Esses organismos estão inclusos em 1.025 famílias e 4.661 gêneros. Conforme os autores, 97% das espécies são consideradas nativas do domínio Pampa. A Figura 4 a seguir, expressa os principais táxons, famílias e número de espécies ocorrentes no domínio conforme o trabalho da Andrade *et al.* (2023).

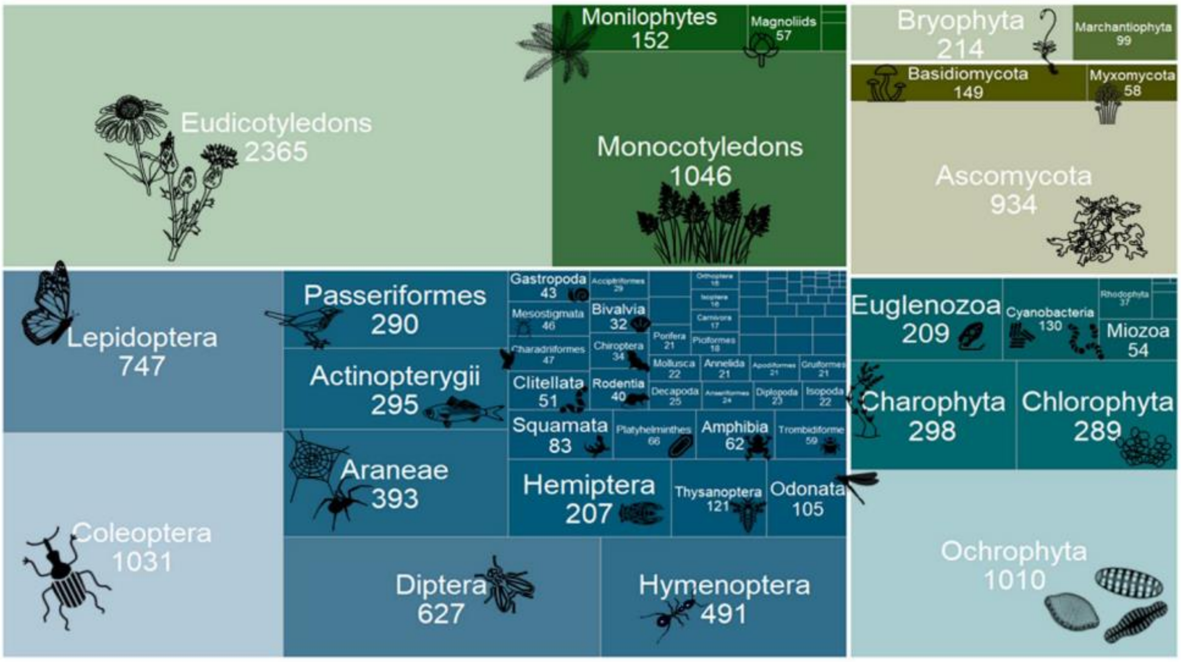

Figura 4: Riqueza de espécies de plantas, animais, fungos e bactérias conhecidas da região do Pampa brasileiro. As espécies estão organizadas em cinco conjuntos de dados: plantas vasculares (em verde), briófitas (em oliva), fungos (em caqui), algas (em verde pinheiro) e espécies animais (em azul).
Fonte: Andrade *et al.* (2023)

Com relação à flora, sabe-se que as plantas vasculares, incluindo angiospermas (Eudicotiledônea e Monocotiledônea), gimnospermas e pteridófitas (Lycophyta e Monilophyta), totalizam 3.642 espécies, distribuídas em 191 famílias e 1.108 gêneros no domínio. Embora as espécies de monocotiledôneas, em particular as gramíneas, tenham um papel determinante na fisionomia dos ecossistemas campestres, a maioria das espécies do Pampa consiste em eudicotiledôneas, com uma maior diversidade entre as famílias Asteraceae (476 espécies), Poaceae (423 espécies), Fabaceae (292 espécies), Orchidaceae (162 espécies) e Cyperaceae (155 espécies). Dentre as pteridófitas, as famílias mais ricas são Pteridaceae (33 espécies), Polypodiaceae (23 espécies) e Aspleniaceae (13 espécies), Lycopodiaceae (7 espécies) e Selaginellaceae (4 espécies) (Cordeiro & Hasenack 2009, Boldrini *et al.* 2009, Bencke 2016, Bencke *et al.* 2016, Christenhusz & Byng 2016, PPG 2016, Andrade *et al.* 2018*,* 2023, Reflora 2023) Já as Briófitas das divisões Anthocerotophyta, Bryophyta e Marchantiophyta, apresentam 318 espécies, 137 gêneros e 69 famílias (Andrade *et al.* 2023, Reflora 2023). As algas contêm 2.046 espécies e 2.378 táxons (espécies, variedades e formas) de 478 gêneros, 213 famílias e 11 divisões. A divisão mais rica é Ochrophyta (1.152 espécies), seguida por Charophyta (381 espécies), Chlorophyta (328 espécies) e Euglenozoa (275 espécies). Desmidiaceae (282 espécies), Euglenidae (181 espécies), Bacillariaceae (126 espécies), Naviculaceae (104 espécies) e Eunotiaceae (112 espécies) são as famílias com maior número de espécies (Guiry 2012, Andrade *et al.* 2023). Já os fungos apresentam 1.141 espécies de 293 gêneros e 107 famílias. Predominam as espécies nos filos Ascomycota (934 espécies), seguidas de Basidiomycota (149 espécies) e Myxomycota (58 espécies)

Com relação à fauna, o Pampa apresenta 5.358 espécies registradas, pertencentes a 2.652 gêneros e 445 famílias. Os vertebrados totalizam 1.136 espécies reconhecidas (Andrade *et al*. 2023). As aves formam o grupo de vertebrados com maior riqueza (567 espécies), seguido por Actinopterygii (295 espécies), Mammalia (120 espécies), "répteis" (90 espécies), Amphibia (62 espécies) e Chondrichthyes (2 espécies) (Bernils *et al.* 2007, Garcia *et al.* 2007, Develey *et al.* 2008, Santos *et al*. 2014, Bencke 2016, Segalla *et al.* 2016, Queirolo 2018, Pacheco *et al.* 2021, Andrade *et al.* 2023). Já os invertebrados totalizam 4.222 espécies. Os grupos mais ricos são Coleoptera (1.031 espécies), Lepidoptera (747 espécies), Diptera (627 espécies) e Hymenoptera (491 espécies) (Ferreira *et al.* 2010, Rieff *et al.* 2010, Rodrigues *et al.* 2010, Silva *et al.* 2012, Podgaiski *et al.* 2013, Maestri *et al.* 2013, Feitosa *et al.* 2015, Mendonça Jr. *et al.* 2015, Ferrando *et al.* 2016, Garcia *et al.* 2016; Silva *et al.* 2017, Andrade *et al.* 2023).

A fauna de invertebrados no Pampa ainda é pouco estudada. Atualmente têm-se os registros de 28 ordens de artrópodes para o domínio, incluindo grupos megadiversos como Hemíptera, Díptera, Hymenoptera, Coleóptera, Lepidóptera, Orthoptera, Araneae, Sarcoptiformes, etc. (Benck, 2016; Andrade *et al.* 2023). No que diz respeito à riqueza e diversidade de Collembola, temos apenas o registro de uma única espécie nominal (*Cyphoderodes xenopus* Börner, 1913) no Pampa. Essa situação é intrigante, pois, embora já existam estudos iniciais com o grupo Collembola explorando aspectos ecológicos e taxonômicos (ligados aos estudos ecológicos), trabalhos de síntese, como o de Andrade et al. (2023), não fornecem informações sobre o grupo. No entanto, por meio dos esforços desta tese, sabemos que Collembola apresenta 35 gêneros e 15 famílias no Pampa. Esses dados são provenientes de compilações de publicações recentes envolvendo os colêmbolos, como Winck et al. (2017, 2019), Jorge et al. (2022, 2023) e Silva et al. (2022). Mais detalhes sobre essa fauna serão apresentados no Capítulo 3 desta tese. De forma geral, os invertebrados constituem uma teia complexa de relações que asseguram a integridade das paisagens campestres e de seus serviços ambientais (Bencke 2009, Pillar & Langer 2015, Pillar *et al.* 2016).

Apesar da riqueza biológica existente no Pampa, sabe-se que o ritmo acelerado em que os campos naturais estão desaparecendo para dar lugar a áreas agrícolas ou para práticas de pecuária extensiva e silvicultura, lançam sérias dúvidas sobre o futuro da conservação no domínio. Esta situação está intimamente ligada a episódios históricos envolvendo a agricultura comercial. No RS ela teve início no decorrer do século XVIII, com o plantio de trigo pelos colonos açorianos. Até esse ponto, a agricultura presente no Estado estava ligada apenas a práticas de subsistência pelos povos indígenas. O primeiro registro de cultivo de soja no Brasil data de 1914 no município de Santa Rosa (região Noroeste do RS), porém, somente na década de 1970 é que a soja se consolidou como a principal cultura do agronegócio brasileiro, onde 80% do volume produzido na época se concentrava nos três estados da Região Sul do Brasil (Embrapa 2005). Desde então o Pampa tem sofrido grande perda de biodiversidade e de habitats devido ao acelerado processo de expansão agrícola, e têm se agravado recentemente pelos planos para conversão de extensas áreas de campos em monoculturas (soja, trigo, milho, silvicultura, etc.) (Pillar *et al.* 2016, MMA 2010), restando, muitas vezes, apenas pequenos remanescentes originais em uma paisagem predominantemente agrícola (Risser 1997, Bencke 2009).

Conforme dados divulgados pelo Projeto Mapbiomas (2023), entre 1985 e 2021 (últimos 36 anos), o Pampa sofreu profundas transformações no uso da terra, perdendo cerca de 3,4 milhões de hectares de vegetação nativa. Assim, no ano de 2021 o domínio apresentava 43,20% de cobertura vegetação nativa, 46,70% da vegetação suprimida para uso antrópico, 9% ocupado por água e 1,10% de praia dunal e areal (Figura 5). Dessa forma, verifica-se que atualmente o Pampa abriga mais áreas antropizadas que de vegetação nativa (Projeto Mapbiomas 2023).

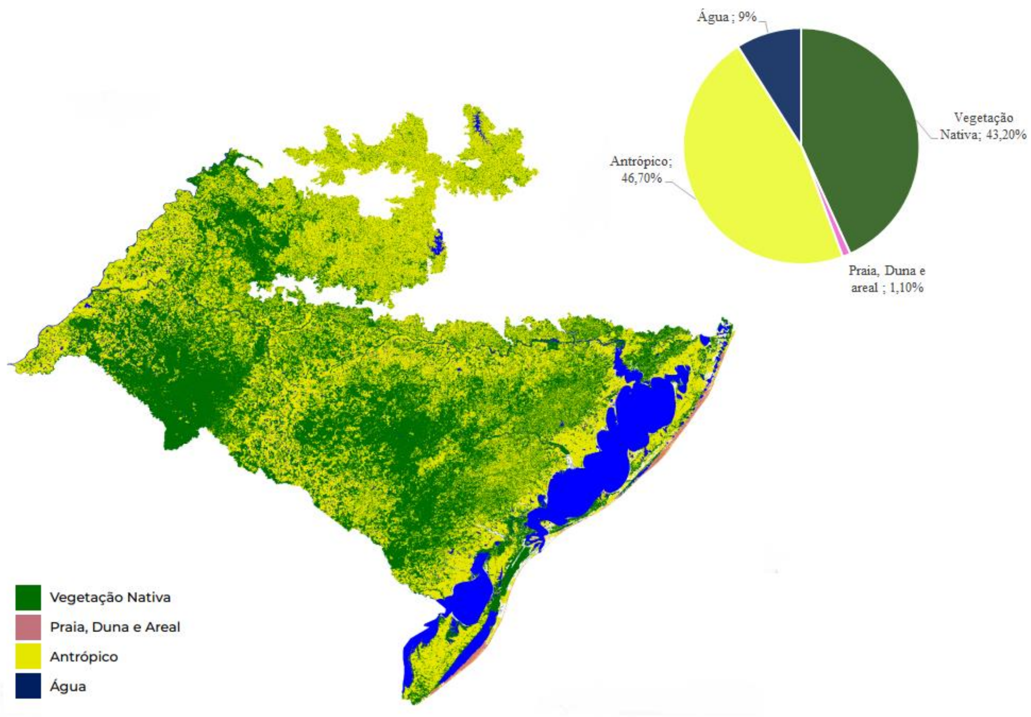

Figura 5: Distribuição geral do uso do solo em áreas do Pampa Brasileiro.
Fonte: Modificado de Mapbiomas, 2023.

Dentre as diversas destinações de áreas do Pampa para o uso antrópico destaca-se conversão dos campos nativos em silvicultura, visto que esta é a classe de mudança do uso da terra que mais cresce atualmente no domínio. Sabe-se que a extensão do plantio de eucalipto aumentou fortemente desde 2006, ocupando hoje cerca de 480.000 hectares (Projeto Mapbiomas 2023), representando um crescimento de mais de 15.5% ao ano, sendo que 60% destas áreas são ocupadas por espécies de *Eucalipto* spp. (Projeto MapBiomas 2023). A maioria das áreas convertidas possui solos rasos, que por sua vez também são áreas mais suscetíveis à degradação (Roesch *et al.* 2009). Além disso, há pouco entendimento de como a plantação de eucalipto afeta a biodiversidade local no Pampa e, consequentemente, as funções ecológicas relacionadas à biodiversidade.

Nos últimos anos, alguns estudos investigaram o impacto da conversão de campos nativos do Pampa em plantações de eucalipto na diversidade de plantas e animais que habitam a superfície do solo (Rodrigues *et al.* 2010, Souza *et al.* 2013, Saccol *et al*. 2017, Sabatté *et al*. 2021). Esses estudos confirmaram principalmente efeitos negativos nos indicadores de biodiversidade. Estudos conduzidos por Winck *et al.* (2017, 2019) e Jorge *et al.* (2022, 2023) evidenciaram efeitos negativos, como a redução da diversidade taxonômica e funcional, em resposta à intensificação do uso da terra, incluindo as plantações de eucalipto. Essas pesquisas têm contribuído para avançar o conhecimento sobre os efeitos da conversão dos campos nativos do Pampa, especialmente por incluírem análises baseadas em atributos funcionais.

Sabe-se que a destinação de áreas para uso antrópico compromete a biodiversidade e consequentemente o potencial de desenvolvimento sustentável da região, seja por perda de espécies de valor forrageiro, alimentar, ornamental e medicinal, seja pelo comprometimento dos serviços ambientais proporcionados pela vegetação campestre, como o controle da erosão do solo e o sequestro de carbono que atenua as mudanças climáticas, por exemplo (Tornquist & Bayer 2009, MMA 2010). Por este motivo, áreas envolvendo o domínio vem recebendo atenção especial do Ministério do Meio Ambiente como ação prioritária para a conservação da biodiversidade (Hasenack *et al.* 2007) e práticas de inventários (MMA 2010).

Em relação às áreas naturais protegidas no Brasil, o Pampa é o bioma que menor tem representatividade no Sistema Nacional de Unidades de Conservação (SNUC), representando apenas 3,3% da área continental brasileira protegida por unidades de conservação (UC). A Convenção sobre Diversidade Biológica (CDB), da qual o Brasil é signatário, em suas metas para 2020, previu a proteção de pelo menos 17% de áreas terrestres representativas da heterogeneidade de cada bioma (Tornquist & Bayer 2009, MMA 2010, Vélez-Martini *et al.* 2015, Vieira & Overbeck 2015, Echer *et al.* 2016).

As "Áreas Prioritárias para Conservação, Uso Sustentável e Repartição de Benefícios da Biodiversidade Brasileira", atualizadas em 2007, resultaram na identificação de 105 áreas do bioma Pampa. Destas, 41 (um total de 34.292 km^2) foram consideradas de importância biológica extremamente alta (MMA 2010, Vélez-Martini 2015, Echer *et al.* 2016). Estes números contrastam com apenas 3,3% de proteção em UC's (2,4% de uso sustentável e 0,9% de proteção integral), com grande lacuna de representação das principais fisionomias de vegetação nativa e de espécies ameaçadas de extinção da fauna e da flora (Vélez-Martini 2015, Vieira & Overbeck 2015, Bencke, 2016). Diante desse cenário, é fundamental ressaltar a importância da conservação das áreas do Pampa para a conservação da biodiversidade da região, especialmente a fauna de Collembola. Dado o crescente aumento de conversão do uso do solo que está ocorrendo, acreditamos que várias espécies podem estar enfrentando riscos de extinção local, muitas das quais ainda não foram identificadas, registradas ou descritas.

1.4. JUSTIFICATIVA

No Brasil, assim como em outras partes do mundo, o conhecimento sobre a Classe Collembola ainda apresenta importantes lacunas. Essa situação está relacionada ao reduzido número de taxonomistas especializados no grupo atuando no país, como apontado por Bellini & Godeiro (2017). Associado a isto, ainda é perceptível que a maioria dos estudos envolvendo esses organismos estão diretamente ligados a região onde estão inseridos os principais especialistas, como por exemplo, a região Norte, Nordeste e Sudeste, onde predominam os domínios fitogeográficos da Amazônia, Caatinga e Mata Atlântica. Dentro desse contexto, diversas áreas do Brasil e seus respectivos domínios, apresentam poucos estudos detalhados sobre os colêmbolos, como é o caso do Pampa, exclusivo do estado do RS.

Até o ano de 2012, somente duas espécies de colêmbolos haviam sido registradas no RS: *Lepidocyrtus pallidus* Reuter, 1890 (com registro incerto, pois trata-se de uma espécie holártica sem distribuição clara) e *Cyphoderodes xenopus* Börner, 1913 (Abrantes *et al.* 2010; 2012). Embora não seja possível atribuir claramente o primeiro registro a nenhum bioma em particular, *C. xenopus* foi coletado na região de São Leopoldo (Börner, 1913), que fica na zona de transição entre a Mata Atlântica e o Pampa. Essa é a única espécie nominal de colêmbolos registrada no Pampa brasileiro até o momento. Existe um terceiro registro publicado de uma espécie nominal no RS, a espécie *Salina maculipenis* Oliveira & Cipola, 2018, coletada no município de Estrela Velha, situado na Mata Atlântica (Oliveira *et al.* 2018; Zeppelini *et al.* 2023). Nas últimas décadas foram iniciados estudos com enfoque ecológico, investigando a composição e a estrutura das comunidades de colêmbolos em relação conversão de campos nativos em monoculturas, com abordagens funcionais e taxonômicas, bem como pesquisas que avaliavam a presença de filtros ambientais e a diferenciação de nichos dentro das comunidades de colêmbolos do Pampa (Winck *et al.* 2017, 2019, Jorge *et al.* 2022, 2023).

Apesar da crescente conversão de extensas áreas de campos em monoculturas e diferentes usos de solos, ocasionando grande perda de biodiversidade ainda não conhecida, o domínio do Pampa ainda apresenta uma diversidade de fitofisionomias a serem exploradas. Dessa forma, pode-se sugerir que exista um número muito maior de famílias, gêneros e espécies de colêmbolos para o estado do que o descrito nas atuais produções cientificas divulgadas. O limitado registro e a ausência de descrições taxonômicas para as espécies do RS refletem a carência de informações e a necessidade de se ampliar o número de estudos focados na taxonomia e ecologia da Classe Collembola no estado do RS e para o Pampa.

1.5. OBJETIVOS

1.5.1. Objetivo geral

Avaliar os efeitos de diferentes usos da terra na composição taxonômica e propriedades ecológicas em comunidades de Collembola (Arthropoda: Hexapoda) do solo no Pampa brasileiro.

1.5.2. Objetivos específicos

- Conhecer a fauna de Collembola em áreas do Pampa no RS;

- Realizar uma revisão na literatura sobre os registros de Collembola para o Pampa;
- Produzir chaves de identificação e diagnoses supragenéricas para ordens, famílias e gêneros registrados no Pampa, RS.
- Analisar a composição e diversidade de Collembola em diferentes usos de terra do Pampa (campos nativos e plantações de eucaliptos).
- Descrever possíveis novas espécies de Entomobryoidea para o Pampa.

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CAPÍTULO 1

DIVERSITY LOSS OF EPIGEIC COLLEMBOLA AFTER GRASSLAND CONVERSION INTO *EUCALYPTUS* FORESTRY IN BRAZILIAN PAMPA DOMAIN

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Article

Diversity Loss of Epigeic Collembola after Grassland Conversion into *Eucalyptus* Forestry in Brazilian Pampa Domain

Clécio Danilo Dias da Silva [1], Bruno Cavalcante Bellini [1,*], Vitor Mateus Rigotti [1], Rudy Camilo Nunes [1,2], Luciana da Silva Menezes, [3] and Bruna Raquel Winck [4,*]

[1] Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte,
59078-970 Natal, Brazil; danilodiass18@gmail.com (C.D.D. S.);
vmrigotti@hotmail.com (V.M.R.); rudy@ifpi.edu.br (R.C.N.)
[2] Biodiversity and Biotechnology Research Group of North Center Piaui, Federal Institute of Education, Science and Technology of Piaui, 64000-040 Teresina , Brazil
[3] Grassland Vegetation Laboratory, Department of Botany, Federal University of Rio Grande do Sul,
90010-150 Porto Alegre, Brazil; lu.silva.menezes@gmail.com
[4] Institut National De La Recherche Agronomique Clermont-Auvergne-Rhônes-Alpe, INRAE, 63000, Clermont-Ferrand, France
* Correspondence: bru.winck@gmail.com (B.R.W.); entobellini@gmail.com (B.C.B.)

Abstract: The Brazilian Pampa is a rich domain mainly represented by grasslands. Conversion of native vegetation into *Eucalyptus* plantation leads to soil degradation and losses on local fauna and flora. The objectives of this study were to compare the taxonomic structure and abundance of epigeic springtails (Collembola) in two different types of land-use in the Brazilian Pampa, native grassland and *Eucalyptus* plantation, as well as to understand the processes that may cause species loss after grassland afforestation. Specimens were sampled in 10 paired plots of grasslands and *Eucalyptus* in southern Brazil. After sampling, all specimens were sorted, counted and identified. We evaluated the taxonomic composition, alpha and beta diversity, and used Random Forest Analysis to understand the influence of environmental factors on the structure and composition of Collembola communities. We sampled 1249 specimens in 26 morphospecies, and our data support there are significant losses in native Collembola communities after the conversion of grasslands into *Eucalyptus* plantations regarding abundance, species composition, richness, and alpha diversity. Species turnover better explained the beta diversity, and plant richness and dominance were the main environmental factors driving the Collembola diversity. These results deepen the knowledge of the impacts of native grassland conversion on soil fauna.

Keywords: land-use; native grasslands; soil ecology; soil mesofauna; springtails

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1. Introduction

The Brazilian Pampa consists of remnants of very old natural ecosystems which witnessed cold and dry climates recorded even before the expansion of the Atlantic Forest in the extreme south of the country, currently the Rio Grande do Sul state (RS) [1,2]. In Brazil, this biome covers an area of 178,243 km^2, corresponding to 63% of RS and 2.07% of the national territory [3,4], structured in three main types of phytoecological units: native forest, with 9591.05 km^2 of coverage (currently 5.38% of the biome in Brazil), native grassland, with 41,054.61 km^2 (23.03%), and native transitional vegetation, with 23,004.08 km^2 (12.91%) [5].

Behind the apparently uniformity of the Pampa, studies found that this domain is highly diverse. For instance, Menezes et al. [6] recorded 56 plant species per square meter within their native vegetation. Likewise, the soil organism richness is quite high in native grasslands, such as for springtails, beetles and spiders [7–13]. Unsurprisingly, the land-use intensification, more precisely the conversion of native vegetation, is one of the main causes of local biodiversity loss [14–16]. In Brazilian Pampa the native vegetation has lost more than 50% (2.5 million hectares) of its natural extent during the past 35 years, and in 2018, converted areas (7,893,373 ha) surpassed the native areas (6,519,015 ha) in terms of their extension, while it seems the conversion rate is still rising [17].

Eucalyptus spp. represent the most planted trees in the world, and Brazil is their largest producer, holding about 7.5 million hectares of cultivation. In the Pampa, the extension of *Eucalyptus* plantation strongly increased since 2006, now occupying about 480,000 hectares [17]. However, most of the converted areas occurred in shallow soils, which in turn are also areas more susceptible to degradation [18]. In addition, there is little understanding of how the *Eucalyptus* plantation affects the local biodiversity in Pampa, and consequently, the biodiversity-related ecological functions.

Native vegetation loss is thought to affect secondary trophic levels (i.e., soil fauna) by changing the quantity and quality of food resources, as well as physicochemical properties of the soil [19,20]. Such disturbances strongly affect soil fauna, which occupies a key role in the maintenance of terrestrial ecosystems. As they are very diverse and belong to several functional groups, soil fauna can directly influence ecological functions, such as: biological control (predators, herbivores, parasites), soil decomposition and fertility (decomposers, fungivores), water regulation and soil formation (ecosystem engineers) [21–24]. Moreover, the diversity within each functional group strongly affects important ecosystem processes such as nutrient cycling, pest control, and primary productivity [25–29]. Springtails (Collembola) are among the most common, widespread and abundant forms of soil decomposers [30]. Besides being the base of food chains involving small predators, i.e., mites, beetles, pseudoscorpions, spiders, they directly feed on organic debris and fungi, impacting the rate of organic matter decomposition in the soil [30–32]. Therefore, as Collembola influence nutrient cycling and soil fertility, it is crucial to deepen our understanding about their response to the environmental changes caused by grassland afforestation.

A recent study demonstrated that Collembola diversity is lower in *Eucalyptus* plantation compared to native grassland [7]. However, considering this study was carried out in a single site of the Brazilian Pampa, our work had as main objective to investigate the impact of *Eucalyptus* plantation on epigeic Collembola communities at a regional scale and identify whether those patterns observed by Winck et al. [7] holds true at a broader scale. Precisely, we addressed the following questions:

(i) How is the epigeic Collembola diversity affected after changes in land-use/land-cover (LULC) from native grassland to *Eucalyptus* plantation?
(ii) Is the species composition of epigeic Collembola communities in the *Eucalyptus* plantation a subgroup of the community present in the original native vegetation? Or is it originated from species replacement?
(iii) What were the most important environmental factors affecting the structure and composition of the epigeic Collembola community?

Our basic hypothesis is that the conversion to *Eucalyptus*, by significantly altering the diversity of plants, the vegetation structure and soil properties, led to the reduction of diversity within epigeic Collembola communities and altered its composition mainly via species replacement as seen in previous studies [7,21].

2. Materials and Methods

2.1. Sites Description and Sampling Design

Our experimental sites were located in the Brazilian Pampa, RS, southern Brazil. The region has a subtropical humid climate with regular monthly rains, being classified as "CFa" climate according to the Köppen-Geiger system [33]. Average temperatures range between 16 and 22 °C, being the coldest month of the year July (with lows down to 10 °C) and the hottest February (with highs of 38 °C). The predominant soils are Acrisols and Leptsols and the dominant vegetation consists of a mosaic of grasses, shrubs, and forbs [34,35].

To explore the effects of grassland conversion to *Eucalyptus* plantation (timber production), we established a paired experimental design in four sites in Brazilian Pampa, with a high coverage of both land-use types: Pinheiro Machado (PIM), Jaguarão (JAG), Lavras do Sul (LAV) and São Gabriel (SAG) (Figure 1). All grassland sites were managed under extensive grazing with high animal pressure. For *Eucalyptus* plantations, plant density was about 0.11 kg/m^2 and the plantations were installed between 2007 and 2011. Within these sites we defined 10 paired plots: 10 of Grasslands and 10 of *Eucalyptus* (GE) (further details are presented in Table A1, Appendix A). All of the samplings were carried out once between November 2018 (late spring) and March 2019 (summer) in two land-use types in Brazilian Pampa, however, the pairs of GE were always sampled at the same time, in the same day.

At each plot and along a 250 m transect, soil properties were measured in three subplots spaced 83 m apart. Sites from the same pair (GE) were sampled always in the same day, controlling possible variation of climatic conditions. Soil texture, expressed as the percentages of sand, silt and clay, were measure at three standard depths (10, 20, 30 cm) using the Bouycous method, as described by [36]. For soil bulk density, three core soil samples of 8.5 cm diameter and 5.0 cm depth were taken along the 250 m transect. Each sample was dried at 105 °C and then weighted to obtain its density in g/cm^2. Vegetation was sampled in ten 1 m^2 subplots, five adjacent to the Collembola sampling subplots and extra five equally spaced along the 250 m transect for a better characterization of the vegetation. In each subplot we measured: plant species composition, plant functional groups [37], and habitat structure (plant height, measured with a ruler, one measure on each corner of the 1 m^2 square subplot and one at the center). From plant functional classification, we obtained richness of functional groups, as non-grass-like species and rosettes (*Eryngium* spp. like species). Finally, from raster layer datasets, we described for each plot: the annual temperature and precipitation (resolution of 1000 m, WorldClim), annual evapotranspiration (resolution of 250 m, MODIS Web), land-surface temperature (resolution of 250 m, MODIS), and elevation (resolution of 90 m, SRTM DEM)[38–40].

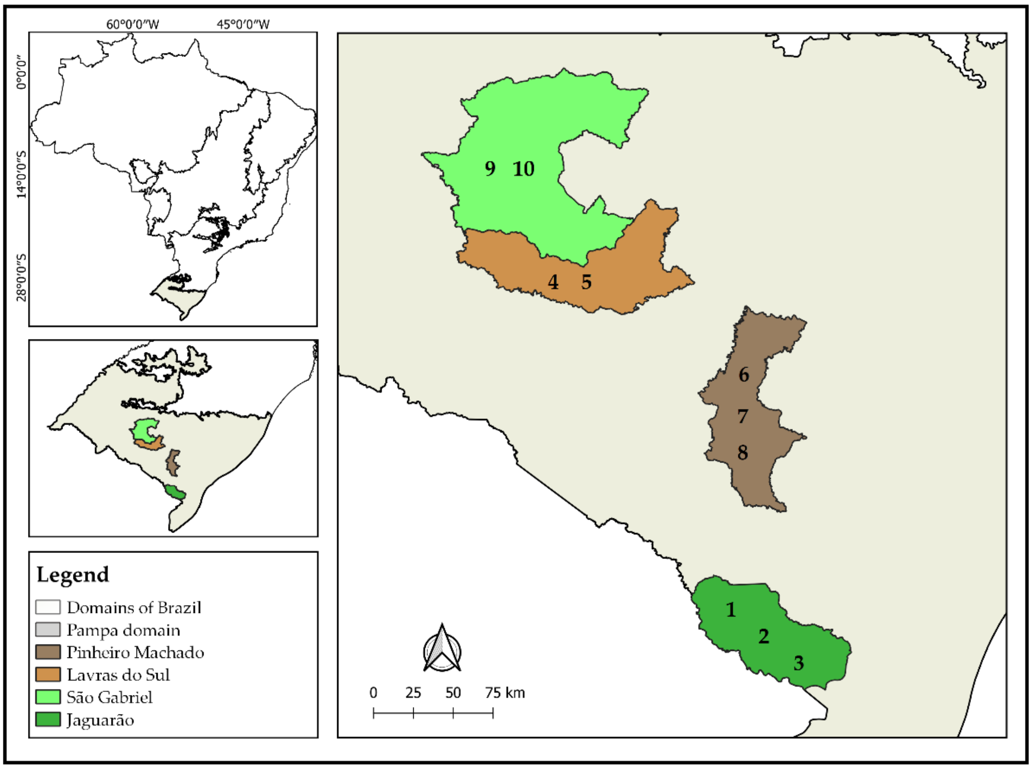

*Figura 6: Sampled sites (***Figure 1.** Sampled sites (municipalities of RS, Brazil) distribution within the Brazilian Pampa. The numbers within each site represent the IDs and locations of the paired plots of Grasslands and Eucalyptus (GE).

2.2. Collembola Sampling and Taxonomic Identification

Collembola was surveyed in five subplots spaced 50 m apart. The specimens were sampled using pitfall traps which consisted of 50 mL Falcon tubes with 30 mm of diameter filled with 70% ethanol plus a drop of detergent. At each subplot we placed three pitfalls, adding up to 15 traps per transect (land-use) and 30 per sampled pair. Traps remained installed for 24 h. We choose such sampling methodology since we were aiming to investigate the epigeic springtails. However, it is important to state that pitfall traps show limitations in sampling all springtail communities, as many taxa live belowground (as the euedaphic Isotomidae) and would be better sampled by the use other methodologies such as Berlese-Tullgren funnels.

After the collections, the biological material was investigated using a stereomicroscope and the springtails were sorted, quantified, and morphotyped. We considered as rare species the taxa with 10 or less specimens per land-use. Posteriorly, glass slides were mounted following Arlé and Mendonça [41] and Jordana et al. [42] methods combined, in which the specimens were cleared in Nesbitt's and Arlé's fluids and were mounted in glass slides in Hoyer's medium. Glass slides were dried at 50 °C for about three days and were studied using a Leica DM750 optical microscope with phase contrast. The taxonomic identification was made following specially the keys and diagnoses provided by Jordana et al. [42], Massoud [43], Betsch [44], Christiansen and Bellinger [45], Bretfeld [46], Potapov [47], Bellini and Godeiro [48], Cipola et al. [49], and Bellinger et al. [50]. The specimens were deposited at the Collembola Collection of the Biosciences Center, Federal University of Rio Grande do Norte, Brazil (CC/UFRN).

2.3. Ecological Data and Statistical Analysis

All statistical analyses were performed using the R software (version 4.1.2). Our data were organized into two matrices: **matrix W**, with the abundance and species richness of springtails of each community in different land-uses (native grasslands and *Eucalyptus* plantation), and **matrix E**, with the environmental data.

2.3.1. Species Composition

Species composition was investigated using Principal Coordinate Analysis (PCoA) based on Euclidian distance after Hellinger transformation. We used "*vegan::vegdist*" to calculate the distance matrix, and "*stats::cmdscale*" function to run PCoA [51]. Then, a Permutation Multivariate Analysis of Variance (PERMANOVA) with 999 permutations ("*vegan::adonis*" function) was calculated to explore differences in species composition between both land-uses.

2.3.2. Beta Diversity

For each pair of LULC, we identify whether the species composition of Collembola in *Eucalyptus* plantation resulted from species replacement after the conversion or represented a subset of species which previously inhabited the original grasslands. For that, we used the function "*betapart::beta.temp*" [52] to compute the temporal dissimilarity using Sørensen dissimilarity index (βSOR). Here we are considering that the native grassland sites were a state prior to the *Eucalyptus* plantation. We also computed both turnover (Simpson index of dissimilarity, βSIM) and nestedness (nestedness resultant index of dissimilarity, βSNE) components [53–55].

2.3.3. Alpha Diversity

We calculated the total abundance of Collembola and alpha diversity indices of each community. Species richness (S) was estimated by rarefaction method using the "*iNEXT::iNEXT*" function [56]. We also calculated the Shannon index (H'), which considers the species richness and each species relative abundances, and Pielou evenness index (J') which indicates if the different species have similar or divergent abundances in the investigated communities [57,58]. Both H' and J' were calculated using the "*vegan::diversity*" function [51]. The total abundance and alpha diversity were tested for their normality and homoscedasticity using Shapiro-Wilk and Levene tests, respectively. For that, we used both "*stats::shapiro.test*" and "*DescTools::LeveneTest*" functions. Posteriorly, the effects of land-use types on alpha diversity were determined by Linear Mixed Models (LMM), which were calculated using the "*nlme::lme*" function [59]. Land-use types (grasslands and *Eucalyptus* plantation) were the predictor variables (fixed effect), and each pair nested within the sites were inserted as random effects in the models to account for paired experimental design.

2.3.4. Effects of the Environmental Factors on the Epigeic Collembola Community

To explore the responsiveness of the epigeic Collembola community to environmental factors, we run the Principal Component Analysis (PCA) and the Random Forest Analysis (RF). The PCA was applied to identify the collinearity among variables and select those which could be used in RF (Figure A1, Appendix A), using "*FactorMineR::PCA*" function, and correlated variables were removed from the dataset. To estimate the importance of different environmental factors on Collembola diversity we used the increases in MSE (mean squared error) of variables, in which higher MSE% values imply on more important variables. The RF analyses were run using "*randomForest*" and "*rfpermute*" packages [60,61].

3. Results

3.1. Epigeic Collembola Community in the Two Land-Use Types

From a 24-h sampling, we collected a total of 1249 specimens of springtails belonging to 26 morphospecies, 19 genera and 11 families in both native grasslands and *Eucalyptus* plantation. The taxonomic composition, total and relative abundances of each taxon in both land-use types are detailed in Table 1. We could not clearly assign any species to taxa already recorded in Brazil or other countries of the Neotropical Region, suggesting at least part of these morphospecies may be actually new to the science.

Table 1. Morphospecies and abundance of epigeic springtails (Collembola) in different land-use types in Brazilian Pampa grasslands.

Family/Morphospecies		**Native Grassland**		***Eucalyptus***	
		Total Abundance	**Relative Abundance (%)**	**Total Abundance**	**Relative Abundance (%)**
Bourletiellidae	*Rastriopes* sp.1	01	0.10	00	0.00
	Prorastriopes sp.1	14	1.43	00	0.00
	Prorastriopes sp.2	03	0.30	00	0.00
Brachystomellidae	*Brachystomella* sp.1	04	0.40	00	0.00
Dicyrtomidae	*Ptenothrix* sp.1	00	0.00	04	1.48
Entomobryidae	*Entomobrya* sp.1	192	19.61	02	0.74
	Entomobrya sp.2	62	6.33	00	0.00
	Entomobrya sp.3	174	17.77	06	2.22
	Entomobrya sp.4	10	1.02	53	19.63
	Entomobrya sp.5	10	1.02	00	0.00
	Lepidocyrtus sp.1	111	11.33	99	36.67
	Seira sp.1	06	0.61	00	0.00
Hypogastruridae	*Hypogastrura* sp.1	14	1.43	00	0.00
	Xenylla sp.1	70	7.15	19	7.04
Isotomidae	*Desoria* sp.1	80	8.17	12	4.44
	Desoria sp.2	65	6.63	00	0.00
	Folsomia sp.1	22	2.24	00	0.00
	Isotomurus sp.1	18	1.83	00	0.00
	Proisotoma sp.1	26	2.65	00	0.00
Katiannidae	*Katianna* sp.1	13	1.32	00	0.00
	Katianna sp.2	03	0.30	00	0.00
	Sminthurinus sp.1	02	0.20	00	0.00
Neanuridae	*Pseudachorutes* sp.1	16	1.63	07	2.59
Orchesellidae	*Dicranocentrus* sp.1	00	0.00	31	11.49
Paronellidae	*Trogolaphysa* sp.1	00	0.00	37	13.70
Sminthurididae	*Sphaeridia* sp.1	63	6.43	00	0.00

Linear Mixed Model

Land-Use Types	**Total Abundance**	**F Value**	***p* Value**
Grassland	979	12.86	0.0059
Eucalyptus	270		

The LMM revealed significant differences in epigeic Collembola abundances between both land-use types ($p = 0.0059$, Table 1). Furthermore, the abundance within each taxonomic level varies between land uses. For example, we recorded a total of 979 individuals belonging to 17 genera and 23 morphospecies in native grasslands. The family with the highest abundance was Entomobryidae (with 57.69%), followed by Isotomidae (21.52%), Hypogastruridae (8.58%), Sminthurididae (6.43%), Bourletiellidae (1.83%), Katiannidae (1.92%), Neanuridae (1.63%), and Brachystomellidae (0.40%). In *Eucalyptus* plantation, however, we only found a total of 270 individuals belonging to 8 genera and 10 morphospecies. As observed for native grasslands, the family with the highest abundance was Entomobryidae (with 59.26%), but it was followed by Paronellidae (13.70%), Orchesellidae (11.49%), Hypogastruridae (7.04%), Isotomidae (4.44%), Neanuridae (2.59%), and Dicyrtomidae (1.48%).

Regarding morphospecies abundance, we recorded 10 abundant species in native grasslands, with *Entomobrya* sp.1 and *Entomobrya* sp.3 as the most abundant ones, respectively. We also found 13 rare species, and *Rastriopes* sp.1 and *Sminthurinus* sp.1 were the rarest taxa. On the other hand, in the *Eucalyptus* plantation we observed four abundant species, with *Lepidocyrtus* sp.1 and *Entomobrya* sp.4 as the most abundant taxa, and six rare species, being *Entomobrya* sp.1 and *Ptenothrix* sp.1 the rarest ones (Table 1).

3.2. Effects after Grassland Conversion into Forestry

The PERMANOVA analysis revealed that native grassland conversion to *Eucalyptus* strongly affects epigeic springtails morphospecies composition ($F = 6.304$; $R^2 = 0.25957$; $p < 0.001$). This result is evidenced in PCoA (Figure 2), which represent 51% of the data variation, and we found a clear separation between both native grassland and *Eucalyptus* plantation. Furthermore, we found an association of *Entomobrya* sp.1 and *Entomobrya* sp.2 to the native grasslands, while *Dicranocentrus* sp.1 and *Entomobrya* sp.4 were associated with *Eucalyptus*. In addition, *Eucalyptus* crops PCoA values were more dispersed than the native grasslands ones, indicating high variability of morphospecies composition in the former land-use.

Even though seven morphospecies were shared by the two land-uses, we found 16 morphospecies restricted to grasslands and only three to *Eucalyptus* plantations. The restricted species found in grassland sites were *Prorastriopes* sp.1, *Prorastriopes* sp.2, *Rastriopes* sp.1, *Brachystomella* sp.1, *Entomobrya* sp.2, *Entomobrya* sp.5, *Seira* sp.1, *Hypogastrura* sp.1, *Desoria* sp.2, *Folsomia* sp.1, *Isotomurus* sp.1, *Proisotoma* sp.1, *Katianna* sp.1, *Katianna* sp.2, *Sminthurinus* sp.1 and *Sphaeridia* sp.1, while those ones restricted to *Eucalyptus* plantation were *Ptenothrix* sp.1, *Dicranocentrus* sp.1, and *Trogolaphysa* sp.1. (Table 1, Figure 2). Furthermore, after exploring β-diversity components in each pair of LULC (Table A2, Appendix A), we observed that the differences in species composition between both LULC resulted more from species turnover (βSIM ranging from 0.5 to 1) rather than species nestedness (βSNE ranging from 0 to 0.2).

We found clear evidence that grassland conversion into *Eucalyptus* lead to a decrease of species richness (Figure 3A), resulting in a significant difference between both LULC ($p = 0.0038$). Specifically, epigeic Collembola richness was 2.3-fold higher in native grasslands ($S' = 23$) compared to *Eucalyptus* plantations ($S' = 10$). The alpha diversity analysis also remarked that grassland areas had a higher species diversity ($H' = 2.317$, $p = 0.0032$) compared to *Eucalyptus* ($H' = 1.545$) (Figure 3B). However, no statistical difference was observed in the evenness index (Figure 3C, $p = 0.31$).

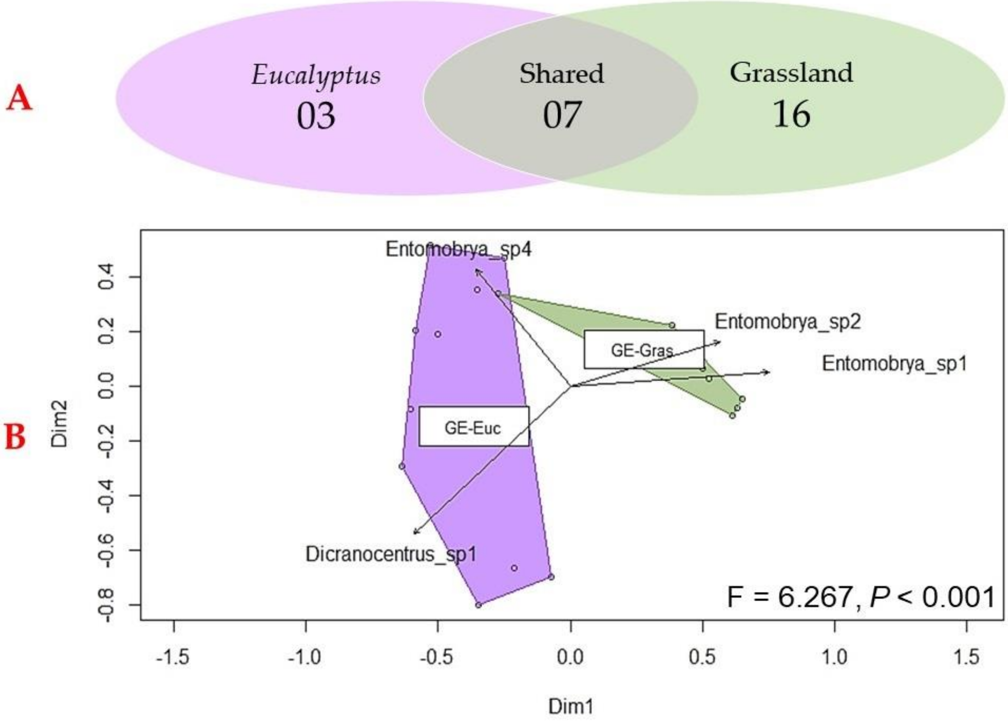

Figure 2. Comparison between epigeic Collembola communities in different LULC in Brazilian Pampa grasslands: (**A**) Venn diagrams showing shared morphospecies between Grassland and *Eucalyptus*; (**B**) Species composition (green polygon—grasslands, and purple polygon—*Eucalyptus* plantation).

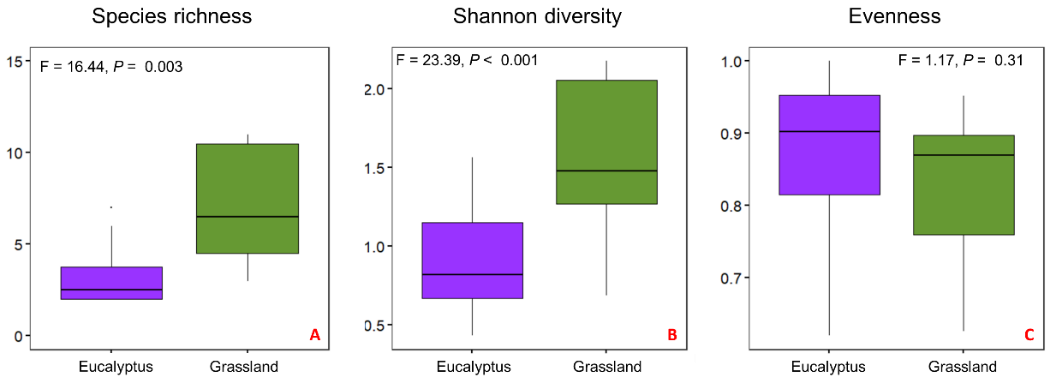

Figure 3. Comparison between epigeic Collembola communities in different LULC in Brazilian Pampa grasslands: (**A**) species richness; (**B**) Shannon index and; (**C**) evenness index.

Lastly, Random Forest analyses showed that plant richness and plant dominance were the major driving factors influencing epigeic Collembola abundance and composition in the sampled sites, while plant richness was the main predictor favoring epigeic Collembola diversity (Figure 4).

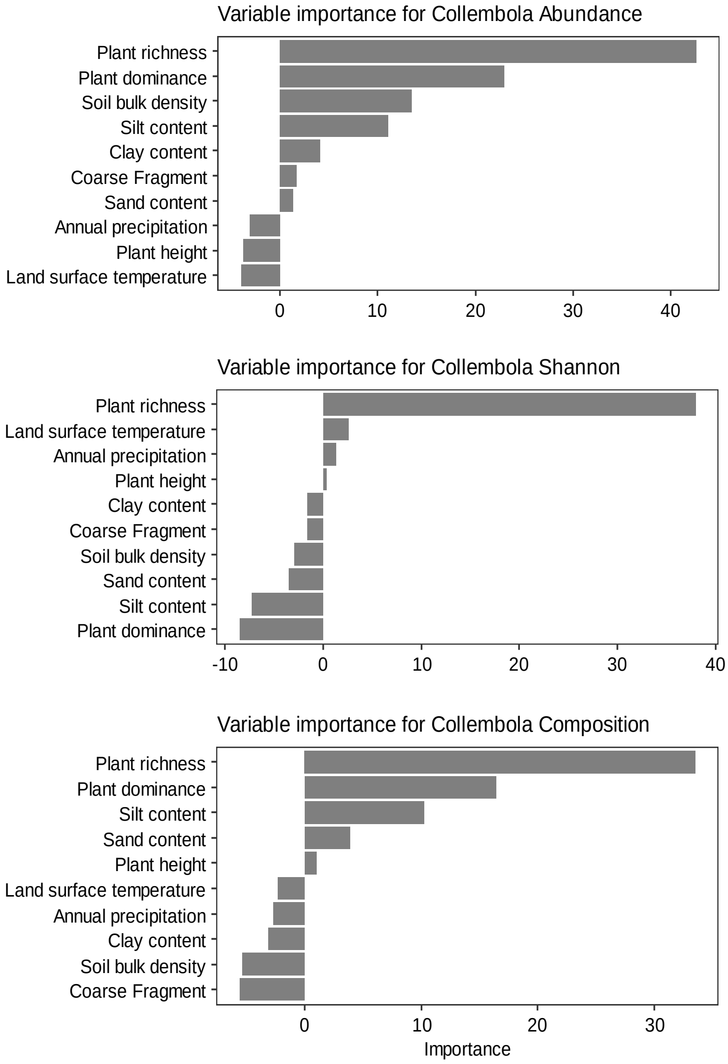

Figure 4. Effect of environmental variables on epigeic Collembola composition and structure using Random Forest Analysis. The accuracy importance measure was calculated for each tree and averaged over the forest (5000 trees). High percentage increase in the MSE (mean squared error) values implies in more important predictors.

4. Discussion

4.1. Taxa Occurrence in the Brazilian Pampa

Here we have compiled so far the most comprehensive taxonomically verified checklist of Collembola from the Pampa biome, considering different LULC types. Most of the studies that used Collembola as a model group to describe soil fauna communities were performed in few sites of the Pampa [7,8,62], while we carried out our study on a broad scale comprising sites with high potential of grassland afforestation. Also, although our identification has been up to the genus level for all collected families, as the species could not be clearly assigned to any nominal taxa, this is one of the few studies that detailed the communities of Collembola until such taxonomic resolution. Such results improved our understanding about the Collembola biodiversity in Brazilian Pampa, as well as allowed us to better identify the real impact of grassland afforestation. Currently, only three nominal (described) species of springtails are known for the RS state, and none of them were recorded from the Pampa domain [63], while we were able to sample 26 morphospecies (Table 1). These data highlight the limited taxonomic efforts concerning the Collembola in Pampa, a fauna which has an elevated potential of endemism but it is not known in its most basic aspects.

All families of springtails herein recorded were already registered in Brazil, while most genera gather nominal species previously recorded to the country, with the exception of *Rastriopes*, *Prorastriopes* (both Bourletiellidae) and *Katianna* (Katiannidae) [63]. Even so, the first two genera were previously recorded from the northeastern Brazil with morphospecies, while all of the three genera have nominal species found in the Neotropical Region [50,64].

We observed that Entomobryidae was the most abundant and rich family in both LULC types (Table 1). This pattern is expected, since this is the most diverse family of Collembola, with more than 1700 species and 40 genera described [50], and our methods tend to favor the sample of this group of organisms [65]. In Brazil, Entomobryidae is the most studied Collembola family, with 106 species described so far [63], and we identified that the dominant genera and species vary among the Brazilian regions. For instance, in Caatinga, a semiarid phytogeographic domain seen in northeastern Brazil, preliminary data point out *Seira* spp. as the major components of the Collembola communities [66,67], while *Entomobrya* spp. are notably the most representative in the Pampa, as found in previous works and in our study [7,8]. This variation is probably a consequence of the habitat characteristics (climatic, soil, and vegetation) of each region, which contribute significantly in structuring Collembola communities. However, detailed analysis of the influence of habitat characteristics on Collembola in a large geographic scale is still missing in Brazil for soil organisms.

4.2. Effects of LULC Changes on Epigeic Collembola Community

We tested the effects of grassland afforestation on the responses of Collembola communities in the Pampa biome. We found that (i) *Eucalyptus* plantation reduced the abundance and diversity of epigeic Collembola communities (Figure 3); and (ii) caused changes in species composition by the replacement of taxa possibly more adapted to closed canopy habitats. Also, as indicated by the Venn diagram (Figure 2A), (iii) native grassland areas present a higher number of unique morphospecies compared to *Eucalyptus* plantations, and most of them were classified as rare. Finally, we also found that (iv) the main environmental factors influencing the epigeic Collembola community were plant richness and dominance.

Our results agree with those from other studies previously carried out in the Brazilian Pampa which compared different land-use types and agricultural intensification [7,62]. In general, they found that *Eucalyptus* plantations cause reduction in functional and/or taxonomic diversity, and also alter species composition within the Collembola community. However, our study provides complementary information. For example, we identified that both LULC types shared only seven morphospecies out of 26, and the epigeic Collembola composition in *Eucalyptus* plantation resulted from species turnover (replacement) rather than nestedness. Such findings support the hypothesis that the conversion to *Eucalyptus* caused local extinctions, selecting species most adapted to the new conditions (i.e., shade habitat and niche simplification).

Although the natural communities were dominated by a few numbers of morphospecies (i.e., *Entomobrya* sp.1 and *Entomobrya* sp.2), the high richness and diversity found in the grassland could be related to the high number of habitat and feeding niches provided by a heterogeneous plant community [68–71]. Due to the selective grazing behavior of the animals (cattle and sheep) in native grasslands, the vegetation structure represents a mosaic of intensely grazed and ungrazed patches (i.e., hard leaves species such as *Eryngium* sp. and *Baccharis* sp. are less preferred by grazers) [72]. Such heterogeneous vegetation structure favors the emergence of different microhabitats and also contributes to a greater amount of available food resources for soil fauna communities [73]. More specifically for the Collembola community, since springtails are tiny organisms mostly ranging from 1 to 5 mm [50], it is expected that even microclimate variations within a given habitat strongly influence the composition and structure within the communities [74–76]. Plant diversity may favor the co-occurrence between different species with different food preferences, considering they feed on a wide range of food, such as living and dead plant tissues, pollen, grain, soil mesofauna, and fungi [31,77]. Finally, the presence of ungrazed patches can act as a refuge for diversity [73], as a shelter for rare species [78]. This statement may explain the high number of rare morphospecies found in grassland sites in our study.

In addition to the habitat simplification caused by grassland afforestation, some studies also supported that *Eucalyptus* strongly alters the physicochemical properties of the soil, which in turn act as ecological filters on the regional pool of species [7,79]. For instance, soils under *Eucalyptus* plantations tend to be drier, more acidic and nutrient-poor [80,81], and present low microbial biomass and activity [82]. Such constraints not only affect Collembola microhabitats, but also influence their food sources. Even further, these ecological filters induced by *Eucalyptus* plantation may select species with functional traits more adapted to lower pH, and closed habitats (with reduction of eyes and pigmentation, for example). In fact, such soil modifications may negatively affect the physiological functions of most Collembola, with consequences on their reproduction rates, life cycles, and overall survival [30,83–86]. So, the conversion of native grasslands into *Eucalyptus* results in changes in epigeic Collembola communities as we observed, which can include local extinctions [87].

4.3. Conservation Perspectives of Soil Fauna in the Brazilian Pampa

Our results support an alarming view of the strong negative effects of native grasslands conversion into *Eucalyptus* forestry on the epigeic Collembola diversity. If our data are representative of what happened in most converted areas, it is possible to expect an overall local loss of more than half of the species richness and more than two thirds of the total abundance of epigeic Collembola, with potentially devastating effects for the edaphic ecosystems and, consequently, for the ecosystem services provided by these animals [30–32]. In this scenario and considering the continuous losses of native grasslands in the Brazilian Pampa [17], it is expected that a significant amount of its Collembola diversity has been locally lost without ever been catalogued, described or studied. This is also probably valid for other representatives of the edaphic fauna as well, and conservation strategies must be implemented to preserve what remains of the native soil mesofauna diversity in the Brazilian Pampa. It is important to expand taxonomic inventories in the remaining fragments of native vegetation, in addition to studies that aim to understand the mesofauna community indexes and how the diversity is influenced by the conversion of natural landscapes. Furthermore, conservation strategies specifically designed for the soil invertebrates are rare or non-existent in most of Brazil, prevailing policies which aim to conserve vertebrates [88]. Although vertebrate management and conservation plans involve the protection of large areas, which end up protecting an entire biota associated with them including the edaphic fauna, it is not possible to affirm that such strategies cover the specific needs of the latter fauna [30,74].

5. Conclusions

The obtained results allow for better understanding on how native grassland conversion into *Eucalyptus* forestry impacts the epigeic Collembola community in Brazilian Pampa. We found the establishment and growth of such crops decrease the native abundance, species richness and alpha diversity of epigeic springtails, and the composition between the two different land-uses is modified due to species turnover. Moreover, our models support the loss of plant richness and dominance in artificial forests of *Eucalyptus* are key features to explain the decrease on abundance and composition of epigeic springtails in the sampled sites. All of these data combined with the known negative impacts of changes in land-use, especially in growing *Eucalyptus* monocultures, may have conservationist and applied ramifications, as they can point to more sustainable methods of land use.

Author Contributions: Conceptualization, C.D.D. S., B.C.B., and B.R.W.; methodology, C.D.D. S., B.C.B., L. S.M., and B.R.W.; software, C.D.D. S., V.M.R., and B.R.W.; validation, C.D.D. S., B.C.B., and B.R.W.; formal analysis, C.D.D. S. and B.R.W.; investigation, C.D.D. S.; resources, B.C.B. and B.R.W.; data curation, C.D.D. S., V.M.R., and B.R.W.; writing—original draft preparation, C.D.D. S., B.C.B., R.C.N., and B.R.W.; writing—review and editing, B.C.B., V.M.R., R.C.N., L. S.M., and B.R.W.; visualization, B.C.B., V.M.R., R.C.N., L. S.M., and B.R.W.; supervision, B.C.B. and B.R.W.; project administration, B.C.B. and B.R.W. ; funding acquisition, B.C.B. and B.R.W. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Ethical review and approval were waived for this study, due to Brazilian laws which do not require permission from an institutional ethics committee on the use of animals for taxonomical/ecological studies with microarthropods.

Informed Consent Statement: Not applicable.

Data Availability Statement: All data are contained within the article. All biological material is deposited at CC/UFRN as previously stated.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

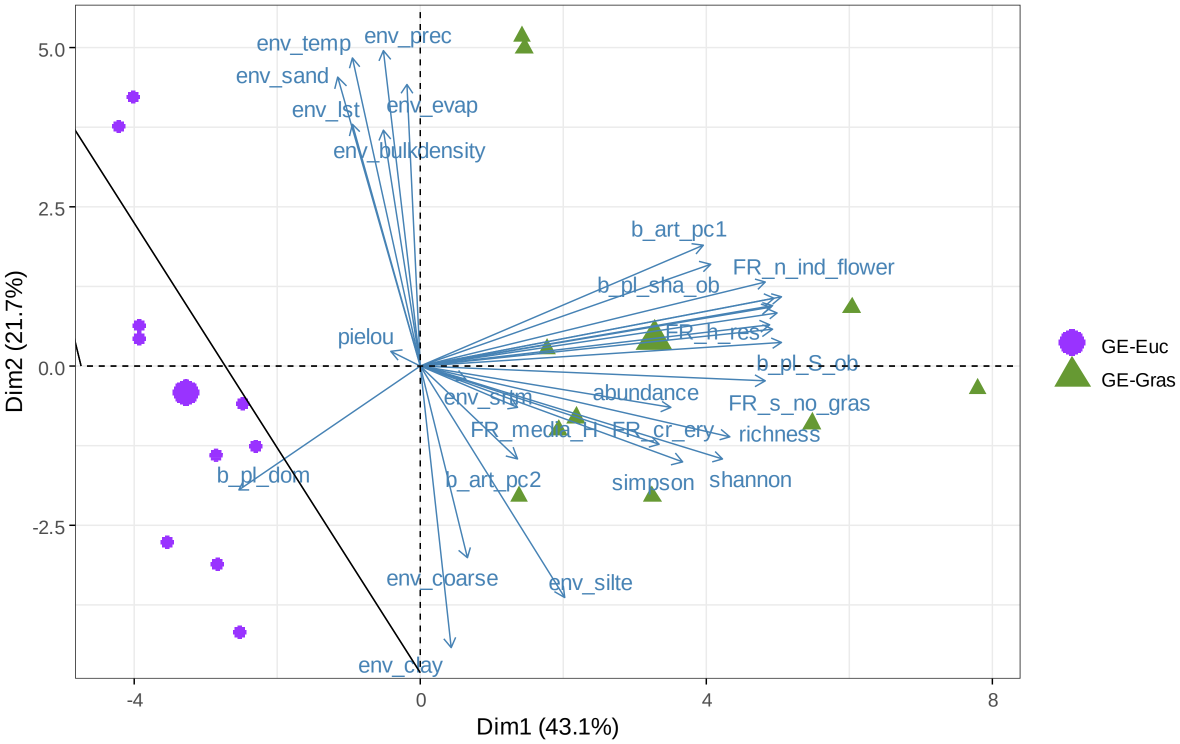

Figure A1. Principal component analysis of all ecological indices and environmental factors (plant community, climate, and soil) in different land-use types across Brazilian Pampa region.

Table A1. Sites, pairs and parcels identifications, different land-uses (Gras = native grassland, Euc = *Eucalyptus* plantation) and coordinates of the sampled sites of this study.

Site	Par	Lulc	Parcel	Geographic Coordinates	
				Longitude	Latitude
JAGUARÃO (JAG)	1	Gras	GE_JAG_Gras_1	−53,397,067	−32,239,946
		Euc	GE_JAG_Euc_1	−53,365,464	−32,239,994
	2	Gras	GE_JAG_Gras_2	−53,319,039	−32,210,709
		Euc	GE_JAG_Euc_2	−53,349,856	−32,240,435
	3	Gras	GE_JAG_Gras_3	−53,304,145	−32,227,443
		Euc	GE_JAG_Euc_3	−53,301,572	−32,245,974
LAVRAS DO SUL (LAV)	4	Gras	GE_LAV_Gras_2	−54,263,648	−30,885,178
		Euc	GE_LAV_Euc_2	−5,431,076	−30,860,155
	5	Gras	GE_LAV_Gras_3	−54,267,129	−30,962,529
		Euc	GE_LAV_Euc_3	−54,252,869	−309,676
PINHEIRO MACHADO (PIM)	6	Gras	GE_PIM_Gras_1	−53,602,698	−31,339,271
		Euc	GE_PIM_Euc_1	−5,359,796	−31,343,839
	7	Gras	GE_PIM_Gras_2	−53,577,106	−31,385,678
		Euc	GE_PIM_Euc_2	−53,571,586	−31,391,762
	8	Gras	GE_PIM_Gras_3	−53,499,849	−31,402,764
		Euc	GE_PIM_Euc_3	−53,509,913	−31,412,028
SÃO GABRIEL (SAG)	9	Gras	GE_SAG_Gras_1	−54,324,136	−30,059,119
		Euc	GE_SAG_Euc_1	−54,320,563	−30,049,282
	10	Gras	GE_SAG_Gras_2	−54,321,307	−30,083,604
		Euc	GE_SAG_Euc_2	−54,327,398	−30,069,851

Table A2. Beta diversity partitioning for each pair of Grassland and Eucalyptus (GE) plantation.

LULC Pairs	βSIM	βSNE	βSOR
GE_JAG_1	0.71	0.04	0.75
GE_JAG_2	1	0	1
GE_JAG_3	0.75	0	0.75
GE_LAV_2	0.5	0.1	0.6
GE_LAV_3	0.5	0.25	0.75
GE_PIM_1	0.67	0.2	0.87
GE_PIM_2	0.67	0.21	0.88
GE_PIM_3	1	0	1
GE_SAG_1	0	0.5	0.5
GE_SAG_2	1	0	1

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CAPÍTULO 2

MULTIPLE-TRAIT APPROACHES SUPPORT THAT EPI- AND ENDOGEIC SPRINGTAILS RESPOND DIFFERENTLY TO GRASSLAND AFFORESTATION BY EUCALYPTUS IN BRAZILIAN PAMPA

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Multiple-trait approaches support that epi- and endogeic springtails respond differently to grassland afforestation by *Eucalyptus* in Brazilian Pampa

Clécio Danilo Dias da Silva[1]*, Bruna Claudia S. Jorge[a3]*, Bruno C. Bellini[1], Luciana Regina Podgaiski[3], Valério Pillar[3], Bruna Raquel Winck[2]

[1]Department of Botany and Zoology, Biosciences Center, Universidade Federal do Rio Grande do Norte, Natal, RN, 59078-970, Brazil;

[2]Institut National De La Recherche Agronomique Clermont-Auvergne-Rhônes-Alpe, INRAE, 63000 Clermont-Ferrand, France

[3]Department of Ecology, Biosciences Center, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, 91501-970, Brazil

* Corresponding authors: brunnaclaudia@hotmail.com / danilodiass18@gmail.com

Highlights

- We evaluated the effects of grassland conversion for *Eucalyptus* on different aspects of Collembola functional diversity and composition
- We observed that the conversion of grasslands resulted in changes in the composition of springtails, with epigeic communities associated with native grasslands and endogeic communities associated with *Eucalyptus* crops.
- We detected a stronger effect of grassland afforestation on the richness of epigeic Collembola compared to the endogeic community.

Abstract

Exotic tree afforestation is seen as a sustainable land-use practice, yet evidence on its impact on soil diversity is scarce. Springtails ecological role depends on functional traits, which may serve as indicators for environmental changes and functional shifts in the soil community. Here we evaluate the effects of grassland afforestation by *Eucalyptus* on the functional diversity and composition of Collembola communities life-forms. The study was conducted in 20 paired areas of native grasslands and *Eucalyptus* plantations in the Brazilian Pampa. We sorted and measured the specimens traits and categorized morphospecies as epigeic or endogeic, using an ecomorphological index. Diversity indices were calculated, and the impact of *Eucalyptus* afforestation was assessed using effect size analyses. The study revealed significant effects of land use types on morphospecies ($p=0.04$) and life forms ($p<0.05$). Grassland areas had more epigeic communities, while endogeic ones were associated with *Eucalyptus.* Afforestation had no impact on epigeic communities' functional indices but positively affected body size, appendages size, and presence of scales. In endogeic communities, *Eucalyptus* afforestation negatively affected richness and functional divergence, leading to reduced body pigmentation, ocelli, legs and furca sizes. These findings emphasize the impact of *Eucalyptus*-driven reforestation on springtails in distinct soil compartments.

Keywords: Biodiversity conservation; Functional Ecology; Land-use change; Soil fauna; Collembola.

Introduction

Anthropogenic activities, such as afforestation, have been shaping biological communities over the last century, determining patterns of taxonomic, functional and phylogenetic biodiversity (Decaëns et al., 2006). Efforts of conservation ecology are traditionally focused on measures of species diversity of the aboveground wildlife, while soil biodiversity is often neglected. Conversely, soil biodiversity comprises more than 25% of terrestrial biodiversity (Bardgett and Van Der Putten 2014), driving terrestrial nutrient cycling through the trophic chain of decomposition, and also supporting and regulating ecosystem functioning through its effects on primary productivity (Jónsson and Davíðsdóttir 2016; Briones 2018).

Springtails (Collembola) are broadly used as a model group of the study of soil communities, being useful bioindicators as they respond to changes in soil chemistry, pH, moisture, litter quality and land-use type and management (Santos et al., 2018; Pompeo et al., 2016; Rossetti et al., 2015). Springtails have massive abundance in soil environments, with numerous species affecting ecosystem functioning at the local scale through decomposition and mineralization processes, especially by feeding on a wide range of microorganisms and organic sources (Hopkin 1997; Salmon et al., 2014; Čuchta et al., 2019).

The ecological role of springtails relies on their functional traits - which are morphological, physiological and behavioral characteristics linked to the ecological niche of the species (Violle et al., 2007; Abgrall et al., 2017). Springtails present a wide range of eco-morphological and life-history traits, whose states can be clustered into life-form types related to the vertical distribution in soils and dispersal ability (Parisi et al., 2005; Martins et al., 2015). Collembola which live on the soil surface (epigeic or epedaphic) are usually highly pigmented, presenting large body sizes (~2mm), well-developed appendices (antennae, legs, and/or furca), high ocelli number (~ 6 or 8), while some taxa may have scales and/or extra body chaetae. Most epigeic taxa feed on litter or fungi (Martins da Silva et al., 2016; Potapov et al., 2020). On the other hand, Collembola which live within the soil (endogeic or euedaphic) show smaller and usually cylindrical bodies, are less mobile, present shorter appendices, a reduction or absence of body pigmentation and ocelli, but may have some better developed sensorial organs (i.e., post-antennal organ and antennal sensilla) (Salmon et al., 2014;

Martins da Silva et al., 2016). In general, endogeic species feed mostly on soil microbiota (Potapov et al., 2016).

Since springtails life-form comprises a set of traits linked to an ecological role, changes in the trait composition and distribution (functional diversity) within a community may indicate relevant effects on ecosystem functioning (Eckert et al., 2023). Functional diversity (FD) is the distribution of species and abundance of a community in a niche space, and it is composed by three major independent components: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Mason et al., 2005). While FRic regards the amount of niche space occupied by a species within a community, FEve corresponds the evenness of the distribution of abundance in a niche space, and FDiv answers how abundance is distributed within the volume of functional trait space occupied by species (Villéger et al., 2008). Regarding functional composition, the community-weighted mean trait values (CWM) reflects the dominance of each functional trait within a given community, where this dominance depends on the abundance or biomass of the species (Garnier et al., 2004, Ricotta and Moretti, 2011).

The Pampa biome comprises biodiversity-rich grasslands ecosystems, which are often misunderstood as degraded or as a stage of secondary succession process. In South Brazil, Pampa grasslands were aggressively converted into monocultures summing up a loss of more than 50% (2.5 million) of its natural extent during the past 35 years, and in 2018, converted areas (7.893.373 ha) surpassed the extension of native areas (6.519.015 ha) (MapBiomas, 2022). Artificial afforestation is the land-use category with a major increase in the last ten years (with an annual increase above 5%), and afforested areas now occupy about 480.000 ha of the Brazilian Pampa, with about 60% of the plantations being of *Eucalyptus* trees (MapBiomas, 2022). Although the afforestation effects on Pampa grasslands were evaluated for plant and vertebrate communities (Pillar et al., 2002; Souza et al., 2013; Dias et al., 2013; Saccol et al., 2017), there is a clear gap of knowledge regarding the response of soil communities to such disturbance. Winck et al. (2017), Silva et al. (2022), and Jorge et al. (2023) investigated the effects of Pampa afforestation using springtails as model organisms, however such studies did not evaluate its effects on all components of functional diversity.

The aim of this study was to measure the effects of grassland afforestation by *Eucalyptus* on the different dimensions of the functional diversity and composition of springtails communities. Moreover, we proposed a compartmentalized analysis to evaluate separately the effects on epi- and endogeic species. We firstly hypothesized that the grassland afforestation with *Eucalyptus* would modify the functional composition and structure of springtails, reducing the functional richness and diversity in both epigeic and endogeic compartment. We expected that the abrupt transition from an open environment to a closed one (Martins da Silva et al., 2016; Winck et al., 2017, 2019; Silva et al., 2022), besides the changes in habitat heterogeneity, would select and modify traits related with the body size, appendages, pigmentation level, and the presence of scales and sensorial organs, promoting the recruitment of more tolerant to the new conditions of closed areas (Salmon et al. 2014; Pollierer and Scheu, 2017; Jorge et al., 2023, Eckert et al., 2023).

Material and Methods

Site description

The study was carried out in the Pampa, in the state of Rio Grande do Sul, Brazil. The climate of the region is CFa - humid subtropical with hot summer without dry season (Köppen-Geiger system; Peel et al., 2007; Alvares et al., 2013). The annual precipitation across the study sites ranges from 1400 to 1700 mm, with no marked seasonality (Wrege et al., 2012). The mean annual temperature is 18.8 °C (Moreno 1961). The predominant types of soils are Acrisols and Leptsols (Modernel et al., 2016). The natural vegetation consists of a mosaic of grasses, shrubs, and forbs depending on grazing intensity (Fischer et al., 2019; Ferreira et al., 2020).

Sampling design

Springtails communities were sampled using a paired transect design. We selected 10 sites located in four municipalities in the Rio Grande do Sul state: Pinheiro Machado (PIM), Jaguarão (JAG), Lavras do Sul (LAV) and São Gabriel (SAG). At each site, we placed a transect of 200 m on native grassland which was paired with another transect with the same length on a nearby *Eucalyptus* plantation. The number of pairs at each site ranged from two to four, and each site was chosen at least 1 km apart from each other. The transect lines were installed at least 100 m away from the grassland/*Eucalyptus* edge. Each transect pair was located on the same soil and relief conditions. All grassland sites were managed under extensive grazing by cattle and sheep. All *Eucalyptus* plantations were about 10 years-old during the samplings, and were planted on areas of previous native grassland. See Table S1 for more sampling details.

Springtails community data

At each transect the springtails were sampled at every 50 m, resulting in five subplots per transect line. We used two sampling methods in order to encompass all soil springtails life forms: *1- Pitfall sampling*: at each subplot, three pitfall traps remained installed for 24h. Each pitfall trap consisted of a 50mL falcon tube with 30 mm of diameter filled with 70% ethanol; *2 - Soil-core extraction*: at each subplot we extracted a soil sample with a steel cylinder (Ø 6 cm, 5 cm depth). At the laboratory, Collembola were extracted from soil samples using Berlese-Tullgren funnels for 14 days, and were stored in 70% ethanol.

All sampled specimens were sorted, counted and mounted on slides for taxonomic identification, following specific literature. To separate the morphospecies, we firstly sorted the specimens by orders, shape, color patterns, and other noticeable features under a stereomicroscope. Slides of few specimens of each morphospecies were prepared and investigated under an optical microscope to confirm their identities at the genus level, and to verify if each morphospecies encompassed a single species.

The data were pooled to provide transect-level data, and was organized in a matrix (W) with presence/absence data of springtails taxa in each community. The matrix **W** is presence/absence based since it combines data of different sampling methods.

Functional trait data

We evaluated 10 functional traits related to springtails habitat preferences, drought tolerance, and sensorial ability (Salmon et al., 2014). We investigated the traits on slide-mounted specimens under an optical microscope. The number of individuals used to measure the traits varied based on the abundance of individuals of each morphospecies: for taxa with an abundance of 10 or less sampled specimens, all individuals were studied; if the abundance was above 10, it was used at least 10% of the specimens, but never less than 10 individuals. Description of each trait, data type, and their environment roles are presented in Table 1.

Life form analysis

We categorized each morphospecies as epigeic or endogeic according to its eco-morphological index score (EMI; Parisi et al., 2005). The EMI separates springtails morphospecies according to their degree of adaptation to the soil profile. We calculate the EMI scores following the trait codification described by Vandewalle et al. (2010). The epigeic (surface-living) morphospecies got EMI scores below 10, while endogeic (deep soil-living) morphospecies got EMI scores above 12 (Parisi et al., 2005). If the EMI ranged between 10 and 12, the morphospecies was categorized accordingly with its most common habitat, as described in the literature for each genus. See Table S3 for the EMI scores and life forms of the morphospecies.

Functional metrics

We calculated the three functional diversity indices of Villéger et al. (2008): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv), as well as the functional dispersion (FDis; Laliberté and Legendre 2010), Rao's quadratic entropy (Rao) (Botta-Dukát 2005), and the community-level weighted means of trait values (CWM; e.g. Lavorel et al. 2008) based on matrices **W** and **B** (function *dbFD*, *FD* R package; Laliberté et al., 2022).

Statistical analyses

We evaluated the effect of grassland afforestation by *Eucalyptus* on springtails functional indexes by calculating effect sizes, which provide both the magnitude and precision of the effect estimation (Nakagawa and Cuthill, 2007) using Hedges' unbiased standardized effect size estimator (Hedges, 1981). We calculated 95% bootstrap confidence intervals, with 10000 iterations and the bias-corrected-and-accelerated (BCa) method, to test if observed effects were different from what is expected by chance within the dataset (*BootES* R package; Kirby and Gerlanc, 2013). We controlled the block effect (pair) by subtracting the mean values of each block from each observed value prior to effect size estimation. Significant results were addressed on a given variable as positive or negative when the confidence interval did not overlap zero.

Life form compartmentalized analysis

In order to evaluate the effect of grassland afforestation on the communities of Collembola above- and belowground, we performed all the above analyses in two datasets derived from the compartmentalization of our original dataset. Here, we organized two matrices **W** and **B** based on the life form (epigeic and endogeic).

Functional composition

We tested for differences between land-use types on trait-weighted morphospecies composition based on Gower distances of matrix **X** with multivariate analysis of variance (Pillar and Orlóci, 1996) with 1023 permutations (function *adonis*, *vegan* R package; Oksanen et al. 2020). The matrix **X** was created by weighting the species in matrix **W** by their degree of belonging to fuzzy sets of traits (*matrix.x,* function, *SYNCSA* R package; Debastiani and Pillar, 2012) that describe similarities between the morphospecies (Pillar et al., 2009). Matrix **X** actually indicates the probabilities for every specimen being present in the plot given its similarity to the individuals that actually were in the plot. Finally, we explored the variation in trait-weighted morphospecies composition using unconstrained non-metric multidimensional scaling (NMDS; *metaMDS* function, *vegan* R package; Oksanen et al. 2020), in which we added a biplot with all functional indexes which significantly varied between the land-use types and obtained correlation scores (*envfit* function, *vegan* R package; Oksanen et al. 2020).

Table 1. Description of springtails functional traits evaluated in this study with their presumed ecological responses to land-use change.

Functional Trait	**Potential Function**	**Data Type**		**References**
Antennal length	Sensorial ability; detection and selection of available resources; reproduction, modified antennae (through clasping organ) in some genera to hold females during the courtship	Continuous	Millimeters	Hopkin (1997), Bretfeld (1999); Cipola et al. (2018)
Body pigmentation	UV protection, thermoregulation and camouflage	Categorical	0 = absent; 1 = weakly pigmented/difused light pigment; 2 = with stripes or complex color patterns; 3 = totally darkly pigmented	Hopkin (1997), Salmon et al. (2014); D'Alba et al. (2019), Vanthournout et al. (2021)
Body size	Metabolic demands, dispersal ability, predator–prey interactions and resistance to desiccation	Continuous	Millimeters	Hopkin (1997); Makkonen et al. (2011)
Eco-morphological score (EMI)	Defines Collembola functional group based on its degree of adaptation to the soil profile	Continuous	EMI score	Parisi et al. (2005)
Furcal development	Predator avoidance and active dispersal abilities of the species	Continuous	Millimeters	Hopkin (1997); Bellini (2016); Cipola et al. (2018); Oliveira (2022)
Leg length	Disperse and movement; predator escaping; reproduction, modified setae on tibiotarsus III, in some genera, that aid in spermatophore transfer	Continuous	Millimeters	Hopkin (1997); Bretfeld (1999); Chahartaghi et al. (2006)
Ocelli number	Habitat preference; sensorial ability; defense against predators	Continuous	Count	Hopkin (1997), Salmon et al. (2014)

Post-antennal organ (PAO)	Sensory organ; detection of food, water and temperature change	Binary	0 = absent 1 = presente	Hopkin (1997), Salmon et al. (2014)
Pseudocelli	Repugnatorial glands; predator escaping	Binary	0 = absent 1 = present	Hopkin (1997); Negri (2004)
Scales	Desiccation protection, thermoregulation potentially predation avoidance	Binary	0 = absent 1 = present	Hopkin (1997), Salmon et al. (2014), Hawes and Greenslade (2015); D'Alba et al. (2019), Vanthournout et al. (2021)

Results

In total, we sampled 1458 springtails specimens, distributed in 43 morphospecies and 12 families: Brachystomellidae, Bourletiellidae, Dicyrtomidae, Entomobryidae, Hypogastruridae, Isotomidae, Katiannidae, Neanuridae, Odontellidae, Onychiuridae, Orchesellidae, Sminthurididae (Table S2). We found 20 exclusive morphospecies for native grasslands and only four exclusive for *Eucalyptus* forests, respectively (Table S2). *Entomobrya* sp. 3, *Entomobrya* sp. 1, and *Entomobrya* sp. 2 were the most frequent morphospecies in this study, all three highly associated with native grasslands. In *Eucalyptus* plantations, the most frequent morphospecies was *Thalassaphorura* sp. 1 and *Lepidocyrtus* sp.1 (Table S2).

Regarding the different sampling methods, we collected 1249 and 209 individuals using pitfall traps and soil-core extraction, respectively. Although both methods were useful for sampling epi- and endogeic morphospecies, the proportion of life forms was different, highlighting their complementarity (Figure S1).

Functional Composition

The multivariate analysis of variance showed that the springtails trait-weighted morphospecies composition (Matrix **X**) was distinct between land-use types ($F_{1,19} = 3.25$; $R^2 = 0.14$; $p=0.04$), with a significant correlation ($p<0.05$) of the life-form proportion. Here we confirmed that epigeic morphospecies were associated with grassland sites, while endogeic taxa were most associated with *Eucalyptus* forests (Figure 1).

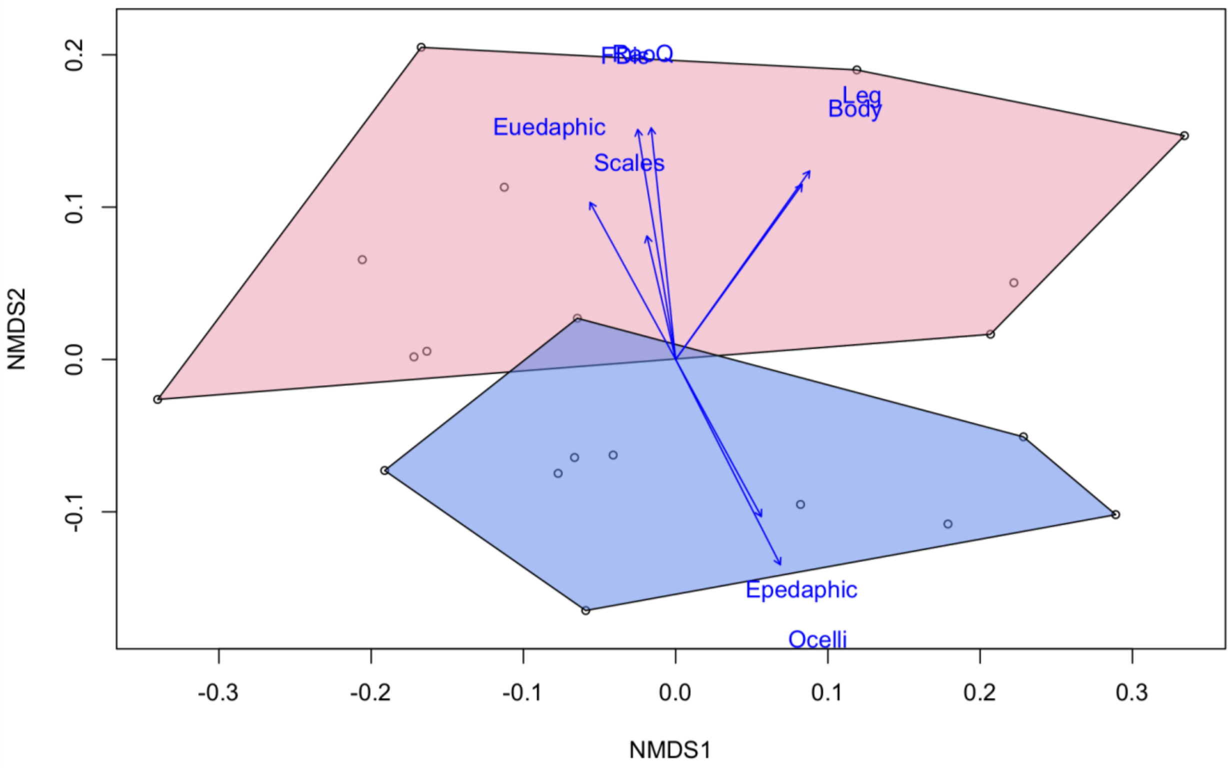

Figure 1. Non-metric multidimensional scaling (NMDS) based on the Gower distance matrix calculated using Matrix **X** (stress = 0.09). Biplot of springtails CWM traits and functional indexes that varied significantly between two land-use types (Pink = *Eucalyptus* crops and Blue = Grasslands) in southern Brazilian Pampa.

Life form richness and CWM

Regarding the life forms, 29 morphospecies were classified as epigeic and 14 were classified as endogeic (Table S2). We detected a negative effect of grassland afforestation with *Eucalyptus* on morphospecies richness of both life forms (Figure 2), with a stronger effect on epigeic springtails.

Grassland afforestation with *Eucalyptus* showed a negative effect on the number of ocelli, while positive for CWM values of scales, legs and body length. The CWM values of body pigmentation, furca length, EMI and antenna length overlapped between de land-use types, indicating no significant effects (Figure 2).

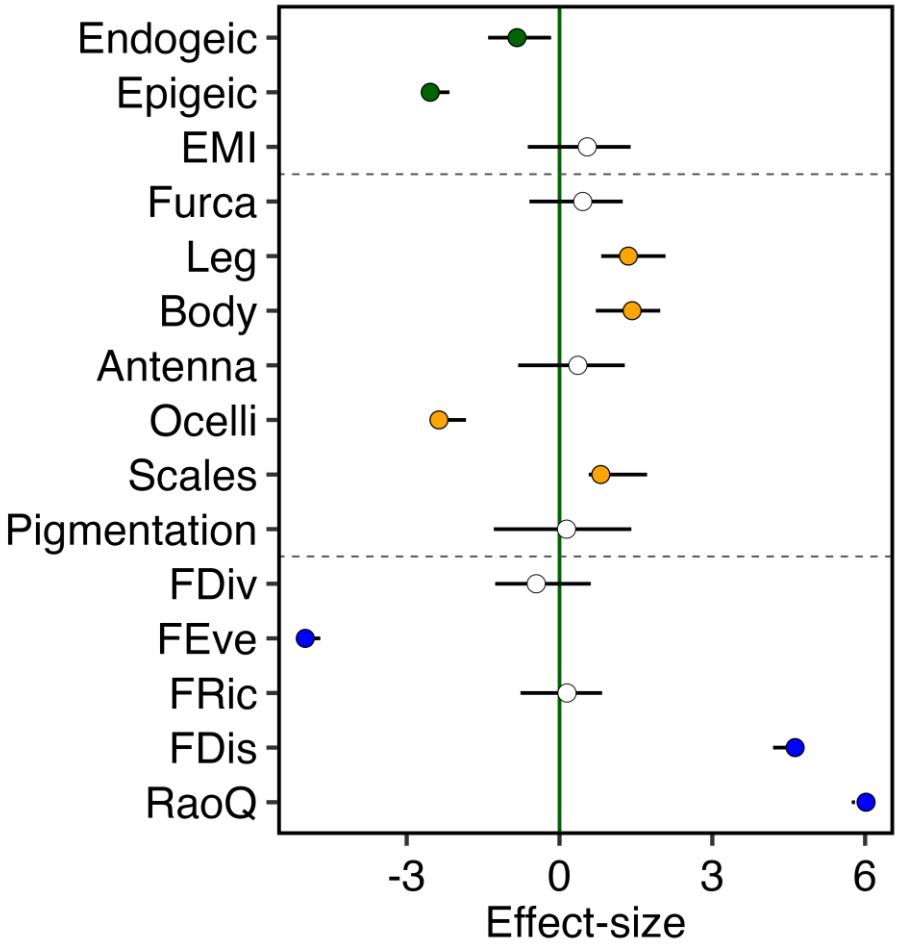

Figure 2. Mean effect size (Hedges' g) of grassland afforestation by *Eucalyptus* on the springtails community of southern Brazilian Pampa. Error bars represent bootstrap 95% confidence intervals. Treatment effect is significantly (filled circles) positive or negative when intervals do not overlap with zero.

Functional indexes

Rao's Q index and FDis were positively affected and FEve negatively by grassland afforestation, while FRic and FDiv indices were not clearly affected (Figure 2).

Compartmentalized communities

Regarding epigeic springtails communities, none of the functional metrics were clearly affected by grassland afforestation with *Eucalyptus*. However, we observed an increase in the presence of species with larger body, antenna, legs and furca sizes, with the presence of scales (Figure 3A) (See Table S3 for epigeic community data). In endogeic community, we found that FRic and FDiv were negatively affected by grassland afforestation with *Eucalyptus*, while RaoQ, FDis and

FEve were not. However, the CWM value of PAO increased in *Eucalyptus* plantation, while the body pigmentation, number of ocelli, legs and furca size (Figure 3B) were all reduced. See table S3 for endogeic community data.

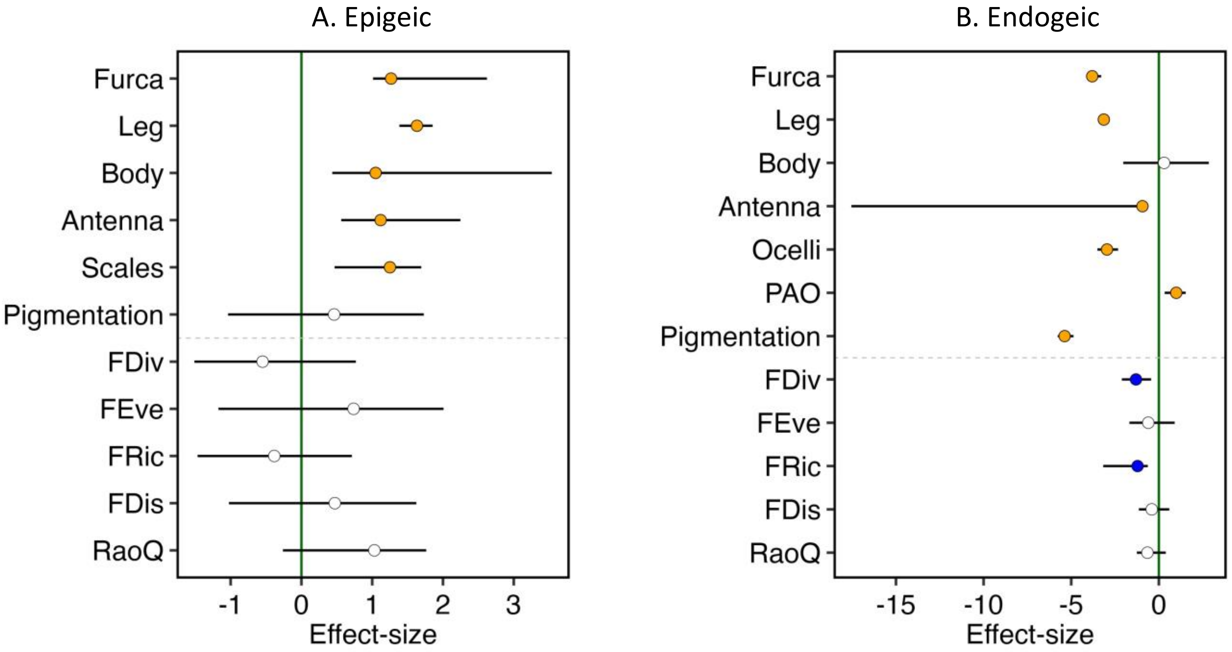

Figure 3. Mean effect size (Hedges' g) of grassland afforestation with *Eucalyptus* on springtails community in southern Brazilian Pampa. Error bars represent bootstrap 95% confidence intervals. Treatment effect is significantly (filled circles) positive or negative when intervals do not overlap with zero.

Discussion

The results corroborate our hypotheses that the afforestation of native grasslands with *Eucalyptus* affects the composition of soil community life forms, especially the species richness. However, part of the functional diversity indices did not showed significant effects of the distinct land-use between endogeic and epigeic springtails communities. There is plenty of evidency in the literature that the conversion of natural ecosystems into agricultural systems leads to changes in environmental conditions, resulting in significant outcomes on below and above-ground biodiversity (Walther, 2010; Oliveira Filho et al., 2016; Machado et al., 2019; Ortiz et al., 2020). Thus, the effects on life form and traits of springtails may reflect the state of conservation of the soil, making them suitable indicators not only for environmental changes but also for functional changes in the soil community (Pflug and Wolters, 2002; Oliveira Filho et al. al., 2016).

Our results showed that the conversion of native grasslands into *Eucalyptus* plantations impacted the composition and richness of springtails life forms, with species and their data set of functional characteristics being selected based on their habitat preferences. This resulted in changes in springtails communities inhabiting both above and below-ground. Epigeic communities were more associated with native grasslands, while endogeic communities showed some preference for *Eucalyptus* plantations. These changes are likely associated with the differences in the vertical structure of the two ecosystems. Native grasslands are open areas, typically characterized by shorter vegetation and greater exposure to solar radiation (Pillar and Lange 2015). This is a habitat that better suits epigeic taxa, as they are more adapted to drier and warmer conditions. Therefore, they have the advantage of being able to access the heterogenous resources of that environment. These organisms can tolerant higher temperatures and better support the incidence of UV rays and dehydration due to a more intense body pigmentation, modifications of the cuticle, plurichaetosis (presence of a secondary set of extra body chaetae), and/or presence of scales (Salmon et al., 2014; Potapov et al., 2016). Grassland afforestation into *Eucalyptus* forests transform a previously open and species-rich environment into a closed and homogeneous one, leading to habitat simplification. Studies indicate that this change also causes significant alterations in the physicochemical properties of the soil and litter, which may act as ecological filters on the regional pool of springtails species (Riutta et al., 2012; Martins da Silva et al., 2016; Winck et al., 2017; Gomes et al., 2022).

For instance, soils in *Eucalyptus* plantations tend to exhibit low soil moisture, high acidity, and reduced nutrient availability (Leite et al., 2010; Gomes et al., 2022). Additionally, these soils display homogeneous food resource availability, low biomass quality and microbial activity (Rzeszowski et al., 2017; Jorge et al., 2023). The chemical alterations under *Eucalyptus* plantation can select endogeic species with functional traits (e.g. body and reduced pigmentation) better adapted to acidic and closed environments. Such species may share with endogeic taxa reduced visual structures, i.e. number of ocelli, and pigmentation, as well as reduced mobility and or the presence of morphological traits which facilitate the exploration of such environment, i.e. more developed sensory structures to forage food resources (Salmon et al., 2014; Chauvat et al., 2014; Martins da Silva et al., 2016). Indeed, these soil changes may have negative effects on the physiological functions of most springtails, impacting their reproduction rates, life cycles, and overall survival (Van Straalen et al., 1997; Fountain and Hopkin, 2005; De Boer et al., 2010).

The complete dataset of life forms showed a increase in RaoQ and FDis indices with grasslands afforestation. The springtail community, including below and above-ground populations, becomes richer in terms of functional traits, resulting in an increase in the functional space occupied by each species. This is due to the greater heterogeneity and complexity of the community, allowing species to perform distinct functions and provide a wide variety of ecosystem services (Purschke et al., 2013). When investigating the afforestation of grasslands on springtails communities, Jorge et al. (2023) found similar results. The authors observed that RaoQ increased by approximately 34% in *Eucalyptus* areas. The increase in functional diversity is likely linked to the preservation of certain grassland-adapted species in the converted sites, along with a rise in the relative abundance of species with traits suited to closed habitats, which are sparsely found in native grasslands (Jorge et al., 2023). However, when analyzing the epigeic and endogeic communities in a compartmentalized manner, the effects on these indices are not the same. Within each life form, functional traits are highly correlated, resulting in less divergence and functional diversity. This leads the species to have similar or overlapping functional traits, resulting in a more functionally homogeneous ecosystem (Cianciaruso et al., 2009; Purschke et al., 2013).

Considering that grassland afforestation with *Eucalyptus* affects springtail life forms, and has significant effects on their functional traits, our compartmentalized analyses have expanded our understanding of these effects on each trait and functional index of both epigeic and endogeic springtails. At first glance, it can be observed that grassland afforestation likely causes a kind of disruptive filtering, favoring extreme traits of each life form.

Grasslands afforestation with *Eucalyptus* leads to a reduction of epigeic and endogeic communities richness. The epigeic communities showed positive effects related to the increase of scales, body size, antennae, leg, and furca. However, diversity indices were not affected. In contrast, the endogeic communities exhibited a positive effect on PAO, but negative effects on pigmentation, presence of ocelli, antennae size, legs, and furca. Additionally, the FRic and FDiv indices were reduced with the grassland afforestation process. These findings reinforce and confirm the functional patterns of endogeic organisms. Being in a light-deprived environment, these organisms have less developed eyes but greater sensory capacity from other functional traits. Moreover, and as previously discussed, they possess lower mobility, resulting in the absence or reduction of legs and furca (Salmon et al. 2014, Martins da Silva et al. 2016, Potapov et al. 2016). In contrast, the functional trait response of epigeic organisms was mainly related to the body and appendages increasing, adaptations more commonly found in open areas, such as native grasslands (Winck et al., 2017, Potapov et al. 2020).

Our findings raise several inquiries, such as: What were the ecological filters in *Eucalyptus* plantation which selected larger epigeic organisms and endogeic organisms with reduced mobility structure? Why did scales have positive effects on epigeic organisms in *Eucalyptus* plantations? Why the functional diversity metrics were unaffected in epigeic communities, while FRic and FDiv were reduced in endogeic communities?

To answer the first question, we hypothesize that the body size of the sampled epigeic springtails is linked to the quality and quantity of plant litter, which favors the growth of microorganisms (fungal) that are part of the food preference of the springtails. The litter layer in *Eucalyptus* plantations exhibits distinct characteristics compared to grassland areas. Since the *Eucalyptus* plantations are about 10 years old, there was a significant accumulation of vegetal residues on their soil surface, forming a dense and thicker layer of litter (Barbosa et al., 2017; Inkotte et al., 2023). Moreover, the litter of *Eucalyptus* contains more lignin and a high CN ratio, and specialist fungi are favored to grow in such conditions rather than bacteria, because of their ability to release specific enzymes for the decomposition of recalcitrant organic material (Algora et al., 2021; Tunlid et al., 2022). Therefore, organisms able to inhabit the *Eucalyptus* litter and adapted to consume such resource have plenty of food sources, even though they are more homogeneous (Daghighi et al., 2017; Gomes et al., 2022). In such conditions of abundance of feeding sources, a raise in the body size is expected.

In grasslands, animal grazing cause frequent plant defoliation, which favor the dominance of short grasses and other herbaceous plants, as legumes and forbs, and the litter layer is thinner, sometimes completely absent, compared to afforested areas (Heinen et al., 2020). By presenting constant high plant diversity and constant growth, mainly during the growing season (September-April), the grassland litter tends to be more palatable to the decomposer community and major environmental heterogeneity (Scherer-Lorenzen, 2008; Liu et al., 2010). These conditions favor a greater diversity and coexistence of different trophic levels in the soil, making the soil food web more complex. Although we did not evaluate other soil organisms, our data suggest that overall soil fauna as whole is richer in grasslands compared to *Eucalyptus*. However, the competition for food resources is likely higher in the native grasslands, making the food availability somewhat limited. In fact, limiting resources is the main ecological theory that explains high diversity within heterogeneous systems (MacArthur and Levins, 1967; Pacala and Tilman, 1994; Chesson, 2000; Levine and Lambers, 2010).

The positive association of body scales in epigeic organisms in *Eucalyptus* plantations was firstly unexpected, since such structures are strongly associated with functions such UV protection and thermoregulation, influencing the amount of reflected light or playing a role in dehydration protection by retaining a layer of water or air between the cuticle and scales (Nickerl et al., 2014; Hawes and Greenslade, 2015; D'Alba et al., 2019). However, *Eucalyptus* plantations in the Brazilian Pampa are planned with high tree spacing, resulting in semi-open thin canopies which allow trespassing light and higher temperatures reaching the litter layer. Consequently, individuals with scales may benefit from these structures even inside artificial forests. Additionally, individuals with scales may be under selection for providing an antipredator mechanism as they can be easily detached from the body, allowing the animal to escape more easily. The scales can also become darkened like the plant litter, favoring the camouflage of these organisms (Vanthournout et al., 2021) or even provide chemical protection to springtails, protecting the contact of undesirable substances with the organisms cuticle (Hensel et al., 2016; D'Alba et al., 2019). However, experimental studies are needed to elucidate the functionalities of scales in taxa associated with eucalyptus crops (Nickerl et al., 2014; D'Alba et al., 2019).

Endogeic springtails have lower mobility, which implies less access and opportunity to choose food. In this case, they are limited to the microorganisms available in the soil pores, which can lead to reduced food intake and, consequently, results in smaller body sizes. The low dispersal capacity of these organisms requires a habitat and food resources of good quality (Oliveira Filho et al., 2016), which are minimized in *Eucalyptus* plantations compared to native grassland areas. Another factor to be highlighted is the decomposition of *Eucalyptus* litter which tends to be slower due to the presence of lignin and chemical compounds, such as essential oils and phenolic compounds, which may have low palatability to decomposers and reduce microbial activity (Silva et al., 2018; Ferreira et al., 2020; Valadão et al., 2020). A study led by Jorge et al. (2023) indicates that grassland afforestation causes a significant reduction in microbial biomass carbon and its metabolic processes, such as respiration and specific enzymatic activities, through alterations in above and below-ground habitats. We also observed a positive correlation to the presence of the PAO in the endogeic community, which is well-documented in the literature (Salmon et al., 2014; Martins da Silva et al., 2016; Winck et al., 2017), and it is related to these organisms' ability to select specific food resources, such as microorganisms (Hopkins, 1997; Chahartaghi et al., 2005; Chauvat et al., 2014).

Despite the significant response of functional traits of the epigeic community, the functional diversity indices (FRic, FEve, FDiv, and FDis) did not differ significantly between the native grassland and *Eucalyptus* afforestation. Considering the functional diversity approaches proposed by Mason et al. (2005) and Laliberté and Legendre (2010), the total functional space occupied by the communities, their diversifications, specializations, and uniformity of functional trait distribution did not vary significantly between habitats. On the other hand, the endogeic community showed significant reductions in FRic and FDiv indices, and this decrease was related to the scarcity of distinct traits in the species composing the endogeic community, resulting in a reduction in ecological interactions and functions performed by the species. Our results align with the discussions by Mason et al. (2005), who emphasized that the decrease in functional divergence is associated with the reduction of the richness of functional characteristics among the sampled species.

Studies demonstrate that endogeic communities present in subtropical grassland soils are less abundant and species-rich (Rieff et al., 2016; Sabatté et al., 2021; Jorge et al., 2023), especially compared to tropical, European, and African soils (Salmon et al. 2004, Sabais et al., 2011; Filho et al. 2016; Susanti et al., 2021, Eckert et al., 2023). Therefore, the reduction in richness and abundance already associated with endogeic communities could render this group more susceptible to negative effects from *Eucalyptus* plantations. It is known that richer communities in species are more likely to have similar species regarding their functional traits, which, in turn, regulate the same function (Folke et al., 2004; Biggs et al., 2020). This can promote greater environmental stability, as several species can perform the same functional role (Joner et al., 2011; Joner and Pillar, 2012). We believe that the process of grassland afforestation in Pampa biome may be intensified functional redundancy (although this metric was not evaluated in this study) within endogeic springtail communities. This is due to the predominance of a single dominant species in the vegetation (*Eucalyptus* sp.), constraints on the establishment of other plant communities, and the reduction in soil fauna and microbiota, favoring the predominance of individuals of springtail performing similar functions. However, in the process of reforestation of grasslands, this functional redundancy can indicate a negative signal, because when combined with the reduction in richness and functional divergence, they can lead to the emergence of empty niches (Loreau, 2004; Flynn et al., 2009). When empty niches occur, negative impacts on the ecosystem can arise, such as imbalances in the food chain, reduced resilience, and diminished capacity to respond to environmental changes (Joner et al., 2011; Joner and Pillar, 2012; Biggs et al., 2020).

Conclusion

Our results showed the influence of *Eucalyptus* plantation on the functional composition of springtails communities, with epigeic species more associated with native grasslands and endogeic species with *Eucalyptus* plantations. Moreover, *Eucalyptus* plantation has negative effects on the overall sprintgtails species richness, with endogeic communities reducing body structures and appendages, as well as their functional diversity.

As few studies have been conducted assessing both epigeic and endogeic springtails after grassland afforestation, we emphasize the importance of this study for a better understanding of the response of springtails communities. Knowing that these organisms are abundant and significantly affect soil decomposition processes, these changes are expected to cause implications in important ecosystem functions.

Studies like this allow us to comprehend the effects of grassland afforestation in a more detailed manner, contrasting with more generalized approaches. Understanding the resulting impacts of these conversions is of paramount importance for developing effective conservation strategies and sustainable management of grassland ecosystems, especially in light of ongoing land use changes in the Brazilian Pampa region.

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Supplementary Material

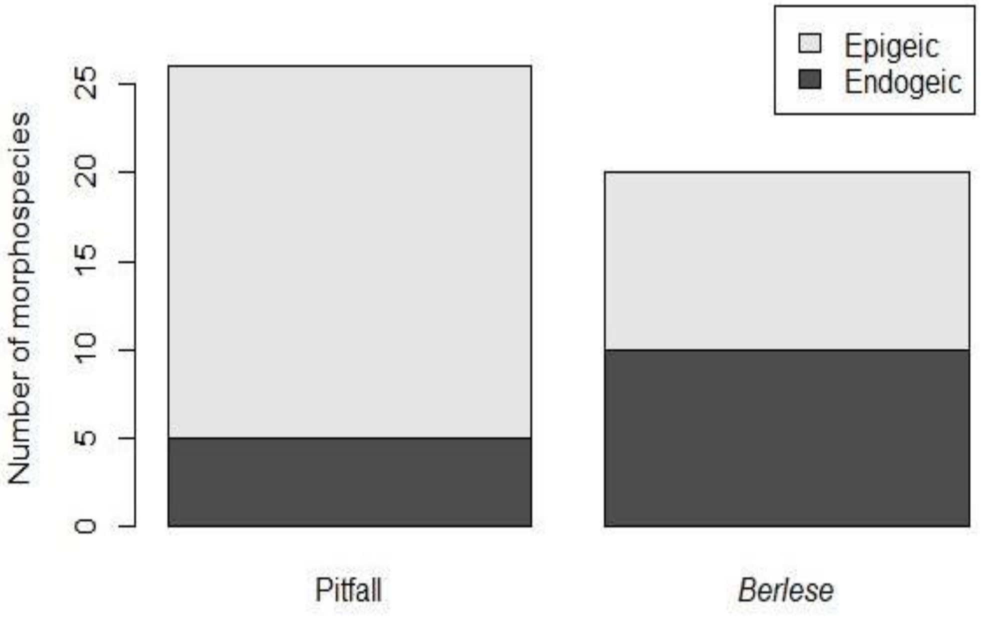

Figure S1. Number of epigeic and endogeic springtails morphospecies sampled by pitfall traps and soil-core extraction in Grasslands and *Eucalyptus* plantations in southern Brazilian Pampa.

Table S1. Description of the sampled areas in this study. Gras = native grassland; Euc = *Eucalyptus* plantation.

Municipality	**Pair**	**Land-use**	**Sampling date**	**Season**	**Geographic Coordinates**	
					Longitude	**Latitude**
JAGUARÃO	1	Gras	April 5, 2019	Autumn	−53,397,067	−32,239,946
		Euc	April 5, 2019	Autumn	−53,365,464	−32,239,994
	2	Gras	April 6, 2019	Autumn	−53,319,039	−32,210,709
		Euc	April 6, 2019	Autumn	−53,349,856	−32,240,435
	3	Gras	April 7, 2019	Autumn	−53,304,145	−32,227,443
		Euc	April 7, 2019	Autumn	−53,301,572	−32,245,974
LAVRAS DO SUL	4	Gras	May 7, 2019	Autumn	−54,263,648	−30,885,178
		Euc	May 7, 2019	Autumn	−5,431,076	−30,860,155
	5	Gras	May 8, 2019	Autumn	−54,267,129	−30,962,529
		Euc	May 8, 2019	Autumn	−54,252,869	−309,676
PINHEIRO MACHADO	6	Gras	November 11, 2018	Spring	−53,602,698	−31,339,271
		Euc	November 11, 2018	Spring	−5,359,796	−31,343,839
	7	Gras	November 12, 2018	Spring	−53,577,106	−31,385,678
		Euc	November 12, 2018	Spring	−53,571,586	−31,391,762
	8	Gras	November 13, 2018	Spring	−53,499,849	−31,402,764
		Euc	November 13, 2018	Spring	−53,509,913	−31,412,028
SÃO GABRIEL	9	Gras	April 23, 2019	Autumn	−54,324,136	−30,059,119
		Euc	April 23, 2019	Autumn	−54,320,563	−30,049,282
	10	Gras	April 24, 2019	Autumn	−54,321,307	−30,083,604
		Euc	April 24, 2019	Autumn	−54,327,398	−30,069,851

Table S2. Collembola morphospecies and their number of occurrences sampled by pitfall traps and soil core extraction in Grasslands and *Eucalyptus* plantations in southern Brazilian Pampa.

Order	Family	Genera	Morphospecies	Life Form	Number of Occurrences		
					Grassland	*Eucalyptus* plantation	Total
Entomobryomorpha	Entomobryidae	*Entomobrya*	*Entomobrya*_sp1	Epigeic	9	1	10
		Entomobrya	*Entomobrya* _sp2	Epigeic	8	0	8
		Entomobrya	*Entomobrya*_sp3	Epigeic	10	5	15
		Entomobrya	*Entomobrya*_sp4	Epigeic	2	5	7
		Entomobrya	*Entomobrya*_sp5	Epigeic	3	0	3
		Lepidocyrtus	*Lepidocyrtus*_sp1	Epigeic	5	6	11
		Lepidocyrtinus	*Lepidocyrtinus*_sp1	Epigeic	2	0	2
		Seira	*Seira*_sp1	Epigeic	4	0	4
		Trogolaphysa	*Trogolaphysa*_sp1	Epigeic	0	4	4
	Isotomidae	*Arlea*	*Arlea*_sp1	Endogeic	1	0	1
		Ballistura	*Ballistura*_sp1	Endogeic	2	1	3
		Desoria	*Desoria*_sp1	Epigeic	5	1	6
		Desoria	*Desoria*_sp2	Epigeic	4	0	4
		Desoria	*Desoria*_sp3	Epigeic	3	1	4
		Desoria	*Desoria*_sp4	Epigeic	0	1	1
		Folsomia	*Folsomia*_sp1	Endogeic	3	0	3
		Isotomodes	*Isotomodes*_sp1	Endogeic	3	5	8
		Isotomurus	*Isotomurus*_sp1	Epigeic	4	2	6
		Pseudanurophorus	*Pseudanurophorus*_sp1	Endogeic	1	1	2
		Proisotoma	*Proisotoma*_sp1	Endogeic	4	0	4
	Orchesellidae	*Dicranocentrus*	*Dicranocentrus*_sp1	Epigeic	0	7	7
Poduromorpha	Brachystomellidae	*Brachystomella*	*Brachystomella*_sp1	Endogeic	5	0	5
		Brachystomella	*Brachystomella*_sp2	Endogeic	1	0	1
	Hypogastruridae	-	Hypogastruridae_sp1	Endogeic	0	1	1
		Hypogastrura	*Hypogastrura*_sp1	Endogeic	3	0	3
		Xenylla	*Xenylla*_sp1	Epigeic	4	4	8
	Neanuridae	*Pseudachorutes*	*Pseudachorutes*_sp1	Endogeic	3	1	4

	Odontellidae	-	Odontellidae_sp1	Endogeic	1	1	2
	Onychiuridae	*Thalassaphorura*	*Thalassaphorura*_sp1	Endogeic	2	8	10
		Thalassaphorura	*Thalassaphorura*_sp2	Endogeic	1	2	3
Symphypleona	Bourletiellidae	*Prorastriopes*	*Prorastriopes*_sp1	Epigeic	2	0	2
		Prorastriopes	*Prorastriopes*_sp2	Epigeic	1	0	1
		Rastriopes	*Rastriopes*_sp1	Epigeic	1	0	1
		-	Bourletiellidae_sp1	Epigeic	3	0	3
	Dicyrtomidae	*Ptenothrix*	*Ptenothrix*_sp1	Epigeic	1	1	2
	Katiannidae	*Katianna*	*Katianna*_sp1	Epigeic	2	0	2
		Katianna	*Katianna*_sp2	Epigeic	1	0	1
		Sminthurinus	*Sminthurinus*_sp1	Epigeic	3	0	3
	Sminthurididae	*Sphaeridia*	*Sphaeridia*_sp1	Epigeic	4	0	4
		Sminthurides	*Sminthurides*_sp1	Epigeic	1	0	1
		Parasminthurides	*Parasminthurides*_sp1	Epigeic	2	1	3
		-	Sminthurididae_sp1	Epigeic	1	1	2
	-	-	Symphypleona_sp.1	Epigeic	2	2	4

Table S3. Collembola morphospecies described by functional traits sampled by pitfall traps and soil core extraction in Grasslands and *Eucalyptus* plantations in southern Brazilian Pampa.

Genera	Morphospecies	Body Pigmentation Level	Scales	PAO	Ocelli number	Pseudocelli	Antenna length (mm)	Body length (mm)	Furca length (mm)	Leg length (mm)	EMI	Life form
Entomobrya	*Entomobrya*_sp1	1	0	0	8	0	1.059	1.668	0.8	0.7	8	Epigeic
Entomobrya	*Entomobrya* _sp2	2	0	0	8	0	0.6	1.12	0.841	0.722	6	Epigeic
Entomobrya	*Entomobrya*_sp3	2	0	0	8	0	0.606	1.078	0.595	0.561	6	Epigeic
Entomobrya	*Entomobrya*_sp4	2	0	0	8	0	1.173	1.459	0.8	0.811	6	Epigeic
Entomobrya	*Entomobrya*_sp5	2	0	0	8	0	0.6	1.08	0.7	0.395	6	Epigeic
Lepidocyrtus	*Lepidocyrtus*_sp1	1	1	0	8	0	0.33	0.879	0.36	0.454	6	Epigeic
Lepidocyrtinus	*Lepidocyrtinus*_sp1	2	1	0	8	0	0.626	1.322	0.098	0.558	8	Epigeic
Seira	*Seira*_sp1	1	1	0	8	0	1.411	1.273	0.642	0.595	4	Epigeic
Trogolaphysa	*Trogolaphysa*_sp1	2	1	0	8	0	0.84	1.401	1.067	0.889	2	Epigeic
Arlea	*Arlea*_sp1	0	0	1	0	1	0.175	0.568	0.019	0.153	18	Endogeic
Ballistura	*Ballistura*_sp1	3	0	1	8	0	0.215	0.71	0.184	0.216	12	Endogeic
Desoria	*Desoria*_sp1	3	0	1	8	0	0.185	0.62	0.222	0.333	10	Epigeic
Desoria	*Desoria*_sp2	3	0	1	8	0	0.6	1.512	0.8	0.711	10	Epigeic
Desoria	*Desoria*_sp3	3	0	1	8	0	0.194	0.581	0.194	0.194	10	Epigeic

Desoria	*Desoria*_sp4	3	0	1	8	0	0.19	0.415	0.113	0.142	10	Epigeic
Folsomia	*Folsomia*_sp1	0	0	1	0	0	0.124	0.519	0.074	0.074	16	Endogeic
Isotomodes	*Isotomodes*_sp1	0	0	1	0	0	0.177	0.679	0.086	0.145	18	Endogeic
Isotomurus	*Isotomurus*_sp1	2	0	1	8	0	0.423	1.006	0.204	0.446	6	Epigeic
Pseudanurophorus	*Pseudanurophorus*_sp1	0	0	0	0	0	0.144	0.569	0	0.157	20	Endogeic
Proisotoma	*Proisotoma*_sp1	1	0	1	6	0	0.164	0.51	0.4	0.223	10	Endogeic
Dicranocentrus	*Dicranocentrus*_sp1	2	1	0	8	0	1.41	2.137	1.444	1.411	2	Epigeic
Brachystomella	*Brachystomella*_sp1	3	0	0	8	0	0.194	0.789	0.148	0.202	16	Endogeic
Brachystomella	*Brachystomella*_sp2	3	0	0	8	0	0.842	0.372	0	0.157	18	Endogeic
-	Hypogastruridae_sp1	3	0	1	8	0	0.076	0.702	0.063	0.147	10	Endogeic
Hypogastrura	*Hypogastrura*_sp1	3	0	1	8	0	0.166	0.711	0.778	0.223	10	Endogeic
Xenylla	*Xenylla*_sp1	3	0	0	8	0	0.124	0.542	0.049	0.124	10	Epigeic
Pseudachorutes	*Pseudachorutes*_sp1	1	0	1	8	0	0.177	0.69	0.345	0.198	10	Endogeic
-	Odontellidae_sp1	0	0	0	0	0	0.038	0.77	0	0.094	20	Endogeic
Thalassaphorura	*Thalassaphorura*_sp1	0	0	1	0	1	0.15	0.622	0	0.127	20	Endogeic
Thalassaphorura	*Thalassaphorura* _sp2	1	0	1	0	1	0.143	0.718	0	0.142	20	Endogeic
Prorastriopes	*Prorastriopes*_sp1	2	0	0	8	0	0.456	0.81	0.444	0.401	6	Epigeic

Prorastriopes	*Prorastriopes*_sp2	2	0	0	8	0	0.661	0.81	0.333	0.5	6	Epigeic
Rastriopes	*Rastriopes*_sp1	2	0	0	8	0	1.32	1.441	0.985	0.601	6	Epigeic
-	Bourletiellidae_sp1	1	0	0	8	0	0.196	0.253	0.114	0.125	6	Epigeic
Ptenothrix	*Ptenothrix*_sp1	2	0	0	8	0	1.112	1.766	0.911	0.789	6	Epigeic
Katianna	*Katianna*_sp1	1	0	0	8	0	0.542	0.712	0.311	0.443	8	Epigeic
Katianna	*Katianna*_sp2	1	0	0	8	0	0.64	0.69	0.345	0.493	8	Epigeic
Sminthurinus	*Sminthurinus*_sp1	1	0	0	8	0	0.436	0.527	0.281	0.303	8	Epigeic
Sphaeridia	*Sphaeridia*_sp1	1	0	0	8	0	0.207	0.211	0.069	0.111	10	Epigeic
Sminthurides	*Sminthurides*_sp1	1	0	0	8	0	0.278	0.332	0.027	0.228	10	Epigeic
Parasminthurides	*Parasminthurides*_sp1	1	0	0	8	0	0.201	0.208	0.153	0.139	8	Epigeic
-	Sminthurididae_sp1	1	0	0	8	0	0.287	0.304	0.171	0.181	6	Epigeic
-	Symphypleona_sp.1	1	0	0	8	0	0.532	0.21	0.135	0.346	6	Epigeic

CAPÍTULO 3

SPRINGTAILS (COLLEMBOLA: HEXAPODA) OF THE BRAZILIAN PAMPA: NEW RECORDS, GENERA AND FAMILY DIAGNOSES AND AN IDENTIFICATION KEY TO THE SUPRASPECIFIC TAXA

Preparado para submissão no periódico *Zootaxa* em colaboração com Gleyce da Silva Medeiros, Rudy C. Nunes, Bruna Cláudia S. Jorge, Bruna R. Winck e Bruno C. Bellini. Formatado conforme as normas da revista.

Springtails (Collembola: Hexapoda) of the Brazilian Pampa: new records, genera and family diagnoses and an identification key to the supraspecific taxa

CLÉCIO DANILO DIAS DA SILVA[1] GLEYCE DA SILVA MEDEIROS[1], BRUNA CLAUDIA JORGE[2], RUDY CAMILO NUNES[3], BRUNA RAQUEL WINCK[4] & BRUNO CAVALCANTE BELLINI[1]

[1]Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte (UFRN), Highway BR-101, Lagoa Nova, Campus Universitario, Natal 59072-970, RN, Brazil
[2]Quantitative Ecology Lab, Department of Ecology, Federal University of Rio Grande do Sul, Porto Alegre, 90040-060, Brazil
[3]Biodiversity and Biotechnology Research Group of North Center Piaui, Federal Institute of Education, Science and Technology of Piaui, Teresina 64000-040, Brazil
[4]Institut National De La Recherche Agronomique Clermont-Auvergne-Rhônes-Alpe, INRAE, 63000 Clermont-Ferrand, France
Corresponding author: Clécio Danilo Dias da Silva (danilodiass18@gmail.com)

Abstract

The springtails from the Brazilian Pampa are still understudied, and there is a single nominal species recorded for the domain published so far. In this study we surveyed the current knowledge of this particular fauna, providing a list of families and genera recorded from the Pampa of Rio Grande do Sul, Brazil, with new records, further nominal species recognized, diagnoses to the recorded families and genera, and an identification key for the suprageneric taxa. Our literature review was carried out based on different databases and papers. We reassessed the identification and records of the inventory of Silva *et al.* (2022). Thus, combining previously published data with the records of Silva *et al.* (2022), we found a total of 35 genera of springtails distributed in 15 families for the Pampa. Many species are potentially new to science and need a formal description. These data demonstrated the need to expand inventories and more detailed taxonomic studies in the Pampa, a domain with large potential biodiversity, but still understudied for the Collembola fauna.

Keywords: Brazilian southern region; edaphic fauna; species list; taxonomic survey.

Introduction

The class Collembola holds small insect-like hexapods with fusiform, dorsoventrally flattened or globose bodies, ranging in size from 0.12 to 17 mm (Hopkin 1997, Bellinger *et al.* 1996–2023). The group includes four well-circumscribed orders: Entomobryomorpha, Poduromorpha, Symphypleona, and Neelipleona. The representatives of the first two orders have elongated bodies with well-defined trunk segments, while the last two orders gather specimens with a globose body with most of the trunk segments largely fused with each other (Hopkin 1997, Bellinger *et al.* 1996–2023).

Springtails are apterous and their body plan is divided into head, thorax, and abdomen, like other hexapods. The head have a pair of primarily four-segmented antennae, and the mouthparts are hidden inside the mouth cavity, a condition denominated entognathy. Contrarily, insects are ectognathous, and show exposed mouthparts (Grimaldi & Engel 2005). The thorax of springtails has three segments, although in the Symphypleona and Neelipleona these are partially or entirely fused to each, with each of them holding a pair of legs. The abdomen has six segments, but some taxa may show a fusion of some of them as well, and it has three characteristic appendages, considered as the main synapomorphies of Collembola: the ventral tube (or collophore), the tenaculum (or retinaculum), and the furca (or furcula), located on the ventral side of the first, third and fourth abdominal segments, respectively (Hopkin 1997, Zeppelini 2012, Mendonça *et al.* 2014, Bellini 2016, Bellinger *et al.* 1996–2023).

Currently, there are more than 9.400 extant nominal species of springtails recorded worldwide. However, estimates support up to 500.000 living species across the globe (Cicconardi *et al.* 2013, Bellinger *et al.* 1996–2023). Most taxa were recorded and described from the Palaearctic and Nearctic Regions (Bellinger *et al.* 1996–2023). Otherwise, more than 1.300 species were already recorded from the Neotropical Region, with 475 of them known from Brazil, whilst 328 species are considered endemic from the country (Abrantes *et al.* 2010, 2012, Zeppelini *et al.* 2023). Even so, the current taxonomic knowledge of the Brazilian fauna shows important and large gaps, considering the vast majority of the known fauna was sampled from the Atlantic Forest, Amazon and Caatinga phytogeographic domains (Zeppelini *et al.* 2023).

The Pampa is an exclusive biome seen in South America, covering part of Rio Grande do Sul state (Brazil), Argentina and Uruguay. In Brazil, it covers about 176,000 km² and its natural landscapes are mainly characterized by grasslands, which shelter an extraordinary biodiversity that is still underexplored (Overbeck *et al.* 2007; Pillar *et al.* 2012; Ferreira *et al.* 2020). For instance, Menezes *et al.* (2018) recorded 56 different plant species per square meter in native grasslands areas. Likewise, the soil organisms richness is quite high in limited degraded areas, such as ants, mites, grasshoppers, beetles, and spiders (Ferreira *et al.* 2010, Rieff *et al.* 2010, Rodrigues *et al.* 2010, Silva *et al.* 2012, Podgaisk *et al.* 2013, Feitosa *et al.* 2015, Ferrando *et al.* 2016, Garcia *et al.* 2016, Silva *et al.* 2017). However, studies related to the taxonomy of Collembola have been neglected for decades for the Brazilian Pampa. Until 2012, there was only two records of springtails to Rio Grande do Sul state (RS): *Lepidocyrtus pallidus* Reuter, 1890 (a uncertain record, since it is a holarctic species, without clear distribution) and *Cyphoderodes xenopus* Börner, 1913 (Abrantes *et al.* 2010, 2012). While the first record cannot be clearly assigned to any biome, *C. xenopus* was collected from São Leopoldo municipality (Börner 1913), a region in the ecotonal zone between the Atlantic Forest and Pampa biomes. This is the sole nominal species of springtail recorded from the Brazilian Pampa so far. The third and last published record of a nominal species from RS was the description of *Salina maculipenis* Oliveira & Cipola, 2018 from Estrela Velha municipality, located in the Atlantic Forest biome (Oliveira *et al.* 2018, Zeppelini *et al.* 2023). Recent prolific research has been developed with an emphasis on the functional diversity of Collembola in different land use systems in areas of the southern Brazil (Oliveira Filho *et al.* 2016, 2020, Santos *et al.* 2018, Machado *et al.* 2019, Ortiz *et al.* 2019). However, possibly due to taxonomic impediments like the small size and complexity of specimens, the absence of collembologists studying and describing the fauna of southern Brazil, and lack of reliable identification keys of the South American springtails, only a few studies have explored the taxonomic diversity of this group in areas of the Brazilian Pampa (Winck *et al.* 2017, 2019, Jorge *et al.* 2022, 2023, Silva *et al.* 2022), all of them based only on morphospecies. This situation was observed by Mendonça Jr. *et al.* (2015), who claimed that there are not even adequate records of springtails for the Brazilian Pampa which can contribute to a real understanding of the taxonomic richness of the group for the domain.

In this scenario, the development of detailed inventories and the description of the Collembola fauna of the Pampa are relevant efforts to support other studies, especially dealing with population ecology, distribution patterns and phylogenetic reviews (Bellini 2014). Activities of this nature may also contribute for planning and implementing environmental conservation policies. So, the main objectives of this paper are: I) to present a survey of the current taxonomical knowledge of Collembola from Brazilian Pampa based on previously published literature; II) to review the specimens of Silva *et al.* (2022), looking for the specific identification of part of the taxa; III) and to provide identification key and diagnoses for the families and genera which occur in the Brazilian Pampa.

Methodology

Reassessing Silva et al. (2022) inventory

In the recently published ecological evaluation of the effects of the conversion of Pampa's native grasslands into *Eucalyptus* artificial forests, an inventory of the morphospecies was provided (Silva *et al.* 2022). At first we could not assign any taxa to already described species, but now we assess again these specimens to confirm part of their identities. The original inventory was carried out in four municipalities in RS, Brazil: Jaguarão – JAG, Pinheiro Machado – PIM, São Gabriel – SAG and Lavras do Sul – LAV (Table 1). All municipalities are under the influence of a humid subtropical climate with regular monthly rainfall, a "CFa" climate according to the Köppen-Geiger system (Kottek *et al.* 2006). Average temperatures range between 16 and 22 °C, with minimums of -10 °C and maximums of 38 °C. The natural vegetation of the sampled areas is predominantly of grassland, with some occasional shrubs and different forest types (Pilar; Lange, 2015). This mosaic of phytophysiognomies can be divided into: I) shallow soil grasslands; II) deep soil grasslands; III) sandy areas of grassland, IV) savonnoid vegetation; V) grasslands of the center of the state; VI) coastal grasslands; and VII) grasslands with *Aristida* spp., regionally known as "barba-de-bode" (Boldrini *et al.* 2010).

In the original study, 20 sampling sites were defined within the four municipalities. The sample method was based in the use of pitfall traps, and so the majority of the sampled taxa are of epigeic species. Further details on the methodology are described in Silva *et al.* (2022).

TABLE 1. Description of the sampled areas in Silva *et al.* (2022).

Municipality	Sampling units	Land-use	Sampling date	Season	Geographic Coordinates	
					Longitude	Latitude
JAGUARÃO	01	Gras	April 5, 2019	Autumn	−53,397,067	−32,239,946
	02	Euc	April 5, 2019	Autumn	−53,365,464	−32,239,994
	03	Gras	April 6, 2019	Autumn	−53,319,039	−32,210,709
	04	Euc	April 6, 2019	Autumn	−53,349,856	−32,240,435
	05	Gras	April 7, 2019	Autumn	−53,304,145	−32,227,443
	06	Euc	April 7, 2019	Autumn	−53,301,572	−32,245,974
LAVRAS DO SUL	07	Gras	May 7, 2019	Autumn	−54,263,648	−30,885,178
	08	Euc	May 7, 2019	Autumn	−5,431,076	−30,860,155
	09	Gras	May 8, 2019	Autumn	−54,267,129	−30,962,529
	10	Euc	May 8, 2019	Autumn	−54,252,869	−309,676
PINHEIRO MACHADO	11	Gras	November 11, 2018	Spring	−53,602,698	−31,339,271

	12	Euc	November 11, 2018	Spring	−5,359,796	−31,343,839
	13	Gras	November 12, 2018	Spring	−53,577,106	−31,385,678
	14	Euc	November 12, 2018	Spring	−53,571,586	−31,391,762
	15	Gras	November 13, 2018	Spring	−53,499,849	−31,402,764
	16	Euc	November 13, 2018	Spring	−53,509,913	−31,412,028
SÃO GABRIEL	17	Gras	April 23, 2019	Autumn	−54,324,136	−30,059,119
	18	Euc	April 23, 2019	Autumn	−54,320,563	−30,049,282
	19	Gras	April 24, 2019	Autumn	−54,321,307	−30,083,604
	20	Euc	April 24, 2019	Autumn	−54,327,398	−30,069,851

Legends: Gras = native grassland; Euc = *Eucalyptus* plantation.

Literature survey of the Collembola records from the Brazilian Pampa

Our literature review was structured in four stages. First we surveyed the "Taxonomic catalog of Brazilian Fauna" to check the nominal species records for springtails from the Pampa of RS and the original records (Zeppelini et al. 2023). In the second stage, we searched for scientific articles on the Scientific Electronic Library Online (SciELO), Google Scholar, Scopus and Web of Science Core databases. We cross-searched the descriptors: "Springtails", "Collembola"; Pampa", "Grassland", "Southern Region", "Brazil". In the third stage, we read and explored the sampled papers. The studies included in our survey were the ones which: i) were published between 2000 and 2022; ii) presented the descriptors in the title, abstract and/or keywords; iii) exploited the richness and/or the taxonomic diversity of Collembola; and iv) presented records of species/morphospecies within the phytogeographic domain of the Pampa. In the fourth and final step, a database was created with the taxonomic and other information extracted from the articles (order, family, genus, species, municipality, geographic coordinates, collection method, year, etc.). These data were used to create a table with the taxa records, plus the identification key and the list of families and genera diagnoses.

Analysis of species records, elaboration of identification keys and supraspecific diagnoses

We performed a cross-reference comparative analysis between the revised records of Silva et al. (2022) (topic 2.1) and the database from the literature review (topic 2.2), using taxa presence and absence to confirm new records for the Pampa. After, we manually built an identification key for orders, families, and genera of springtails. In its structure, a single key was provided, with the steps for orders and families in Arabic numerals and genera with letters. For families with a single genus recorded, a brief diagnosis of it is presented in a single step. The following abbreviations were used in the key: Abd. – abdominal segment; Ant. – antennal segment; Mac – Macrochaeta; Mic – Microchaeta; MTO – Metatrochanteral Organ; PAO – Postantennal organ; Th. – Thoracic segment, VT – Ventral tube. In addition, we also provide diagnoses for all supraspecific recorded taxa found based on information available in the specialized literature, such as Massoud (1967), Betsch (1980), Jordana *et al.* (1997), Christiansen & Bellinger (1998), Bretfeld (1999), Potapov (2001), Cipola *et al.* (2018a); Bellinger *et al.* (1996–2023).

Results

Reassessment of Silva et al. (2022) inventory of the Collembola fauna from the Brazilian Pampa

In Silva *et al.* (2022) study carried out in four municipalities of the Brazilian Pampa (Table 1), a total of 26 morphospecies, 18 genera, 10 families, and three orders were recorded. These records are depicted in Table 2 above. Of the original 26 morphospecies, we were able to identify two of them, while other seven had a closer related species marked with *cf.* = "to be compared with" and *aff.* = "affinis".

TABLE 2. Collembola species and morphospecies recorded in the sampled areas (municipalities) of the Pampa domain, Rio Grande do Sul, Brazil.

Taxa	Sampled municipalities			
	JAG	LAV	PIM	SAG
ENTOMOBRYOMORPHA Börner, 1913				
ENTOMOBRYIDAE Schäffer, 1896 *sensu* Godeiro *et al.* 2022	+	+	+	+
ENTOMOBRYINAE Schäffer, 1896	+	+	+	+
Entomobrya sp. 1	+	+	+	+
Entomobrya sp. 2	+	+	+	+
Entomobrya sp. 3	+	+	+	+
Entomobrya sp. 4	+	-	+	+
Entomobrya sp. 5	+	-	+	-
LEPIDOCYRTINAE Wahlgren, 1906	+	+	+	+

Lepidocyrtus cf. *nigrosetosus* Folsom, 1927	+	+	+	-
SEIRINAE Yosii, 1961	-	-	-	+
Seira sp.1	-	-	-	+
PARONELLINAE Börner 1906 *sensu* Godeiro *et al.* 2022	+	-	+	-
Trogolaphysa aff. *piracurucaensis* Nunes & Bellini, 2018*	+	-	+	-
ORCHESELLIDAE Börner, 1906 *sensu* Zhang *et al.* 2019	+	+	+	+
HETEROMURINAE Absolon & Kseneman, 1942	+	+	+	+
Dicranocentrus sp. nov.*	+	+	+	+
ISOTOMIDAE Schäffer, 1896 *sensu* Potapov, 2001	+	+	+	-
ANUROPHORINAE Börner, 1901	+	+	+	-
Folsomia sp.1	+	-	+	-
Proisotoma sp.1	+	-	+	-
ISOTOMINAE Schäffer, 1896				
Desoria aff *trispinata* MacGillivray, 1986	+	+	+	-
Desoria aff. *ruseki* Fjellberg, 1979	+	-	+	-
Isotomurus sp.1*	+	-	+	-
PODUROMORPHA Börner, 1913				
HYPOGASTRURIDAE Börner, 1906	+	+	+	+
Hypogastrura aff. *devia* Christiansen & Bellinger, 1980*	-	-	+	+
Xenilla welchi Folsom,1916*	+	+	-	+
BRACHYSTOMELLIDAE Stach, 1949	+	-	-	-
Brachystomella saladaensis Weiner & Najt, 2001*	+	-	-	-
NEANURIDAE Börner, 1901	+	+	-	-
PSEUDACHORUTINAE Börner, 1906	+	+	-	-
Pseudachorutes aff. *auricularious* Cassagnau & Rapoport, 1962*	+	+	-	+
SYMPHYPLEONA Börner, 1901 *sensu* Massoud, 1971				
DICYRTOMIDAE Börner, 1906*	+	-	-	-
PTENOTHRICINAE Richards, 1968 sensu Bretfeld, 1999	+	-	-	-
Ptenothrix sp.1*	+	-	-	-
KATIANNIDAE Börner, 1913 *sensu* Bretfeld, 1999				
Katianna sp. nov.*	-	+	-	-
Katianna sp.1*	-	+	-	-
Sminthurinus sp.1	-	+	-	-
BOURLETIELLIDAE Börner, 1913, *sensu* Bretfeld, 1994	-	-	+	-
Rastriopes sp.1*	-	-	+	-
Prorastriopes sp.1*	-	-	+	-
Prorastriopes sp.2*	-	-	+	-
SMINTHURIDIDAE Börner, 1906 *sensu* Betsch & Massoud, 1970*	+	-	+	-
Sphaeridia cf. *lobata* Bretfeld & Gauer, 1994*	+	-	+	-

Legends: * = New records for the Brazilian Pampa; + = present; - = absent; sp. = specie; aff. = affinis; cf.= confers; JAG = Jaguarão; PIM = Pinheiro Machado; LAV = Lavras do Sul; SAG = São Gabriel.

Concerning the sampled municipalities, we observed the species *Dicranocentrus* sp. nov., *Entomobrya* sp.1, *Entomobrya* sp.2 and *Entomobrya* sp.3 were the only ones found in all the four sampled municipalities (SAG, PIM, LAV and JAG). *Brachystomella saladaensis* Weiner & Najt, 2001 and *Ptenothrix* sp.1 were found exclusively in JAG. *Katianna* sp. nov., *Katianna* sp.2 and *Sminthurinus* sp.1 were found only in LAV, while *Rastriopes* sp.1, *Prorastriopes* sp.1 and *Prorastriopes* sp.2 were found only in PIM, and *Seira* sp.1 only in SAG (Table 2).

Considering species and morphospecies, the families with the highest specific richness were Entomobryidae (08 spp.) and Isotomidae (05 spp.), respectively. Less representative families were Bourletiellidae (03 spp.), Katiannidae (03 spp.) and Hypogastruridae (02 spp.), while all other families were represented by a single species/morphospecies (Figure 1).

Among the municipalities sampled in Silva et al. (2022), the genus with the highest number of morphospecies was *Entomobrya* (05 spp.). On the other hand, with the exception of *Desoria* (02 spp.), *Katianna* (02 spp.) and *Prorastriopes*

(02 spp.), all other genera had only one single assigned morphospecies/species. *Dicranocentrus* sp. nov., *Katianna* sp. nov. and *Hypogastrura* aff. *devia* are new taxa and are currently under description.

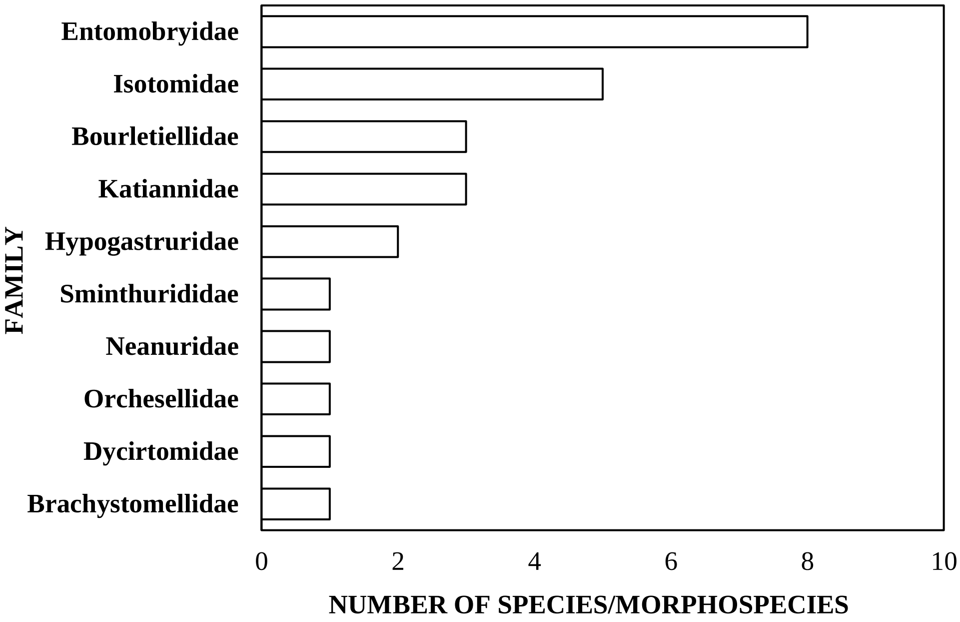

FIGURE 1. Number of Collembola species/morphospecies per family recorded in Silva *et al.* (2022), from the Brazilian Pampa.

Literature review on the Collembola records from the Brazilian Pampa

In literature databases only four scientific papers, other than Silva *et al.* (2022), met our determined search criteria. We also added *Cyphoderodes xenopus* to our list, since it is the sole nominal species from the Brazilian Pampa previously recorded in the literature (Börner 1913, Abrantes *et al.* 2010, 2012, Zeppelini *et al.* 2023). From all these sources, a total of 25 genera were recorded for the phytogeographic domain of the Pampa, distributed in 14 families and three orders (Figure 2, Table 3).

Among the registered genera, we highlight *Entomobrya* Rondani, 1861 and *Lepidocyrtus* (*Lepidocyrtus*) Bourlet, 1839, since they were found in most sites registered by the authors in the publications (Eldorado do Sul – EDS; Jaguarão – JAG; Pinheiro Machado – PIM; Lavras do Sul – LAV and São Gabriel – SAG). However, many genera have records in a single municipality, for example, *Agraphorura* Pomorski, 1998 was only observed in JAG, and *Pseudosinella* Schäffer, 1897, *Cryptopygus* Willem, 1901, *Isotomiella* Bagnall, 1939, *Onychiurus* Gervais, 1841, *Mesaphorura* Börner, 1901, *Cyphoderus* Nicolet, 1842, and *Folsomides* Stach, 1922, were found only in EDS.

Regarding the genera richness per family, Isotomidae (11 genera), Entomobryidae (7 genera) and Onychiuridae (3 genera) were the richest. All other families had only a single genera recorded (Figure 2).

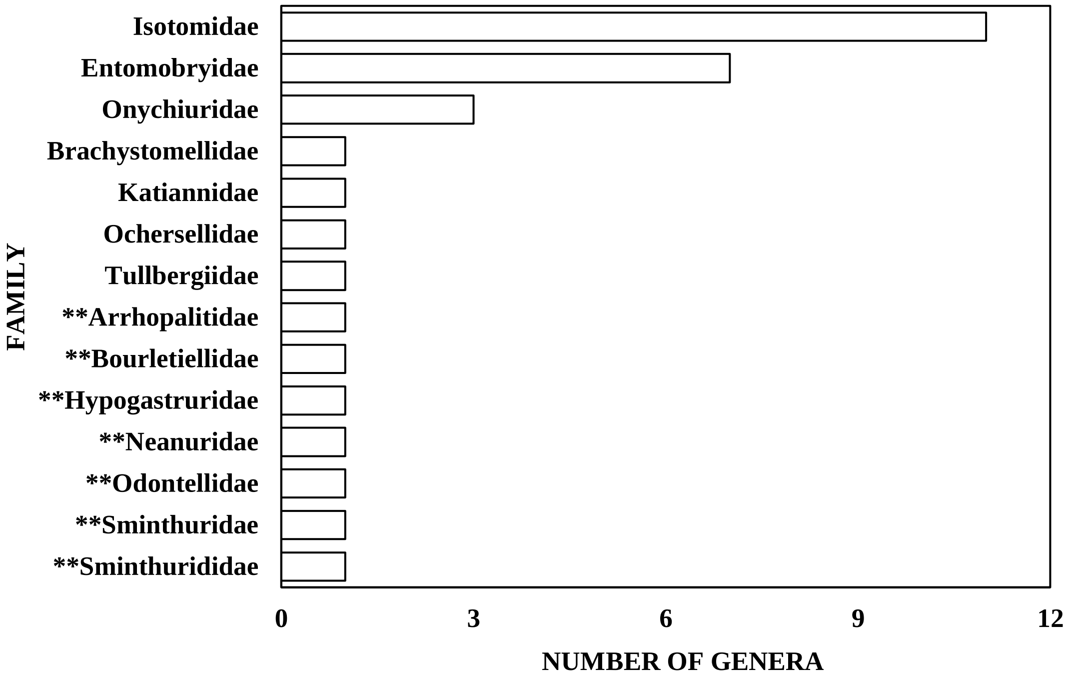

FIGURE 2. Number of Collembola genera per family recorded in the literature for Pampa, Rio Grande do Sul, Brazil. Legend: ** = Families with unidentified genera.

TABLE 3. Records of Collembola from the Brazilian Pampa, Rio Grande do Sul, Brazil, available in the literature*.

Taxa	Municipalities						Collections Methods	References
	EDS	JAG	PIM	LAV	SAG	SL		
ENTOMOBRYOMORPHA								
ENTOMOBRYIDAE	+	+	+	+	+	-		
ENTOMOBRYINAE	+	+	+	+	+	-		
Entomobrya Rondani, 1861	+	+	+	+	+	-	Berlese and pitfall	Winck *et al.* (2017), Winck *et al.* (2019), Jorge *et al.* (2022, 2023)
LEPIDOCYRTINAE	+	+	+	+	+	-		
Lepidocyrtus (*Lanocyrtus*) Yoshii & Suhardjono, 1989	+	-	-	-	-	-	Berlese and pitfall	Winck *et al.* (2017), Winck *et al.* (2019), Jorge *et al.* (2022)
Lepidocyrtus (*Lepidocyrtus*) Bourlet, 1839	+	+	+	+	+	-	Berlese and pitfall	Winck *et al.* (2017), Winck *et al.* (2019), Jorge *et al.* (2022, 2023)
Pseudosinella Schäffer, 1897	+	-	-	-	-	-	Berlese and pitfall	Winck *et al.*. (2019), Jorge *et al.* (2022)
						-		
SEIRINAE	+	+	+	+	+	-		
Lepidocyrtinus Börner, 1903	-	+	+	+	+	-	Berlese	Jorge *et al.* (2023)
Seira Lubbock, 1870	+	+	-	-	-	-	Berlese and Pitfall	Jorge *et al.* (2022, 2023)
PARONELLINAE	+	-	-	-	-	+		
Cyphoderus Nicolet, 1842	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
Cyphoderodes xenopus Börner, 1913	-	-	-	-	-	+	-	Börner (1913), Zeppelini *et al.* (2023)
ORCHESELLIDAE	+	-	-	-	-	-		
HETEROMURINAE	+	-	-	-	-	-		
Dicranocentrus Schött, 1893	+	-	-	-	-	-	Berlese And Pitfall	Jorge *et al.* (2022)

	-	-	-	-	-	-		
ISOTOMIDAE	+	+	+	+	+	-		
ANUROPHORINAE	+	+	+	+	-	-		
Arlea Womersley, 1939	+	-	+	-	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022, 2023)
Cryptopygus Willem, 1901	+	-	-	-	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022)
Isotomiella Bagnall, 1939	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
Isotomodes Axelson, 1907	+	+	+	+	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022, 2023)
Pseudanurophorus Stach, 1922	-	+	+	-	-	-	Berlese and Pitfall	Jorge *et al.* (2023)
ISOTOMINAE	+	+	+	-	+	-		
Desoria Agassiz & Nicolet, 1841	+	+	+	-	-	-	Berlese and Pitfall	Winck *et al.* (2017); Winck *et al.* (2019), Jorge *et al.* (2023)
Psammisotoma Greenslade & Deharveng, 1986	+	-	-	-	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022)
Ballistura Börner, 1906	-	+	+	-	+	-	Berlese	Jorge *et al.* (2023)
Folsomides Stach, 1922	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
Folsomia Willem, 1902	+	-	-	-	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022)
Proisotoma Börner, 1901	+	-	-	-	-	-	Berlese and Pitfall	Winck *et al.* (2019), Jorge *et al.* (2022)
PODUROMORPHA								
BRACHYSTOMELLIDAE	-	+	+	+	-	-		
Brachystomella Ågren, 1903	-	+	+	+	-	-	Berlese	Jorge *et al.* (2023)
HYPOGASTRURIDAE	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
NEANURIDAE	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
ODONTELLIDAE Massoud, 1967* **	-	-	+	-	-	-	Berlese	Jorge *et al.* (2023)
ONYCHIURIDAE Börner, 1913	+	+	+	+	+	-		
Agraphorura Pomorski, 1998	-	+	-	-	-	-	Berlese	Jorge *et al.* (2023)
Onychiurus Gervais, 1841	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
Thalassaphorura Bagnall, 1949	-	+	+	+	+	-	Berlese	Jorge *et al.* (2023)
TULLBERGIIDAE Bagnall, 1935	+	-	-	-	-	-		
Mesaphorura Börner, 1901	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
SYMPHYPLEONA								
ARRHOPALITIDAE Stach, 1956, *sensu* Bretfeld, 1999* **	+	-	-	-	-	-	Berlese	Winck *et al.* (2019)
BOURLETIELLIDAE	+	-	+	-	-	-	Berlese and Pitfall	Winck *et al.* (2017), Jorge *et al.* (2023)
KATIANNIDAE	-	-	+	-	+	-		
Sminthurinus Börner, 1901	-	-	+	-	+	-	Berlese	Jorge *et al.* (2023)
SMINTHURIDAE Lubbock, 1862, *sensu* Deharveng, 2004* **	+	-	-	-	-	-	Pitfall	Winck *et al.* (2017)
SMINTHURIDIDAE	+	-	+	+	+	-	Berlese and Pitfall	Winck *et al.* (2017), Winck *et al.* (2019), Jorge *et al.* (2023)

Data based in: Börner (1913), Winck *et al.* (2017), Winck *et al.* (2019), Jorge *et al.* (2022), Jorge *et al.* (2023), Zeppelini et al. (2023). Legend: *= other than Silva et al. (2022); *** = Genus unknown/not identified by the authors; + = present; - = absent; EDS = Eldorado do Sul; JAG = Jaguarão; PIM = Pinheiro Machado; LAV = Lavras do Sul; SAG = São Gabriel; SL = São Leopoldo.

Identification key

Below we present an identification key for orders, families and genera found so far in the Brazilian Pampa, as listed in Tables 2 and 3. For a better understanding of the external morphology and specific terms used as diagnostic structures of Collembola taxa, we recommend the reading of: Hopkin (1997), Fjellberg (2007), Cipola *et al.* (2018) and Bellinger *et al.* (1996–2023).

IDENTIFICATION KEY FOR ORDERS, FAMILIES AND GENERA OF THE BRAZILIAN PAMPA

1 Elongated body, with distinct tergal segmentation.. **2**
1' Globular body, formed by the fusion of thoracic and abdominal segments .... **Symphypleona 10**

2 Pronotum (protergite) absent, prothorax without chaeta or papillae... **Entomobryomorpha 3**
2' Pronotum present, with chaeta and/or dorsal papillae .... **Poduromorpha 5**

3 Abd. IV length less than 2.0 times the Abd. III in the midline.. **4**
3' Abd. IV length greater than 2.0 times the Abd. III in the midline.. **Entomobryidae**

a - Dens crenulate, tapering at the apex, mucro short with 1–2 curved teeth .... **b**
a' - Dens smooth and cylindrical, mucro otherwise .... **f**
b - Mucronal spine present .... **c**
b' - Mucronal spine absent.. **d**
c - Scales absent; dorsal chaetotaxy usually polymacrochetotic (with many macrochaetae)
.... *Entomobrya* Rondani, 1861
c' - Scales present; dorsal chaetotaxy oligomacrochetotic (with few macrochaetae) .... **e**
d - Antennae longer than or subequal to body; mesothorax strongly projecting over head; unguis with large lateral teeth; dens dorsally usually with long, blunt chaetae..*Lepidocyrtinus* Börner, 1903
d' - Antennae length smaller than body length; mesothorax rounded, not projecting over head; unguis with small lateral teeth, dens dorsally without blunt chaetae ....*Seira* Lubbock, 1870
e - Head with 6+6 or less eyes .... *Pseudosinella* Schäffer, 1897
e' - Head with 8+8 eyes .... *Lepidocyrtus* Bourlet, 1839
f Dens dorsally with long fringed scales... **g**
f' Dens dorsally without fringed scales .... *Trogolaphysa* Mills, 1938
g Mucro styliform with truncate apex.. *Cyphoderodes*, Silvestri, 1911
g' Mucro apically claw-shaped with variable number of teeth .... *Cyphoderus* Nicolet, 1842

4 Antennae with four segments; body without scales; usually with homogeneous dorsal chaetotaxy, with little differentiation between different types of chaetae; dorsal Mac, if present, apically pointed … .... **Isotomidae**

a - Specimens usually with distinct color patterns, Abd. III longer than other abdominal segments, VT with anterior chaetae, furcula well developed, ventral manubrium densely covered by chaetae.. **c**
a' - Specimens usually with difused or weak pigmentation, sometimes entirely pale, Abd. III shorter than other abdominal segments, VT without anterior chaetae, furcula variable, sometimes reduced or entirely absent, ventral manubrium mostly with 10+10 or less chaetae .... **b**
b - Body with few sensilla; anal spines present, furcula absent or reduced.. **e**
b' - Body with many sensilla; anal spines absent, furcula present and well developed... **i**
c - Abdominal segments without bothriotricha... *Desoria* Agassiz & Nicolet, 1841
c' - Abdominal segments with bothriotricha.. **d**
d - Mucro with 3 teeth .... *Psammisotoma* Greenslade & Deharveng, 1986
d' - Mucro with 4–5 teeth... *Isotomurus* Börner, 1903
e - Abdomen with individualized Abd. V and VI . ... **f**
e' – Abdomen with fused Abd. V–VI. .... **g**
f - Furcula present .... *Isotomodes* Axelson, 1907
f' - Furcula absent .... *Pseudanurophorus* Stach, 1922
g - Bothriotricha absent... *Arlea* Womersley, 1939
g' - Bothriotricha present.. **h**
h - PAO absent.. *Isotomiella* Bagnall, 1939
h' - PAO present .... *Cryptopygus* Willem, 1901

i - Manubrium without ventral chaetae ....**j**
i' - Manubrium with ventral chaetae ....**k**
j- Mucro without lamella...*Folsomides* Stach, 1922
j' - Mucro with lamella.. *Ballistura* Börner, 1906
k - Abd. V–VI separated...*Proisotoma* Börner, 1901
k' - Abd. IV–VI fused...*Folsomia* Willem, 1902

4' Antennae with four to six segments; body with or without scales, with heterogeneous dorsal chaetotaxy; dorsal Mac blunt or foot-shaped .... **Orchersellidae**

a – Scales present, antennae with six segments, Ant. I–II basally subdivided, Ant. III–IV annulated, abdominal segment IV short, less than twice the length of Abd. III in its midline, mucro bidentate with basal spine .... *Dicranocentrus* Schött, 1893

5 Pseudocelli present on the body and/or head; eyes always absent... **6**
5' Pseudocelli absent on body and head; eyes present or absent **7**

6 Ant. III sense org with none or one small inner papilla; sense rods partially hidden by weakly developed tegument fold ....**Tullbergiidae**

a - Specimens without pigmentation; antennae shorter than the head length. Abd. VI dorsally with proximal cuticular crescentic ridges, with two anal spines on short papillae…………………………………………………………………………….*Mesaphorura* Börner, 1901

6' Ant. III sense organ hidden by well-developed conical tegument papillae.. **Onychiuridae**

a - Furcula reduced to a finely granulated area with 2+2 Mic in two rows; Abd.VI with or without anal spines .... **b**
a' - Furcula reduced to a finely granulated area with four Mic in one transverse row; Abd.VI with anal spines ....*Onychiurus* Gervais, 1841
b - PAO with compound vesicles; tibiotarsus with seven chaetae in the distal whorl; Abd.VI devoid of anal spines .... *Agraphorura* Pomorski, 1998
b' - PAO with simple vesicles; tibiotarsus with nine or more chaetae in the distal whorl; Abd.VI with or without anal spines .... *Thalassaphorura* Bagnall, 1949

7 Maxillae without the cardo, Ant. IV triangular .... **Odontellidae**
7' Maxillae with the cardo, Ant. IV clavate **8**

8 Mandibles with molar plate .... **Hypogastruridae**

a - Eyes 4+4 or 5+5; PAO absent; unguiculus absent...*Xenylla* Tullberg, 1869
a' - Eyes 8+8; PAO present; unguiculus present with enlarged basal lamella ....*Hypogastrura* Bourlet, 1842

8' Mandibles absent or, if present, lacking molar plates.. **9**

9 Mandibles absent in Neotropical genera, maxillae with short capitulum, with rostral or internal teeth ....**Brachystomellidae**

a - Eyes 8+8 to 2+2; oral cone short and triangular; apex of maxillae globular with up to 10 rostral teeth; furcula present, with a distinct mucro …. ....*Brachystomella Ågren, 1903*

9' Mandibles usually present, maxillae elongated, sometimes styliform .... **Neanuridae**

a - PAO present, rounded or elliptical, formed by a single row of small vesicles; elongated oral cone; mandibles present with two or more apical teeth; maxillae styliform with one, two or three lamellae; furcula usually well developed ....*Pseudachorutes* Tullberg, 1871

10 Females with subanal appendage; males without prehensile antennae... **11**
10' Females without subanal appendage, male with antennae modified between Ant. II–III in prehensile structures ....**Sminthurididae**

a - Ant. II and Ant. III weakly modified in males, with only elements **b1** in Ant. II and **c3** in Ant. III. Tibiotarsus III with chaetae **IIIpi** and **IVpi** generally serrated on females, **IIpe**, **IIIpi** and **IVpi** generally modified on males, mucronal chaeta absent .... *Sphaeridia* Linnaniemi, 1912

11 Ant. IV subequal or longer than Ant. III; antennae elbowed between Ant. III–IV **12**
11' Ant. IV shorter than Ant. III; antennas antennae elbowed between the Ant. II–III .... **Dicyrtomidae**

a - Head, clypeal region with two median unpaired thick spiniform chaetae. Adults with bothriotricha **A**–**D**; Tibiotarsus III posteriorly with two to three serrated chaetae .... *Ptenothrix* Börner, 1906

12 Subanal appendage directed towards the anus; trochanteral organ absent **14**
12' Subanal appendage directed backwards or towards the genital pore; trochanteral organ present **13**

13 Eyespatches reduced and lacking pigments, with 0+0 to 2+2 eyes .... **Arrhopalitidae**
13 Eyespatches developed and dark, with 6+6 to 8+8 eyes .... **Katiannidae**

a - Furcula base without neosminturoid chaeta; head with thick frontal spines, simple **a0** chaeta on small abdomen .... *Katianna* Börner, 1906
a' - Base furcula with neosminturoid chaeta; head with normal chaetae, **a0** chaeta forked on small abdomen .. .. *Sminthurinus* Börner, 1901

14 Abd. V with two pairs of bothriotricha (**D**–**E**); capitate tenent hairs mostly present and usually dilated on all tibiotarsi; mucro spatulated with lateral borders smooth .... **Bourletiellidae**

a - Tibiotarsus with rastral organ and without obliquely truncated chaetae .... *Rastriopes* Börner, 1906
a' - Tibiotarsus without rastral organs and with obliquely truncated chaetae .... *Prorastriopes* Delamare Deboutteville, 1947

14' Abd. V with a pair of bothriotricha (**D**); capitate tenent hairs mostly absent on all tibiotarsi; mucro gutter-like, usually with at least one border toothed .... **Sminthuridae**

Families and genera diagnoses for the Collembola from the Brazilian Pampa

All diagnoses were organized alphabetically by families and genera.

ARRHOPALITIDAE Stach, 1956, *sensu* Bretfeld, 1999
Eyes reduced, 2+2 to 0+0. Trochanters II and III with trochanteral organ. Bothriotricha A–C equidistant, lying behind Abd. I and forming an angle opening anteriorly. Tibiotarsus with or without capitate tenent hairs. VT elongate and with smooth sacs, retinaculum with 4+4 teeth. Mucronal chaeta absent (adapted from Bretfeld 1999).

BRACHYSTOMELLIDAE Stach, 1949
Specimens with varied coloration, present or absent pigmentation. Pronotum present, with associated chaetae. Ant. III and Ant. IV fused dorsally and well separated ventrally. Apical bulb in Ant. IV present. Sensory organ in Ant. III with two variable-shaped sensory rods and two guard sensilla. Variable number of eyes (from 0+0 to 8+8). PAO present, with variable shape and number of vesicles, or absent. Mandibles completely absent (vestigial only in *Probrachystomellides* Weiner & Najt, 1991). Maxilae present and with cardo, apical denticles in rostral or anterolateral position. Apex of maxillae globulous (or square) or elongated. Unguis present; unguiculus absent. Furcula present or absent. Anal spines absent (adapted from Massoud 1967, Jordana *et al.* 1997, Mendonça & Fernandes 1997, Bellini & Godeiro 2017).

Brachystomella Ågren, 1903
Specimens usually dark blue pigmented, some taxa with reduced pigments or colorless. Ant. IV with apical bulb with one to three vesicles, with five to eight dorsal sensilla; ventral region without a modified set of several reduced sensilla (sensory field). PAO present, with three to ten vesicles in one single circular row. Eyes present (2+2 to 8+8). Oral cone short and triangular. Mandibles totally absent. Apex of maxillae globular with up to ten rostral teeth. Tibiotarsus with or without tenent hairs, with simple or dilated apex. Unguiculus usually absent. Furcula present, well developed (with 5–7 dental chaetae and long mucro), reduced (with 3–4 dental chaetae and reduced mucro), or vestigial (with dental chaetae and mucro) (Adapted from Massoud 1967, Queiroz & Weiner 2011, Bellini *et al.* 2018).

Remarks. The specimens of *B. saladaensis* identified in this study show a range in the number of vesicles of the apical bulb of the Ant. IV (1–3).

BOURLETIELLIDAE Börner 1913

Specimens pigmented, from pale yellow to dark black or violet, with uniform pigmentation or distinct color patterns. Antennae flexed between Ant. III and Ant. IV; Ant. IV longer than Ant. III; Ant. IV clearly subsegmented. 8+8 eyes. Five pairs of abdominal bothriotricha: three pairs on the large abdomen (A–C); two pairs (rarely one pair) on the small abdomen (D–E). Bothriotricha A, B and C aligned. Subanal appendage in females present, curved anteriorly towards the anus. Rastral organ present on the tibiotarsus. Trochanter III without trochanteric organ. VT with short sacs. Mucronal chaetae absent. Mucro usually spatulate (adapted from Bretfeld 1999, Bellini & Godeiro 2017)

Rastriopes Börner, 1906

Specimens with variable pigmentation, with stripes or complex color patterns. Eyes 8+8. Mouthparts normal. Small abdomen with regular chaeta **a0** in both sexes. Tenaculum with 3 teeth plus a basal tubercle. Tibiotarsus III with rastral organ constituted by 5–6 thick, rough or toothed chaetae (adapted from Betsch 1980, Bretfeld 1999).

Prorastriopes Delamare-Deboutteville, 1947

Specimens with variable pigmentation, with stripes or complex color patterns. Eyes 8+8. Ant. IV short, with about seven subsegments. Mouthparts normal. Parafurcal area with 15 chaetae. Small abdomen with regular chaeta **a0** in both sexes. Female with seven dorsal cicumanal chaetae smooth or with small teeth. Male genital papilla as large as one ventral anal valve, with more than 30 chaetae. Trochanter I without a distal oval organ. Tibiotarsus I–III with rastral organ constituted by obliquely truncated chaetae. Tibiotarsus I–II without the chaeta **jp**. Empodium without lamellae, with long external filament (adapted from Delamare-Deboutteville 1947, Betsch 1980, Bretfeld 1992, Bretfeld, 1999).

DICYRTOMIDAE Börner, 1906

Specimens pigmented, from pale yellow to dark brow-violet, uniformly pigmented or with distinct color patterns. Ant. IV shorter than Ant. III, antennae flexed between Ant. II and Ant. III. Ant. IV and distal part of Ant. III sometimes subsegmented. Eyes 8+8. Three or four pairs of long abdominal bothriotricha (A–C or A–D). Subanal appendage of females present, directed posteriorly or towards the anus. Tibiotarsus III usually with two or three spiniform chaetae in posterior position. VT with long sacs. Mucro without chaeta (adapted from Bretfeld 1999, Bellini & Godeiro 2017).

Ptenothrix Börner, 1906

Specimens with thick and spiniform chaetae on the frontal head (clypeal region with two median), anterior large abdomen and Abd. VI. Dorsolateral large abdomen with two or more longitudinal rows of small spines. Large abdomen without a dorsoposterior protuberance. Abdominal bothriotricha A–D present. Neosminthuroid chaetae absent on the parafurcal area. Tibiotarsus III posteriorly with two to three serrated chaetae. Unguis usually without tunica. Tenaculum with 4+4 teeth. Dorsal internal and external chaetae of the dens usually serrated or toothed (adapted from Betsch 1980, Bretfeld 1999, Cipola *et al.* 2018a).

ENTOMOBRYIDAE Schäffer, 1896 *sensu* Godeiro *et al.* 2022

Pronotum absent. Heterogeneous dorsal chaetotaxy, with chaetae of different sizes and shapes. Scales present or absent. Dorsal ciliated macrochaeta present, sometimes truncated or enlarged at the apex. PAO usually absent. Eyes present or absent. Post-ocular bothriotricha present. MTO present, with small, smooth spiniform chaetae. Abd. IV with length variable, longer than Abd. III in its midline more than 2.0 times. Dens dorsally smooth or crenulated, sometimes tapered at the apex and curved at the distal region; dental spines present or absent. Mucro always present, with variable morphology (adapted from Christiansen & Bellinger 1998, Soto-Adames *et al.* 2008, Zhang & Deharveng 2014, Bellini & Godeiro 2017, Zhang *et al.* 2019).

Entomobrya Rondani, 1861

Body colour pattern variable, from reduced to entirely pigmented; most species with clear longitudinal and/or transversal stripes or spots of pigment on dorsal body. Eyepatches black. Body and appendages without scales, secondarily covered by several ciliate small to medium-sized ciliate chaetae; dorsal chaetotaxy variable, but mostly with many Mac. Antennae without subsegments; Ant. IV usually as the longest segment, with an apical bulb; Ant. I mostly shorter than the head length. Eyes 8+8. Trunk sensilla usually as 2,2/1,2,2,+,3 from Th. II to Abd. V; Abd. IV with 2+2 bothriotricha. Abd. IV about 2.5 times or more the length of Abd. III in the midline. MTO well developed, with several spine-like smooth chaetae. Dens crenulate and tapering next to the apex, lacking spines. Mucro bidentate, sometimes with one strongly reduced apical tooth; mucronal spine present (adapted from Jordana 2012, Zhang & Deharveng 2015, Santos *et al.* 2020).

Cyphoderus Nicolet, 1842

Specimens pale, scales present. Antennae relatively short; Ant. IV not subdivided or ringed. Eyes absent. Maxillae palp with terminal appendage and basal chaeta both smooth, MTO normally **L** or **V** shape with a variable number of chaetae. Tenaculum with four teeth on each branch and one anterior chaeta on corpus; Unguis with three teeth on external lamella, two lateral and one medial, inner lamella with two well-developed basal teeth and variable number of unpaired teeth, unguiculus well developed. Dens smooth and straight, without spines but with large modified dorsal plumose scales and a few ciliate chaetae. Mucro with a single dorsal lamella with variable number of teeth, but never styliform and/or with a truncate apex (Delamare-Deboutteville 1948, Jantarit *et al.* 2014, Oliveira *et al.* 2023)

Cyphoderodes, Silvestri, 1911
Specimens pale, scales present, overall morphology similar to *Cyphoderus*. Mandibles normal, maxillae with well-developed capitulum. Mucro styliform with a truncate apex. Unguis more or less globular, deformed, bearing recognizable anterior and posterior teeth. Unguiculus without modifications (Delamare-Deboutteville 1948).

Lepidocyrtinus Börner, 1903
Specimens variably pigmented. Eyepatches black. Heavily ciliated scales present on body and appendages. Antennae with four segments; Ant. IV weakly to heavily annulated, with an apical bulb; Ant. III annulated or normal. Antennae length greater than or equal to body length. Head dorsal chaetotaxy mostly lacking postoccipital Mac (except for **Pa5** behind the eyes). Trunk macrochaetotaxy moderately developed, each segment with dorsal clusters of Mac. Th. II mostly projected anteriorly and with one anterior extra group of at least eight Mac (**a5** group). Th. II strongly projecting over head. Th. II–Abd. V sensilla formula as 1,1/0,2,2,+,3, respectively. Abd. IV well developed, much longer than the Abd. III length in midline. Abd. IV with 3+3 bothriotricha. Distal manubrium and dens usually with dorsal blunt Mac; dens crenulate and tapering next to the apex, lacking spines. Mucro falcate, without the basal spine (adapted from Cipola *et al.* 2020a, Godeiro *et al.* 2021).

Lepidocyrtus Bourlet*,* 1839
Specimens variably pigmented, many species with diffused body pigments. Eyepatches black. Finely ciliated scales present at least on the head, trunk, manubrium and ventral surface of dens. Dorsal chaetotaxy with few Mac other than those present on the Th. II collar. Antennae with four segments, none subdivided; Ant. IV apical bulb usually absent on Neotropical taxa. Eyes 8+8. Oral cone normal, not elongate. Trunk sensilla usually as 1,1/0,1,1,+,3 from Th. II to Abd. V. Abd. IV with 2+2 bothriotricha. Abd. IV about 2.5 times or more the length of Abd. III in the midline. MTO well-developed, with more than 15 smooth spiny chaetae. Dens crenulate and tapering next to the apex, rarely with proximal spines; proximal dens usually with an enlarged dorsal projection (dental lobe). Mucro bidentate with the basal spine (adapted from Zhang & Deharveng 2015, Bellini *et al.* 2015, Cipola *et al.* 2018b, Cipola *et al.* 2019).

Pseudosinella Schäffer, 1897
Specimens variably pigmented, most species with reduced body pigments or entirely pale. Finely ciliated scales present at least on the head, trunk, manubrium and ventral surface of dens. Dorsal chaetotaxy with few Mac other than those present on the Th. II collar. Antennae with four segments, none subdivided; Ant. IV apical bulb present or absent. Eyes 6+6 to 0+0. Oral cone normal, not elongate. Trunk sensilla usually as 1,1/0,1,1,+,3 from Th. II to Abd. V. Abd. IV with 2+2 bothriotricha. Abd. IV about 2.5 times or more the length of Abd. III in the midline. MTO variably developed. Dens crenulate and tapering next to the apex, without spines; proximal dens without the dental lobe. Mucro bidentate with the basal spine (adapted from Soto-Adames 2010, Zhang & Deharveng 2015, Cipola *et al.* 2020b).

Seira Lubbock, 1870
Specimens variably pigmented. Eyepatches black. Heavily ciliated scales present on body and appendages. Antennae with four segments; shorter than the body length. Head dorsal chaetotaxy mostly with clusters of Mac other than **Pa5** behind the eyes. Trunk macrochaetotaxy moderately developed, each segment with dorsal clusters of Mac. Eyes 8+8. Th. II to Abd. V sensilla formula as 1,1/0,2,2,+,3, respectively. Abd. IV well developed, about 2.5 times or more the length of Abd. III in the midline. Abd. IV with 3+3 bothriotricha in Neotropical species. MTO developed, with more than 15 smooth spiny chaetae. Neotropical taxa males without sexually dimorphic fore legs distal manubrium and dens without dorsal blunt Mac; dens crenulate and tapering next to the apex, lacking spines. Mucro falcate, without basal spine. (adapted from Zhang & Deharveng 2015, Cipola *et al.* 2018a).

Trogolaphysa Mills, 1938
Specimens variably pigmented, most taxa uniformly yellowish, bluish or pale. Finely ciliate scales distributed on Ant. I–II (at least), head, dorsal trunk and ventral face of manubrium and dens. Dorsal chaetotaxy with few Mac other than those present on the Th. II collar. Ant. IV not subsegmented, slightly annulated or smooth, apical bulb absent. Eyes 8+8 to 0+0. Labial chaetae **L1** and **L2** subequal, **L2** never reduced. Post-labial basal region usually with several chaetae organized in one or two transversal rows. Chaetotaxy of Th. II–III and Abd. I in adults mostly few Mic. Th. II to Abd. V sensilla formula as 1,1/0,1,1+2–3. Abd. IV with 3+3 bothriotricha; Abd. IV elongated, at least three times the length of the Abd. III. Manubrium without clear spines like the ones on dens. Dens straight and smooth, with one or two rows of ciliate spines. Mucro square (shorter), subrectangular or rectangular (longer), with 3–5 teeth (adapted from Soto-Adames *et al.* 2014, Soto-Adames 2015, Bellini & Cipola 2017, Nguyen & Soto-Adames 2018, Souza 2021).

HYPOGASTRURIDAE Börner, 1906
Pigmented specimens, with the exception of cavernous or euedaphic species. Pronotum present, with associated chaetae. Head and trunk without pseudocelli. Mandibles present and well developed, with evident molar plates; maxilae with six

lamellae each. Variable number of eyes (from 0+0 to 8+8), PAO present, unguiculus, tenaculum and furcula present or absent. Usually with two anal spines (adapted from Jordana *et al.* 1997, Christiansen & Bellinger 1998, Thibaud *et al.* 2004, Bellini & Godeiro 2017, Cipola *et al.* 2018a).

Hypogastrura Bourlet, 1842
Specimens pigmented, usually dark. Dorsal head and trunk chaetotaxy mostly uniform, with chaetae with similar sizes, with the exception of long sensilla. Antennae shorter than the head length, with four articles. Ant. IV with a simple or trilobed apical bulb, with up to ten dorsal sensilla, ventral region with or without a modified set of several reduced sensilla (sensory field); Ant. IV and ant. III separation without eversible sac. Eyes 8+8 to 5+5, OPA present with 3–6 vesicles. Mandibles molar plates fully developed, maxillae without modifications. Dorsal head chaetotaxy complex, with several chaetae. Th. II usually with **m2** chaeta. Unguiculus present. Furcula always present, dens with 5–7 chaetae. Anal spines present and usually short. (adapted from Jordana *et al*. 1997, Christiansen & Bellinger 1980, Thibaud *et al.* 2004).

Xenilla Tullberg, 1869
Specimens usually dark blue pigmented. Dorsal head and trunk chaetotaxy mostly uniform, with chaetae with similar sizes, with the exception of long sensilla. Antennae shorter than the head length, with four articles. Ant. IV and Ant. III separation without eversible sac. Eyes 5+5 or 4+4. PAO absent. Tibiotarsus usually with two tenent hairs with capitate apexes. Unguiculus absent. Anal spines mostly present and small. Tenaculum and furcula rarely absent. Mucro present or absent; if present fused or not to the dens (adapted from Jordana *et al.* 1997, Thibaud *et al*. 2004, Bellini & Godeiro 2017).

ISOTOMIDAE Schäffer, 1896
Pronotum absent. Pigmentation present or absent. Usually homogeneous dorsal chaetotaxy, with few differences between different types of chaetae, dorsal Mac, if present, apically pointed. Scales absent. Antennae with four segments.. PAO present or absent, when present, elliptical or oval. Eyes present or absent. Post-ocular bothriotricha absent. MTO absent. Abdominal bothriotricha present or absent. Abd. IV usually smaller than or subequal to Abd. III in length. Abd. IV, V and VI individually or fused together (IV+V+VI, IV+V or V+VI). Anal spines present or absent. Furcula present or absent. Mucro present or absent, with varied morphology (adapted from Potapov 2001, Soto-Adames *et al.* 2008, Bellini & Godeiro 2017).

Arlea Womersley, 1939
Specimens pale, lacking pigments. Eyes 2+2 or absent (more common). PAO very large and oval, without central constriction. Abd. V–VI fused to each other. Unguiculus present. Furcula usually well developed, with manubrium, dens and mucro individualized. Manubrium ventrally with 5+5 or less distal chaetae. Dens tapering apically and crenulate. Mucro falcate and small, without lamellae and the mucronal spine (adapted from Arlé 1939, Rapoport & Rubio 1968, Mendonça & Arlé 1987, Barra 1997, Abrantes & Mendonça 2005, Mendonça *et al.* 2006).

Ballistura Börner, 1906
Specimens pigmentation varying from pale to dark. Eyes 8+8 to 5+5. PAO oval to elliptical, usually small. Abd. IV, V and VI not fused to each other. VT with 4+4 or more laterodistal chaetae and, usually with only a single pair of posterior chaetae. Clavate tenant hairs present or absent. Unguis usually simple without tooth. Unguiculus present, usually with wide lamellae and an apical filament. Ventral side of the manubrium without chaetae. Dens mostly medium-sized, thick and cylindrical, not crenulate. Mucro large, bidentate and lamellate, lacking the mucronal spine (adapted from Potapov 2001, Potapov *et al*. 2006).

Cryptopygus Willem, 1901
Specimens usually pale. Body chaetae mostly short. Apical bulb of Ant. IV absent, eyes 8+8 to 0+0. PAO usually broad, oval or elliptical, with or without constriction. Abd. V and Abd. VI fused to each other. Clavate tenent hairs present or absent. Unguiculus present. Furcula present and well-developed, mucro bidentate. Manubrium with few chaetae on the ventral side, usually 1+1 or 2+2. Dens slender, crenulate, continuously narrowed (adapted from Potapov 2001, Fjellberg 2007).

Desoria Agassiz & Nicolet, 1841
Specimens mostly pigmented. Dorsal Mac present. Eyes 8+8 or rarely 6+6. PAO present, small and elliptical, without constriction. Mandibles normal, strong, unmodified. Maxillae modified in some species. Abd. V and Abd. VI separated, rarely fused. Furcula present and well-developed. Manubrium with several ventral chaetae. Dens slender, crenulated, continuously narrowed. Mucro with 3–5 teeth; mucronal spine present or absent (adapted from Potapov 2001, Fjellberg 2007, Bellini & Godeiro 2017).

Folsomia Willem, 1902
Specimens usually pale or weakly pigmented, rarely dark. Apical bulb of Ant. IV absent. Eyes 8+8 to 0+0. PAO present, with variable morphology. Abd. IV–VI fused. Retinaculum with 4+4 teeth and one chaeta. Furcula present, variably

developed. Manubrium with a variable number of ventral chaetae, usually less than 10+10. Dens mostly crenulated, continuously narrowed, mucro with 2–3 teeth. (adapted from Potapov 2001, Fjellberg 2007)

Folsomides Stach, 1922
Specimens usually with a slender body, mostly pale or weakly pigmented. Dorsal Mac present. Apical bulb of Ant. IV absent. Eyes 6+6 to 1+1. PAO organ present, oval to elongated. Abd. V and VI separated, abdomen bent between Abd. IV and Abd. V. VT with 3+3 distal chaetae. Clavate tenant hairs absent. Furcula mostly present and short Manubrium without ventral chaetae. Dens short, without crenulations. Mucro usually bidentate or entirely missing. Mucronal spine absent (adapted from Potapov 2001, Fjellberg 2007).

Isotomiella Bagnall, 1939
Specimens pale, lacking pigments. Body chaetae heterogeneous, Mac present. Ant. IV with six broadened leaf-like sensilla. Eyes and PAO absent. Abd. V and VI fused to each other. Unguis without teeth, unguiculus present. Furcula well-developed. Manubrium with 1+1 to 9+9 ventral chaetae Dens mostly medium-sized to long, slender and crenulated. Mucro short, with 1–3 teeth (adapted from Potapov 2001).

Isotomodes Axelson, 1907
Specimens pale, lacking pigments. Dorsal Mac present, usually medium-sized. Eyes absent. PAO present, mostly elliptical. Abd. V–VI separated from each other. Clavate tenant hairs absent. Furcula present and short. Manubrium without ventral chaetae. Dens short and smooth, lacking crenulations. Mucro with two teeth (adapted from Potapov 2001).

Isotomurus Börner, 1903
Specimens usually large, with more than 2 mm, mostly pigmented. Dorsal chaetotaxy heterogeneous and complex, chaetae usually ciliated, Mac present. Eyes 8+8. PAO without constrictions and small. Abd. V–VI separated from each other. Ciliate bothriotricha present at least on Abd. III–IV. Tibiotarsi II–III usually with ciliated Mac. VT anterior and posterior faces with many chaetae. Furcula present and well-developed, long. Manubrium ventral side densely covered by chaetae. Dens long, slender and crenulated, rarely tuberculated. Mucro short, with four teeth, mucronal spine present or absent (adapted from Potapov 2001, Bellini & Godeiro 2017).

Proisotoma Börner, 1901
Specimens pale to dark. Dorsal chaetae usually short, Mac present at least on the abdominal segments. Ant. IV without the apical bulb. Eyes 8+8 to 0+0. PAO present, with variable morphology. Abd. V and Abd. VI separate from each other. VT with 4+4 laterodistal and more than two posterior chaetae. Unguis simple, without tooth. Unguiculus present Clavate tenant hairs present or absent. Furcula present, short to medium-sized. Manubrium with few ventral chaetae. Dens usually thick, crenulate or smooth. Mucro with 2–3, mucronal chaeta absent (adapted from Potapov 2001, Potapov *et al.* 2006, Fjellberg 2007).

Psammisotoma Greenslade & Deharveng, 1986
Specimens pigmented, grayish to bluish. Dorsal chaetotaxy complex, with a dense cover of fine smooth chaetae, Mac absent. Eyes 8+8 to 3+3 to 8+8. PAO present, large and elliptical, without constriction. Abd. V and Abd. VI separate from each other; Abd. IV with 2+2 ciliated bothriotricha. Tenaculum with 4+4 teeth and one chaeta on corpus. Tibiotarsus II with at least one dorsal modified chaeta. Furcula present and well-developed. Manubrium with numerous ventral chaetae. Dens long and crenulated. Mucro small, with three teeth, mucronal chaeta absent (Greenslade & Deharveng 1986, Thibaud *et al.* 1994, Abrantes & Mendonça 2009).

Pseudanurophorus Stach, 1922
Specimens with or without pigments. Eyes 4+4 to 0+0. PAO present. Ant. IV without the apical bulb. Clavate tenent hairs absent; unguiculus present. Furcula entirely absent (excluding the Siberian species *P. mobillis* Potapov, 1997). Abd. IV and Abd. V separate (adapted from Potapov 2001, Fjellberg 2007).

KATIANNIDAE Börner, 1913
Specimens pigmented, from pale yellow to dark black, uniformly pigmented or with distinct color patterns. Ant. IV sometimes subsegmented. Eyes 8+8. Large abdomen with three pairs of bothriotricha (**A–C**) with a triangular pattern, small abdomen with Abd. V, with one pair of bothriotricha (**D**). Subanal appendage usually curved, directed towards the genital pore and apically split into several branches. Metatrochanter with a clear trochanteral organ, with a rounded, oval or triangular socket. Tibiotarsus with or without capitate tenent hairs. Tenaculum usually with 3+3 teeth and one basal appendix on each ramus and a corpus tenaculum with 0–2 chaetae (adapted from Bretfeld 1999, Palacios-Vargas & Vacaflores-Argadoña 2020).

Sminthurinus Börner, 1901
Specimens pigmented, usually yellowish with dark stripes or spots or entirely black. Head and body with regular chaetae, without large spines. Ant. IV undivided, at least two times longer than Ant. III; Ant. III with a simple papilla or with 2–4

vesicles. Mouthparts normal. Abdominal bothriotricha **A–D** present. Neosminthuroid chaeta present on parafurcal area. Sacs of VT smooth. Tenaculum with 4+4 teeth and 1–2 chaetae. Abd. V included or not on small abdomen. Females with furcated (bifid) chaeta **a0** on Abd. VI, circumanal chaetae winged, expanded at base (regular shape on males). Subanal appendage usually curved. Metatrochanteral chaeta present with a small chaeta on an enlarged socket. Tibiotarsi with or without capitate tenent hairs (if present, generally with 4–5). Unguis with or without pseudonychia and tunica. Unguiculus with an apical filament present, longer on first leg. Dens with ventral chaetotaxy reduced, mucronal chaeta absent, at least one edge of mucro serrated. Males generally present, smaller than females (adapted from Delamare-Deboutteville & Massoud 1963, Bretfeld 1999; Fjellberg 2007, Dányi & Park 2016).

Katianna Börner, 1906
Specimens with variable pigmentation, with stripes or complex color patterns. Spiniform striated or ciliated chaetae on frontal head and usually long chaetae on basal half of Ant. III and posterior large abdomen. Ant. IV. subdivided or annulated. Ant. III. with a single papilla. Ventral head-back without spur. Abdominal bothriotricha **A–D** present. Neosminthuroid chaeta absent. Tenaculum with 4+4 teeth. Small abdomen with normal chaeta **a0** on males and females. Metatrochanteral chaeta present with a small chaeta on an enlarged socket. Tibiotarsi with capitate tenent hairs. Mucronal chaeta absent (adapted from Börner 1907, Womersley 1939, Delamare-Deboutteville & Massoud 1963, Betsch 1980, Bretfeld 1999).

NEANURIDAE Börner, 1901
Specimens with variable size and color, present or absent pigmentation. Pronotum present. Oral cone usually elongated; mandibles present, with varied morphology, with or without lamellae and teeth; mandibles present (rarely absent), without molar plate; PAO absent or present, when present, of moruliform or simple type; variable number of eyes (0+0 to 8+8); furcula present or absent; anal spines present or absent, when present, mucro with a variable morphology (Massoud 1967, Jordana *et al*. 1997).

Pseudachorutes Tullberg, 1871
Specimens usually dark bluish or greyish. Antennae four segmented; Ant. IV apical bulb with 1–3 lobes; Ant. IV–III dorsally fused. Eyes 8+8. PAO present, rounded or elliptical, formed by a single row of small vesicles (not moruliform). Elongated oral cone; mandibles present with two or more apical teeth; maxillae styliform with one, two or three lamellae. Unguiculus absent. Furcula usually well developed; dens with at least 4+4 chaetae, mucro mostly present. Anal spines absent (adapted from Massoud 1967, Palacios-Vargas & Mejía-Madrid 2012).

ODONTELLIDAE Massoud, 1967
Specimens with varied color, with body varying from blue to completely depigmented. Number of eyes varying from 0+0 to 5+5. PAO present. oral cone short or long. Maxillary palp present. Maxillae cardo absent. Maxillary capitulum without lamellae. Mandibles reduced, without molar plates. Furcula present; dens with two to seven dorsal chaetae; mucro with variable morphology. Retinaculum present. Anal spines present or absent on Abd. IV (adapted from Massound 1967, Deharveng 1981, Jordana *et al.* 1997).

ONYCHIURIDAE Börner, 1913
Specimens generally depigmented, sometimes pale. Antennae shorter than the head length. Ant. IV without apical bulb, with a dorso-external subapical microsensilla. Ant. III sense organ hidden by well-developed conical tegument papillae. PAO present. Eyes absent. Pseudocelli present. Inner tooth of unguis present or absent. Furcula usually absent, if present, reduced. Mucro absent. Retinaculum with 1–2 teeth. Abd. II and Abd. III with ventral organ formed by some thickened chaetae. Abd. IV with or without anal spines (Jordana *et al.* 1997, Pomorski 1998, Beruete *et al*. 2021, Cipola *et al.* 2018a).

Agraphorura Pomorski, 1998
Ant. IV with two sensilla; apical organ of Ant. III with 4–5 guard papillae. PAO with composed granulated vesicles. Furcula absent, furcal region covered by a fine granulation, with 2+2 posterior small chaetae arranged in two rows. Tibiotarsus usually with seven distal chaetae, rarely with nine. Anal spines absent (adapted from Pomorski 1998, Arbea 2005, Weiner & Busmachiu 2022).

Onychiurus Gervais, 1841
Ant. III apical organ with two smooth clubs and five guard papillae; PAO with composed vesicles. Furcula absent, furcal region covered by a fine granulation, with four small chaetae in a single tranversal row. Anal spines present (adapted from Pomorski 1996, 1998, Weiner 1996, Arbea 2012, Greenslade & Ireson; 2022).

Thalassaphorura Bagnall, 1949
PAO with simple vesicles. Tibiotarsi with reduced chaetotaxy, distal whorl with nine chaetae. Furcula absent, furcal region covered by a fine granulation, with 2+2 posterior small chaetae arranged in two rows. Anal spines present (adapted from Fjellberg 1998, Pomorski 1998, Greenslade & Ireson 2022).

ORCHESELLIDAE Börner, 1906 *sensu* Zhang *et al.* 2019
Heterogeneous dorsal chaetotaxy, with chaetae of different sizes and shapes. Scales present or absent. Antennae with four to six segments; Ant. I and Ant. II subsegmented or not. apical bulb of Ant. IV present or absent. Eyes present or absent. PAO present or absent. Post-ocular bothriotricha present. MTO present. Abd. IV less than 2.0 times the length of the Abd. III in the midline. Clavate tenent hair present or absent. Mucro always present, with variable morphology (adapted from Christiansen & Bellinger 1998, Soto-Adames *et al.* 2008, Zhang & Deharveng 2015, Zhang *et al*. 2019, 2020)

Dicranocentrus Schött, 1893
Specimens mostly pigmented, colour patterns variable. Eyepatches black. Heavily ciliated scales present on body and appendages. Antennae usually with six segments; Ant. I and Ant. II basally subdivided; Ant. III–IV annulated; Ant. III usually longer than Ant. IV; Ant. IV apical bulb absent. Eyes 8+8. PAO absent. Prelabral chaetae simple (not bifurcate). Post-labial quadrangle chaetae (anterior ones surrounding the cephalic groove) smooth or rough, never ciliate. Th. II not projected over head. Th. II to Abd. V sensilla as 2,2/1,3,3,+,4–7. Abd. IV short, less than twice the length of Abd. III in its midline. Dens crenulate and tapering next to the apex, with or without simple (not ramificated or ornamented) dental spines. Mucro bidentate with the basal spine (adapted from Mari-Mutt 1979, Cipola *et al.* 2016, Xisto & Mendonça 2016, Bellini *et al*. 2020, 2022, Zhang *et al*. 2020).

SMINTHURIDAE
Specimens usually pigmented, from pale to dark brown or black, color patterns variable. Ant. IV longer than Ant. III, antenna elbowed between Ant. III and Ant. IV. Ant. IV clearly subsegmented or not. Eyes 8+8 to 0+0. Mostly with four pairs of bothriotricha: **ABCD**; **B** and **D** rarely missing in adults; **ABC** with a triangular pattern. Subanal appendages of females directed towards the anus, long and simple. Tibiotarsi tenent-hairs usually acuminate. Ungues often with pseudonychia and/or tunica. Unguiculus usually with an apical filament present. VT with long and warty sacs. Retinaculum with 3+3 teeth. Mucro apex asymmetrical or symmetrical, one of the edges usually toothed; mucronal chaeta present or absent (adapted of Bretfeld 1999).

SMINTHURIDIDAE Börner, 1906 *sensu* Betsch & Massoud, 1970
Specimens pigmented, from yellowish to dark blue, most taxa uniformly pigmented. Ant. IV longer than Ant. III, subsegmented or simple. Ant. II and Ant. III of males strongly modified into a clasper organ, with large spiniform chaetae and other specific structures. Eyes 6+6 to 8+8. Trunk with five pairs of abdominal bothriotricha, three pairs on the large abdomen (**A–C**); two pairs in the small abdomen (**D–E**). Subanal appendage in females absent. VT with short spherical sacs. Mucronal chaeta present or absent (adapted from Bretfeld 1999, Bellini & Godeiro 2017, Medeiros *et al.* 2022).

Sphaeridia Linnaniemi, 1912
Specimens pigmented, bluish grey to reddish, sometimes with dark blue on large abdomen. Small specimens (body length up to 0.6 mm in females and 0.35 mm in males). Head and large abdomen with normal chaeta, posterior dorsal large abdomen with long chaeta, sometimes short and thick chaeta on head and thorax. Ant. II and Ant. III weakly modified in males, with only elements **b1** (Ant. II) and **c3** (Ant. III) present. Ant. IV in both sexes without subdivisions. Thorax III without vesicles on males. Abdominal bothriotricha A–E present. VT generally modified with the presence of process on males. Tibiotarsus III with chaetae **IIIpi** and **IVpi** generally serrated on females, and chaetae **IIpe**, **IIIpi** and **IVpi** generally modified on males. Distal tibiotarsus III organ absent. Dens with basal inner process. Dental chaetae **E1** and **J1–3** spiniform. Mucro narrow, with at least one serrated edge. Mucronal chaeta absent (adapted from Betsch, 1980, Bretfeld 1999, Medeiros *et al*. 2022).

TULLBERGIIDAE Bagnall, 1935
Body elongated, slender, with short antennae and legs. Eyes absent; pigmentation usually absent. Ant. III sense organ with none or one small inner papilla; sense rods partially hidden by weakly developed tegument fold. PAO present with variable morphology. Pseudocelli present. Abd. VI with 1+1 (rarely 2+2) smooth anal spines. Dorsal side of Abd. IV usually with spine-like processes or tubercles. Abd. VI dorsally with or without 1+1 crescent-shaped integumental. Furcula and retinaculum absent. Tibiotarsus usually only with simple chaetae; ungues without teeth; unguiculi usually reduced or absent. VT with 6+6 or 7+7 chaetae (Jordana *et al.* 1997, Dunger & Schlitt 2011, Cipola *et al.* 2018a)

Mesaphorura Börner, 1901
Specimens pale, without pigmentation, small (usually with 0.4–0.8 mm) and slender. Antennae shorter than the head length. Antennae four-segmented; Ant. IV with five large dorsal sensilla; Ant. III apical organ with two large modified guard sensilla, plus two short sense rods partially hidden by a tegumentary fold. Eyes absent. PAO present, elliptical, with 18–55 rod-like simple vesicles arranged in two rows. Pseudocelli star-like or rosette-like shaped. Abd. VI dorsally with proximal cuticular crescentic ridges, with two anal spines on short papillae (Jordana *et al.* 1997, Dunger & Schlitt 2011, Bu & Gao 2017).

Discussion

According to our survey and results, there are now 15 families, 35 genera and three nominal species registered from the Brazilian Pampa. The higher species/morphospecies richness of Entomobryidae found in Silva *et al.* (2022) is corroborated by the literature, as this family is the most diverse of Collembola, with more than 1700 described species worldwide, and most taxa are epigeic (Bellinger *et al.* 1996–2023). In Brazil, Entomobryidae is also the richest family of springtails, with 234 species and 31 genera recorded so far (Zeppellini *et al.* 2023). On the other hand, concerning our literature survey, Isotomidae was the most representative in number of recorded genera, supporting the euedaphic and hemiedaphic fauna of the Pampa is likely highly diverse to this taxon. Isotomidae is also one of the most diversified groups of the Entomobryomorpha, with about 1472 described species worldwide, with 78 species and 21 genera recorded from Brazil so far (Bellinger *et al.* 1996–2023; Zeppelini *et al.* 2023).

In Silva *et al.* (2022), *Entomobrya* was the richest genus in number of morphospecies. This is the largest genus of Collembola, with more than 330 nominal species recorded worldwide (Bellinger *et al.* 1996–2023). Specimens of *Entomobrya* do not have scales on their body, but usually hold numerous dorsal ciliated mesochaetae (Jordana 2012). Species can be recognized based on their color patterns, but similar patterns may hide very distinct taxa, and dorsal macrochaetotaxy is likely a more reliable feature to separate them (Jordana 2012, Katz *et al.* 2015). In Brazil, the genus has 15 recognized species, of which 10 are considered endemic to the country (Zepellini *et al*. 2023).

Regarding the fauna sampled in Silva *et al.* (2022), we emphasize that the observed diversity is a direct result of the use of pitfall traps, which samples mostly epiedaphic and hemiedaphic species, such as those of Entomobryoidea and Symphypleona (Table 2). In contrast, for the records found in other studies, we observed a better representation of euedaphic groups, such as many Isotomidae, and all Onychiuridae and Tullbergiidae (Table 3). Such results are due to the use of Berlese-Tüllgren funnels in the evaluated studies (Winck *et al.* 2017, Winck *et al.* 2019, Jorge *et al.* 2023), as well as the association of this method with pitfall traps (Jorge *et al.* 2022). There is no single method capable of efficiently sampling all groups of edaphic fauna at the same time (Barreta *et al.* 2011), and so, the selection of sampling methods and their combined use must be considered to cover the largest possible number of springtails groups, in order to obtain a more representative view of sampled areas.

The listing presented in this study adds new records of species for the Brazilian Pampa. However, our results illustrate the lack of taxonomists working with the Collembola fauna from this biome, in view of its potential taxonomic richness which is still understudied. Thus, further taxonomic efforts concerning the fauna of this biome is urgent, given that, possibly, a large part of this fauna is being lost without even having been described (Bellini 2014, Bellini & Godeiro 2017, Silva *et al.* 2022).

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CAPÍTULO 4

A NEW SPECIES OF *DICRANOCENTRUS* SCHÖTT (COLLEMBOLA, ORCHESELLIDAE) FROM THE BRAZILIAN PAMPA

Preparado para submissão no periódico *Zootaxa* em colaboração com Rudy Camilo Nunes e Bruno C. Bellini. Formatado conforme as normas da revista.

A new species of *Dicranocentrus* Schött (Collembola, Orchesellidae) from the Brazilian Pampa

CLÉCIO DANILO DIAS DA SILVA[1], RUDY CAMILO NUNES[2] & BRUNO CAVALCANTE BELLINI[1]

[1]Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte (UFRN), Highway BR-101, Lagoa Nova, Campus Universitario, Natal 59072-970, RN, Brazil
[2]Biodiversity and Biotechnology Research Group of North Center Piaui, Federal Institute of Education, Science and Technology of Piaui, Pedro II 64255-000, Brazil

Corresponding author: Clécio Danilo Dias da Silva (danilodiass18@gmail.com)

Abstract

Here we describe and illustrate the first species of *Dicranocentrus* Schött, 1893 recorded from Rio Grande do Sul (RS) state and for the Brazilian Pampa domain. The species was collected in the municipality of Jaguarão, RS, Brazil. *Dicranocentrus* sp. nov. is unique within the genus by antennae Ib and IIb ventrally with two smooth acuminate chaetae each; labium scaled, with chaeta **M1** ciliated and others smooth; tenent hair capitate; manubrial plate with 13 ciliate chaetae plus nine pseudopores, manubrium ventro-apical region with two ciliate chaetae, among other features. The species belongs to the *gracilis*-group *sensu* Mari Mutt. Additionally, we have included a comparative table that encompasses all species of *Dicranocentrus* of *gracilis*-group worldwide.

Keywords: Chaetotaxy, Entomobryoidea, Entomobryomorpha, South Brazil, Taxonomy.

Introdution

Orchesellidae Börner, 1906 *sensu* Zhang *et al.* (2019) is currently composed of four subfamilies: Orchesellinae Börner, 1906, Bessoniellinae Soto-Adames, 2008, Heteromurinae Absolon & Kseneman, 1942, and Nothobryinae Zhang & Deharveng, 2015 *sensu* Nunes *et al.* 2020 (Zhang et al., 2019; Godeiro *et al.* 2022; Bellinger *et al.* 1996–2023). The last two subfamilies are recorded from Brazil, with five genera known for the country: *Heteromurtrella* Mari-Mutt, 1979, *Mastigoceras* Handschin, 1924, *Dicranocentrus* Schött, 1893, *Nothobrya* Arlé, 1961 and *Capbrya* Barra, 1999; and 18 species (Bellini *et al.* 2020, Bellinger *et al.* 1996–2023).

Dicranocentrus belongs to Heteromurinae and has a Pantropical distribution, it is the second largest genus of Orchesellidae, with 69 nominal species. Its main diagnostic features are antennae with six segments (antennal segments I and II subdivided), 8+8 eyes, absence of the postantennal organ, regular prelabral chaetae (not bifurcate), ungues with a single outer tooth and dental spines, if present, simple (Mari-Mutt 1979, Cipola *et al.* 2016, Zhang *et al.* 2020, Bellini *et al.* 2020). Mari Mutti (1979) proposed four species-groups for the genus based on dorsal head macrochaetatoxy. Species of the *circulatus*-group have $\mathbf{A_1}$ and **Ps present**, while $\mathbf{S_2}$ is absent and their **P** group consists of up to 16 macrochaetae. The *sundanensis*-group taxa have $\mathbf{S_2}$ **present**, but lack $\mathbf{A_1}$ and **Ps** and their **P** group has up to eight macrochaetae. The *marias*-group species do not present $\mathbf{A_1}$, $\mathbf{S_2}$ and any macrochaetae in the **P** group. Finally, the *gracilis*-group taxa lack $\mathbf{A_1}$ and $\mathbf{S_2}$, and usually have six macrochaetae present in the **P** group (Mari-Mutt 1979). Even so, for species of the latter group, the number of macrochaetae in the **P** group may be higher (Bellini *et al.* 2020).

Among the species of the genus, 30 of them belong to the *gracilis*-group, with 16 of them occurring in the Neotropical Region, and six species recorded from Brazil: *D. albicephalus* Xisto & Mendonça, 2017, *D. cuprum* Xisto & Mendonça, 2016, *D. heloisae* Arlé & Mendonça, 1982, *D. magnus* Xisto & Mendonça, 2017, *D. marimutti* Xisto &

Mendonça, 2017 and *D. melinus* Xisto & Mendonça, 2016. All these described species were recorded in the phytogeographic domain of the Atlantic Forest (Mari-Mutt 1979, Bellini *et al.* 2020, Bellinger *et al.* 1996–2023).

In this study, we present the description of a new species of *Dicranocentrus* of the *gracilis*-group from Brazil. Additionally, we provide a comparative table including all species from the *gracilis*-group. It is important to highlight that this is the first species description of the genus within the phytogeographical domain of the Pampa and of the State of Rio Grande do Sul, Brazil.

Materials and Methods

Specimens were firstly preserved in 70% ethanol at 6°C. After, they were clarified in Nesbitt's solution, washed in Arlé's liquid and mounted in glass slides in Hoyer medium, following Arlé & Mendonça (1982) and Jordana *et al.* (1997), with few adaptations. The habitus of the new species was photographed in 70% ethanol under a Leica S8APO stereomicroscope attached to a Leica EC4 camera, using LAS v. 4.12 software. Morphological studies and raw drawings were made under Leica DM750 microscope with phase contrast and a drawing tube attached. Final figures were covered, improved, and organized in plates with CORELDRAW 2022 software. The type series was deposited at the Collembola Collection of Centro de Biociências of Universidade Federal do Rio Grande do Norte (CC/UFRN) and Invertebrate Collection of the National Institute for Research in the Amazon (CI/INPA). Brazil.

The chaetotaxy terminology used in this study follows mainly: Fjellberg (1999) to the labial palp papillae; Gisin (1967) to the labial chaetotaxy, with additions of Zhang & Pan (2020); Cipola *et al.* (2014) to the labral chaetotaxy; Mari-Mutt (1979) to the dorsal head chaetotaxy, with additions of Soto-Adames (2008) and Zhang *et al.* (2020); Szeptycki (1972) and Zhang & Deharveng (2015) to the S-chaetotaxy; and Szeptycki (1979) to the dorsal chaetotaxy, with additions and modifications provided by Soto-Adames (2008), Cipola *et al.* (2016) and Zhang *et al.* (2018, 2019), and using Bellini *et al.* (2020, 2021) as models.

The abbreviations used in the description are: Abd.—adominal segment(s); acc.—accessory S-chaeta(e); al—anterolateral S-chaeta(e); as—anterosubmedial S-chaeta(e); Ant.—antennal segment(s); b.c.—basal chaetae; **l.p**.—lateral process; mac—macrochaeta(e); mes—mesochaeta(e); mic—microchaeta(e); ms—S-microchaeta(e); MTO—metatronchanteral organ; p.c.—proximal chaetae; ps—posterior S-chaeta(e); sens—ordinary S-chaeta(e); Th.—thoracic segment(s), VT—ventral tube. Antennal segments I and II subdivisions are: "a" to proximal subarticle, "b" to distal one.

The symbols used in the drawings to represent the dorsal chaetotaxy schemes are: large blank circles for mac; large black circles for mes; small black dots for mic; blank circles with small black circle inside for mac or mic; black chaetae-like drawings for sens or ms; black circles crossed by a line for pseudopores; a dash above or under any symbol to chaetae present or absent. Taxonomic description and comparisons are based on half body. Chaetae labels (including rows) and labial papillae are marked in bold in the text.

Results

Order Entomobryomorpha Börner, 1913

Superfamily Entomobryoidea Womersley, 1934

Family Orchesellidae Börner, 1906 *sensu* Zhang *et al*. (2019)

Subfamily Heteromurinae Absolon and Ksenemann, 1942 *sensu* Zhang & Deharveng (2015)

Tribe Heteromurini Absolon and Ksenemann, 1942 *sensu* Zhang *et al.* (2020)

Genus *Dicranocentrus* Schött, 1893

Dicranocentrus sp. nov. Silva & Bellini

Type material. Holotype: male on slide, Brazil, State of Rio Grande do Sul, Jaguarão municipality (−53,349,856, −32,240,435), *Eucalyptus* plantation in the phytogeographic domain of the Pampa, 06/IV/2019, L.R. Podgaisk col., pitfall traps. Paratypes: two males and five females, same data as holotype.

Species diagnosis: Bluish pigments on Ant. II–IV, mouthparts and tibiotarsus. Ant. III longer than Ant. IV, Ant. IIb and Ib ventrally with two smooth acuminate chaetae each. Labral papillae rounded. Dorsal head **An**, **A**, **M**, **S** and **Ps** series with 10, 5, 5, 7, 0 mac, respectively; seven posterior mac (**Pa5**, **Pa3?**, **Pm3?**, **Pp3**, **Pp7**, **Pe2–3**,) and three interocular chaetae present. Maxillary outer lobe basal chaeta acuminate, labial papilla **E** with l.p. finger-shaped, not reaching the papilla apex. Labial chaetae **M1** ciliated and **m2**, **r**, **a1**, **a2**, **l1**, and **l2** smooth, labium with four scales. Post-labial chaetotaxy with about 39 chaetae, almost smooth. Th. II with five **m** and six **p** mac, **p5** as mic; Th. III with 7, 3, 3 mac on rows **a**, **m** and **p**, respectively; Abd. I with five mac; Abd. II with three mac, Abd. III with four mac; Abd. IV with 12 mac, 5 of them internal, **B6** as mac; Abd. V with four sens. MTO with about 35 spine-like smooth chaetae. Tibiotarsi I–III without smooth chaetae, except for the distal chaeta on tibiotarsus III. Tenent hair capitate; ungues with one tiny internal apical tooth; unguiculi lanceolate, antero-internal lamella wide, postero-external with a single tooth. Ventral tube anterior face with three mac and about 22 ciliated chaetae; posterior face with about 34 ciliated chaetae and at least one smooth chaeta on each side, midline with at least three smooth and two ciliated chaetae. Lateral flap with about 18 smooth and 31 ciliated chaetae. Tenaculum corpus with a single rough chaeta. Manubrial plate with 13 ciliate chaetae plus nine pseudopores, manubrium ventro-apical region with two ciliate chaeta. Dens with 45 to 64 spines distributed in 3–5 rows in proximo-internal region.

Description: Habitus typical of the genus (Figure 1). Body length (head + trunk) of holotype = 2.76 mm, range of type series = 2.74–3.60 mm; average body length of adult females = 3.22 mm, average body length of adult males = 2.90 mm, average body length of adults = 3.08 mm. Specimens fixed in 70% ethanol with yellowish background, Ant. I distally, Ant. II–IV, mouthparts and distal tibiotarsi dark blue (Figure 1). Coarsely ciliate scales present on Ant. I, Ant. IIa, head (dorsally and ventrally), dorsal trunk, legs (all segments), ventral tube anterior and posterior faces, ventral manubrium and ventral dens. Dorsal head and trunk mac, mes and mic ciliate.

Figure 1. *Dicranocentrus* sp. nov. habitus, specimen fixed in 70% ethanol (lateral view).

Head (Figures 2–3). Antennae shorter than the trunk, ratio antennae: body = 1:1.39 (holotype). Ant. III longer than Ant. IV, antennal ratio Ant. Ia–IV of holotype = 1:6.0:2.2:7.2:22.0:10.2. Ant. IV subapical organite not seen, apparently missing, Ant. IV with a ventral subapical bifurcated pin projection (Figure 2B). Ant. III sense organ with 2 slightly swollen sensory rods and three guard surrounding sensilla (Figure 2C). Ant. IIb and Ib with two ventral smooth acuminate chaetae each (Figure 2D and 2E). Labral papillae rounded, internal larger, marked and more oval, external more discrete (Figure 2F); Labral formula with 4 (**a1–2**), 5 (**m0–2**), 5 (**p0–2**) smooth chaetae, **p0** longer than others, **a** chaetae slender, prelabral chaetae larger than the labral ones (Figure 2G). Eyepatches largest lens **A**, **B–F** subequal, **G–H** smaller than the others, with one mac and two mes as interocular chaetae (Figure 2A). Head dorsal chaetotaxy rows with 10 antennal (**An**), five anterior (**A0, A2–3, A5–6**), five medial (**M0–3**); seven sutural (**S0–1, S3–6**), two post-occipital anterior (**Pa3**?, **Pa5**), one postoccipital medial (**Pm3?**), two postoccipital posterior (**Pp3**, **Pp7**) and two postoccipital external (**Pe2–3**) mac, respectively (Figure 2A). Sublobal plate with four chaeta-like appendages, lateral one slightly reduced, interno-basal one slightly smaller than the interno-apical ones (Figure 3C). Labium with six papillae (**H**, **A**–**E**), with 2, 0, 5, 0, 4, 4 guard chaetae, respectively, **l.p.** of papilla **E** finger-shaped, not reaching the papilla apex (Figure 3A); labium with five proximal chaetae, **an2**–**3** slightly smaller than others; labial basomedial and basolateral fields chaetotaxy formula as **M1m2r1–2el1–2a1–5**, with **r1** smaller than **r2**, both not reduced; labium with four scales (Figure 3B). Post-labial chaetotaxy with about 39 rough, rough chaetae, four of them surrouding the cephalic groove (Figure 3D).

Trunk dorsal chaetotaxy (Figures 4–5). Th. II, excluding anterior collar, with one anterior (**a5**), five medial (**m1–2**, **m4–4p**) and six posterior (**p1–3**) mac, **p4–6** as mic (Figure 4A). Th. III with seven anterior (**a1–7**), three medial (**m4**, **m6p**, **m6e**) and three posterior (**p1–3**) mac; with at least four pseudopores in the postero-lateral region (Figure 4B). Abd. I with two anterior (**a2–3**), three medial (**m2–4**) mac; with at least five pseudopores in the postero-lateral region (Figure 4C). Abd. II with three medial (**m3–3e**, **m5**) mac; with at least seven pseudopores in the postero-lateral region (Figure 4D). Abd. III with one anterior (**a3**), two medial (**m3**, **pm6**) and one posterior (**p6**) mac; with at least eigth pseudopores in the posterior region (Figure 5A). Abd. IV with five central (**A3**, **A6**, **B2e?**, **B5–6**, **B6**) and seven lateral (**D3**, **E2–4**, **F1–3**, **Fe4**) mac, **as** sens just above and internal to **A3**, at least 12 central long sens (possibly many more), with at least five pseudopores in the posterior region (Figure 5B). Ratio Abd. III:IV of holotype 1:1.4. Abd. V macrochaetotaxy with one anterior (**a6e?**), three medial (**m2–3**, **m5**) and five posterior (**p1**, **p3**, **p4–5**, **5pe**) mac, with three internal and one lateral sens and at least four pseudopores in the postero-lateral region (Figure 5C).

Legs (Figure 6A–B): Trochanteral organ with about 35 spine-like smooth chaetae (Figure 6A). Tibiotarsi lacking smooth chaetae, except for the distal chaeta on tibiotarsus III. Tenent hairs discretely capitate, two small pretarsal chaetae present, tibiotarsus III distal smooth chaeta shorter than the tenent hair (Figure 6B). Ungues with four inner teeth: two paired basal teeth on proximal 1/3, one unpaired median tooth on proximal 3/5 with the same size of the basal teeth, and a shorter apical tooth on distal 1/8, apparently absent in some specimens due to size and position; unguiculi lanceolate, antero-internal lamella wide, all lamellae smooth except for the postero-external lamella with a large tooth on its proximal 1/2.

Abdominal appendages (Figure 6C–E, 7): Ventral tube anterior face with three mac and about 22 ciliate chaetae with different sizes (Figure 5C); posterior face with approximately 34 ciliated chaetae and at least one smooth chaeta on each side, midline with at least three smooth and two ciliated chaetae (Figure 6D). Lateral flap with about 18 smooth and 31 ciliated chaetae (Figure 6E). Tenaculum corpus with a single rough chaeta, each ramus with four teeth. Dorsal manubrium without smooth acuminate chaetae, manubrial plate with 13 ciliate chaetae plus nine pseudopores (Figure 7A), manubrium ventro-apical region with two ciliate chaetae (Figure 7B). Dorsal dens with one smooth acuminate chaeta on its dorsoproximal region, dens with 45 to 64 ciliate spines in 3–5 rows in proximo-internal region (Figure 7C). Mucro apical tooth larger than the basal one, mucronal spine reaching the apex of the basal tooth (Figure 7D).

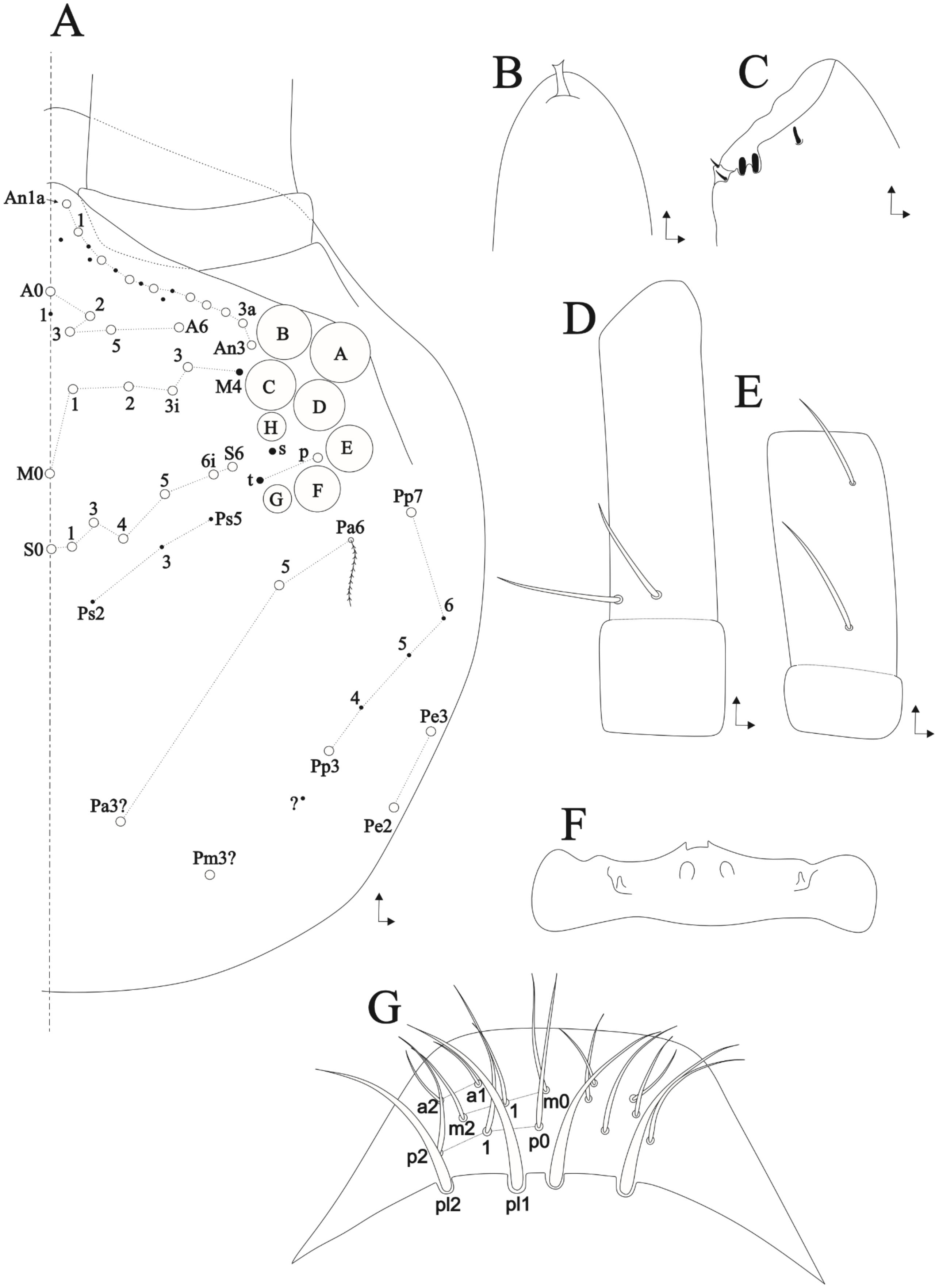

Figure 2. *Dicranocentrus* sp. nov. head: (A) dorsal head chaetotaxy and eyes (right side); (B) apical Ant. IV (ventro-lateral view); (C) apical organ of Ant. III (ventro-lateral view); (D) ventral Ant. IIa and Ant.IIb smooth acuminate chaetae; (E) Ia and Ib smooth acuminate chaetae; (F) labral papillae; (G) labral and pre-labral chaetotaxy.

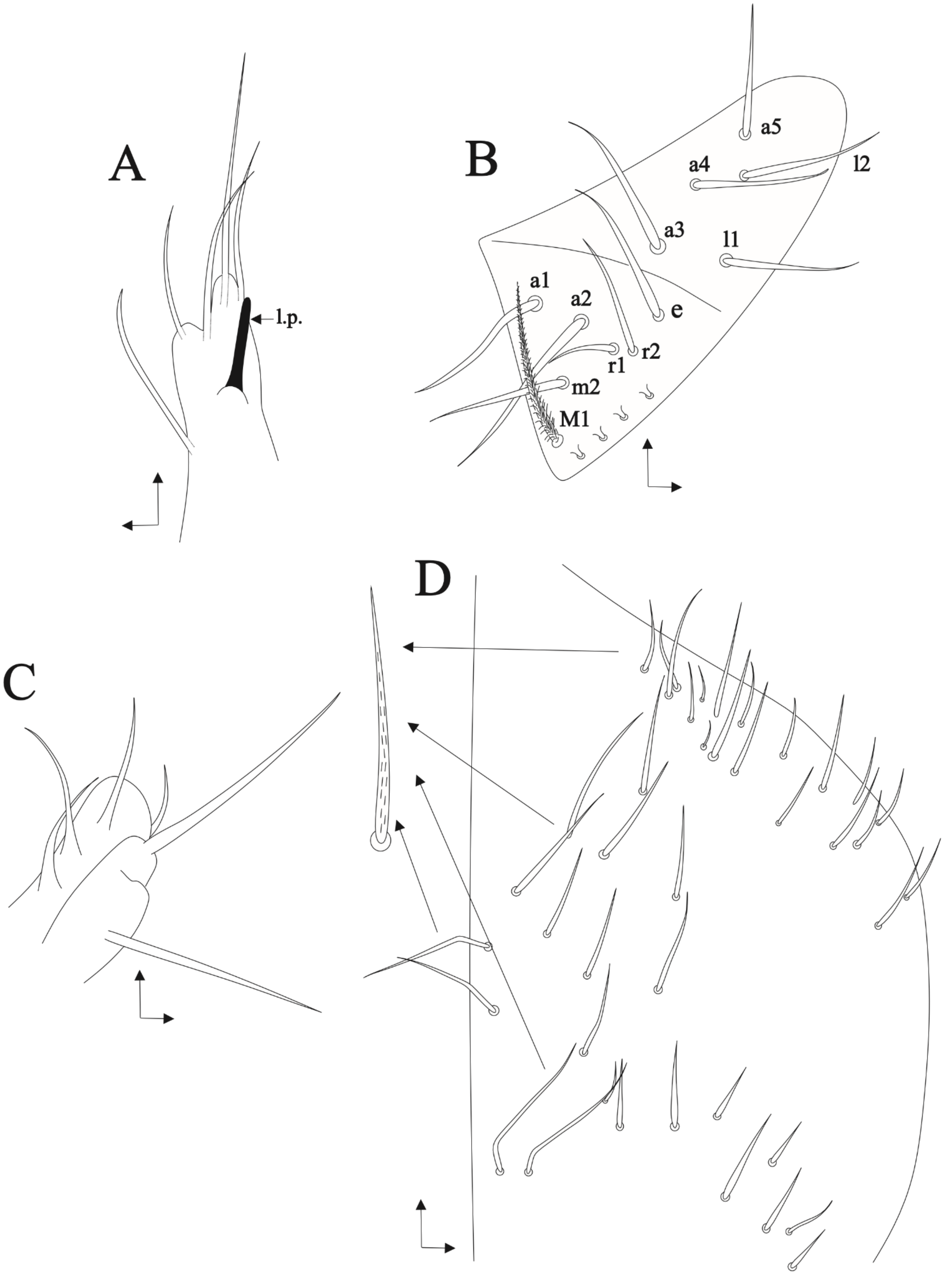

Figure 3. *Dicranocentrus* sp. nov. ventral head: (A) labial papilla E (left side), arrow indicates the lateral process (l.p.); (B) labial basomedian and basolateral fields (right side); (C) Labial palp and sublobal plate (right side); (D) post-labial chaetotaxy (rigth side), arrows point to the detailed morphology of all post-labial chaetae.

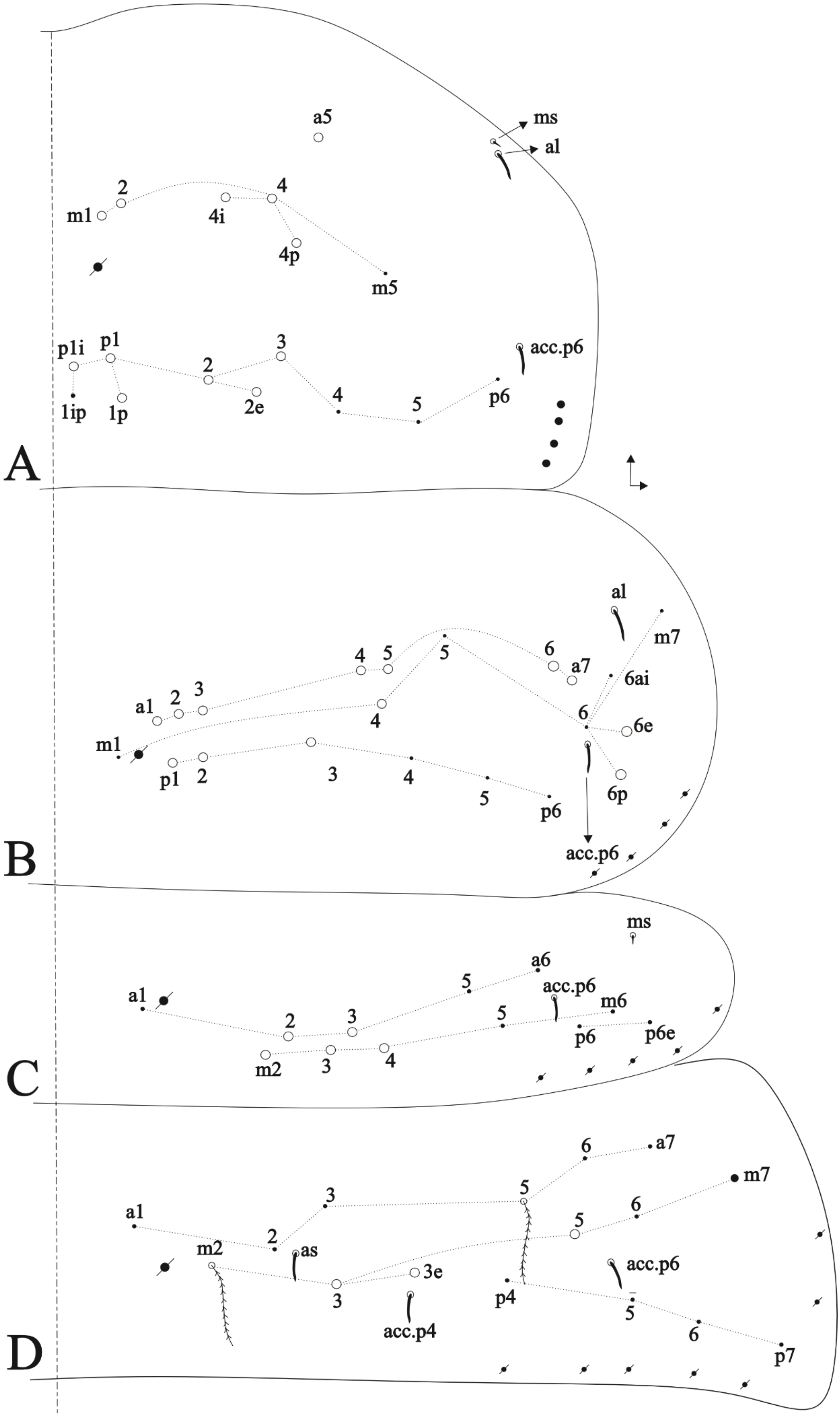

Figure 4. *Dicranocentrus* sp. nov. trunk dorsal chaetotaxy (right side): (A) Th. II; (B) Th. III; (C) Abd. I; (D) Abd. II.

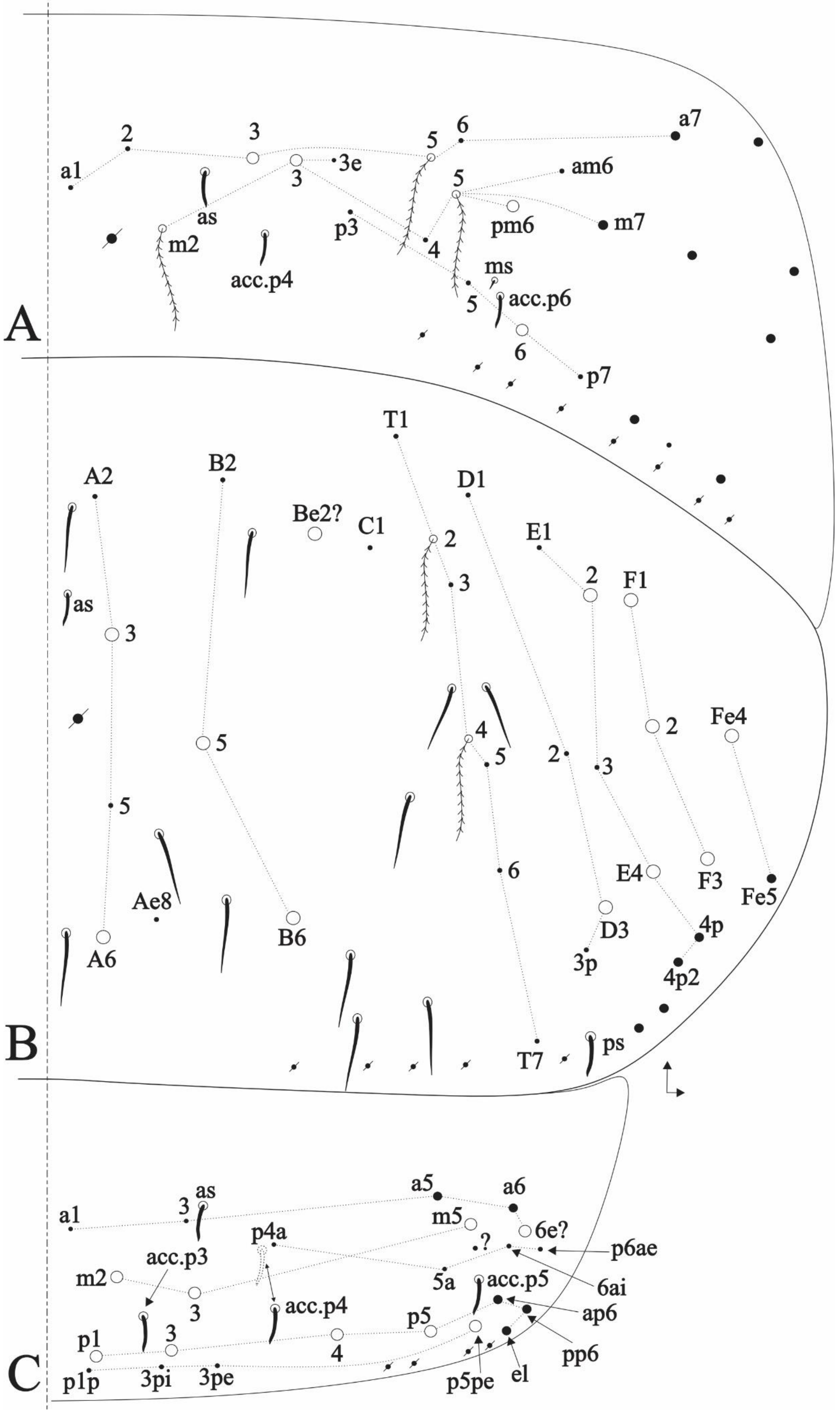

Figure 5. *Dicranocentrus* sp. nov. trunk dorsal chaetotaxy (right side): (A) Abd. III; (B) Abd. IV; (C) Abd. V.

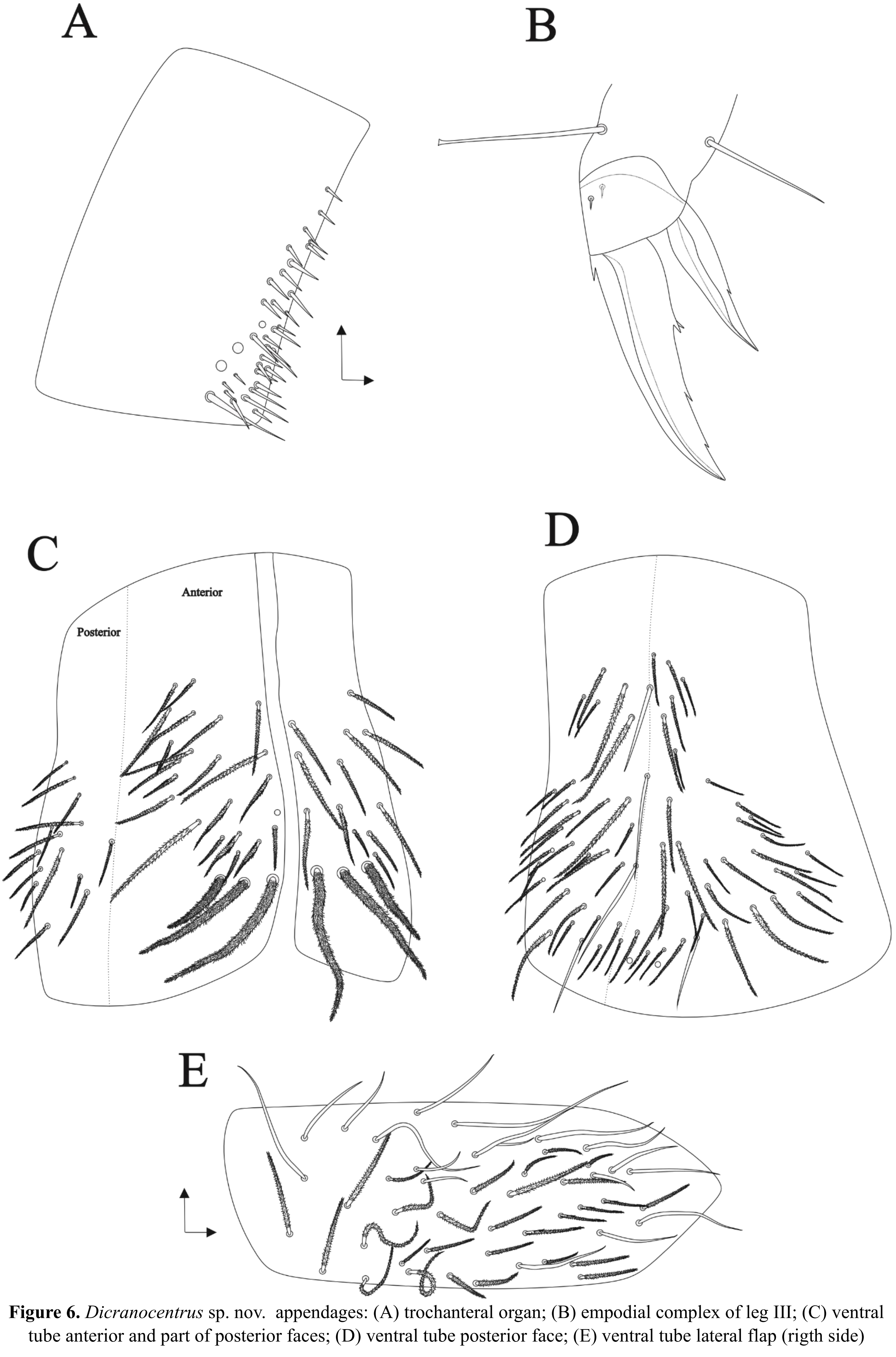

Figure 6. *Dicranocentrus* sp. nov. appendages: (A) trochanteral organ; (B) empodial complex of leg III; (C) ventral tube anterior and part of posterior faces; (D) ventral tube posterior face; (E) ventral tube lateral flap (rigth side)

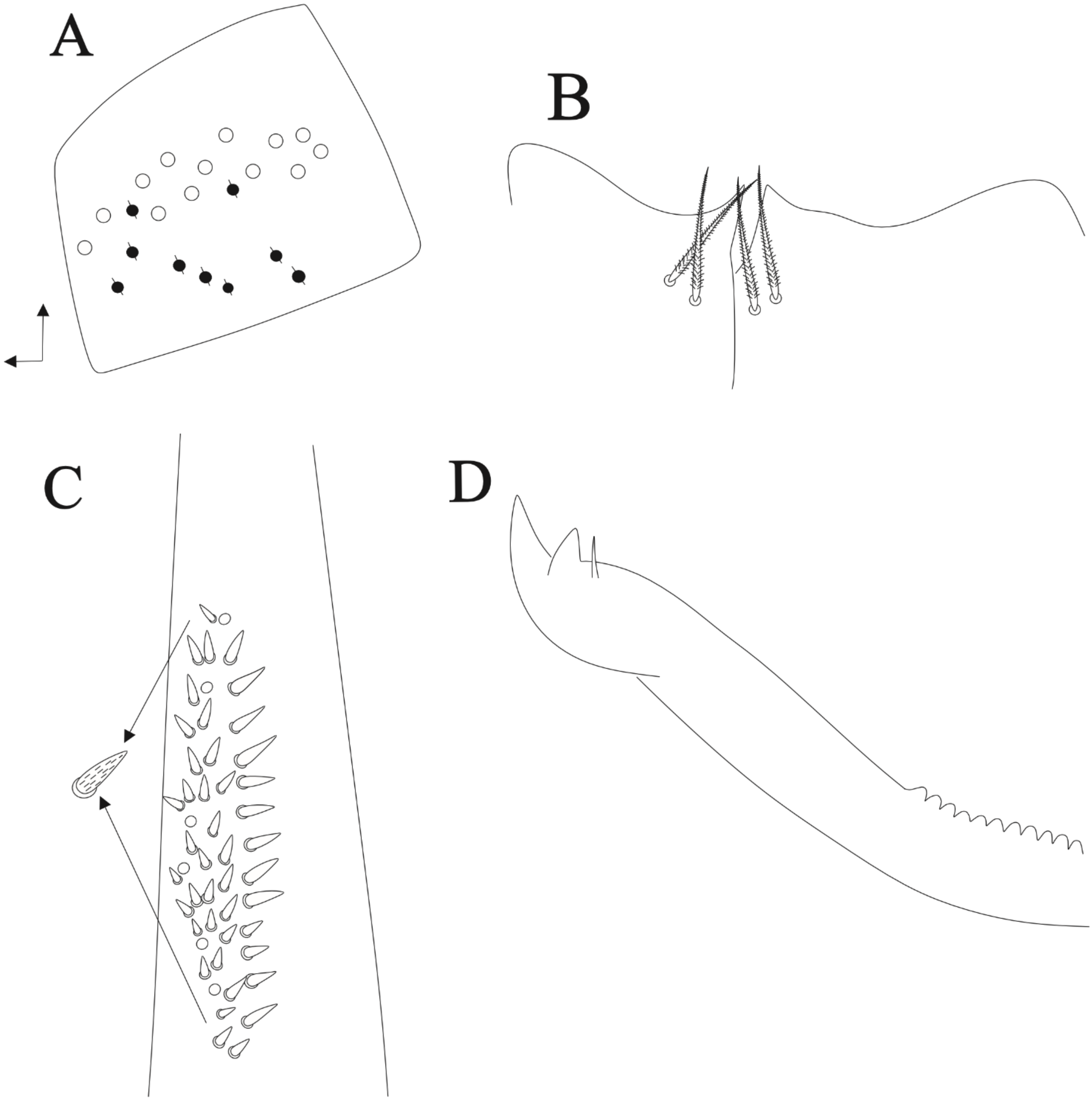

Figure 7. *Dicranocentrus* sp. nov.: (A) manubrial plate (left side); (B) manubrium ventro-distal chaetae; (C) spines on basal dens (internal view of right side), arrows point to the detailed morphology of all spines; (D) distal dens and mucro (left side).

Table 1. Comparison between *Dicranocentrus* species from the *gracilis*-group.

Species	**Body bluish/violetish pigmented areas**	**Interocular chaetae**	**Smooth chaetae in Ant. Ib**	**Smooth chaetae in Ant. IIb**	**Ant. IV subapical bifurcated projection (pin seta)**	**Basomedian and basolateral labial fields chaetae**							**Mac head – group P**	**Mac on dorsal tergites**							**Chaetae on tenaculum**		**Pseudopores in manubrial plate**	**Manubrium ventro-distal chaetae**	**Trochanteral organ chaetae**	**Tibiotarsus inner smooth chaetae**	**Tenent hair**	**Dental spines**	
						R (smaller)	**M1**	**M2**	**A1**	**A2**	**E**	**Scales**		**Th.II**	**Th.III**	**Abd. I**	**Abd. II**	**Abd. III**	**Abd. IV**	**Abd. V**	**Number**	**Type**						**Number**	**distribution**
D. sp. nov.	Ant.II–IV, tibiotarsus and mouthparts	3	2	2	+	S	C	S	S	S	S	+	5	12	13	5	3	4	12	9	1	C	9	2	±35	-	CP	45-64	3-5 rows
D. albicephalus [17]	Th. and Abd; Ant., trochanters, VT and manubrium	5	0?	1	+	C	C	S	S	S	S	-	4	12	9	5	3	4	5	?	1	S	?	?	±40	+	AC	±50	4-5 rows
D. assimilis [2,5,8]	Entire body, except dorsal head and trunk and ventral dens	?	?	?	?	?	?	?	?	?	?	?	5	11	9	3	2	2	4	?	?	?	?	?	?	+?	AC	-	-
D. bidentatus [12]	Ant. Ib-IIb, distal part of the Ant. III-IV, Th., Abd., and tibiotarsus	-?	?	?	?	C	C	C	S	S	S	-	1	?	?	?	?	?	?	?	?	?	?	?	42	+	AC	18	1-2 rows
D. capitaneus [14]	side body, head, base of ant., legs, mouthparts	5	?	?	?	?	?	?	?	?	?	?	4	13	9	5	2	6	5	?	1	?	?	?	±100	+	CP	±20	3-4 rows
D. colombiensis [5,9]	Ant., mouthparts, tibiotarsus	?	?	?	+	S	C	S	S	S	S	+	3	12	9	5	2	2	5	?	?	?	?	?	?	-	AC	29	2 rows
D. cuprum [16]	Ant., entire head, Th. And in the legs, except in the tibiotarsus.	4	-?	-?	+	S	S	S	S	S	S	-	1	10	9	5	3	4	5	?	1	C	?	?	±70	+	AC	±50	2-3 rows
D. deharvengi [10]	Ant. And legs	-?	?	?	+	C	C	C	S	S	C	-	9	15	10	6	3	5	6	?	?	?	?	?	?	-	CP	-	-
D. delamarei [8]	Ant., head and legs (except coxa)	-?	?	?	?	S	S	S	S	S	S	-	3	12	10	5	3	4	5	?	?	?	?	?	?	-	CP	10-14	1 row
D. edicitae [6]	Not specified	-?	?	?	?	?	?	?	?	?	?	?	3	12	7	4	2	2	4	0	?	?	?	?	?	?	?	?	?

Species	Body bluish/violetish pigmented areas	Interocular chaetae	Smooth chaetae in Ant. Ib	Smooth chaetae in Ant. IIb	Ant. IV subapical bifurcated projection (pin seta)	Basomedian and basolateral labial fields chaetae							Mac head – group P	Mac on dorsal tergites							Chaetae on tenaculum		Pseudopores in manubrial plate	Manubrium ventro-distal chaetae	Trochanteral organ chaetae	Tibiotarsus inner smooth chaetae	Tenent hair	Dental spines	
						R (smaller)	M1	M2	A1	A2	E	Scales		Th.II	Th.III	Abd. I	Abd. II	Abd. III	Abd. IV	Abd. V	Number	Type						Number	distribution
D. fraternus [7]	When present distributed throughout the body. Some individuals are pale.	-?	?	?	+	C	C	C	S	S	S	-	10	11	10	4	3	5	4?	?	1	?	?	?	±38	-	CP	-	-
D. gapudi [14]	Ant., legs, VT	4	?	?	?	?	?	?	?	?	?	?	7	14	12	6	2	4	5	?	6-7	C	?	?	30-40	+	AC	16-25	?
D. gracilis [5,13]	Ant., head, Th. II-III, Abd. I, Legs and VT	?	?	?	?	?	?	?	?	?	?	?	4	11	9	5	2	4	5	?	?	?	?	?	?	-	AC	16	2 rows
D. heloisae [11,15]	Ant., head and tibiotarsus	3	8	6	+	C	S	S	S	S	S	+	1	12	8	5	2	2	14	5	1	C	?	?	±100	+	AC	±60	5 rows
D. indecisus [14]	Ant., legs, VT	6	?	?	?	?	?	?	?	?	?	?	10	16	11	6	4	5	6	?	1	?	?	?	50-61	-	?	-	-
D. inermis [2,5]	Ant., legs, and Abd. V-VII	?	?	?	?	?	?	?	?	?	?	?	3	12	9	3	2	2	4	?	?	?	?	?	?	+	CA	-	-
D. longicornis [3,5]	Ant.,herad, mouthparts, Th., Abd., legs and fúrcula	?	?	?	?	?	?	?	?	?	?	?	?	12	8	5	2	3	0	?	?	?	?	?	?	-	AC	77	5-6 rows
D. *luzonensis* [14]	Ant., legs, VT	?	?	?	-	?	?	?	?	?	?	?	4	13	9	3	3	4	3	?	5-7	?	?	?	24-37	?	CA	14-20	?
D. magnus [17]	Apical part of the antennae, parts of the head, and the entire legs	5	0?	1	+	S	C	S	S	S	S	-	3	13	9	3/ 5	3	4	5	?	1	C	?	?	±100	+	AC	±40	4-5 rows
D. marimutti [17]	Th. III and Abd.; Ant. And distal region of tibiotarsus.	5	0?	4	+	C	C	C	S	S	S	-	3	12	9	5	3	4	5	?	1	S	?	?	±60	+	AC	±90	4 rows
D. melinus [16]	Ant. And Legs	7	0?	0?	+	C	C	S	S	S	S	-	4	12	9	5	3	4	5	?	1	C	?	?	±50	+	CP	±55	3-4 rows
D. meruensis [1,5,8]	Ant., mouthparts,	?	?	?	?	?	?	?	?	?	?	?	5	10	9	3	3	4	4	?	?	?	?	?	?	+	AC	39	1-3 rows

Species	Body bluish/violetish pigmented areas	Interocular chaetae	Smooth chaetae in Ant. Ib	Smooth chaetae in Ant. IIb	Ant. IV subapical bifurcated projection (pin seta)	Basomedian and basolateral labial fields chaetae							Mac head – group P	Mac on dorsal tergites							Chaetae on tenaculum		Pseudopores in manubrial plate	Manubrium ventro-distal chaetae	Trochanteral organ chaetae	Tibiotarsus inner smooth chaetae	Tenent hair	Dental spines	
						R (smaller)	M1	M2	A1	A2	E	Scales		Th.II	Th.III	Abd. I	Abd. II	Abd. III	Abd. IV	Abd. V	Number	Type						Number	distribution
	tibiotarsus and VT																												
D. nepalensis [7]	Ant. And anterior head	?	-?	-?	+	C	C	C	S	S	S	-	9	11	9	3	2	4	4	?	?	?	?	?	?	-	CP	-	-
D. nigritus [5,9]	Entire body	-?	?	?	+	S	C	C	S	S	S	-	5	9	11	5	2	4	4	?	?	?	?	?	?	-	CP	26	2 rows
D. orellanae [6]	Not specified	-?	?	?	?	?	?	?	?	?	?	?	2	14	9	5	2	3	5	4	?	?	?	?	?	?	CP	44	2-3 rows
D. paramoensis [12]	Head, Body and appendages	-?	?	?	?	C	C	C	S	S	S	-	1	10	6	3	3	3	7	10	?	?	?	?	52	-	AC	18	1-2 rows
D. platenses [9]	Ant., mouthparts and legs	?	?	?	+	C	C	S	S	S	S	+	3	12	9	5	3	4	5	?	?	?	?	?	?	-	AC/ CP	±60	4-5 rows
D. schoetti [5,9]	Ant., Head, Th., Abd., legs and VT	-?	?	?	+	S	S	S	S	S	S	+	4	11	9	5	2	4	6	?	?	?	?	?	?	-	CP	64	3-4 rows
D. singularis [7]	Ant., head, Th. II-III, Abd. I-II, and coxa	?	?	?	?	C	C	S	S	S	S	-	8	5	6	2	3	2	2	?	?	?	?	?	?	-	CP	-	-
D. thaicus [4,14]	Ant. And legs	5	?	?	?	C	C	C	S	S	C?	-	10	14	10	6	3	5	5	?	1	?	?	?	60-95	-	AC/ CP	-	-
D. violaceus [10]	Ant., Th., Abd., and legs	-?	?	?	?	C	C	S	S	S	S	-	9	12	9	4	3	5	3	?	?	?	?	?	?	-	CP	-	-

Data based in: 1 – Wahlgren (1908); 2 – Schött (1927); 3 – Handschin (1929); 4 – Yosii (1961); 5 – Mari-Mutt (1979); 6 – Jacquemart (1980); 7 – Mari Mutt, & Bhattacharjee (1980); 8 -Mari-Mutt (1981a); 9 – Mari-Mutt (1981b); 10 – Mari-Mutt (1981c); 11 – Arlé & Mendonça (1982); 12 – Mari-Mutt (1983); 13 – Schött (1893); 14 – Mari-Mutt (1985); 15 – Xisto & Mendonça (2014); 16 – Xisto & Mendonça (2016); 17 – Xisto & Mendonça (2017). Legends: (+) present; (−) absent; (±) approximately; (/) or; (?) unknown/unclear; (S) smooth; (C) ciliate; (AC) cuminate; (CP) capitate; (Abd.) abdomen; (Th.) thorax; (VT) ventral tube.

Remarks. *Dicranocentrus* sp. nov. is unique within the genus by the combination of the following features: antennae IIb and Ib ventrally with two smooth acuminate chaetae each; labial triangle with chaeta **M1** ciliated and **m2**, **r**, **a1**, **a2**, **l1**, and **l2** smooth, labium with four scales; MTO with about 35 spine-like smooth chaetae; tenent hair capitate;manubrial plate with 13 ciliate chaetae plus nine pseudopores, manubrium ventro-apical region with two ciliate chaeta; dens with 45–64 spines and bluish pigments on Antennae II–IV, mouthparts and tibiotarsus.

Dicranocentrus sp. nov. belongs to the *gracilis*-group *sensu* Mari-Mutt (1979) specially due to the absence of the **A1** and **S2** chaetae. It is mostly similar to other Neotropical species of the genus, such as *D. albicephalus*, *D. colombienses*, *D. heloisae*, *D. magnus* and *D. melinus* in terms of the subapical bifurcated projection and chaeta of the tenaculum, smooth **m2**, **a1**, **a2**, and **e** chaetae, as well as scales in the labial triangle, the subapical bifurcated projection on the Ant. IV, and some similarities in the labial triangle. However, the new species differs in several aspects. Firstly, in the number of mac in the **P** group of the dorsal head. *Dicranocentrus* sp. nov. has five mac, *D. albicephalus* and *D. melinus* have four, *D. colombiensis* and *D. magnus* have three and *D. heloisae* has one. Secondly, the number of interocular chaetae varies, with *Dicranocentrus* sp. nov. having three, *D. albicephalus* and *D. magnus* five. Thirdly, the number of MTO spine-like chaetae differs, with *Dicranocentrus* sp. nov. having about 35, *D. albicephalus* about 40, *D. melinus* about 50 and *D. magnus* and *D. heloisae* about 100, each one. Lastly, the spines in the proximo-internal region of the dens also show variation, with *Dicranocentrus* sp. nov. having 45–64 spines, *D. albicephalus* about 50, *D. colombiensis* about 29, *D. magnus* about 40, *D. melinus* about 55 and *D. heloisae* about 60. *Dicranocentrus* sp. nov. resembles *D. colombiensis* in the presence of scales in the labial triangle, while these scales are absent in *D. magnus* and *D. albicephalus*. The **r** chaeta in the labial triangle is smooth in *Dicranocentrus* sp. nov., while in *D. melinus* and *D. heloisae* it is ciliated. In terms of interocular chaetae, both *Dicranocentrus* sp. nov. and *D. heloisae* have three, while *D. melinus* has seven. Furthermore, *Dicranocentrus* sp. nov. differs from these species by having a capitate tenent hair, while in *D. albicephalus*, *D. colombiensis*, *D. magnus* and *D. heloisae* it is acuminate. *Dicranocentrus* sp. nov. and *D. melinus* have a ciliated **M1** chaeta while in *D. heloisae*, **m1** chaeta is smooth. Considering all the facts mentioned above, it is possible to conclude that *Dicranocentrus* sp. nov. is a new species, differing significantly from its congeners, specifically of the *gracilis*-group. For further comparisons with more species see table 1.

Habitat. The type material was found in *Eucalyptus* plantations with a semi-open canopy with considerable input of sunlight and a dense and dark layer of plant litter on the soil.

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CONCLUSÃO GERAL

Diante dos resultados encontrados, esta tese apresenta uma significativa contribuição ao conhecimento da fauna de colêmbolos no Pampa, tanto no estado do Rio Grande do Sul como em escala nacional. Nossos achados permitiram uma compreensão profunda dos impactos resultantes da conversão de campos nativos para plantações de *Eucalyptus* sobre as comunidades de colêmbolos.

Os resultados encontrados sustentam que o processo de conversão supracitado está causando perdas substanciais na diversidade taxonômica dos colêmbolos no Pampa. Esses achados são alarmantes, especialmente à luz da extensa transformação das áreas naturais em diversos usos do solo (cultivos de *Eucalyptus*, soja, arroz, etc.). Consequentemente, considerando este cenário, podemos sugerir que muitas espécies de colêmbolos possam ter sido extintas localmente antes mesmo de serem identificadas, registradas e até mesmo descritas.

Além disso, nossos resultados relativos à diversidade funcional destacaram a influência direta do plantio de *Eucalyptus* na composição funcional das comunidades de colêmbolos. Observamos uma associação de espécies epigéicas com os campos nativos e de espécies endogéicas com as plantações de *Eucalyptus*. Adicionalmente, ficou evidente que o processo de conversão tem efeitos negativos na riqueza geral de espécies de colêmbolos, incluindo reduções nas estruturas e apêndices corporais, bem como na diversidade funcional dessas comunidades.

Este trabalho também resultou na criação de um conjunto de informações sobre ordens, famílias e gêneros de colêmbolos que ocorrem no Pampa, acompanhado da elaboração de uma chave de identificação e diagnoses supragenéricas que certamente contribuirão para a expansão e aprimoramento das pesquisas relacionadas a Taxonomia e Ecologia Collembola nesta região.

Por meio dos dados gerados e consolidados nesta tese, agora dispomos de registros de três espécies nominais, 15 famílias e 35 gêneros para o Pampa. Além disso, descrevemos e ilustramos a primeira espécie de *Dicranocentrus* Schött para o Rio Grande do Sul e para a região do Pampa brasileiro, pertencente ao grupo *gracilis sensu* Mari-Mutt. Com base nesses avanços, elaboramos uma tabela comparativa abrangendo todas as espécies de *Dicranocentrus* do grupo *gracilis* em todo o mundo.

Em suma, esta tese contribui significativamente para o entendimento da taxonomia, ecologia e conservação de colêmbolos no contexto do Pampa brasileiro. Destacamos a importância de estudos aprofundados sobre o impacto das práticas de uso da terra na biodiversidade dessas comunidades e enfatiza a necessidade de conservar os campos nativos e adotar práticas sustentáveis nas plantações de *Eucalyptus* para garantir a manutenção da diversidade desses animais e o equilíbrio ecológico do domínio do Pampa.