Role of Microhabitats and Environment Variation on Collembola (Hexapoda: Entognatha) Populations in The Luquillo Experimental Forest: A Montane Environment

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List of abbreviation

A. General

CTE	canopy trimming experiment
DCA	detrended correspondence analysis
LEF	The Luquillo Experimental Forest
LTER	Long-Term Ecological Research
m a.s.l.	Meters above sea level
PCA	principal component analysis
PERMANOVA	permutational multivariate analysis of variance
SIMPER	Similarity Percentage

B. Collembola Morphology

Abd	abdominal segment
Ag	ante-genital
Af	antenno-frontal
An	anal
Ant	antennal segment
Cl	clypeal
Cx	coxa
De	dorso-external
Di	dorso–internal
DL	dorso–lateral
Fe	femur
Fu	furcal vestige
L	lateral
M	long macroseta
mi	microseta
Oc	ocular
PAO	Post antennal organ
S	sensillum
Scx	subcoxa
Sgd	dorsal guard sensillum of Ant. III
Sgv	ventral guard sensillum of Ant. III
ss	sensorial seta
So	subocular
Th	thoracic segment
Ti	tibiotarsu
Tr	trochanter
V	ventral
Ve	ventro-external
Vi	entro-internal
Vl	ventro-lateral
VT	ventral tube

Author's Biography

Claudia Marcela Ospina Sánchez was born in Bogotá, Colombia in March 29, 1980. She is the second of the three offspring's of Luis Ovidio Ospina and María Adela Sánchez. In 2017 her daughter Emilia was born in San Juan, Puerto Rico.

In December of 2004, Claudia completed a degree in agronomic engineering from the Universidad Nacional de Colombia, sede Bogotá. Since, she developed an interest in Collembola Taxonomy. Her thesis, springtails associated with cultivated grasses in three Holdridge life zones located in the Antioquia department (Colombia), was published in Agronomía Colombiana, being one of the first references of Collembola in Colombia.

Before her graduation she joined the International Center for Tropical Agriculture (CIAT) for an internship about springtails associated with cotton and maize crops. After the graduation she got enrolled in CIAT as a research assistant working on the impact of biotechnology on biodiversity, while also continuing her work in Collembola Taxonomy.

With the motivation to continue her work in Collembola taxonomy at an academic level, in August 2008 she was admitted to the Master degree in Biology at the University of Puerto Rico, Mayagüez campus. In 2010 she completed the grade focused in Springtails populations in litter in a Secondary Forest. After graduating she returned to Colombia to participate in the improvement of Taxonomic Collections in Collaboration with CIAT and the Entomology Museum form Universidad Nacional de Colombia - Agronomía (UNAB).

The interest of Claudia Marcela for Collembola continued growing with the time, and in August of 2012 she was enrolled as a Ph. D student in the biology intercampus doctoral program at the University of Puerto Rico. This time she described 14 new Collembola species, and worked in the ecology of Collembola in a Tropical Forest.

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Abstract

It is well understood that complex abiotic and biotic factors influence soil dynamics. To better understand these interactions, the ability to discuss focal taxa at a species level could be incredibly informative, albeit difficult to accomplish due to limited knowledge of existing taxa diversity. The utilization of microhabitats by different species may be important in explaining community compositions among forest types. Collembolans represent a unique focus group to help understand soil dynamics because they respond strongly to physico-chemical and/or biological changes that occur within environments even over a small geographic range. This study was conducted along an altitudinal gradient in the Luquillo Mountains of Puerto Rico. We sampled in tabonuco, (*Dacryodes excelsa*, 300-520 m a.s.l.) palo colorado (*Cyrilla racemiflora,* 750-820 m a.s.l.), and elfin (*Tabebuia rigida,* 950-1050 m a.s.l.) forest types. Sampling occurred in nine plots every four months from August 2014 to August 2015, with three plots in each forest type. In each plot, we selected five trees of the dominant species and sampled soil, leaf litter and epiphytes from the adjacent area of each tree. Berlese funnels were used to extract all arthropods and collembolans were identified to species. In total, 8335 collembolans were collected and found to represent 51 species, 2 subspecies and 6 forms that belong to 15 families. Fourteen new species and 2 subspecies were described, and 22 species were reported for the Island. The QRL analyses showed the influence of environmental conditions over the morphological traits in Collembola species, and allowed the separation in to functional group based in mobility characters. According to a principal component analysis (PCA) there was a clear separation of Collembola communities according to the elevation among the three forests type. Community composition varied among forests, in species richness and abundances. Palo colorado forest had the highest number of species 52, followed by the efin with 42 and Tabonuco with 37. These results show the importance of several microhabitats for collembolans, especially epiphytes in the elfin forest, which were found to contain high abundance. For soil samples we found two endemic species, while in epiphytes and leaf litter had 6 and 9 exclusive species respectively. This study highlights the dearth of taxonomic information for collembolans in tropical forests and the importance of their distribution along microhabitats as well as their participation in the decomposition process.

Chapter 1 : Distribution of the microarthropods in Tropical Forests: Study on Collembola (Hexapoda: Entognatha) Populations in The Luquillo Experimental Forest in Puerto Rico

1. Introduction

The study of the distribution patterns of living organisms and the factors that drive the organization of such patterns is a central theme in ecology (Rahbek 2005). Arthropods distribution patterns along gradients are of interest because they reflect ecological and evolutionary responses to environmental change. As a consequence, variation in soil biodiversity presents strong local and taxonomic specificity. Studies in biological soil communities point to consistent patterns in soil diversity and distribution (Bardgett et al. 2005). However, at species levels there is a dearth of fundamental information as to how soil diversity responds to environmental gradients at specific geographic scales, or what biotic or abiotic factors control soil diversity. The aim of this study is to characterize the richness and diversity of Collembola along a tropical mountain gradient, as well as the correlation of richness and diversity with biotic and abiotic microhabitats characteristics within three forest types along the elevation gradient in the Luquillo Mountains.

Montane environments allow exploration, within short geographical distances, of the effects environmental gradients in temperature and humidity on ecosystem processes (Rahbek 2005, González et al. 2013, Maunsell et al. 2013). These changes in climate have large influence on vegetation, leaf litter composition and soil type (Jordan 1985). In addition, the decomposition process is controlled by soil organisms whose functions are influenced by environmental conditions and the chemical composition of the litter (Swift et al. 1979, Seastedt 1984, Lavelle et al. 1993, Aerts 1997, Wardle et al. 2004, Lavelle et al. 2006). The biodiversity of decomposers is controlled by climate, soil type, vegetation composition, plant species diversity, and mixing of plant litter types (Wardle et al. 1999, González and Seastedt 2001, Bardgett and van der Putten 2014).

Studies on belowground diversity and their impact for ecosystem functioning form a relatively new field in ecology, still largely unexplored and little understood (Bardgett et al. 2005, Bardgett and Wardle 2010). Belowground decomposers drive essential ecosystem functions, such as organic matter turnover and nutrient cycling (Wardle et al. 2004, Bardgett and Wardle 2010) and are therefore key determinants of soil fertility and nutrient uptake by plants (Coleman et al. 2004, Wardle et al. 2004, Bardgett and Wardle, 2010). Collembola (springtails) are among the most abundant and diverse decomposers and are known to modify plant growth through the nutrient recycling (Hopkin 1997, Wardle 1999). Collembola have well differentiated morphological life-forms which enable the functional role that they play in ecosystems to be recognized to some degree (Rusek 1998). However, environmental conditions that determine springtail species composition in tropical ecosystems is little studied (Petersen 2002). The main objective of this dissertation is to identify and compare the composition and abundance of Collembola in a mountain gradient in soil, leaf litter and epiphyte microhabitats in three forest types in the Luquillo Experimental Forest in Puerto Rico. Additionally, I characterize the environmental conditions in soil, vegetation and atmosphere that influence the Collembola population's assemblages and would serve as criteria to determinate the functional adaptations of the species to an ecological role.

1.1. Microhabitats and decomposition

The soil is an important natural resource for a number of ecosystem and biosphere processes. These processes include: plant production, cycling of organic matter and nutrients, storage of carbon and water; and also release of nitrous oxides, carbon dioxide and methane

(Swift et al. 1979, Lavelle and Spain 2001). Forest soil is commonly covered by plant debris in different decomposition states. Decomposition can be considered as a two-stage process. First, litter is broken down by detritivores to small pieces which can be chemically reduced. Second, through the activities of micro-organisms (bacteria and fungi) these small pieces of organic matter are further reduced and mineralized into basic inorganic molecules, such as ammonium, phosphate, carbon dioxide and water. These can be taken up by plants or micro-organisms, leached out of the system or, in the case of gaseous break-down products, released to the atmosphere (Swift et al. 1979, Golley 1983). There are three main levels of litter decomposition control, which operate in the following order: climate> litter chemistry> soil organisms (Swift et al. 1979, Seastedt 1984, McClaugherty et al. 1985, Zak et al. 1990, Lavelle et al. 1993, Aerts 1997, Bengtsson 1998).

In forest ecosystems, the soil is established by ecological processes such as primary production by plants and the decomposition of organic matter by microorganisms. In many tropical and temperate forests, however, a considerable amount of dead organic matter is retained in the canopy, forming epiphyte mats (Fonte and Schowalter 2004). The development of such structures provides a variety of habitats for organisms, and thus contributes to raising species diversity (Takeda and Abe 2001). In these systems, it is known that grazing food webs based on live parts of plants form primarily in the canopy, whereas detritus-based food webs reside primarily in the soil (Takeda and Abe 2001).

The organic matter in the canopy is composed of shoots and roots of vascular and non-vascular plants, abscised leaves of host trees, and epiphytes that have been intercepted by branches (Nadkarni et al. 2002). These mats form communities of meso- and microarthropods, fungi, and other microorganisms that are distinct from floor communities, yet that interact with whole-forest processes (Nadkarni et al. 2002). The canopy organic matter influences nutrient cycling by altering ecosystem nutrient pools, pathways, and rates of fluxes (Coxson and Nadkarni 1995).

Microclimate has a direct effect on litter decomposition due to the effects of temperature and moisture (Swift et al. 1979, Swift and Anderson 1989, Coleman and Crossley Jr 2004, Wardle et al. 2004). The moisture environment of litter and soil depend on the supply of water to it by precipitation, the interception by vegetation, and the losses from it by evapotranspiration (Swift et al. 1979, Lavelle et al. 1993). The relative importance of these factors is influenced by temperature, the physical nature of the soil, and the character of the vegetation cover (McClaugherty et al. 1985, Swift and Anderson 1989, Lavelle et al. 1993, Aerts 1997). Moreover, fluctuations in temperature and location of the liquid, in films, or in empty spaces have a marked influence in the soil biota, because many soil animals absorb and lose water through their integuments (Coleman and Crossley Jr 2004).

1.2. Soil Arthropods

Soil arthropods are important to many ecosystem processes, such as leaf litter breakdown, soil formation, and nutrient cycling (D'Haese 2013). Soils also host high biodiversity, with significant bio indication potential (Paoletti 1999). Soil moisture is one of the principal soil characteristics that influence distribution of soil macroarthropods, because their survival can be affected negatively by both low and high soil moisture values (Blanchart et al. 1987, Ausden et al. 2001, Adis and Junk 2002). The chemical composition of plant residues and the nature of the decomposer community play an important role in decomposition and nutrient availability to plants (Tian and Brussaard 1993). Faunal influences are strongest in the tropics (Heneghan et al. 1998, González and Seastedt 2001). The amount and quality of the litter layer may control the diversity and action of important soil organisms (Crossley et al. 1992, Wall and Moore 1999, Wardle et al. 1999, González and Seastedt 2001).

Arthropods and epiphytes are significant biodiversity components of tropical forest canopies. These two biological elements share a link in forests via the presence of epiphyte mats—accumulations of living and dead plant material on the upper surfaces of branches (Yanoviak et al. 2004) that harbor a diverse but inconspicuous arthropod fauna. This material also provides habitat for other diverse invertebrate fauna, which includes many of the major groups of decomposers found in terrestrial soil (Nadkarni and Longino 1990). Entomologists have documented that the dead organic matter is inhabited by numerous species of invertebrates in both tropical and temperate forest canopy mats (Nadkarni and Longino 1990). This system is dominated by mites (Acarina), springtails (Collembola), ants (Hymenoptera: Formicidae), and minute beetles (Coleoptera) (Yanoviak et al. 2004, Richardson et al. 2005, Yanoviak et al. 2007). Many species are canopy specialists, which are never encountered on the forest floor (Nadkarni and Longino 1990, Paoletti et al. 1991). Additionally, recent studies have documented numerous forest types where canopy organic matter is abundant: tropical montane forests, temperate rainforests, elfin woodlands, and some lowland forests (Coxson and Nadkarni 1995).

Soil invertebrate taxa composition within decomposing substrates is determined by: (i) the quality and structure (including pore space) of litter, which (assuming stable litter input quality over time) depends mostly on the stage of decomposition (Berg et al. 1998, Berg and Bengtsson 2007) and varies between soil horizons; (ii) vertical gradients of abiotic factors such as temperature and moisture (Briones et al. 2007); and (iii) an interaction between i and ii (Swift et al. 1979, Aerts 1997). For instance, differences in organic matter quality may influence water retention capacity, insulation capacity or albedo, affecting moisture and temperature regimes and thereby species assemblages (Krab et al. 2010).

Intra-taxonomic comparative studies of the altitudinal and latitudinal gradients represent a convenient natural system for investigating the effect of climate on mechanisms determining geographical variation in species richness (Rahbek 2005). Nevertheless, this approach remains largely unexplored. For this work, Collembola are chosen as a soil-arthropod biodiversity indicator because of their high taxonomic diversity, their richness in narrowly distributed species, and their high abundance in all terrestrial habitats, especially in soils and leaf litter of some forests where they constitute one of the most numerous arthropods. Previously, altitudinal studies on Collembola indicate that, as a group, they respond strongly to the physico-chemical and/or biological changes that occur with increasing elevation, even over a relatively small elevation range (Cutz-Pool et al. 2010, García-Gómez et al. 2011, Maunsell et al. 2013).

1.3. Altitudinal gradients

Understanding patterns in biodiversity along environmental gradients is a central theme in ecology (Ricklefs 2004). Of particular interest are arthropods and the changes that they experiment along elevation gradients because they are remarkably diverse. Additionally, arthropods have a major role in shaping aboveground biodiversity and the functioning of terrestrial ecosystems, as well as their ecological and evolutionary responses to environmental change (Bardgett and van der Putten 2014). The general observation is that arthropod abundance and richness decrease with elevation. This pattern has been related to temperature patterns (McCain and Grytnes 2010). Yet, it is often reported that these same variables change in a humped-back pattern. In this case the peak in precipitation occurs in middle elevations. For most terrestrial animal species, precipitation effect may be indirect through its effect in resource availability (Rahbek 2005, McCain and Grytnes 2010). Alternatively, these differences may be related to biotic factors as the taxonomic focus group (Rahbek 1995, 2005), for example decomposers and their response to changes in leaf litter compositions along altitudinal gradients.

Although many studies of species richness and diversity along elevational gradients have been published, most of them are focused in plant and are carried in the temperate zones. However, the global majority of terrestrial organisms are tropical arthropods and knowledge of their richness patterns along altitudinal gradients is still very poor (Brehm et al. 2007). Some examples include groups such as butterflies and ants, which show a maximum diversity in tropical regions below 1000 m (Brühl et al. 1999, Fisher 2002). Whereas, evidence is still limited because only a very few insect studies have investigated complete elevational gradients. So far, only a few exceptions to an overall declining diversity of insects at elevations higher than 1000 m have been documented. Examples include arctiid and geometrid moths in Ecuador (Brehm et al. 2003) and Costa Rica (Brehm et al. 2007). The last study confirms that Geometrid moths have a predominantly montane distribution with exceptionally high species richness at elevations up to 2100 m. Richness at the lowest elevations is markedly lower, and also decreases towards higher elevations at the mountain summit (Brehm et al. 2007).

Differences in environmental variables that influence diversity are often taxon or functional group specific (Chust et al. 2004, Vanbergen et al. 2007). Recent studies in Collembola communities point out that they could change because of litter composition (Santos et al. 2008), soil chemistry (Salamon and Alphei 2009) altitude (Cutz-Pool et al. 2010, García-Gómez et al. 2011, Maunsell et al. 2013), vegetation type (Vanbergen et al. 2007, Cutz-Pool et al. 2010) and microhabitat heterogeneity (García-Gómez et al. 2009, García-Gómez et al. 2011). Moreover, Collembola is a very diverse group in soil, litter, and vegetation while being an efficient instrument for diversity studies in those habitats (Deharveng 1996).These meso-arthropods have well differentiated morphological life-forms which enable the functional role that

Collembola play in ecosystems to be recognized in some degree (Rusek 1998). Each functional group shows special adaptations for a particular microhabitat (Salmon and Ponge 2012).

1.4. Ecological Studies of Arthropod Communities in Puerto Rico

In Puerto Rico, most of the studies of arthropod communities have been done in the Luquillo Mountains. Designated a U.S. Experimental Forest in 1956, it became part of the International Network of Biosphere Reserves in 1976 (Richardson 1999, Quiñones et al. 2018). Four distinguishable forest types are dominated by different tree species. The tabonuco *(Dacryodes excelsa* Vahl) forest occupies areas below 600 m.a.s.l., the mid-elevation. palo colorado *(Cyrilla racemiflora* L.) forest occurs in areas above the cloud condensation level from 600-900 m. The elfin forest (dominant tree *Tabebuia rigida* Urban), with stunted vegetation and waterlogged anoxic soils, is located only on the highest peaks above 900 m. Palm forests *(Prestoea montana* (R. Grah.) Nichols) occur at all elevations, principally on windward slopes, in wet gullies, and in stream valleys (Gould et al. 2006).

In a survey conducted by Pfeiffer (1996), arthropod densities and their dynamics were documented in the litter layer of the Tabonuco forest over one annual cycle. The samples were taken during the 1984-85, when the dry period extended from 22 February to 1 May. In this study low collembolan densities were recovered (1,292 ind. m^{-2}) when compared with desert and steppe habitats. It was expected because, in general, densities of Neotropical litter and soil systems also fall near the low end of the range of estimates from a variety of habitats. For this study, in Tabonuco forest litter, Entomobryidae *sensu lato*, constituted the dominant family of Collembola. It represented 69% of the mean annual collembolan density, containing about half of the fifteen or so species extracted from the 1984- 85 samples. Dominant entomobryid species included *Dicranocentrus* sp*., Dicranocentruga* sp. (= *Troglolaphysa*), and *Lepidocyrtus s*p., while

Ptenothrix sp. and *Sphyrotheca* sp. comprised nearly all of the Sminthuridae and *Proisotoma* sp. the majority of the Isotomidae (Pfeiffer 1996).

Richardson (1999) and Richardson et al. (2005) studied the arthropod communities in several strata in the montane forest. The first study focused on the composition of complex bromeliad microcosms. It demonstrated that the total area available for animal colonization of bromeliads increases markedly in these forests with increasing elevation. Bromeliad species sampled were facultative epiphytes of similar morphological type *(Guzmania* and *Vriesiu* spp.) growing on trunks and lower branches within arms reach. Twenty plants were collected from each of the three major forest types during each of two periods (December 1993-January 1994 and December 1994-January 1995). A total of 15,599 animals were gathered. In each forest, the six most abundant species made up at least 70 percent of the total abundance. Scirtid beetle larvae *(Scirtes* sp.), the most abundant species in the two lower forests, were absent from the Elfin forest, as were the hydrophilid beetles, *Omicrus ingens.* Many detritivores present in all three forests *(e.g.*, *Gentepohlia dominicana*, *Culex* spp. larvae, and isopod crustaceans) showed a marked reduction in abundance in the elfin forest. The exception was the larva of a cased chironomid midge (Tanytarsini), which was the most abundant organism in the bromeliads there. Sixty eight collembolans were collected, representing the 0.43% of the identified animals (Richardson 1999).

In a follow up study to Richardson (1999), 10 plants were sampled from the Tabonuco and Palo Colorado forests at heights of up to 12 m above the ground in comparison with 10 control plants collected near ground level to determine whether there were any differences in animal species composition and litter interception in the lower canopy. Abundance was significantly lower in the elfin forest and animals were smaller. The additional data confirmed (Richardson 1999) that species richness was highest in the Palo Colorado. Mean invertebrate size followed the same pattern as bromeliad plant size, being largest in the intermediate Palo Colorado forest and smallest in the elfin forest. No different species assemblages were found in plants collected from higher in the trees within the same forest, but there were some significant differences in species distribution. Cased chironomid (Tanytarsini) and elaterid *(Platycrepidius* sp.) larvae were more frequent in the high level plants and scirtid beetle larvae were more frequent in the low level plants (Richardson et al. 2000).

Richardson et al. (2005) studied litter invertebrate communities, comparing the influence of elevation and forest type on forest floor faunal diversity. They sampled sierra palm litter and tree litter in Tabonuco, Palo Colorado, and Elfin forest from January to March during each of three years (1999-2001). The invertebrate species richness was significantly greater in palm forest stands than in forest types at the same or similar (elfin forest) elevation. There was only a very slight and non-significant decline in species richness with increasing elevation in palm forests. There were no significant differences between years or species richness in elfin forest non-palm litter was significantly lower than in all other forests, where the amount of litter was significantly lower than in other type of tree litter. Between litter types, palm litter and non-palm litter communities the species richness were similar in all years of the study in the Tabonuco forest, but became increasingly dissimilar in the palo colorado and the elfin forests. In all forests and for all years the most widely distributed and most abundant invertebrate population were Acari, Formicidae, Collembola, Isoptera, Coleoptera adults and Hemiptera/Homoptera, in total comprising 80% of the fauna. Collembolans were all classified as microbivores in these studies. Although their abundant (9.9% total fauna), they contribute only contributed 1.2% of total invertebrate biomass. The dominant family was Entomobryidae *sensu lato* , as in the earlier study (Pfeiffer 1996). The differences in Collembola abundance were found for forest type, palm/non-palm, and across the years. The significant interactions were in forest x palm/non-palm and palm/non-palm x year. According to analysis of variance in abundance, significant differences were found in Collembola population between tabonuco - palo colorado, tabonuco - elfin and palo colorado - elfin in non-palm litter (Richardson et al. 2005).

The Luquillo Experimental Forest (LEF) is subject to frequent disturbances that temporarily alter the estructure of forest communities (Scatena et al. 2012). During the past 25 years, this site experienced two major hurricanes (Hugo 1989 and George 1998) that broke or toppled trees on windward slopes over large areas. Schowalter and Ganio (1999) evaluated the invertebrate communities at the Luquillo Experimental Forest following Hurricane Hugo. They surveyed six tree species, collecting branches at 10- 12 m heights during dry (January – March) and wet (May – November) season, in 1991, 1992, 1994 and 1995. They found hurricane related effects in defoliators, sap-suckers, mollusks and detritivores but not in predators. In this study Collembola populations were differently affected by the disturbances ($p<0.05$). They were more abundant in intact forest than in tree-fall gaps. Additionally they found more detrivores abundance in branches of *Cecropia* and *Prestoea* trees ($p< 0.01$)(Schowalter and Ganio 1999).

In 2004, a canopy trimming experiment (CTE) was initiated in a hurricane-structured tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER). This experiment was designed to indicate the relative importance of canopy opening and a pulse of debris to the forest floor as factors affecting biotic responses to hurricane disturbance (Schowalter et al. 2003). In CTE four treatments were used (1) canopy trimmed (Trim) with debris plot to simulate conditions created by hurricanes; (2) Trim with cut material removed from the plot to simulate canopy opening without debris deposition; (3) canopy undisturbed (No trim) with trimmed material from treatment 2 to simulate debris deposition without canopy opening; and (4) No trim and no debris alterations occurred at the forest floor). In this area, canopy and litter arthropod abundance and community composition were evaluated (Richardson et al. 2010, Schowalter et al. 2014).

To evaluate canopy arthropods abundance and composition, seven tree species were selected by Schowalter et al. (2014). In each plot at each sampling time, one branch was collected from one tree of each species. Canopy invertebrates were sampled prior to treatment during June 2004. Following treatment application, all plots were sampled during June–July, 2005–2007 and 2009. As a result, 105 taxa were collected yet only 13 taxa were used for statistical analysis. Six taxa showed a significant response to treatments (miscellaneous moths, *Wasmania tropicus,* and Salticids on *Sloanea berteriana*, *C. rubens* on *Manilkara bidentata*, and Collembola on *Dacryodes excelsa*). No taxa responded significantly to trim treatment alone. Collembola showed significant trim x time interactions on *D. excelsa* ($p = 0.021$, $n = 43$, $F = 5.94$). In general, this result indicated that debris treatment had a more pervasive effect on canopy arthropods than did canopy removal. This is most likely due to indirect effects of debris on the availability of nutrients for new foliage production on host trees (Schowalter et al. 2014)

Richardson et al. (2010) evaluated the effect of canopy removal and debris deposition of litter invertebrate communities and provided a useful proxy for litter fauna. In order to collect arthropods, they used litter bags that were placed in all plots on 20–23 June 2005 and recovered after 2, 4, 7, 10, 13, 16 and 19 months in the field. Invertebrates from each bag were extracted using Tullgren funnels. In this survey they found all community parameters (abundance, biomass, diversity, taxonomic composition and trophic structure) changed significantly during the experiment. Total animal counts peaked in the first three sample periods (August 2005–January 2006) and then declined to approximately 35% of the initial level by January 2007. Numerically, mites dominated the fauna throughout the experiment, accounting for 66% of the 52,035 animals collected. Over time they became numerically less important in relative terms (from 75% to 55%) and in absolute numbers. Individual taxa responded differently to the trimming of the canopy, causing a major shift in community composition. Acarina, Collembola, and Psocoptera responded positively with higher abundance in trimmed plots whereas Homoptera, Hemiptera, Isopoda, and Diplopoda responded negatively. Collembolans, isopods, millipedes, and ostracods responded positively to debris addition. In conclusion, litter arthropods responded to trimming, but not to debris deposition. The result of this study indicate that the primary effect of hurricane disturbance on litter arthropods is through changes in habitat conditions resulting from canopy opening rather than from the pulse of debris to the forest floor (Richardson et al. 2010, González et al. 2014)).

In most LEF studies, Collembola is an important group because of their abundance in soil and litter, and their responses to changes in disturbance, altitude and vegetation type (Schowalter and Ganio 1999, Schowalter et al. 2003, Richardson et al. 2005, Richardson et al. 2010, Schowalter et al. 2014). Even though not many Collembola were found in bromeliads (Richardson 1999), the canopy provides microhabitats where the arthropod communities composition is similar to those in the floor (Yanoviak et al. 2007, Rodgers and Kitching 2011). For many collembolan species in the Cloud forest, leaf litter suspended in epiphytes represents a microhabitat resource that occurs as patches isolated within a matrix of very different habitat types. Although strictly epiphyte-associated collembolans may not exist, the presence of epiphytes may represent an important resource for species that do have a strong association with forest canopy habitats more broadly (Palacios-Vargas et al. 1998, Rodgers and Kitching 2011). These observations are evidence that soil forest floor, leaf litter and, suspended litter of the forest canopy are all microhabitats which host significantly different assemblages of collembolan species waiting to be studied.

1.5. Taxonomic Studies of Collembola in Puerto Rico

More than 8,805 Collembola species are known in the world and around 90 new species are described each year (Janssens 2018). In Puerto Rico the first report was made by Folsom (1927) who described two new species. Wolcott (1948) reported seven genera and (Wray 1953) added nine genera to the list. Mari Mutt (1976, 1977, 1979, 1981, 1982, 1984, 1985a, b, 1986, 1987, 1988) reported more than 60 species and described 27 new species from the Island. Soto-Adames (1988a, b, 2002a) report 39 species from the US Virgin Islands and Puerto Rico and describe nine species. Samalot-Roque (2006) reported 44 species, (6 undescribed) in red mangrove forest (*Rhizophora mangle)* around the Island. Recently, Ospina Sánchez (2011) found 35 species in a secondary forest in Mayagüez. At present 110 Collembola species are known on the Island, they represent 53 genera and 17 families (Ospina 2011). In Puerto Rico, Collembola fauna is well known in comparison with other groups of soil arthropods. However not all Collembola species from LEF have been identified. Likewise, there is a lack of information on the abundance of other arthropods (González and Barberena 2018).

Collembolans colonize several environments and are one of the groups with more biomass contribution to soils (Hopkin 1997). Springtails are common detrivorous and fungivorous and there are found throughout the vertical microhabitats structure of forests from the aboveground parts (canopy and leaf litter suspended in epiphytes) to the belowground parts (soil forest floor leaf litter and humic soils). They play important roles in the functioning of detrital food webs (Seastedt 1984, Petersen 2002) and participate actively in organic material degradation processes, nutrient recycling, and mineralization of useful elements for plants (Palacios-Vargas et al. 2000). Collembolan communities have been related to various habitat factors, such as soil water condition, vegetation, and soil fertility (Hågvar 1982), soil chemistry (Salamon and Alphei 2009) and other organisms (Salmon and Ponge 1999). Moreover, Collembola is a very diverse group in soil, litter, and vegetation while being an efficient instrument for diversity studies in those habitats (Deharveng 1996). Although there have been many studies of the spatial distribution of collembolans in various microhabitats, few studies have examined the spatial patterns between the canopy and soil strata in relation to the vertical structure of dead organic matter (Rodgers and Kitching 2011).

2. Objectives

The objectives of this dissertation are:

1. To identify Collembola species from the Luquillo Mountains associated with Tabonuco, Palo Colorado, and Elfin forests.
    a. To determinate the species Identity of Collembola of three forest types, present in soil, leaf litter and mosses mats.
    b. To update the species list of the Collembola from Puerto Rico and their distribution.
2. To describe the new Collembola species in the survey.
    a. To make a full description of the morphological characteristics of the new species of Collembola.
    b. To compare the new species with the other species of the genera described.
    c. To redefined genera descriptions when necessary.
3. To characterize the Collembola functional groups presents in a tropical environment.
    a. To list the species morphological traits for Collembola in soil, leaf litter and mosses microhabitats.
    b. To compare morphological variation of Collembola species among microhabitats.

    c. To use morphological and ecological data to characterize the Collembola functional groups present in the Luquillo Mountains.

4. To compare environmental variables with Collembola community compositions in three forest types.
    a. To analyze the influence of environmental variables over the Collembola population assemblages.
    b. To compare Collembola richness and abundance within and among three montane forests.
    c. To determinate the environmental factor that takes major effect in the distribution of Collembola species among three forests.

3. Methodology

3.1. Forest Study Sites

This study took place in LEF, Puerto Rico. The sampling areas occur along an elevational gradient from 300 m over sea level to over 1000 m. Three forest types are represented in the study, located in the Luquillo Experimental Forest (LEF) and include the elfin, palo colorado, and tabonuco forest alliances (Wadsworth 1951, Weaver 1994). The elfin forest type represent the *Tabebuia riguda – Eugenia borinquensis* community (Gould et al. 2006) and it is found within the Lower montane wet and rain Holdrige life zones (Ewel and Whitmore 1973). The palo colorado forest type represent the *Cyrilla racemiflora – Micripholis garniifolia* community (Gould et al. 2006) and it is found in the Montane subtropical rain Holdrige life zones (Ewel and Whitmore 1973). The tabonuco forest type represent the *Dacryodes excelsa - Manika bidentate* community (Gould et al. 2006) and it is found in the Subtropical wet Holdrige life zones (Ewel and Whitmore 1973). All sites are on non-calcareous material derived from volcanic bedrock.

Rainfall increases with elevation. The tabonuco, palo colorado and elfin forests receive an annual rainfall of 3537 mm, 4191 mm, and 4849 mm, respectively (Garcia-Martino et al. 1996). The number of rainless days decreases with elevation, such that on average the tabonuco, palo colorado and elfin forest have 97, 69, and 53 rainless days respectively. Mean annual temperatures decline from 23 °C to 19 °C over the same gradient (Weaver and Murphy 1990). Net primary production (NPP) is related to rainfall and declines with elevation (Weaver and Murphy 1990).

The samples were collected during the dry season (February), early wet season (May), mid-wet season (August), and late wet season (November) (Schowalter et al. 2014). Three sampling locations were selected within each of the three forest types (Table 1.1). Samples of soil, lea litter and mosses were collected from five individuals of the most common tree species according to Gould et al. (2006). Only mid-sized trees were selected from the FS inventory (González et al. unpublished data, Table 1.1).

Table 1.1 Forest type, dominant tree species, sampling locations and mid-size range of tree heights used for Collembola survey in LEF, 2001 measures (González et al. unpublished data)

Forest type	**Dominant tree sp.**	**Sampling Location**	**Elevation (m)**	**Mid-size range Total height (m)**		**DBH* (cm)**	
				min	**max**	**min**	**max**
Tabonuco	*Dacryodes excelsa*	El Verde	433.2	11	16	8.5	35.4
		Río Grande	518.2	4.5	18	4	28.3
		Sabana 4	300.6	14	21	34.4	47.1
Palo colorado	*Cyrilla racemiflora*	Pico del Este	759.3	7	8.2	8.2	12.5
		Toro Trail-1	815.3	9.8	13	10.2	45.8
		Toro Trail-2	795.3	16	14	47.9	57.8
Elfin	*Tabebuia rigida*	Pico del Este	987.6	5	8	11.5	14.3
		Pico del Oeste	994.4	3.6	5	4.3	6.5
		Yunque peak	1044.8	3.5	4	4.5	7.5

DBH: Diameter at breast height.

3.2. Microhabitats Sampling

Two samples were collected at a random point in the tree and on the adjacent ground areas.

Soil: At each sampling point, a sample was collected from the soil surface to a 10 cm depth using a core (10 cm in diameter) on the ground areas directly adjacent to the selected tree.

Litter: At each sampling point, a 10 cm^2 litter sample with its entire depth were collected.

Epiphyte mats-Mosses: Using a step ladder to reach the middle branches of each tree, samples of epiphyte mats (contiguous pieces of live and dead mosses perched upon branches of tree) were collected. The epiphyte and their substrate were sampled in an area of 10 cm^2 with the entire depth of the collected brown material. Every sample met two distinct criteria:

1. The epiphyte must to be dominated by bryophytes rather than by large vascular epiphytes such as bromeliads, orchids or woody plants
2. The accumulation of organic material under of the mosses must be larger than 1cm (Yanoviak et al. 2007).

The material collected in soil, litter and epiphyte mats were placed in plastic bags upon collection and transported to the lab for further processing. Here, the fresh weight was recorded. Then, the samples were completely dried in Berlese funnels for seven days in order to extract the arthropods. After the extraction, the dry weight of the samples was measured. The water content in the sample was calculated by the following formula (Arbea and Jordana 1990):

$$\text{Water Content} = \frac{\text{Fresh weight of sample} - \text{Dry weight of sample}}{\text{Dry weight of sample}}$$

The soil samples were sorted by hand into roots and soil. For leaf litter samples they were sorted by hand into three categories: organic matter, entire broad leaves and others (twigs, roots, etc.). The weight of these categories and total sample were register to characterize the physical composition of the microhabitat.

3.3. Collembola Identification

The specimens of Collembola were counted and separated into morphospecies using a dissecting microscope. Two or three specimens of each morphospecies were mounted on slides to be identified using contrast-phase microscopy. These specimens were cleared using Nesbitt solution and fixed in slides using Mac André II solution (Mari Mutt 1976). To harden the solution, the slides were dried in a slide warmer at 45 °C to 50°C for at least seven days. Finally, each specimen was label with its collecting data. In the beginning of the process, Collembolans were identified using Christiansen and Bellinger (1980), key the springtails of Cuba (Díaz - Azpiazu et al. 2004), keys available in www.collembola.org, local keys published by Mari Mutt (1976, 1979, 1984, 1985a-b, 1986, 1987, 1988), we also had the personal advice of Dr. Soto-Adames and Dr. Palacios-Vargas, the major Collembola taxonomist of the Neotropical area.

For the specimens that could not be identified using the above mentioned literature, it was necessary to look for revisions of the group and the original descriptions of the species and genera. Then we determined if the specimens belong of a new species. The principal criteria used for this determination were the morphological differentiations (Gisin 1967, Yoshii 1989, Soto-Adames 2002), in combination with differences in the chaetotaxy (Carapelli et al. 1995, Soto-Adames 2002, Jordana and Baquero 2005).

3.4. Statistical Analysis

3.5.1. Functional Diversity

To characterize functional diversity the morphological differences in cuticular clothing, color pattern and foot complex were studied using slides-mounted specimen (Figure 1.1). The cuticular clothing includes presence or absence of modified setae as spines, multiramosus setae or scales (Figure. 1.1 A-1, A-2. A-3), more setae modifications indicating adaptation to exposed environments (Salmon and Ponge 2012). The color pattern (Figure 1.1 B) allows for the identification species (Yoshii 1989, Soto-Adames 2002b) and the differentiation among geographic areas (Frati et al. 1997, Soto-Adames 2002b, Jordana and Baquero 2005). The foot complex is a character used as evidence of adaptation to substrates, where their hardness results in more and larger teeth in the unguis, but less modification in unguiculus (Christiansen 1965, 1988). Additional modifications include the enlargement and the addition in number of the tenent hair (Figures 1.1 C-1, C-2, C-3). Additionally the collection location was included as trait attribute (Lemey et al. 2009). Finally, the gut content was classified as fungi, bacteria, leaf litter or non seen. The vertical gradient in resource (substrate-microhabitat) quality might also result in differences in colonization by fungi and algae (Osono 2002) that are potential food resources for some collembolan species, and may influence Collembola vertical distributions (Yoshida and Hijii 2005).

For the analysis of the correlation between environmental variables and traits we use QRL analysis perform with R ade4 package (Dray and Dufour 2007). Initially three tables were constructed: Table L for abundance of species; R for environmental variables and Q for traits attributes. Then a separate analysis of each table was performed. Correspondence analysis was applied to the species table. Finally, R, L, and Q tables are linked both by their m rows (sites) and k columns (species), and the ordination of the L-species table represents the link between the R-environment table and the Q-trait table. (Dolédec et al. 1996).

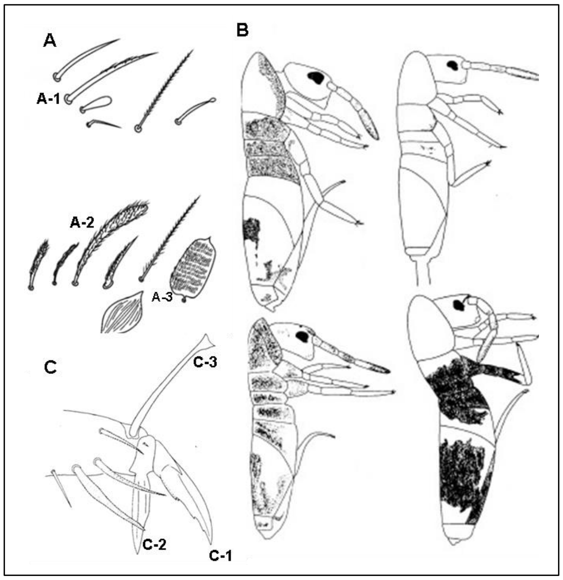

Figure 1.1 Morphological characters of Collembola in A. Cuticular clothing A-1. Spines, A-2.Multitamosus setae, A-3. Scales (Díaz -Azpiazu et al. 2004).B. Color patter variation in *Lepidocyrtus dispar* (Mari Mutt 1988). C. Foot complex C-1. Ungus, C-2 Ungusculus.

3.5.2. Diversity Index

To analyze patterns of Collembola species turnover at multiple spatial scales, I used multiplicative diversity decompositions of effective numbers of species (so-called Hill numbers) in its unweighted form (Jost 2007). Hill numbers (*q*D) represent true diversities, as they obey the replication principle (Jost 2007, Tuomisto 2010). They are in units of 'species', and hence, they can be plotted on the same graph to construct diversity profiles that can be useful to characterize the species abundance distribution of a community and to provide complete information about its diversity (Chao et al. 2012).

To compare the diversity among forest and microhabitat the rarefaction curves was performed with R using the "iNEXT" package (Hsieh et al. 2016) which provides simple functions to compute and plot the seamless rarefaction and extrapolation sampling curves for the three most widely used members of the Hill number family (species richness, Shannon diversity and Simpson diversity). The individual-based abundance data were used, with an end point of 5000, confidence of 0.95 and bootstrapping of 500. To obtain the turnover and nestedness components , the “beta.multi” function on the “betapart” R package was utilized, using the Sorensen index (Baselga and Orme 2012, Team 2014).

3.5.3. Microhabitats Analysis

A Nonmetric Multidimensional Scaling (NMDS) was performed using individual-based abundance and the type of forest and microhabitat using as environmental variables to look for the separation of the Collembola populations. This analysis was made in R using package “vegan 2.9”(Oksanen et al. 2013).

To summarize the varied environmental variables we used the principal component analysis (PCA) performed on PAST 3 (Hammer et al. 2001). To analyze the effect of environmental variables on Collembola abundance and richness the generalized linear models (GLM’s) in R software was used.

A permutational multivariate analysis of variance (PERMANOVA) was used to study Collembola communities along an altitudinal gradient, using the Jaccard index as dissimilarity measure and performing 900 permutations using the “adonis” function in R package “vegan 2.9”(Oksanen et al. 2013).

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Chapter 2 Checklist of Collembola from the Tropical Mountains in Puerto Rico

1. Collembola from Puerto Rico

Puerto Rico is an archipelago located in the northeastern part of the Caribbean (17°57'19"N and 18°29'19"N Latitude; 65°38'04"W and 67°16'13"W) Longitude and has an area of approximately 8900 km^2.The main island accounts for approximately 8746 km^2 of that area, whereas the islands of Vieques and Culebra account for 131 km^2 and 26 km^2, respectively. In the main island the altitude varies between sea level and 1300 m. Temperatures tend to decrease towards higher elevations along the center of the main island (Ewel and Whitmore 1973), and the mean annual temperature ranges from 19°C to 26°C. The ecological life zones of Puerto Rico include subtropical dry forests and subtropical rain forests, among other life zones described by Ewel and Whitmore (1973). In addition, the island can be divided into three major physiographic regions based on topographic features, geologic structure, and rock type: the coastal lowlands, the coastal hills, and the central mountains (Helmer et al. 2002, Parés-Ramos et al. 2008).

Politically the island is divided into 78 municipalities, 48 of them have Collembola species reported (Fig.1.1). According to the present inventory the largest number of species come from Mayagüez (63 spp) followed by Luquillo (36 spp), Arecibo and Cabo Rojo (20 spp. each one). The Collembola fauna in Puerto Rico is distributed in three principal habitats: forest, littorals and caves. In this inventory, 105 species are reported in forest (including mangrove habitats). *Archisotoma gourbaultae, A. interstitialis*, *Spinactaletes aebianus, S. bellingeri, S. calcalectoris* and *S. myoptesimus* are reported form littorals habitats. *Metasinella topotypica, Oncopodura arecibena, Trogolaphysa subterranea,* and *Collophora quadrioculata* were reported in caves.

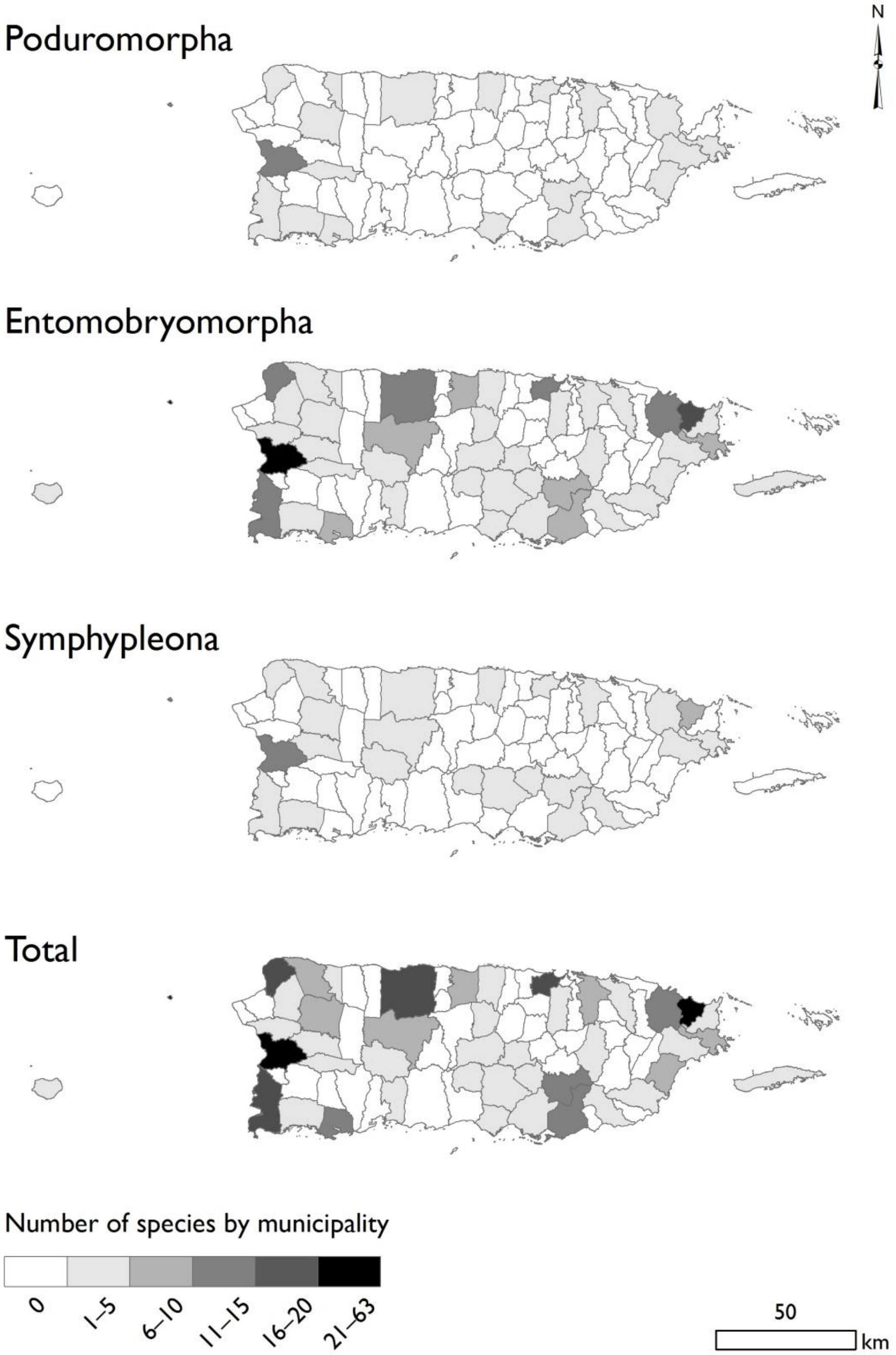

Figure 2.1 Political division of Puerto Rico in 78 municipalities, indicate the number of Collembola species reported for each one (M. Quiñones, 2018)

The first list of Collembola of Puerto Rico was published in 1982, where 39 genera and 59 species were listed including their geographic distribution according to biogeographic zones in the world (Mari Mutt 1982). To the date, we count the Collembola reported since Folsom (1927) who described two new species, Wolcott (1948) that reported seven genera and Wray (1953) added nine other genera to the list. Mari Mutt (1976, 1977, 1979, 1981, 1982, 1984,1985a-b, 1986, 1987, 1988) reported more than 60 species and described 27 new species for the island. Soto-Adames (1988 a-b, 2002a) reported 39 from the U.S. Virgin Islands and Puerto Rico and described nine species. Samalot-Roque (2006) recorded 44 species, in red mangrove forests (*Rhizophora mangle)* around the island. Recently, Ospina (2011) found 35 species in a secondary forest in Mayagüez.

At http://luq.lter.network/datacatalog, a data set of the list of species recorded form Puerto Rico, is based on bibliography cited above. The collection location, habitat and biotope information for each species were obtained from the references cited. The data for global distribution of species was based on Bellinger et al. (2018) using the biogeographical distribution regions stated by Good (1974), modified by Christiansen and Bellinger (1995) and Culik and Zeppelini (2003). Species distributed across at least in four of the major regions were considered cosmopolitan (Mari Mutt 1982, Abrantes et al. 2010). The species reported exclusively from Puerto Rico Bank were listed as Endemic. Nomenclatural organization follows that of Deharveng 2004; Bellinger et al. 2010 and Soto-Adames et al. 2008. The fields given in a database are: Family, genus, specie, world distribution, and Neotropical distribution, Historical reports in P.R., life zone in P.R, Location (municipality) and habitat.

2. Methodology

The study took place in LEF in the altitudinal gradient sites. The sampling sites occur along an elevational gradient from 330 to over 1000 m (Table 1). Rainfall increases with elevation along this altitudinal gradient the. The Tabonuco, Palo Colorado and Elfin forests receive an annual rainfall of 3537 mm, 4191 mm, and 4849 mm respectively (Garcia-Martino et al. 1996). In contrast, the number of rainless days decreases with elevation, such that on average the Tabonuco, Palo Colorado and Elfin forest have 97, 69, and 53 rainless days respectively, most of them during the first semester of each year (Garcia-Martino et al. 1996). Mean annual temperatures decline from 23 °C to 19 °C over the same gradient (Weaver and Murphy 1990).

Within the forest type described above three sampling locations were selected (Table 1). Each sampling location will be visited during the dry season (February), early wet season (May), mid-wet season (August), and late wet season (November, Schowalter et al. 2014). In each forest plot, one set of samples were collected from five individuals of the most common tree species (Gould et al. 2006) away from palms, and another set of samples was collected from a palm brake.

A set of samples were component for two leaf litter samples and two soil samples, in a target plant influence area. At each sampling point, a soil sample was collected from the soil surface to a 10 cm depth using a soil corer (10 cm in diameter). For leaf litter trial, a 10 cm^2 sample with its entire depth will be collected. The soil and leaf litter samples were placed in plastic bags and transported to the lab for further processing. Here, the samples were completely dried in Berlese funnels for seven days in order to extract the arthropods. The springtails were count and separated into morphospecies using a dissecting microscope. Two or three specimens of each morphospecies were mounted on slides and identified using contrast-phase microscopy. These specimens were cleared using Nesbitt solution and fixed in slides using

Mac André II solution (Mari Mutt 1976). To harden the mounting medium, slides will be dry in a slide warmer at 45 °C to 50°C for at least three days and each specimen was label with its collecting data. Finally, Collembolans were identified using keys to North American species (Christiansen and Bellinger 1980), keys to springtails of Cuba (Díaz -Azpiazu et al. 2004), keys available in www.collembola.org, local keys (Mari Mutt 1976, 1981, 1985, 1986b, 1987, 1988) and Dr. Soto-Adames advice.

Specimens that could not be identified using the above mentioned literature, it was necessary to look for revisions of the group and the original descriptions of the species and genera. Then we determined if the specimens belonged of a new species. The principal criteria used for this determination were degree of morphological differentiation (Gisin 1967, Yoshii 1989, Soto-Adames 2002b), including differences in the chaetotaxy (Carapelli et al. 1995, Soto-Adames 2002b, Jordana and Baquero 2005).

3. Results: Collembola from the Luquillo Mountains

For the Luquillo Mountains 16 families, (sensu Deharveng, 2004; Bellinger *et al*., 2010 and Soto-Adames *et al*., 2008), 37 genera and 53 species and seven subspecies have been identified. Fifteen are new species in the genera *Pronura, Arlesia, Furculanurida, Hylaeanura, Pseudachorutes, Brachystomella, Xenylla, Microgastrura, Thalassaphorura, Isotomurus, Entomobya* and *Serroderus.* Moreover*,* two are new subspecies for the species *Folsomiella intermedia* and *Micranurida wladimiri*. In total, we have 22 species as new reports from Puerto Rico (Table 2.2). The complete list of the identify taxa are in table 2.1.

Table 2.1 Taxonomy and list of the Collembola collected in Luquillo Mountains (Puerto-Rico) during 2014 and 2015. Taxonomy follows Deharveng (2004) y Bellinger et al. (2010).

Taxa

- Class Collembola Lubbock, 187
  - Ordo Poduromorpha Börner, 1913
    - Superfamily Neanuroidea Massoud, 1967
      - Family Neanuridae Börner, 1901
        - Subfamily Neanurinae Börner C, 1901, sensu Cassagnau, 1989
          - Genus *Pronura* Delamare Deboutteville, 1953
            - 1.*Pronura* n. sp Ospina et al 2019
        - Subfamily Pseudachorutinae Börner, 1906
          - Genus *Arlesia* Handschin 1942
            - 2. *Arlesia* n. sp. Ospina et al 2019
          - Genus *Furculanurida* Massoud, 1967
            - 3. *Furculanurida bistribus* n. sp. Ospina et al 2019
          - Genus *Hylaeanura* Arlé, 1966
            - 4. *Hylaeanura infima* Arlé, 1966
            - 5. *Hylaeanura aemilia* n. sp. Ospina et al 2019
          - Genus Micranurida Börner, 1901
            - 6. *Micranurida wladimiri* subsp. *caribena*
          - Genus *Neotropiella* Handschin 1942
            - *7. Neotropiella silvestrii* (Denis,1929)
          - Genus *Pseudachorutes* Tullberg, 1871
            - 8. *Pseudachorutes* n. sp1. Ospina et al 2019
            - 9. *Pseudachorutes* n. sp2. Ospina et al 2019
      - Family Brachystomellidae Stach, 1949
          - Genus *Brachystomella* Agren,1903
            - 10. *Brachystomella* n. sp1. Ospina et al 2019
            - 11. *Brachystomella* n. sp2. Ospina et al 2019
          - Genus *Folsomiella* Bonet, 1930
            - 12. *Folsomiella intermedia* sub sp. *ciega*
      - Family Hypogastruridae Börner, 1906
          - Genus *Microgastrura* Stach, 1922
            - 13. *Microgastrura parvaboletus* sp.n.
          - Genus *Xenylla* Tullberg, 1869
            - 14. *Xenylla* n.sp1 Ospina et al 2019
            - 15. *Xenylla* n.sp2 Ospina et al 2019
    - Superfamily Onychiuroidea sensu D'Haese 2002
      - Family Onychiuridae Lubbock, 1867
        - Subfamily Onychiurinae Börner, 1901
          - Genus *Thalassaphorura* Bagnall, 1949
            - 16. *Thalassaphorura smilodonta* n.sp Ospina et al 2019
      - Family Tullbergiidae Bagnall, 1935
        - Subfamily Stenaphorurinae Luciañez & Simón, 1992
          - Genus *Mesaphorura* Börner, 1901
            - 17. *Mesaphorura* cf. *ruseki* Christiansen & Bellinger, 1980
      - Family Odontellidae Massoud, 1967
          - Genus *Superodontella* Stach, 1949
            - 18. *Superodontella* cf. *cornifer* Mills, 1934

- Ordo Entomobryomorpha Börner, 1913 Soto-Adames et al., 2008
  - Superfamily Isotomoidea Szeptycki, 1979
    - Family Isotomidae Schäffer, 1896
      - Subfamily Proisotminae Stach, 1947
        - Genus *Folsomides* Stach, 1922
          - 19. *Folsomides centralis* (Denis, 1931)
          - 20. *Folsomides parvulus* Stach, 1922
        - Genus Folsomina Denis, 1931
          - 21. *Folsomina onychiurina* Denis, 1931
      - Subfamily Anurophorinae Börner, 1901
        - Genus *Hemisotoma* Bagnall 1949
          - 22. *Hemisotoma thermophila* (Axelson 1900).
        - Genus *Isotomiella* Bagnall, 1939
          - 23. *Isotomiella minor* (Schäffer, 1896)
          - 24. *Isotomiella* sp.
      - Subfamily Isotominae Schäffer, 1896
        - Genus *Isotomurus* Börner, 1903
          - 25. *Isotomurus degrade* sp.n. Ospina et al 2019
  - Superfamily Entomobryoidea Womersley, 1934
    - Family Entomobryidae Schäffer, 1896
      - Subfamily Orchesellinae Börner C, 1906, sensu Szeptycki A, 1979
        - Genus *Dicranocentrus* Schött, 1893
          - 26. *Dicranocentrus celatus* Mari Mutt, 1985
          - 27. *Dicranocentrus marias* (Wray,1953)
        - Genus *Heteromurtrella* Mari Mutt, 1979
          - 28. *Heteromurtrella tihuiensis* Mari Mutt, 1985
      - Subfamily Entomobryinae Schäffer, 1896, sensu Szeptycki, 1979
        - Genus *Entomobrya* Rondani, 1861
          - 29. *Entomobrya flavum* sp.n. Ospina et al 2019
          - 30. *Entomobrya longisetae* Soto-Adames, 2002
      - Subfamily Lepidocyrtinae Wahlgren E, 1906, sensu Szeptycki, 1979
        - Genus *Lepidocyrtus* Bourlet, 1839
          - 31. *Lepidocyrtus caprilesi* Wray,1953
          - 32. *Lepidocyrtus dispar* Mari Mutt, 1986
            - Form A
            - Form B
            - Form D
            - Form E
          - 33. *Lepidocyrtus maldonadoi* Mari Mutt, 1986
          - 34. *Lepidocyrtus paracaprilesi* Mari Mutt, 1988
            - Form epifita Ospina et al 2018
        - Genus *Pseudosinella* Schäffer, 1897
          - 35. *Pseudosinella biungiculata* Ellis, 1967
          - 36. *Pseudosinella violeta* Mari Mutt, 1986
        - Genus *Seira* Lubbock, 1870
          - 37. *Seira desapercibida* Soto-Adames, 2002
    - Family Oncopoduridae Carl & Lebedinsky, 1905
        - Genus *Oncopodura* Carl & Lebedinsky, 1905
          - 38. *Oncopodura arecibena* Mari Mutt, 1984
    - Family Paronellidae Börner, 1913, sensu Soto-Adames FN et al., 2008
      - Subfamily Paronellinae Börner, 1913, sensu Soto-Adames *et al*., 2008
        - Genus *Camphylothorax* Schött, 1893
          - 39. *Camphylothorax sabanus* (Wray,1953)

Form epifita Ospina et al 2019
Genus *Salina* MacGillivray, 1894
40. *Salina tristani* Denis, 1931
Genus *Trogolaphysa* Mills, 1938
41. *Trogolaphysa geminata* Mari Mutt 1987
42*. Trogolaphysa jataca* (Wray 1953)
43. *Trogolaphysa luquillensis* (Mari Mutt, 1987)
44. *Trogolaphysa sp.*
Subfamily Cyphoderinae Börner, 1913, sensu Soto-Adames *et al*., 2008
Genus *Cyphoderus* Nicolet, 1842
45. *Cyphoderus similis* Folsom, 1927
Genus *Serroderus* Delamare Deboutteville, 1948
46. *Serroderus yunquensis sp.n. Soto-Adames et al 2019*
Orden Neelipleona Massoud, 1971
Family Neelidae Folsom, 1896
Genus *Neelus* Folsom, 1896
47. *Neelus desantisi* Najt, 1971
Genus *Neelides* Caroli, 1912
48. *Neelides minutus* (Folsom, 1901)
Orden Symphypleona Börner, 1901 sensu Massoud, 1971
Family Sminthurididae Börner, 1906 sensu Betsch & Massoud, 1970
Genus *Sphaeridia* Linnaniemi, 1912
49. *Sphaeridia* n. sp 4.
Superfamily Katiannoidea Bretfeld, 1994
Family Arrhopalitidae Stach, 1956, sensu Bretfeld, 1999
Genus *Arrhopalites* Börner, 1906
50. *Arrhopalites* sp1
Family Sminthuridae Lubbock, 1862
Genus *Shpyrotheca* Börner, 1906
51. *Shpyrotheca aleta* Wray, 1953
Superfamily Dicyrtomoidea Bretfeld, 1994
Family Dicyrtomidae Börner, 1906
Genus *Calvatomina* Yosii, 1966
52. *Calvatomina rufescens* (Reuter, 1890)
Subfamily Ptenothricinae Richards, 1968
Genus *Ptenothrix* Börner, C, 1906
53. *Ptenothrix borincana* Soto-Adames, 1988

After this survey, the inventory of Collembola species identified in the Luquillo Experimental forests increase to 70 species, 44 genera and 15 families (Table 2.2), distributed along the municipalities of Luquillo and Río Grande.

Table 2.2. Collembola species reported for the Luquillo Experimental Forest up to date. A. Poduromorpha B. Entomobryomorpha C. Neelipleona and Symphypleona.

A. Poduromorpha

Family	Specie	Reported By
Neanuridae	*Friesea magnicornis*	1
	*Arlesi*a sp	1
	*Arlesi*a sp.n.*	2
	Neotropiella silvestrii	1,2
	Neotropiella sp.	1
	Furculanurida n.sp*	2
	Paranura sp.	1
	Pronura sp.n.*	2
	*Hylaeanura infima**	2
	Hylaeanura aemilia sp.n*.	2
	Micranurida wladimiri subsp. *caribeña**	2
	Pseudachorutes sp.n1*	2
	Pseudachorutes sp. n2*	2
	*Pseudachorute*s sp.	1
	Paleonura borincana	3
	Sensillanura sp.	1
Brahystomellidae	*Brachystomella agrosa*	1
	*Brachystomell*a sp.	1
	Brachystomella sp.n1*	2
	Brachystomella sp.n2*	2
	Folsomiella intermedia subsp. *ciega**	2
Hypogastruridae	*Microgastrura* sp.	1
	Microgastrura parvaboletus sp.n*	2
	Xenylla sp.n1*	2
	Xenylla sp.n2*	2
Onychiurudae	*Thalassaphorura smilodonta* sp.n*	2
	Onychiurus sp.	1
Tullbergiidae	*Mesaphorura* cf. *ruseki**	2
Odontellidae	*Odontellidae sp.*	1
	Superodontella cf. *cornifer**	2

1.Soto-Adames and Richarson, com pers 2. Present study 3. Palacios-Vargas & Soto-Adames 2017 * New Report for Puerto Rico.

B. Entomobryomorpha

Family	Specie	Reported By
Isotomidae	*Folsomides centralis*	2
	Folsomides parvulus	2
	Folsomides americanus	1
	Folsomina onychiurina	2
	Hemisotoma thermophila	1,2
	Isotomiella minor	1,2
	Isotomiella sp.*	2
	Isotomurus degrade sp.n.*	2
Entomobryidae	*Dicranocentrus celatus*	2
	Dicranocentrus marias	2
	Heterumurus sp.	1
	Heteromurtrella tihuiensis	2
	Entomobrya flavum n.sp*	2
	Entomobrya longisetae	1,2
	Lepidocyrtus caprilesi	1,2,5
	Lepidocyrtus dispar	1,2,3
	Lepidocyrtus maldonadoi	1,2,3,5
	Lepidocyrtus paracaprilesi	2,4

	Pseudosinella biungiculata	2
	Pseudosinella violenta	1,2
	Seira desapercibida	1,2
	Seira dowlingi	1
Oncopoduridae	*Oncopodura arecibena*	2
Paronellidae	*Campylothorax sabanus*	1,2
	Salina tristani	1.2
	Trogolaphysa geminata	2
	Trogolaphysa jataca	2
	Trogolaphysa luquillensis	2
	Trogolaphysa sp	2,1
	Cyphoderus similis	1.2
	Serroderus yunquensis sp.n.	1,2

1. Soto-Adames and Richarson, com pers 2. Present study 3. Mari Mutt (1986a) 4. Soto-adames (2000) 5. Soto-Adames (2002a). * New Report for Puerto Rico

C. Neelipleona and Symplypleona

Family	Specie	Reported By
Neelidae	*Neelus desantisi**	2
	Neelus murinus	1
	Neelides minutus	2
Sminthurididae	*Sphaeridia* n. sp 4	1,2
Arrhopalitidae	*Arrhopalites* sp*	2
Sminthuridae	*Shpyrotheca aleta*	1,2
Dicyrtomidae	*Calvatomina rufescens*	1,2
	Ptenothrix borincana	1,2

1. Soto-Adames and Richarson, com pers 2. Present study* New Report for Puerto Rico

With this last report in the present study, we expand the knowledge of the species of Collembola in LEF. So far, in the Poduromorpha Order 14 species had been reported (Ospina Sánchez et al. 2018), now we expanding to 30 the species reported in this order (Table 2.2A). For the Order Entomobryomorpha, 13 additional species were reported for a total; of 30 species for this Order (Table 2.2B). For the Order Neelipleona, the species *Neelus murinus* was the only reported before, now we have three species (Table2.2C). Finally, for the Order Sympleona, *Arrhopalites* sp. was the only new report of four species reported (Table 2.2C, Ospina Sánchez et al. 2018).

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Chapter 3 : New Collembola Species from the Luquillo Mountains in Puerto Rico

1. Introduction

The projected estimate for Collembola species is approximately 50,000 (Hopkin 1997). Despite its ancient origin, global distribution and abundance in nearly all habitats, the class Collembola is comprised of only 8000 described species. These species frequently exhibit unusually broad geographical ranges for organisms that are minute, strictly soil-dwelling and flightless (Cicconardi et al. 2013). Furthermore, species often comprise geographically isolated populations among which gene flow can be very low (Frati et al. 1997).The prolonged geographic isolation, resulting in genetically divergent populations, should tend to promote speciation. However, identifying Collembola species often is complicated by the lack of strong morphological characters that distinguish them, such as wing patterns or sclerotized reproductive structures which are critical for identifying other hexapods (Frati et al. 1997). However, morphological studies of collembolan have demonstrated that characters such as differences in color patterns may be used to differentiate species (Gisin 1947, Yoshii 1989, Soto-Adames 2002) in combination with differences in the chaetotaxy within allopatric and sympatric species (Carapelli et al. 1995, Jordana and Baquero 2005, Soto-Adames 2002). Additionally, recent molecular studies have presented evidence of taxonomically and geographically pervasive cryptic species diversity within morphologically defined species (Frati et al. 1997, Soto-Adames 2002, Emerson et al. 2011, Cicconardi et al 2013).

2. Methodology

The material used to describe all the Collembola species come from the survey of the Collembola microhabitat project at the Luquillo Mountains along of three forest types (Table 1.1). For this study 8734 specimens of Collembola were separated from 1124 samples.

The specimens of Collembola were separate into morphospecies using a dissecting microscope. Two or three specimens of each morphospecies were mounted on slides to be identified using contrast-phase microscopy. These specimens were cleared using Nesbitt solution and fixed in slides using Mac André II solution (Mari Mutt 1976). To harden the solution, the slides were dried in a slide warmer at 45 °C to 50°C for at least seven days. Finally, each specimen was label with its collecting data. In the beginning of the process, collembolans were Identified using Christiansen and Bellinger (1980b), a keys to springtails of Cuba (Díaz - Azpiazu et al. 2004), keys available in www.collembola.org,and local keys published by Mari Mutt (1976, 1979, 1984, 1985a-b, 1986, 1987, 1988).

For the specimens that could not be identified using the above mentioned literature, it was necessary to look for revisions of the group and the original descriptions of the species and genera. Then we determined if the specimens belong to a new species. The principal criteria used for this determination was morphological differentiation (Gisin 1967, Yoshii 1989, Soto-Adames 2002b), in combination with differences in chaetotaxy (Carapelli et al. 1995, Soto-Adames 2002b, Jordana and Baquero 2005). For the morphological descriptions and comparisons. I also had the advice of Dr. Soto-Adames and Dr. Palacios-Vargas, two international recognized experts in Neotropical springtails taxonomy.

Abbreviations for types of chaetas and general morphology used along the descriptions are listed below. Types of chaetae: M—long macroseta, mi—microseta, S—sensillum, ss—sensorial seta, S.g.d.—dorsal guard sensillum of Ant. III, S.g.v.—ventral guard sensillum of Ant. III. General morphology: Abd.–abdominal segment, Ant.—antennal segment, Th.—thoracic segment. Setal groups and/or tubercles on head and tergites: Af—antenno-frontal, Cl—clypeal, De—dorso-external, Di—dorso–internal, DL—dorso–lateral, L–lateral; Oc—ocular, So—subocular. Setal groups and tubercles of sternites: Ag—ante-genital, An—anal, Fu–furcal vestige; Ve—ventral, Ve—ventro-external, Vi–entro-internal, Vl—ventro-lateral, VT—ventral tube. Legs: Cx—coxa, Fe—femur, Scx2—subcoxa 2, Tr–trochanter, Ti.—tibiotarsu

3. Taxonomic Section

In the present work 15 new species in the genera *Pronura, Arlesia, Furculanurida, Hylaeanura, Pseudachorutes, Brachystomella, Xenylla, Microgastrura, Thalassaphorura, Isotomurus* and *Entomobya* are described. Two new subspecies are described for *Folsomiella intermedia* and *Micranurida wladimiri*. We also include comments for two species with modifications, *Campylothorax sabanus* and *Lepidocyrtus paracaprilesi.*

Table 3.1 Taxonomy of the new species from Luquillo Experimental Forest

Order	**Family**	**Genera**	**Species**
Poduromorpha	Neanuridae	*Pronura*	sp.n.
		*Arlesi*a	sp.n.
		Furculanurida	*bistribus* sp.n.
		Hylaeanura	*Aemilia* sp.n
		Micranurida	*wladimiri* subsp. *caribeña**
		Pseudachorutes	sp1. n.
		Pseudachorutes	sp2. n.
	Brahystomellidae	*Brachystomella*	sp1. n.
		Brachystomella	n. sp2
		Folsomiella	*Intermedia* subsp. *ciega*
	Hypogastruridae	*Microgastrura*	*parvaboletus* sp. n.
		Xenylla	sp1. n.
		Xenylla	sp2. n.
	Onychiurudae	*Thalassaphorura*	*smilodonta* sp. n.
Entomobryomorpha	Isotomidae	*Isotomurus*	*degrade* sp. n.
	Entomobryidae	*Entomobrya*	*flavum* sp. n.
		Lepidocyrtus	*paracaprilesi* Form epiphyte
	Paronellidae	*Campylothorax*	*Sabanus* Form epiphyte

3.1*. Pronura* sp.n. Ospina et al 2018

3.1.1. Genus *Pronura*

The genus *Pronura* was created to accomodate the species *kilimanjarica*, from Tanzania (Delamare Deboutteville 1953). To the date, 53 named species are listed in this genera (Bellinger et al. 2018), all in tropical regions especially in Africa and Southeast Asia and few others from

Australia, southwestern Asian an American regions (Palacios-Vargas et al. 2011). In the Neotropical region three species have been described *P. amazonica* from Brazil, *P. gaucheri* from French Guayana and *P. paraguayana* from Paraguay. The new specie described below is the first record of the genus in Puerto Rico.

This genus include individuals without pigment, with dorsal tubercles poorly developed or absent, usually without reticulations or tertiary granulations. Maxilla needle-like, mandible bidentate or tridentate. With 2 + 2 unpigmented eyes, or eyes absent. Sensilla on Ant. IV subequal. Posterior tergites not fused. Without additional sensorial setae on the lateral abdominal tergites. Di setae, at least Di1, shifted towards De on Abd. V. Tibiotarsi without tenent hairs, unguis without teeth (Palacios-Vargas et al. 2011).

For description of *Pronura* sp.n. the Abbreviations of Palacios-Vargas and Soto-Adames (2017) were used.

3.1.2. Morphological description

Length 287 µm (n = 6).

Color in alcohol white. Granulation fine. Only dorso-lateral tubercles on Abd. III, IV and V well developed. Body setae comprising microsetae; thick, hyaline macrosetae, and acuminate macrosetae, in addition to sensorial setae (Fig.3.2A).

Head. Antenna shorter (ratio 0.47) than head diagonal. Ant. III and IV fused dorsally, ventral separation well marked. Ant IV dorsally with eight subequal sensilla, twelve long and finely setae, four short acuminate setae, no apical or subapical organ differentiated (Fig. 3.2A). Ant III dorsally with two globular sensilla in a cuticular fold and two guard sensilla. S.g.v. almost straight and subequal to S.v.d.; one mesoventral sensilla (mi). Ant II with eleven setae. Ant I with six setae, two with blunt tips (Fig.3.2B).

Postantennal organ (PAO) and eyes absent. Head with two weakly delimited tubercles, dorsal quetotaxy as in Fig. 3.2A and table 3.2A. Mandibles styletiform, maxillae with a hook shape. Labrum elongate, rounded apically (Fig. 3.2E); labrum formula 0/2,4. Labium with four basal, three distal and three lateral setae (Fig.3.2D). Ten setae Vi on ventral side of head.

Thoracic and abdominal dorsal chaetotaxy as in Fig.3.2A and table 3.2B. Abd VI unilobed without tubercle (Fig.3.2G). Number de setae in legs as in table 3.2B. Unguis without teeth (Fig.3.2F).

Ventral tube with 4+4 setae. Furcal vestige with two setae and one microseta. Ventral chaetotaxy reduced (Table 3.2). Male genital plate with 3+3 pregenital, twelve circumgenital and two eugenital setae. Each lateral anal tubercle with twelve setae and two microsetae.

Table 3.2 Complete chaetotaxy of Pronura sp. n. per semi-tergites. A. Cephalic chaetotaxy. B. Body chaetotaxy.

A.Cephalic chaetotaxy

Head setae group	Tubercles	Number of setae	Seta Type	Setae
Cl	-	2	M	F
	-	2	mi2	G
Af	-	4	M	A,B
	-	4	me	C,D
Oc	-	2	M	Ocm
	-	2	mi	Oca
Di	-	4	mi	Di1,Di2
De	+	2	M	De1
	+	2	mi	De2
DL+L+Sc^{1}	-	10	M	DL 1-5
		8	me	L1-4
Total	1	42		

B. Postcephalic, ventral and leg chaetotaxy of *Pronura* sp. nov.

	Thorax & Abdomen DORSAL					Legs			
	Di	De	DL	L	Scx2	Cx	Tr	Fe	T
Th. I	me	Me	M	-			6	12	20
Th. II	2me	M,mi+S	M,mi+S	M,2me		3	5	12	20
Th. III	2mi, me	M, mi+S	M,mi+S	M, 2me		6	3	15	18
						ABDOMEN VENTRAL			
Abd. I	mi, me	mi+S	me, mi	M, 2me			VT:3+3		
Abd. II	mi, me	mi+S	M, me	M, 2me	Ve: 5				
Abd. III	mi, me	S	M, me	M	Ve:3	Fu:3			

Abd. IV	me	2M+S	M	Ve:4	Vl:3	
Abd. V	me	3M+mi+S	M	Ag:3	Vl:1	L:1
Abd. VI		3M, 2me, mi		Ve: 11		

3.1.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter at the Luquillo Mountains, Puerto Rico. Holotype: male, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 19.II.2015 C.M.Ospina. Paratypes: 2 male, 2 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l.,19.II.2015, C.M.Ospina. 1 immature on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak *Tabebuia rigida* forest type, leaf litter 1044.8 m.a.s.l. 4.XI.2014, C.M.Ospina. 1 immature on slide Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 4.XI.2014 C.M.Ospina.

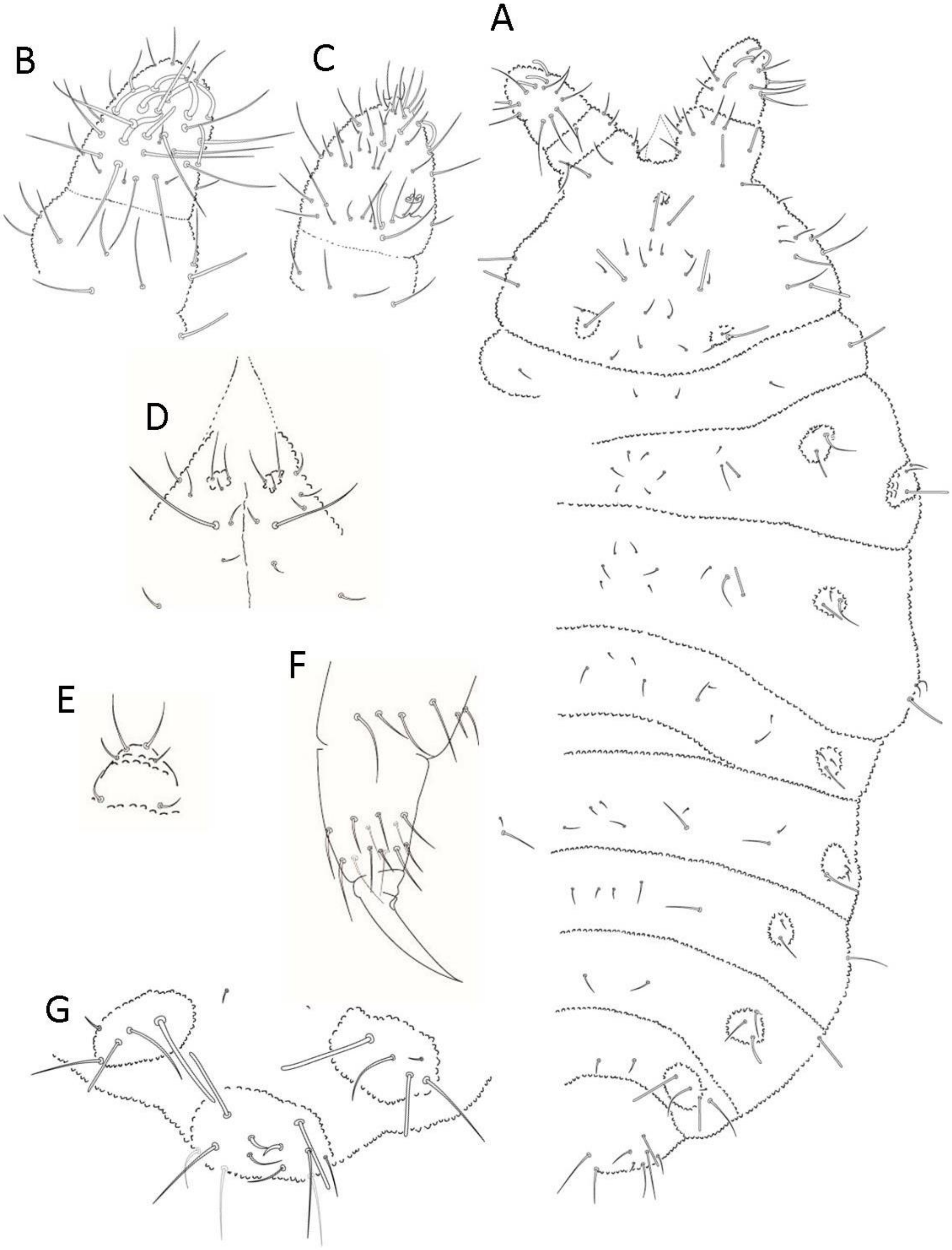

Figure 3.1 ***Pronura* sp.n.** A. Dorsal chaetotaxy B. Ant. IV and III, dorsal view C. Ant. IV and III, ventral view D. Labium E.Labrum F. Leg I G. Abd. V-VI Dorsal view.

3.1.4. Discussion

Among the Tribe Paleonurini there genera, like *Paramanura, Paleonura* and *Pronura*, for which a clear diagnoses are not available. Many species of this genera have been transferred between and above mentioned genera (Palacios-Vargas and Soto-Adames 2017), and even the validaty of the genera is under discussion (Cassagnau 1991). These genera need a deeper study, since there are few characters used to separate them. The location of setae Di in Abd V is the most used character to separate these genera (Fig. 3.2), sometimes the location of the setae is not so clear. In this new species, the seta Di2 is in the middle line, while Di1 seem located in the single tubercle present in Abd V (Fig. 3.2D), this variation also occurs in *P. gaucheri* (Palacios-Vargas et al. 2011).

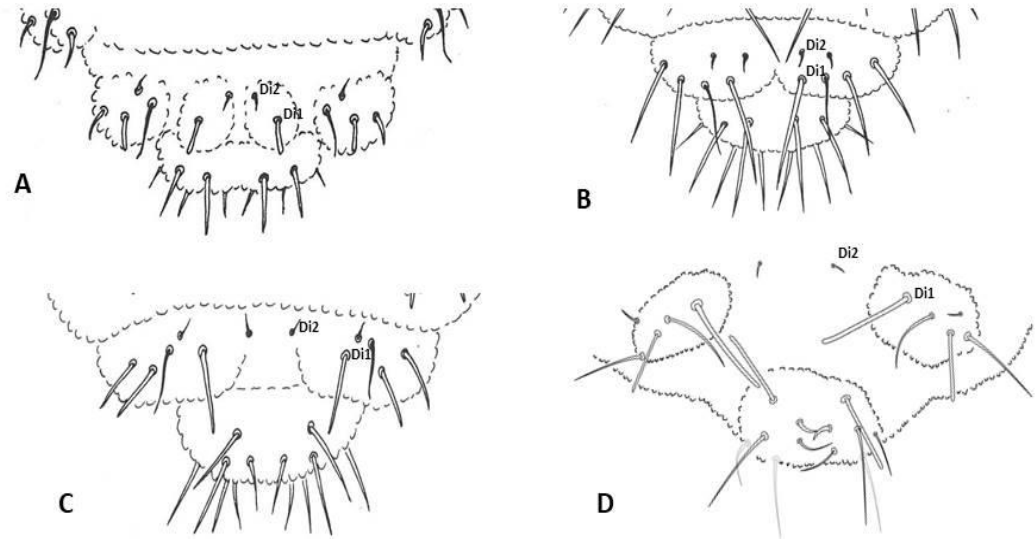

Figure 3.2 Dorsal abdominal chaetotaxy for genera of Paleonurini, showing the position of Di setae in Abd V. A. *Paleonura nuda* B. *Paramanura najtae* C. *Pronura amazonica* (Cassagnau and Pereira de Oliveira 1990)D. *Pronura* sp.n.

The new species is the first Neotropical species without eyes and the combination of the follow characters: single head tubercle (De), Abd IV with Di1 absent, fused De+DL with one acuminated macrosetae, one thick macrosetae, and one microsetae. P. n.sp is very similar to *P. gauchuri* but they differ in the characters mentioned above and other differences in chaetotaxy

(Table 3.3). *P. paraguayana* differs from the new species in the presence of barbulate and relatively long setae and the presence of five tubercles in the head.

Table 3.3 Comparative table of South-American species of *Pronura* and *Paramanura* (Palacios-Vargas et al. 2011), including the new Puerto Rican species of *Pronura*

	Af	Oc	De Th. II-III	De Abd. I-III	De+DL Abd IV	L Abd I-II
P. amazonica	ABCD	Oca, Ocm	2+S	2+S	3+S	2
P. gaucheri	ABCD	Oca, Ocm	2+S	1+S	3+S	2
P. paraguayana	ABD	Oca, Ocm, Ocp	3+S	2+S	4+S	3
P. n.sp	ABCD	Oca, Ocm	2+S	1+S*	2+S	3
Paramanura najtae	ABD	Oca, Ocm	2+S	1+S	4+S	2

*in the new sp. Abd III have 0+S

3.2. *Arlesia* sp.n. Ospina et al 2018

3.2.1. Genus *Arlesia*

The Neotropical genus *Arlesia* was created as part of a revision of *Ceratrimeria* (Handschin 1942), with *A. albipes* (Folsom 1927) as type species. To date seven species have been described: *A. albipes*; *A. arleana* de Mendonça and Fernandes, 1999; *A. cochabambensis* Cassagnau and Rapoport, 1962; *A. fluminensis* Arlé, 1939; *A. intermedia* Fernandes and de Mendonça, 2004; *A. proxima* (Arlé, 1939) and *A. variabilis* Thibaud and Massoud, 1983 from Costa Rica, Brazil, Bolivia and Guadalupe. In Puerto Rico *A. albipes* was reported in mangrove habitats (Samalot 2006) and leaf litter (Ospina Sánchez 2011).

The diagnosis of the genus, includes individuals with a Pseudachorutes aspect, with the antennal segment III and IV fused, the division being visible only at the level of the sensorial organ in Ant. III. Apical bulb on Ant IV trilobed. Ant III sense organ with two straight sensillas in a single fossa. Buccal cone relatively short, maxilla styletiform with two lamellas fused basally, but separated in the distal extreme. Mandible with variable number of teeth. Eyes reduced. OPA absent. Unguis with or without teeth. Furcula present. Chaetotaxy with smooth and short setae. Larger setae are present in the distal border of the Th. II to Abd V (Massoud 1967).

3.2.2. Morphological description

Length 404μm (n = 6).

Color: Individuals in alcohol with head, thorax and legs I white; antenna, ocular patch, legs II and II, abdomen and furcula evenly purple. Granulation well difrenciated, paratergites rounded. Body setae comprising short, smooth and thin setae, sensorial setae long and smooth (Fig.3.3).

Head: Antenna shorter (0.6) than head diagonal. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with an apical vesicle, four subcylindrical thin sensilla and twelve long setae; dorsoexternal microsensillum and subapical organite present; apical bulb trilobed (Fig.3.3B), ventral side with one subcylindrical setae; Ant III sense organ with two small internal sensilla, two subcylindrical guard sensilla (S.g.v. larger and thinner than S.g.d.) and two guard setae; ventral microsensillum present (Fig. 3.3C); Ant. II with 12 setae; Ant. I with six setae. Postantennal organ (PAO) absent. Eyes 3+3 in a pigmented patch. Head dorsal quetotaxy as in figure 3.3A. Buccal cone typical for genus. Labral chaetotaxy 2/252. Mandible with five teeth, two apical short and subequal, one middle short and two basal large (Fig 3.3D). Maxilla styletiform (Fig.3.3E).

Body: Ordinary body setae short and smooth, distributed as in Fig. 3.3F. Sensory setae (s) well differentiated and distributed on Th. I-Abd. V as 022/11111.

Legs: Tibiotarsi with 16 setae in all legs, Tenent hair absent. Claw without teeth. Unguiculus absent (Fig. 3.3G).

Collophore with 3+3 setae; tenaculum with 3+3 teeth and without setae; furcula well developed, ratio mucro: dens = 1:1.2 Dens with 6 setae; mucro long, straight, with tip slightly hooked (Fig 3.3H).

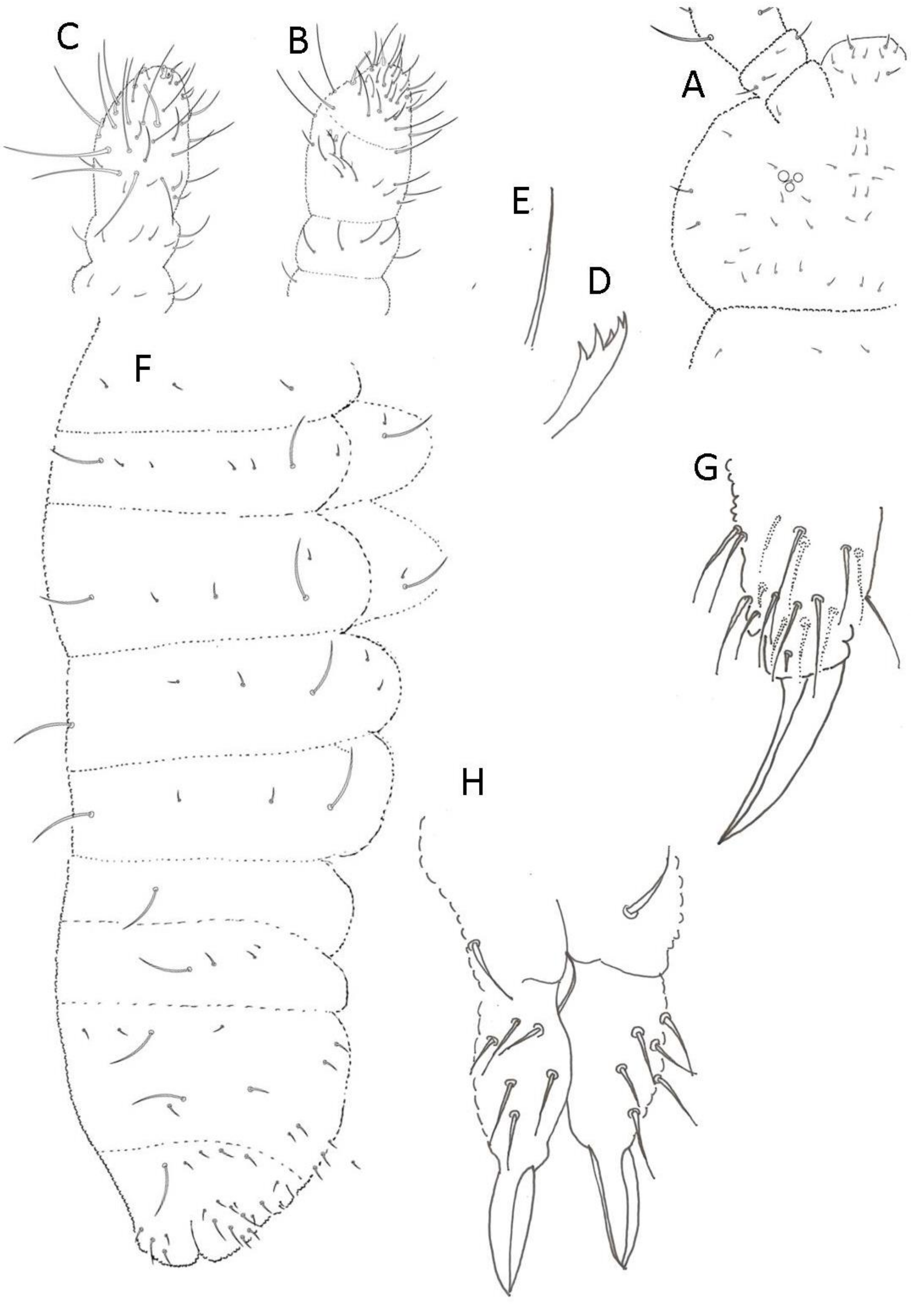

Figure 3.3 ***Arlesia* sp.n.** A. Dorsal view B. Ant. IV and III, dorsal view C. Ant. IV and III, ventral view D. Mandible E. Maxilla F. Body dorsal view G. Leg I H. Furcula.

3.2.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo

Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 04.XI.2014 C.M.Ospina. Paratypes: 3 immatures, 3 male, 3 female on slide , Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 04.XI.2014 C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 15.II.2015, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter 987.6 m.a.s.l. 19.V.2015, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, leaf litter 994.4 m.a.s.l. 29.VI.2015, C.M.Ospina. 1 immature on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, leaf litter 994.4 m.a.s.l. 06.VIII.2015, C.M.Ospina.

3.2.4. Discussion

Arlesia n.sp has a new combination of characters: Unique color pattern, thoothless unguis and 3+3 eyes. The closest species is *A. intermedia*, which differs in the character mentioned before, the presence of 5+5 eyes and two mandibular lamellas, plus the curved shape of the mucro (Fernandes and Mendonça 2004). Three *Arlesia* species has coloration patterns, *A. albipes* have white antennae, *A. arleana* is almost black with antennae, Th II and Abd II,V,VI yellow (Mendonça and Fernandes 1999) and *A. fluminensis* is blue and orange (Arlé 1939). All the described species have 7+7 to 5+5 eyes.

3.3. *Furculanurida bistribus* sp.n. Ospina et al 2018

3.3.1 Genus *Furculanurida*

This genus was created to relocate the species *Microanurida africana* on account of having a well development furcula (Massoud 1967). The mean characters of this genus have been discussed by (Palacios-Vargas and Gao 2009, Queiroz and Fernandes 2011, Zon et al. 2014) and it is clear that some species are dubiously placed in *Furculanurida* (Table 3.4). To the date, the genus holds 14 nominal species distributed in the Neotropical, Ethiopian and the Nearctic regions, each with seven, six and one described species, respectively. The present new species is the first record for the genus in Puerto Rico.

Table 3.4 *Furculanurida* species move to other genus or in discussion

Species	Original genus	Move to	Reason to move
africana (Massoud, Z, 1963) Massoud, 1967	*Microanurida*	*Furculanurida* (type species) Massoud (1967)	Furcula developed
arlei Thibaud & Massoud, 1980	*Furculanurida*	*Stachorutes* Weiner and Najt (1998)	Presence of a microsensillum on Ant IV, mandible with only 2 teeth and a reduced furcula with very small mucro.
		Furculanurida Thibaud and Palacios–Vargas (2000)	Presence of 8 thick sensilla on antennal segment IV and long sensorial setae on the body and a small tooth in the unguis.
ashrafi (Yosii, 1966) Thibaud, J-M & Palacios-Vargas, JG, 2000	*Micranurida*	*Stachorutes* Deharveng and Lienhard (1983)	Furcula reduced
		Furculanurida Thibaud, J. M., and Palacios–Vargas, J. G., (2000)	Is included in the key for *Furculanurida* species
		Stachorutes Benito et al. (2005)	Is include as *Stachorutes* In the phylogenetic analysis
		Furculanurida Palacios-Vargas and Gao (2009)	Is included in the key for *Furculanurida* species
furculata (Salmon, 1956) Massoud, 1967	*Kenyura*	*Furculanurida* Massoud (1967	Furcula developed and post-antennal organ present
perplexa (Salmon, 1956) Massoud, 1967	*Hypanurida*	Thibaud and Palacios–Vargas (2000)	Reduce furcula

According to Queiroz and Fernandes (2011) the genus includes individuals with length 0.6–1.4 mm. Body with blue-gray pigment or without pigment. Ant IV with trilobed apical bulb; dorsolateral microsensillum present or absent; 6–7 sensilla and long ordinary chaetae. PAO circular or elliptical with 4–22 vesicles. Eyes from zero to eight per side. Mandible with 2–10 teeth. Maxilla styliform with two fused lamellae. Tenent hair on tibiotarsi acuminated. Ventral tube with 3–4 chaetae on each side. Tenaculum with 2–3 teeth on each ramus. Furcula complete, with well-developed dens and mucro. Dens with 5–6 chaetae on each side. Mucro separated from dens and with two lamellae tapering. Sensilla on body always long.

3.3.2 Morphological description

Length 462µm (n = 7).

Color: Individuals in alcohol with antenna and abdomen evenly gray, ocular patch dark pigmented; head, legs III and furcula light gray; thorax, legs I and II white to light purple or blue. Granulation coarse. Body setae comprising by smooth and thin setae and sensorial setae long and smooth.

Head: Antenna shorter (0.6x) than diagonal head. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with an trilobed apical vesicle, six subcylindrical thin sensilla and 14 long setae; subapical organite present and dorsoexternal microsensillum absent (Fig. 3.4A); Ant III sense organ with two small internal sensilla, two subequal subcylindrical guard sensilla and two guard setae between them; ventral microsensillum present (Fig. 3.4B); Ant. II with 12 setae; Ant. I with six setae.

Eyes 3+3 in a pigmented patch; postantennal organ (PAO) with 5 or 6 vesicles disposed in a rosette (Fig. 3.4C). Head dorsal quetotaxy as in figure 1.5D. Setae a0 absent

Buccal cone elongate, Labium normal quetotaxy (A to G setae, Fig. 3.4E). Labral chaetotaxy 2/2322 (o 2/252?) (Fig.1.5F). Mandible with four teeth, two apical short and subequal, one middle and one basal large and subequal; maxilla styletiform with two fused lamellae (Fig. 3.4G).

Body: Ordinary body setae smooth, distributed as in Fig. 3.4D. Th I with 3+3 setae. Sensory setae (s) well differentiated, in position p3 y p6 in Th I y II and p3 in Abd I to V and distributed on Th. I-Abd. VI as 022/111110. Female genital plate with 2+2 pregenital setae, six circumgenital setae and 1+1 eugenital setae . Male genital plate with 2+2 pregenital setae, 10 circumgenital setae and 4+4 eugenital setae (Fig.3.4H).

Legs: subcoxae 1, 2; subcoxae 2, 1; coxa 3, trochanter 4, femora 10 and tibiotarsi with 10 setae in all legs, Tenent hair acuminate. Claw without teeth. Unguiculus absent.

Collophore with 3+3 setae; tenaculum with 3+3 teeth and without setae; furcula well developed, manubrium with six setae, dens with three setae, mucro straight and a broad hook like end. Ratio mucro: dens = 1:1.3 (Fig. 3.4I).

Etymology: *Bistribus*, Latin for two times three, in reference the presence of 3+3 eyes and 3+3 setae in dens, unique characters of this new species.

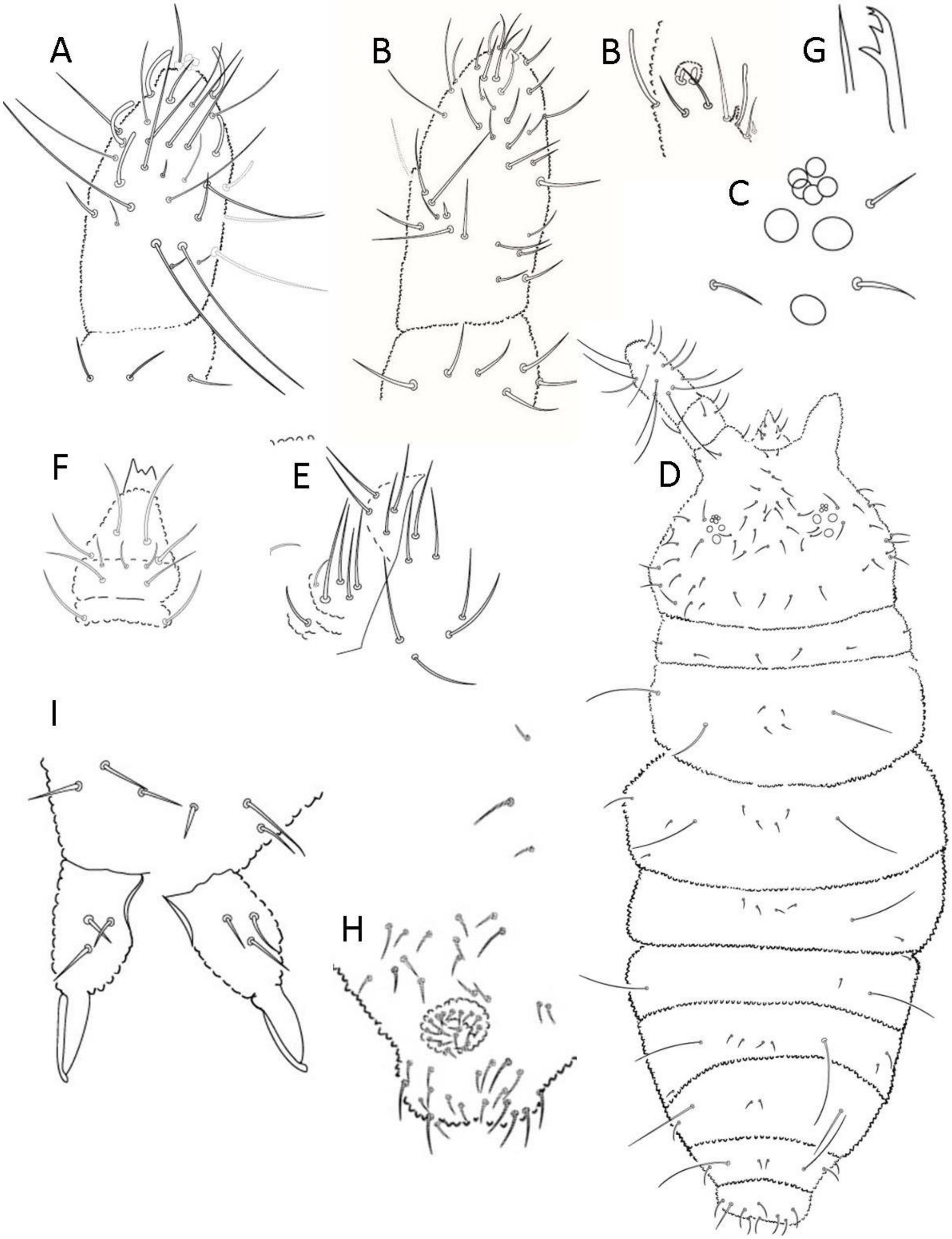

Figure 3.4 ***Furculanurida bistribus*** **sp.n.** A. Ant. IV and III, dorsal view B. Sensorial Organ in Ant. III C. Postantennal Organ D. body dorsal view E. Labium F. Labrum G. Maxilla and Mandible H. Male ventral view I. Manubrium and furcula.

3.3.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter and epiphyte at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 04.XI.2014 C.M.Ospina. Paratypes: 2 immatures, 2 male, 4 female on slide , Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte, 987.6 m.a.s.l., 04.XI.2014, C.M.Ospina. 2 female on slide , Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte, 987.6 m.a.s.l., 19.V.2015, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte, 987.6 m.a.s.l., 11.II.2015, C.M.Ospina. 1 immature on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter 1044.8 m.a.s.l., 4.XI.2014, C.M.Ospina. 1 juvenile on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter, 1044.8 m.a.s.l., 19.V.2015, C.M.Ospina. Other examined material: 5 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 04.XI.2014, C.M.Ospina. 2 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l. 04.XI.2014 C.M.Ospina. 2 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter, 1044.8 m.a.s.l., 04.XI.2014, C.M. Ospina. 12 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 19.V.2015, C.M.Ospina.2 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 29.VII.2015, C.M.Ospina. . 2 individuals, in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter, 1044.8 m.a.s.l., 29.VII.2015, C.M. Ospina.

3.3.4. Discussion

F. bistribus **sp.n.** is place in *Furculanurida* because many of their characters show this relation and fits with the original genera diagnosis: apical bulb trilobed, presence of long setae in Ant. IV, maxilla styliform, furcula full development and setae in the body short but the sensory setae long (Massoud 1967). Although in the genera diagnosis state the presence the teeth in unguis, it is an except for *F. africana* that is toothless (Massoud 1963) as the new species, additionally inner tooth on claw are usually considered as specific, not generic characters (Zon et al. 2014). The new species has other characters that put it closer to *Stachorutes* as the presence of 5 sensillas in Ant IV and 3 setae in dens. The number of S-chaetae on Ant. IV in *Furculanurida* species, when known, is 6 or 7, versus 5 or 6 in *Stachorutes*; hence it is not a diagnostic character (Zon et al. 2014). The number of setae in dens is a character share with *F. perplexa*, but the position of this species in the genera is controversial because the reduction of the furcula (Queiroz and Fernandes 2011); however, the number of setae on the dens and mucro, as well as the shape of the mucro are variable characters among the species (D'Haese 2013).

Although morphological characters seem similar between *Furculanurida* and *Stachorutes*, the geographic separation of the two genera is remarkable. The genera *Furculanurida* was established for three sub-Saharan African neanurids: *Micranurida africana, Kenyura furculata*, and *Hypanurida perplexa* (Massoud 1967). After that, other species was described or include in *Furculanurida* from the Lesser Antilles, Guatemala, Brazil, French Guiana, Tanzania, Morocco, Nepal, and Ivory Coast. These species thus conform to a general Gondwanan distribution. *Furculanurida langdoni* is an exception to this distribution, being found in North America. In contrast to *Furculanurida, Stachorutes* exhibits mostly a Eurasian distribution, with species known from China, France, Poland, Russia, Slovakia, Spain, Tanzania, and the United States (Bernard 2007).

Despite to the differences of the new species with the more recent genus diagnosis, we place *F. bistribus* as *Furculanurida* because their Gondwanan distribution in addition the full development of the furcula (Fig.3.4I) despite the number of setae in dens, enlarging the genera diagnosis to specimens with 3-6 setae in dens. The other characters that put the new species close to *Stachorutes* lack of strong evidence and need more studies (Bernard 2007, Zon et al. 2014).

F. bistribus **sp.n.** has these unique characters combination: 5 sensilla in Ant. IV, 3+3 eyes, 3 setae in dens and the absent of internal tooth in the unguis, additionally with their coloration patterns. Members of *Furculanurida* of have a variable number of eyes between 0 and 8 eyes per side, *F. africana* and *F. emucronata* have no eyes, *F. furculata* 2+2, *F. arawakensis* 4+4, *F. belemensis, F.grandcolasorum, F. guatelmaltensis* and *F. langdoni* have 5+5, *F. duodecimoculata, F. longisensillata* and *F. nissimiani* have 6+6; *F. septemoculata* has 7+7 and one of the most recent described *F. tropicalia* has 8+8. All the described species have 5+5 or 6+6 setae in dens and all have a development furcula as the new species. Leaving aside the unique characters of *F. bistribus* **sp.n.**, it appears close to *F. arawakensis,* been different in the presence of 7 teeth on the mandibles and the variation in 6 to 7 in the number of PAO vesicles; this species has 6 sensilla in Ant. IV and 6 setae in dens. Similar species is *F. longisensillata* that is different to the new species for the presence of 10 teeth on the mandibles and the variation in 5 to 9 in the number of PAO vesicles; this species also has 6 sensilla in Ant. IV and 6 setae in dens.

3.4. *Hylaeanura* aemilia n. sp. Ospina et al 2018

3.4.1. Genus *Hylaeanura*

The genus *Hylaeanura* was created by Arlé (1966) to place *Paranurella infima* described by himself in 1959. So far only four species are known: *H. nohbecana* Vázquez, Cutz-Pool & Palacios-Vargas 1998; *H. nepalensis* (Yosii 1966), first described as *Paranura nepalensis and H. mendoncae* Zeppelini & Palacios-Vargas 2013. The species are distributed in Brazil, French Guiana (Najt et al. 1990), Mexico and Nepal. In this work the genus is first reported from Puerto Rico represented by *H. infima* and *H. aemilia* **sp.n.**

The diagnosis of the genus includes a habitus of *Paranurella* or *Kenyura*, without pigment. Very small, less than 1.0 mm. Without eyes or at most 2 eyes per side. Antenna shorter than half the cephalic diagonal, with 7 sensilla, S8 hypertrophied. Mandible with one to three teeth, maxilla styletiform. Legs very short. Ungues without teeth, no unguiculus or tenant hairs. Ventral tube with 3 + 3 setae. Furcula very reduced, dens with 3 setae, mucro minute or lacking. Body chaetotaxy very reduced and very small setae (Zeppelini and Palacios-Vargas 2013).

3.4.2. Morphological description

Length 332 µm (n = 3).

Color: Specimens in alcohol without color. Granulation coarse without tubercles. Body setae short and smooth, the sensorial setae longer than setae, both acuminate (Fig 3.5).

Head: Antenna smaller (0.47) than diagonal head. Ant. III and IV fused dorsally with a bilobed apical vesicle; 8 subcylindrical sensilla, S8 larger and S3 hypertrophied and 14 long setae dorsally; subapical organite and dorsoexternal microsensillum absent (Fig.3.5B); Ant. III sense organ with two small internal sensilla, two subequal subcylindrical and straight guard sensilla; ventral microsensillum present (Fig.3.5C); Ant. II with 11 setae; Ant. I with six setae.

Eyes 2+2 in a pigmented patch. Postantennal organ (PAO) absent. Head dorsal quetotaxy as in figure (3.5A), umpired setae d1 present. Labium with a total of 11 setae per side with setae A,B,C,D (Fig.3.5D). Labral chaetotaxy 2222 (Fig 1.6E). Mandible with one tooth. Maxilla styletiform.

Body: Ordinary body setae smooth, distributed as in Fig.3.5A . Th I with 3+3 setae. Sensory setae (s) larger and thin than body setae, in position p4 in all segments and distributed on Th. II-Abd. V as 11/11111. Male genital plate not seen. Female genital plate with 3+3 pregenital setae, 7 circumgenital setae and 2 eugenital setae; Each anal lateral lobe with 14 setae(Fig. 3.5F).

Legs: short as the antenna, coxa with 3,6,2; trochanter with 6,6, 4; femora 10,10,10 and tibiotarsi with 12,16,16 setae in legs I, II and III respectively. Tenent hair and unguiculus absent; claw without teeth.

Collophore with 3+3 setae; Tenaculum with 3+3 teeth and without setae (Fig.3.5G); furcula reduced, dens with four setae, mucron absent (Fig.3.5H).

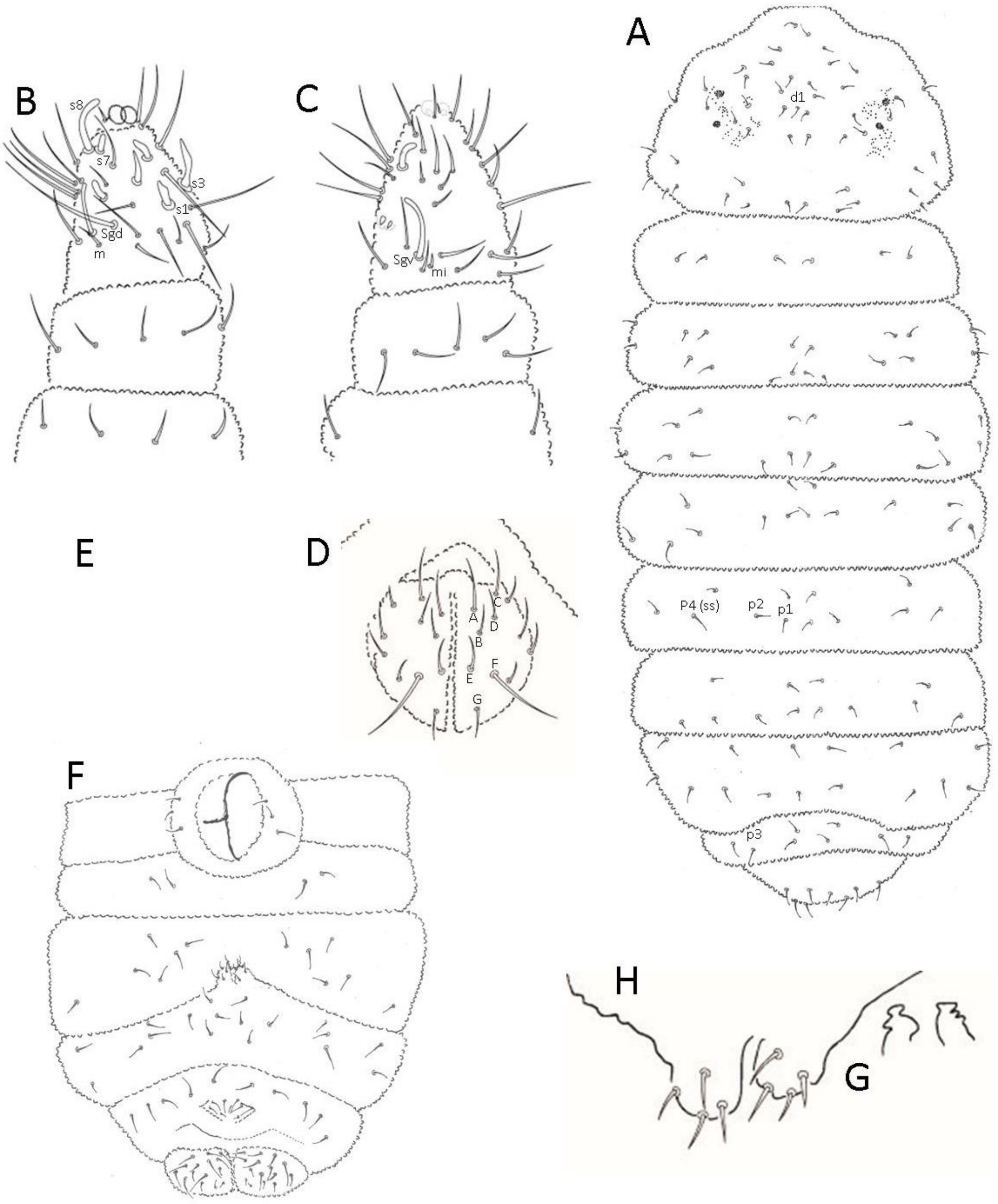

Figure 3.5 ***Hylaeanura aemilia*** **n.sp** A. Dorsal view B. Ant. Dorsal view C. Ant. Ventral view D. Labium E. Labrum F. Ventral view G. Tenaculum. H. Furcula.

Etymology. This species is dedicated to the daughter of the senior Author, Emilia who was born while this research was being conducted.

3.4.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter and soil at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo,

Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, soil, 815 m.a.s.l., 18.XI.2014, C.M.Ospina. Paratypes: 1 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 2, *Cyrilla racemiflora* forest type, leaf litter, 795 m.a.s.l., 18.XI.2014, C.M.Ospina. 1 immature on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815 m.a.s.l, 18.II.2015, C.M.Ospina. Other examined material: 9 individuals in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, soil, 815 m.a.s.l., 18.XI.2014, C.M.Ospina. 2 individuals in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815 m.a.s.l., 18.II.2015, C.M.Ospina. 2 individuals in alcohol, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815 m.a.s.l., 18.VIII.2015, C.M.Ospina

3.4.4. Discussion

H.aemila sp.n. is different from the other *Hylaeanura* for their small size, the enlarge of the sensilla s3 in Ant IV, the absence of modified setae in Abd IV and the manubrium without setae. Using the comparative morphology of the *Hylaeanura* by Zeppelini and Palacios-Vargas (2013), the new species characters combination is different from the species previously described (Table 3.5). According this comparative table the most similar species is *H. nepalensis* but it differ in their size, the presence of 2+2 tenacular teeth and three mandibular teeth (Yosii 1966).

Table 3.5. Comparative morphology of the five species of Hylaeanura (Zeppelini and Palacios-Vargas 2013), including the new species from Puerto Rico**.**

Species	Total length (µ)	Ventral guard sensillum	Dorsal guard sensillum	Eyes per side of head	Tenacular teeth	Shape Abd IV sensillum	Mucro
H. infima	500	?	?	0	?	ss	-
H. nohbecana	1000	st	st	0	3+3	cf	+
H. nepalensis	700	st	st	2	2+2	?	-
H. mendocae	600	si	si	2	3+3	ss	-
H.aemilia **n.sp**	330	st	st	2	3+3	ss	-

st-straight, si-sinuous, cf-candle-flame shaped, and ss-sensillum shaped.

H. infima the smallest of the described species have the sensillum of Abd IV of setae shape, but differ of the new species on the absence of eyes and the presence of the teeth in the mandible (Arlé 1966), unfortunately there is not an extensive description of this species.
H. nohbecana is the biggest species of *Hyleaenura*, is similar to the new species in the straight shape of the guard sensillum in Ant. IV, the differences appear in the chaetotaxy: the absence of umpired d1 setae in head, the presence of setae a3 in Abd II-IV and the position of the ss in Abd. I in p3. additionally, *H. nohbecana* have no eyes, the furcula with two small dens each bearing 3 setae and a small vestigial mucro (Vázquez et al. 1998).

H. mendoncae, the most resent described species differs from the new one in the position of ss from Abd. I to III in position p3, in Abd. IV also in position p3 but in the shape of a sensillum, and in Abd. V in position p2. The furcula is reduced too, the manubrium is totally reduced, but 6 + 6 setae present ventrally on Abd. III, dens with 3 setae each and no mucro (Zeppelini and Palacios-Vargas 2013). Differences of the new species and other species of Hylaeanura are listed in table 3.5.

3.5. *Micranurida wladimiri* subsp. *caribeña*

3.5.1. Genus *Micranurida*

This cosmopolitan genus *Micranurida* was created to place the species *Micranurida pygmea* Börner, 1901, to the date, 28 named species are listed in this genus (Bellinger et al. 2018). In the Neotropic, four species were reported: *M. fluminensis* from Brazil; *M. wladimiri* from M. Malvinas, *M. furcifera* in Mexico and *M. pygmaea* in Argentina, Mexico and Peru (Mari Mutt and Bellinger 1990b). In Puerto Rico this is the first reported of the genus.

This genus include the thick individuals, white or blue, tegument generally thick; apical organ in Ant IV simple or trilobed, with large sensillas and variable in shape. Buccal cone rounded. Mandible of *Anurida* type, constituted to a single capitulum without lamella or tooth.

Eyes present or absent postantenal organ present. Unguiculus and tenet hairs absent. Furcula generally absent, when present is rudimentary. Without anal spines (Massoud 1967).

3.5.2. Morphological description

Length 177µm (n = 2).

Color: Individuals in alcohol white, granulation rather coarse, uniform. Dorsal setae smooth and fine, sensilla thicker and longer (Fig 3.6).

Head: Antenna shorter (0.56) than diagonal head. Ant. III and IV fused dorsally, ventral separation market by a fine tegumentary granulation. Ant. IV with a simple apical vesicle, five flame shape sensillas and several long setae; subapical organite present and dorsoexternal microsensillum absent; Ant III sense organ with two small internal sensilla, two large and subequal subcylindrical guard sensilla and two guard setae between them; Ant. II with 12 setae; Ant. I with six setae.

Eyes 2+2 in a pigmented patch. Postantennal organ (PAO) with seven vesicles disposed in a rosette. Head dorsal quetotaxy as in Fig. 1.7A. Buccal cone round, Mandible with three teeth, Maxilla styletiform.

Body: Ordinary body setae smooth, distributed as in Fig. 3.6 Th I with 3+3 setae. Sensory setae (s) in position p3 and with distribution in the half tergites 001/111110.

Female genital plate with six circumgenital setae and 2+2 eugenital setae (Fig. 3.6B). Male genital plate not seem.

Tibiotarsi with 15 setae in all legs, Tenent hair absent. Unguis simple without inner or lateral teeth Unguiculus absent.

Collophore with 4+4 setae; tenaculum absent; furcula vestigial formed by four setae (Fig 3.6B)

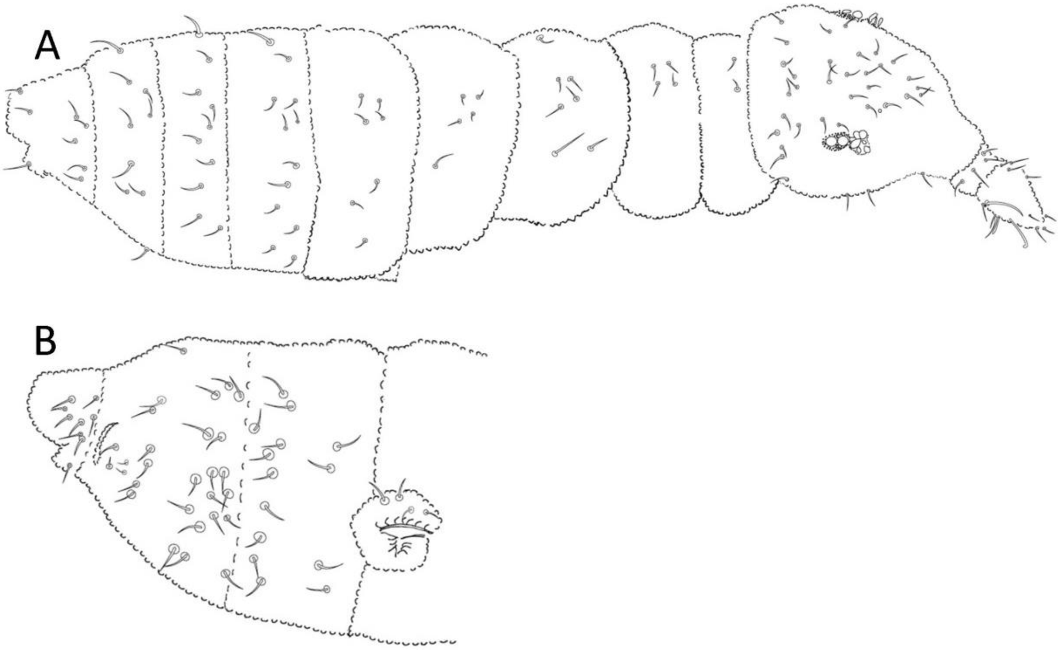

Figure 3.6 ***Micranurida wladimiri*** **sub sp.** ***caribeña*** A. Dorsal view B. Abd I-VI, ventral view.

Etymology. *caribeña* refers to the location of the subspecies in contrast to their species form the Malvinas.

3.5.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l, 18.XI.2014, C.M.Ospina Paratypes: 1 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s,19.II.2015, C.M.Ospina

3.5.4. Discussion

The Puerto Rican species coincide in all the characters included in the original description of *M. wladimiri* (Najt and Rubio 1978), with some differences in size and cephalic chaetotaxy. The body chaetotaxy is not described. Because the lack in details of the closer species and the few specimens examined from Luquillo are not possible explore mayor differences between *M. wladimiri* and the present species.

3.6. *Pseudachorutes* sp1.n. Ospina et al 2018

3.6.1. Genus *Pseudachorutes*

The genus *Pseudachorutes* was established by Tullberg (1871) based on the type species *Pseudachorutes subcrassus*. To the present, it contains 107 species worldwide (Bellinger et al. 2018), 24 have been reported from the Neotropic, seven of them belong to the Caribbean area: *P. difficilis* Denis, 1931, from Costa Rica*; P. legrisi* Thibaud and Massoud, 1983, and *P. reductus* Thibaud and Massoud, 1983 from the Antilles*; P. nica* Palacios-Vargas 1988 from Nicaragua; *P. orghidan*i Massoud and Gruia, 1969, from Cuba; *P.subcrassoides* from Nicaragua (Maes and Palacios-Vargas 1988) and *P. parvulus* from Cuba (Díaz-Azpiazu et al. 1996) and Puerto Rico (Ospina Sánchez et al. 2018).

The genus includes the individuals with Ant. III and IV dorsally fused, Ant. IV generally with 6 sensilla nd apical bulb, Ant. III organ with 2 microsensilla in a cuticular fold, 2 guard sensilla and one microsensillum; buccal cone extended, mandibles with two or several teeth, maxilla often styliform with two lamellae; ocelli 8+8, PAO present in one circle or one ellipse; unguiculus absent furcula well developed, anal spines absent (Stach 1949, Massoud 1967, Christiansen and Bellinger 1980a).

3.6.2. Morphological description

Length 328µm (n = 5).

Color: Individuals in alcohol evenly purple to dark blue, granulation strong. Body setae simple and smooth, with micro and macrosetae and acuminate; sensorial setae longer than macrosetae without other modifications (Fig 3.7).

Head: Antenna shorter (0.62) than diagonal head. Antennal segments ratio I: II: III+IV as 1: 1.34: 3.12. Ant. III and IV fused dorsally; Ant. IV with a simple apical vesicle, five subcylindrical thin sensilla and 14 long setae; subapical organite and dorsoexternal microsensillum absent (Fig. 3.7A); Ant III sense organ with two small straight internal sensilla under a cuticular fold, two subcylindrical subequal guard sensilla and two guard setae between them; ventral microsensillum present (Fig. 3.7B); Ant. II with 12 setae; Ant. I with six setae.

Postantennal organ (PAO) with five to six vesicles disposed in a rosette as larger as the nearby ocelli. Eyes 8+8 in a pigmented patch. Head dorsal quetotaxy as in figure 3.7C; setae a0 on the head absent. Mandible with three short teeth. Maxilla styliform, with one apical hook. Buccal cone elongate. Labral chaetotaxy 2/552, the sclerotization in the shape of ogive. Labium with typical number of setae for the genus (Fig. 3.7D)

Body: Ordinary body setae smooth, dorsal chaetotaxy distributed as in Fig. 3.7C. Th I with 3+3 setae. Setae a2 present on Th. II, but absent from Th. III to Abd. IV, with m3 and m4 present on Abd. IV. Sensory setae on the body in position of p4 and m6 on Th. II and III and p5 from Abd. I–III and p4 on Abd. IV-V. Sensorial formula of the body 022/111110. Sensory setae longer than ordinary setae, sometimes difficult to identify.

Female genital plate with 4+4 pregenital setae, six circumgenital setae and 2+2 eugenital setae (Fig 3.7E). Male genital plate with 4+4 pregenital setae, 16 circumgenital setae and 2+2 eugenital setae (Fig. 3.7F). Each anal valve with 13 setae and 2 hr setae.

Legs: Trochanter with 3 setae each; femora I, II, III with 10, 8, 8 setae respectively; tibiotarsi with 18 setae each, with one acuminate tenet hair. Unguis without teeth; Unguiculus absent.

Collophore with 3+3 setae; tenaculum with 3+3 teeth and without setae; furcula well developed, manubrium with two lateral setae at each side, dens with six setae, mucro straight, apex slightly curve. Ratio mucro: dens = 1:2 (Fig.3.7G).

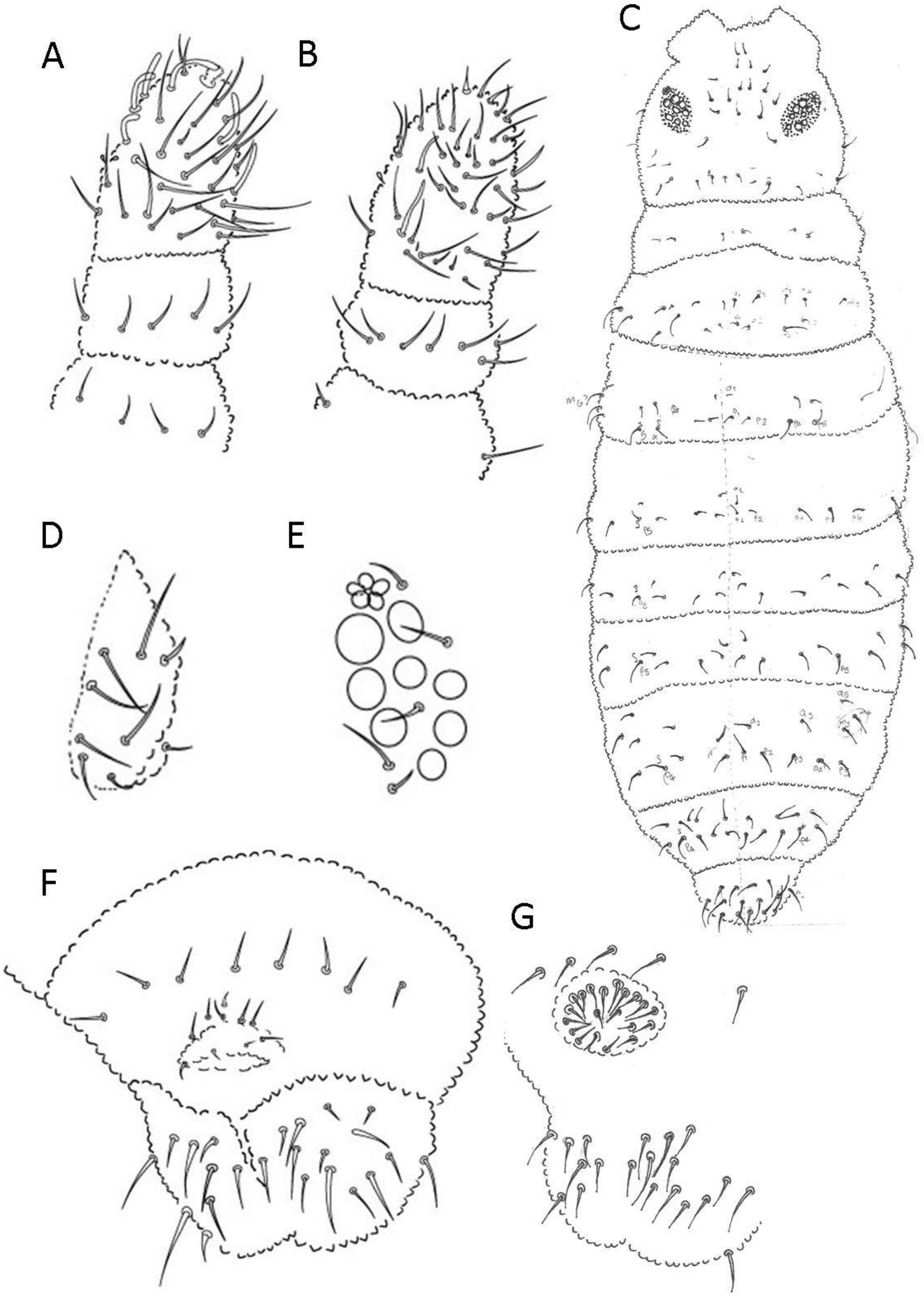

Figure 3.7 ***Pseudachorutes*** **sp1. n.**A. Ant. Dorsal view B. Ant. Ventral view C. Dorsal view D. Labium E. OPA and eyes F. Female genital plate G. Male genital plate.

3.6.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter and epiphyte at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l, 18.XI.2014, C.M.Ospina. Paratypes: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Cyrilla racemiflora* forest type, leaf litter, 759.3 m.a.s.l., 25.VIII.2014, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter, 987.6 m.a.s.l., 04.XI.2014, C.M.Ospina. 1 female on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter 1044.8 m.a.s.l., 4.XI.2014, C.M.Ospina. 1 male, 1 female on slide , Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, leaf litter, 994.4 m.a.s.l., 11.II.2015, C.M.Ospina. 1 immature on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter, 987.6 m.a.s.l., 11.II.2015, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, leaf litter, 994.4 m.a.s.l., 19.V.2015, C.M.Ospina. 1 male on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, epiphyte, 994.4 m.a.s.l., 11.II.2015, C.M.Ospina.

3.6.4. Discussion

Pseudachorutes nsp1 have this novel combination of characters: A simple antennal bulb and five sensilla in Ant IV, PAO with 5-6 vesicles, absent of teeth in the unguis and the presence of one acuminate tenet hair. The new species is the smaller and the one with less OPA vesicles in the region. All the Caribbean species have a trilobed bulb in Ant IV expect for *P. legrisi*, this species differ from the new species in the number of OPA vesicles (10-13), the presence of the inner tooth in unguis and the presence of the capitate tenet hair; the chaetotaxy differences are in the presence of the setae d0 in head, and the absence of setae m in Abd IV (Thibaud and

Massoud 1983). Other differences with the other Caribbean species are presented in the Table 3.6.

3.7. *Pseudachorutes* sp2. n. Ospina et al 2018

3.7.1. Morphological description

Length 626µm (n = 5).

Color: Individuals in alcohol dark blue with thorax, legs and furcula white, granulation strong. Body setae simple and smooth, with micro and macrosetae acuminate; sensorial setae longer than macrosetae without other modifications (Fig 3.8).

Head: Antenna shorter (0.49) than diagonal head. Antennal segments ratio I: II: III+IV as 1: 1.22: 2.51. Ant. III and IV fused dorsally; Ant. IV with a trilobed apical vesicle, five subcylindrical thin sensilla and 16 long setae; subapical organite absent and dorsoexternal microsensillum present (Fig. 3.8A); Ant III sense organ with two small straight internal sensilla under a cuticular fold, two subcylindrical guard sensilla (S.g.v. larger than S.g.d.) and two guard setae between them; ventral microsensillum present (Fig. 3.8B); Ant. II with 10 setae; Ant. I with six setae. Postantennal organ (PAO) with 16 to 20 vesicles disposed in a rosette, 1.3 larger than the nearby ocelli. Eyes 8+8 in a pigmented patch. Head dorsal quetotaxy as in Fig. 3.8C; setae a0 on the head absent, unpaired seta sd1 present. Mandible with two short teeth. Maxilla styliform, with one apical hook. Buccal cone elongate. Labral chaetotaxy 2/522, the sclerotization in the shape of ogive (Fig. 3.8D). Labium with typical number of setae for the genus (Fig.3.8E).

Body: Ordinary body setae smooth, dorsal chaetotaxy distributed as in Fig. 3.8C. Th I with 3+3 setae. Setae a2 present on Th. II, but absent from Th. III to Abd. IV, with m3 and m4 absent on Abd. IV. Sensory setae on the body in position of p4 and m6 on Th. II and III and p5 from Abd. I–V. Sensorial formula of the body 022/111110. Sensory setae longer and thicker in the base, slender in the end than ordinary setae.

Female genital plate with 4+4 pregenital setae, six circumgenital setae and 2+2 eugenital setae (Fig. 3.8F). Male genital plate with 4+4 pregenital setae, 10 circumgenital setae and 2+2 eugenital setae. Each anal valve with 14 setae and 2 hr setae.

Legs: Coxa I, II, III with 3, 7, 7 setae each; Trochanter I, II, III with 6,4,6 setae each; femora I, II, III with 10,12,12 setae respectively; tibiotarsi with 18 setae each, with one acuminate tenet hair. Unguis with one lateral teeth; Unguiculus absent.

Collophore with 4+4 setae (Fig 3.8G); tenaculum with 3+3 teeth and without setae; furcula well developed, manubrium with two lateral setae at each side, dens with six setae, mucro straight, apex slightly curve. Ratio mucro: dens = 1:1.5 (Fig.3.8H).

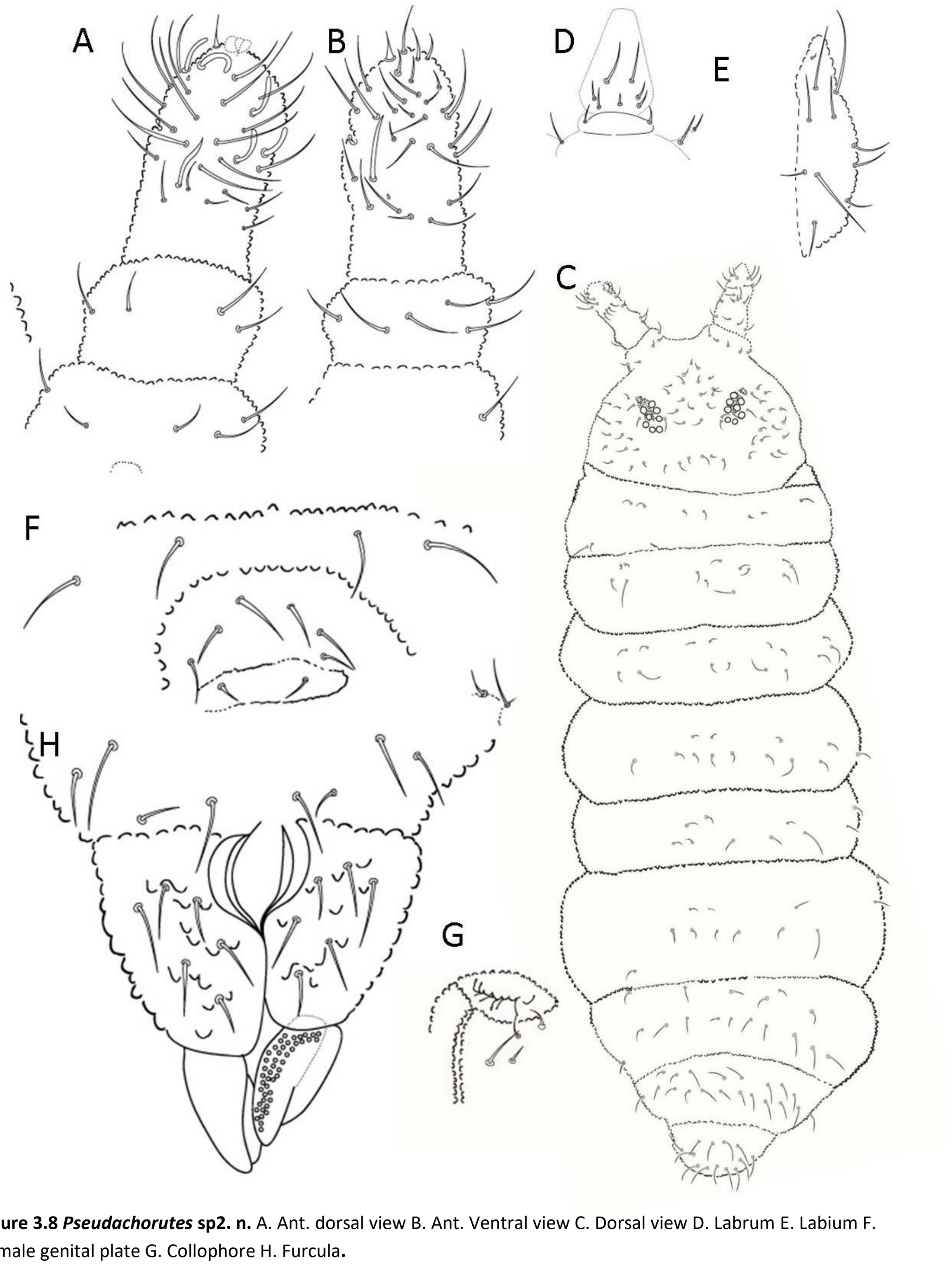

Figure 3.8 ***Pseudachorutes*** **sp2. n.** A. Ant. dorsal view B. Ant. Ventral view C. Dorsal view D. Labrum E. Labium F. Female genital plate G. Collophore H. Furcula**.**

Etymology

3.7.2. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter and epiphyte at the Luquillo Mountains, Puerto Rico. Holotype: Male, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l., 18.XI.2014, C.M.Ospina. Paratypes: 2 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l., 18.XI.2014, C.M.Ospina. 1 male, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l., 19.II.2015, C.M.Ospina.1 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Cyrilla racemiflora* forest type, leaf litter, 759.3 m.a.s.l., 19.XI.2014, C.M.Ospina. 1 female on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter 1044.8 m.a.s.l., 15.VIII.2014, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, leaf litter, 994.4 m.a.s.l., 04.XI.2014, C.M.Ospina.

3.7.3. Discussion

The new species is characterized for their coloration pattern, the presence of an antennal bulb trilobed, 5 sensillas in Ant IV, an OPA with 16-20 vesicles, the ocular setae are macrosetae, the presence of an inner teeth in the unguis and one acuminated tenet hair. This species is close to *P. nica*, the differences are the number of sensillas in the Ant III (6); the type of ocular setae and the absence of tenet hair; other differences in the chaetotaxy are the presence to the well development ventral sensory file with 20-25 setae in Ant IV, and the setae a4 and p2 in the thoracic and abdominal tergites (Palacios-Vargas and Mejía-Madrid 2012). This species is different form the species described above in the presence of a simple antennal bulb in Ant. IV, number of vesicles in the OPA, the absence of tooth in the unguis, the absence of the umpired setae d1 in head, and the position of the SS in the abdominal tergites. Additional differences between the *Pseudachorutes* Caribbean species are presented in Table 3.6.

Table 3.6 Comparison of *Pseudachorutes* Caribbean species (Palacios-Vargas and Mejía-Madrid 2012), including two new species form Puerto Rico. Size in mm; Ant bulb = number of lobes in antennal apical bulb; Ant. IV = number of cylindrical sensilla; PAO = number of vesicles; PAO/E = size PAO/eye ratio; Md = number of mandibular teeth; Ocular = type of ocular setae 1, 2 and 3; Inner u = inner unguis teeth; LUT = lateral unguicular teeth); D = number of dental setae; TH = number of tenet hairs, ac = acuminate, cap = capitate.

Species/ Character	Size	Ant bulb	Ant IV	PAO	PAO/E	Md	Ocular 1 2 3	Inner u	LUT	D	TH
nica	1.4	3	6	14–20	1.0	4	mMm	-	+	6	None
orghidani	1.2	3	5	17	1.1	3	???	+	+	6	None
difficilis	0.5	3	6	6–7	?	3	mmm	-	-	6	1 ac
legrisi	0.8	1	5?	10–13	1.8	3	mmm	+	-	6	1 cap
reductus	0.8	3	6?	8	1.2	5	mmm	+	-	3	1 ac
Sp1	0.3	1	5	5-6	1.0	3	mmm	-	-	6	1ac
Sp2	0.6	3	5	16-20	1.3	3	MMM	+	-	6	1ac

3.8. *Brachystomella* n. sp1. Ospina et al 2018

3.8.1. Genus Brachystomella

The genus *Brachystomella* was created by Ågren to place the species *Brachystomella maritima*; this species was revised by Stach in 1928, and was renamed as *Brachystomella parvula* becoming a type species (Massoud 1967). To the date, 74 species of this genus are described (Bellinger et al. 2018), of these 31 are reported form the Neotropical region (Weiner and Najt 2001). In Puerto Rico, the species *B. agrosa* and *B. bacoensis* have been reported (Ospina Sánchez et al. 2018).

Brachystomella include the individuals mostly blue in the dorsal view, but clear at it ventral side, including the appendages. The apical vesicle in Ant IV simple to trilobed, the head with 8+8 to 2+2 eyes and OPA present with a variable number of vesicles in one line. The mandibles are absent and maxillae have several teeth. The furcula and tenaculum are generally present and development and anal spines absent (Massoud 1967, Bellini et al. 2018).

3.8.2. Morphological description

Length 540µm (n=7)

Color. Individuals in alcohol with head, thorax and furcula evenly purple; thorax and legs white.

Head. Antenna shorter (0.7) than the diagonal head. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with ordinary setae and 7 subcylindrical thin sensilla; dorsoexternal microsensillum subapical and organite absent; apical bulb bilobed (Fig. 3.9A). Ventral side without blunt setae; Ant. III sense organ with two small internal sensilla, two subcylindrical subequal guard sensilla and two guard setae between them (Fig. 3.9B); ventral microsensillum absent Ant. II with 12 setae; Ant. I with 6 setae. Postantennal organ (PAO) with 4 vesicles. Eyes 8+8. Head with setae a0 and, c1 to c7, seta sd1 absent. Buccal cone typical for genus. Labral chaetotaxy 2/2334 Mandible absent, maxilla with 8 teeth (Fig.3.9C).

Body. Ordinary body setae short, distributed as in Fig. 3.9D. Sensory setae (s) well differentiated and distributed on Th. I-Abd. V as 022/21111. Microsensilla present only on Th. II. Prothorax with 2+2 setae Thoracic sterna without setae. Abd. II-IV with setae s= p4; Lateral anal valves each with one hr seta.

Legs. Subcoxae I, II, III with 1, 2, 2 setae; coxae I, II, II with 3, 6, 6 setae; trochanter I, II, III with 5, 5, 4 setae; femora I, II, III with 12, 12, 10 setae; tibiotarsi I, II, III with 19, 19, 18 setae, without capitate setae, seta M present, and seta B7 absent. Tenent hair acuminate, law with inner tooth at half length of its inner edge, without lateral teeth (Fig. 3.9E). Unguiculus absent.

Collophore With 3+3 setae. Tenaculum With 3+3 teeth, without setae. Furcula Well developed, ratio mucro: dens = 1: 1.9; Dens with 6 setae, mucron straight, with tip slightly hooked. (Fig. 3.9F).

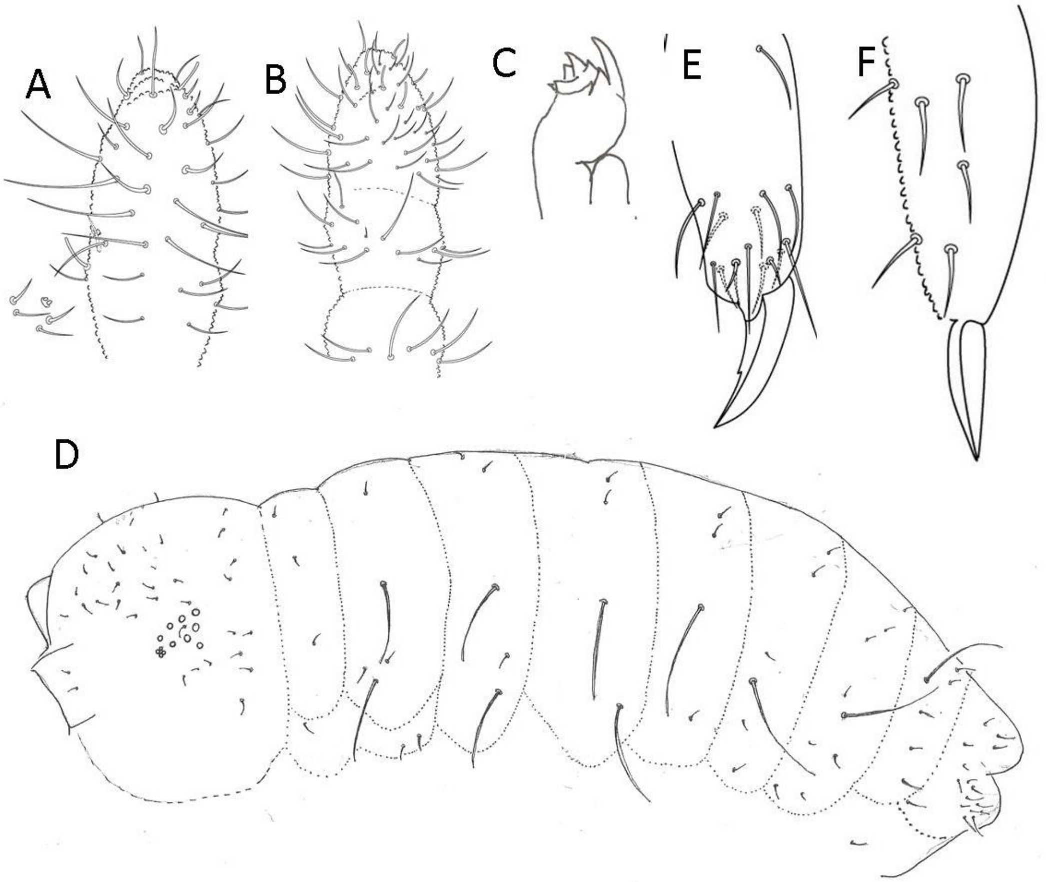

Figure 3.9 ***Brachystomella*** **B/N sp.n.** A. Ant. III dorsal view B. Antenna ventral view C. Maxilla D. Body dorsal view E. Leg F. Furcula.

3.8.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter or soil at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l.,19.II.2015, C.M.Ospina. Paratypes: 1 male, 2 female and 1 immature on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l.,19.II.2015, C.M.Ospina. 1 male on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, soil, 815.3 m.a.s.l., 27.V.2015, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 815.3 m.a.s.l., 18.XI.2015, C.M.Ospina.

3.8.4. Discussion

The combination of a bilobulate apical vesicle in Ant. IV , the number of sensorial setae in Abd. 1 (2+2), the reduction of hr setae (1+1), the number of setae in dens (6-7) and the color patter are characters than make this a unique species. The new species keys out to *B. agrosa* in Weinar and Najt (2001), but the new species differ in the presence of 6-7 normal setae in each dens, a bilobulate apical vesicle in Ant. IV and just one setae hr in the anal valves, additionally *Brachystomella* n. sp. is the only member of the genus with a white band covering the entire thorax. There are 25 Neotropical *Brachystomella* with 8+8 eyes; the new species is the first with a white band in the thorax. The only *Brachystomella* previously reported form Puerto Rico, *B. agrosa* differ from the new species in the number of dental setae (5), their apical vesicle is simple and the number of setae hr in the anal valves are 2. *B. purma* and *B. nordestina* described form Peru and Brazil respectively, are most similar to the new species but they have a different color pattern, 5 dental setae and a trilobed apical vesicle on Ant. IV (Weiner and Najt 2001, Bellini et al. 2018). Other similar Neotropical species with 8+8 eyes and 4 vesicles PAO are *B. stachi* and *B. zapati,* which differ from the new species in having 1+1 setae on Abd 1, number of setae on the tibiotarsi (18, 18, 17) and in having 3+3 hr setae on anal valves and the number of vesicles in the apical organ on Ant. IV (Weiner and Najt 2001).

3.9. *Brachystomella* n. sp2. Ospina et al 2018

3.9.1. Morphological description

Size 358µm (n=12)

Color. Individuals in alcohol with head, body and appendages evenly purple.

Head. Antenna shorter than head (about 0.6 the length of head). Ant. IV with ordinary setae and 6 subcylindrical sensilla; dorsoexternal microsensillum absent, subapical organite absent; apical vesicle simple; Ant. III and IV fused dorsally, ventral separation well marked. Sensory organ of Ant. III consisting of: two small globular internal sensilla, two guard sensilla subcylindrical, the lateral larger and two guard setae (Fig 3.10A-C); ventral microsensillum absent. (Fig. 3.10A). Ant. II with 12 setae Ant. I with 6 setae. Postantennal organ (PAO) bearing 4 vesicles. Eyes 8+8. Head with setae a0 and sd1, c2 and c5 (Fig. 3.10D). Habitus and buccal cone typical for the genus Brachystomella. Mandible absent, maxillae each with 7 teeth (Fig. 3.10E). Labral chaetotaxy 2/2334.

Body. Dorsal chaetotaxy as in Fig 1.11D with very short ordinary setae, with longer sensory setae s. Their formula per half tergum 022/11111. Th. I with 3+3 setae. Microsensilla present on Th. II. Abd I-IV with setae s= p4. Thoracic sterna without setae, Abdominal sternum II with 1+1 setae. Even anal valves each with three setae hr.

Legs. subcoxae "1" I, II and III with 1,2 and 2 setae; coxae I, II and II with 3, 6 and 6 setae; trochanters I, II and III with 5, 5 and 4 setae; femora I, II and III with 12, 12 and 10 setae; Tibiotarsi I, II and III with 20, 20 and 18 setae, respectively, all acuminate setae, seta M present, seta B7 present on tibiotarsu III. Claw without inner or lateral teeth (Fig.3.101F). Empodial appendage absent.

Collophore with 3+3 setae; tenaculum with 3+3 teeth, without setae. Furcula well developed with 5 setae in each dens (Fig. 3.10G). Mucro straight with apex slightly hooked dorsally. Ratio muro:dens = 1:1.3.

Etymology

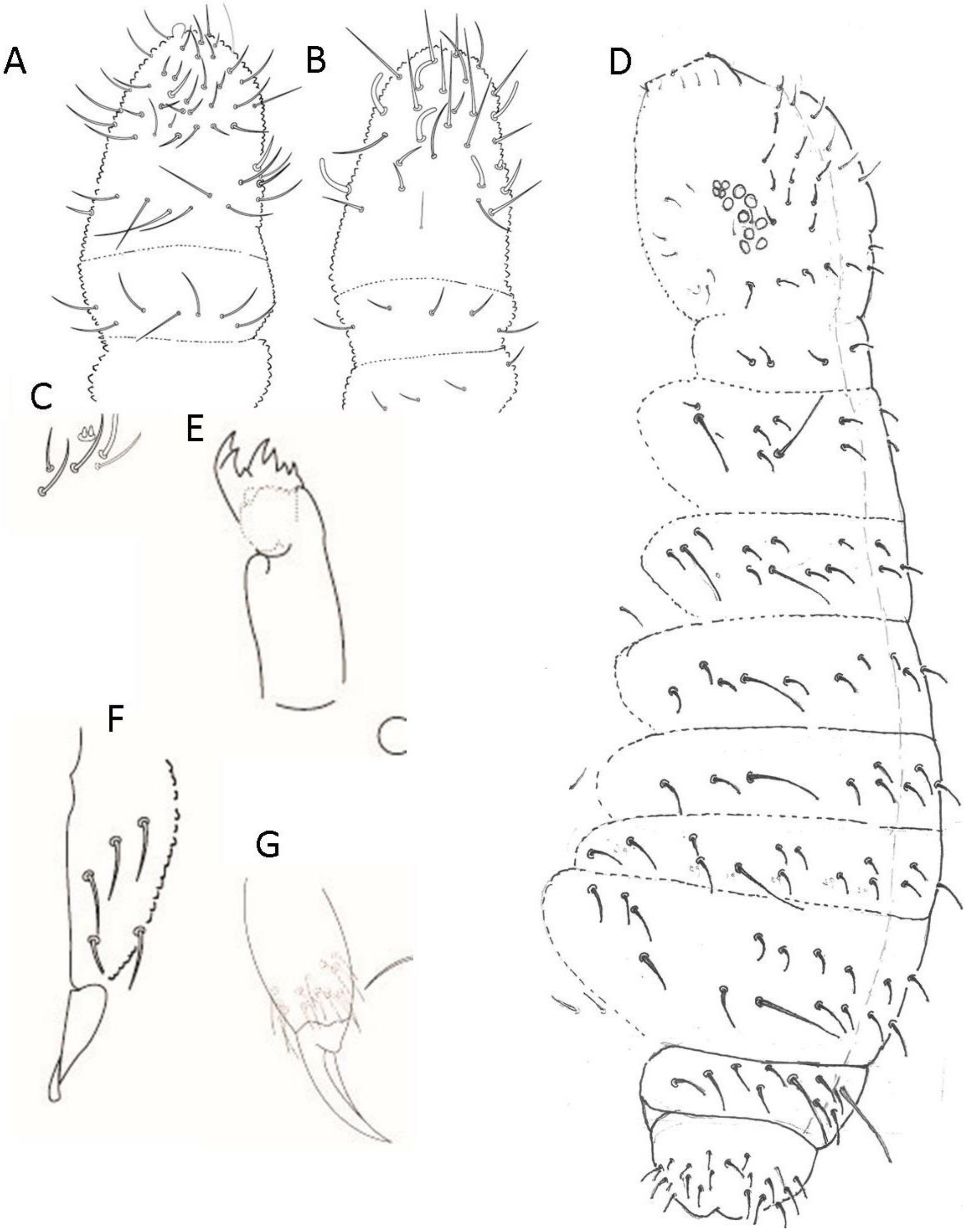

Figure 3.10 ***Brachystomella morada*** **sp.n.** A. Antenna dorsal view B. Antenna ventral view C. Sensorial Organ in Ant. III D. Head and body dorsal view E. Maxilla F. Leg G. Furcula.

3.9.2. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter at the Luquillo Mountains, Puerto Rico. Holotype: female, collected in *Tabebuia rigida* forest type, Río Grande, PR. 11.III.2015. Paratypes: 2 females on slide, Puerto Rico, Río Grande, Luquillo Mountains, El Verde field station, *Tabebuia rigida* forest type, leaf litter, 433.2 m.a.s.l., 25.XI.2014, C.M.Ospina. 2 females and 1 male on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter,815.3 m.a.s.l., 18.XI.2014, C.M.Ospina. 4 females and 2 immatures on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter,815.3 m.a.s.l., collected in *Cyrilla racemiflora* forest type, Toro Trail 1, Luquillo, PR, 19.II.2015, C.M. Ospina.

3.9.3. Discussion

The presence of a simple apical vesicle in Ant. IV, the number of sensorial setae in Th. I (3+3), sensorial setae in Abd. I (2+2), hr setae (3+3) and setae in tibiotarsi I and II (20) make this a unique species. The new species keys out to *B. mataraniensis* in Weiner and Najt (2001), but the new species differ in the presence of one setae s in Th. I; 12, 12, 10 setae in femora I, II, III and 20, 20, 18 setae in tibiotarsu I, II and III respectively; and the presence of 5 setae in dens and the absence of inner teeth in the ungus.

This new purple species looks like *B. agrosa*, but it differs in the number of setae in Th. I (2+2), in tibiotarsu (19,19,18) and in femora (12,11,10). Other species in the region with 3+3 setae in Th. I: *B. barrerai, minimucronata, vilalobosi, globulosa* and *baconaensis* have capitate setae in all tibiotarsu. *B. mataraniensis* and *victoriensis* are species without clavate setae in tibiotarso but differ from the new species in the number of setae in tibiotarsu (19, 19, 18) and femora (12, 11, 10 and 13, 12, 10 respectively).

3. 10. ***Folsomiella intermedia*** subsp. n. *ciega*

3.10. 1. Genus *Folsomiella* Bonet, 1930

The genus *Folsomiella* was stablished for the species *Achorutes (Schoettella) caecus* (Folsom, 1927) from Panama (Massoud 1967). To the date *Folsomiella* include six species (Bellinger et al. 2018), all of them in the Neotropical Region. This new species is the first record for Puerto Rico.

The genus include individuals with pigment and eyes absent; habitus, antenna and buccal parts similar to *Brachystomella*; post-antennal organ with several tubercle arranged in a circle or ellipse; furcula present and mucro usually present (Massoud 1967, De Mendonça et al. 2005).

3.10.2. Morphological description

Size 394µm (n=3)

Color in alcohol light blue to white

Head. Antenna shorter than head (about 0.6X length of head). Ant. I with 6 setae, Ant. II with 12 setae, Ant. III and IV fused dorsally, ventral separation well marked. Sensory organ of Ant. III consisting of: two small globular internal sensilla, two subequal subcylindrical guard sensilla and two guard ; ventral microsensillum present. Ant. IV with ordinary setae and 6 subcylindrical sensilla (Fig. 3.11A-B); Postantennal organ bearing 4-5 vesicles; eyes absent. Head setae a0, c1, c4 and c5 present (Fig. 3.11C) . Labral chaetotaxy 2/2334. buccal cone typical for the genus *Brachystomella*. Mandible absent, maxillae each with 8 teeth (Fig. 3.11D).

Body. Dorsal chaetotaxy as in Fig. 1.12C ordinary setae unusually short, sensory setae s longer, with formula 022/21111. Th. I with 2+2 setae. Microsensilla present on Th. II. Abd. I-IV with setae s= p3. Thoracic sterna without setae, abdominal sternum II with 1+1 setae. Paired anal valves each with two seta hr.

Legs. Subcoxae "1" I, II and III with 1,2 and 2 setae; coxae I, II and II with 2, 5 and 6 setae; trochanters I, II and III with 6, 4 and 4 setae; femora I, II and III with 12, 10 and 10 setae;

tibiotarsi I, II and III with 19, 19 and 18 setae, respectively, without acuminate setae, seta M present, seta B7 absent on tibiotarsu III. Claw with inner tooth at half length of its inner edge, without lateral teeth (Fig. 3.11E). Empodial appendage absent.

Collophore with 3+3 setae; tenaculum with 3+3 teeth, without setae. Furcula well developed with 5 setae in each dens; mucro straight with apex slightly hooked (Fig. 3.11F). Ratio muro:dens = 1: 1.7.

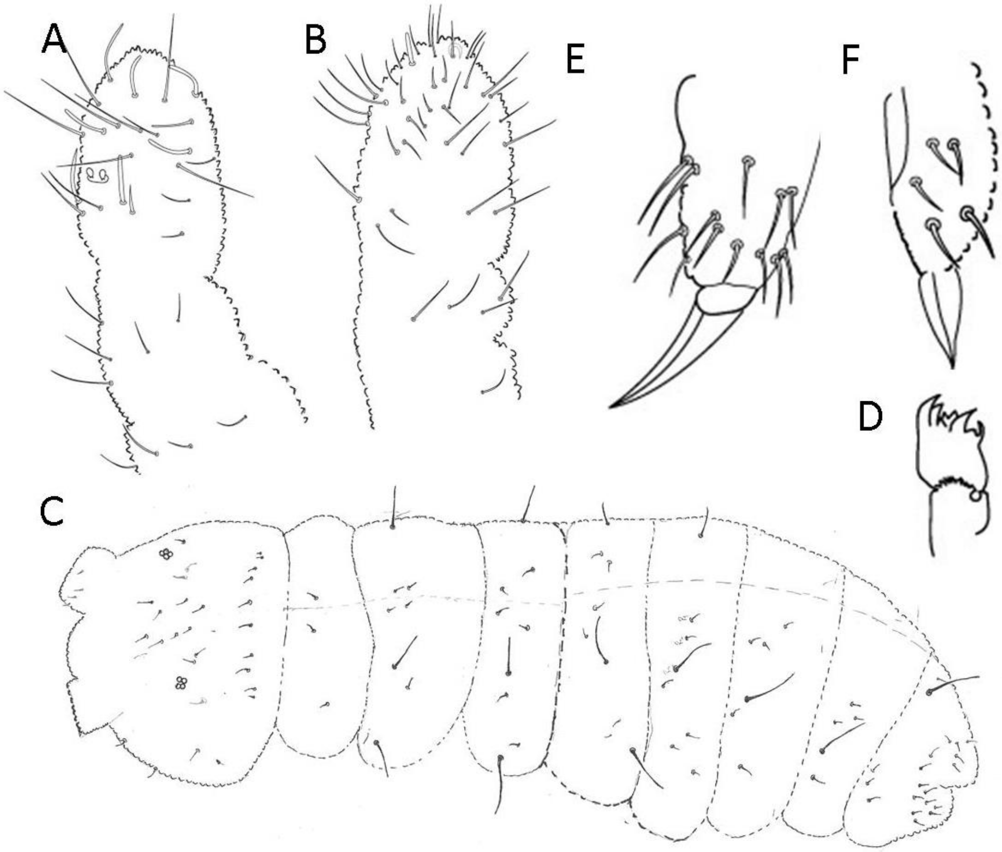

Figure 3.11 ***Folsomiella intermedia*** **subsp. n.** ***ciega*** A. Antenna dorsal view B. Antenna ventral view C. Head and body dorsal view D. Maxilla E. Leg F. Furcula.

3.10.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter; at the Luquillo Mountains, Puerto Rico. Holotype: 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 25.VIII.2014, C.M.Ospina. Paratypes: 1 male on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, leaf litter, 18.XI.2014,C.M.Ospina. 1 male on slide, Puerto Rico, Río Grande, Luquillo Mountains, El Verde field station, *Dacryodes excelsa* forest type, leaf litter, 11.III.2015, C.M. Ospina.

3.10.4.Discussion

The species *F. intermedia* was described for Arlé (1939), as *Brachystomella intermedia* mentioned some diagnostic characters as the lack of pigmentation, the presence of one or two eyes, OPA bearing 7 or 8 vesicles , Ant. IV with a simple apical vesicle, ungus without teeth (inner or lateral) and furcula with 5 lateral setae.

Other *Folsomiella* species, *trisetosa, pseudocaeca* and *albida* have more than 5 OPA vesicles and 3+3 setae in Th.I. *F. caeca* has the apical vesicle trilobed. *F. polylepiana* and *nothofagutalis* have 3 dens setae.

3.11. *Microgastrura parvaboletus* sp.n. Ospina et al 2018

3.11.1. Genera *Microgastrura* Stach, 1922

The *Microgastrura* genus was created by Stach, describing their type species *M. duodecimoculata* in 1922. Since then 6 additional species have been described: *M. jamaicensis* (Massoud and Bellinger, 1963); *M. massoudi* Deharveng, L and Najt, J, 1988; *M. minutissima* (Mills, HB, 1934); *M. nanacatlica* Vázquez, M and Palacios-Vargas, JG, 1997; *M. sensiliata* Jordana, R, 1981 and *M. sofiae* Vázquez, M and Palacios-Vargas, JG, 1997. Three species are known in the Neotropical Region: *M. jamaicensis* from Jamaica*; M. nanacatlica* and *M. sofiae* from Mexico. The new species is the first record of the genus form Puerto Rico.

The diagnosis of the genus includes those forms lacking apical teeth on the mandible and having more or less rudimentary molar plate, but otherwise similar to *Hypogastrura*

(Christiansen and Bellinger 1980a). Ant.IV with 7-10 sensilla, with one or two subapical bulbs, and with "file or Trump setae" ventrally. Postantennal organ with 4 centrally jointed lobes; 6+6 eyes; tibiotarsi without capitate tenent hairs; unguiculus with lamella and sometimes with filament; unguis with inner teeth. Ventral tube with 4+4 or 3+3 setae. Tenaculum with 4+4 teeth and no setae on corpus. Dens with seven setae, some of them spiniform and with subapical bulb. Mucro with external lamella. Mucro distinctly separate from dens. Without anal spines (Vázquez and Palacios-Vargas 1996).

3.11.2. Morphological description

Length 435 μm (n = 6).

Color: Individuals in alcohol gray to dark blue

Head: ratio head: antenna = 1:1.35. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with a simple apical bulb, six thin dorsal sensilla and three thick dorso-external sensilla(Fig. 3.12B), ventral file with 30 to 40 modified setae (Fig 3,12A). Ant III sense organ with two small and widened distally internal sensilla and two guard sensilla. Ant.II with 12 setae and Ant. I with 6 dorsal setae (Figs. 3.12A). 6+6 eyes and postantenal organ with four vesicles of different shape and size; with four ocular setae (Fig. 3.12D). Head dorsal quetotaxy as in figure 3.12E. Mandible thin and elongate (Fig.3.12F). Maxilla with four apical teeth (Fig. 3.12G).

Body: Ordinary body setae smooth, acuminated, and shorter than sensilla; distributed as in Fig. 3.12H. Leg chaetotaxy (I-III): coxae 3, 3, 3; trochanter 5,5,5; femora 10, 10, 8; tibiotarsi 19,19,18. Tenent hairs acuminate. Unguis thin, with one median apical ventral tooth. Ratio tibiotarsi: unguis = 1:1.08. Unguiculus trapezoidal with a fine and short filament (Fig. 3.12I)

Ventral tube with 4+4 setae. Tenaculum with 4+4 teeth. Furcula well developed, manubrium dorsally with ten pair of setae. Dens with seven setae, four spiniform. A bladder ventrally, on distal part of dens. Mucro thin, with small lamella (Fig. 3.12J). Ratio dens: mucro = 1: 1.79.

Etymology. *Parv*a is a Latin for small and *boletus* for a fungi in a seta shape in reference an a form of the sensilla in the sensorial organ in the antenna III

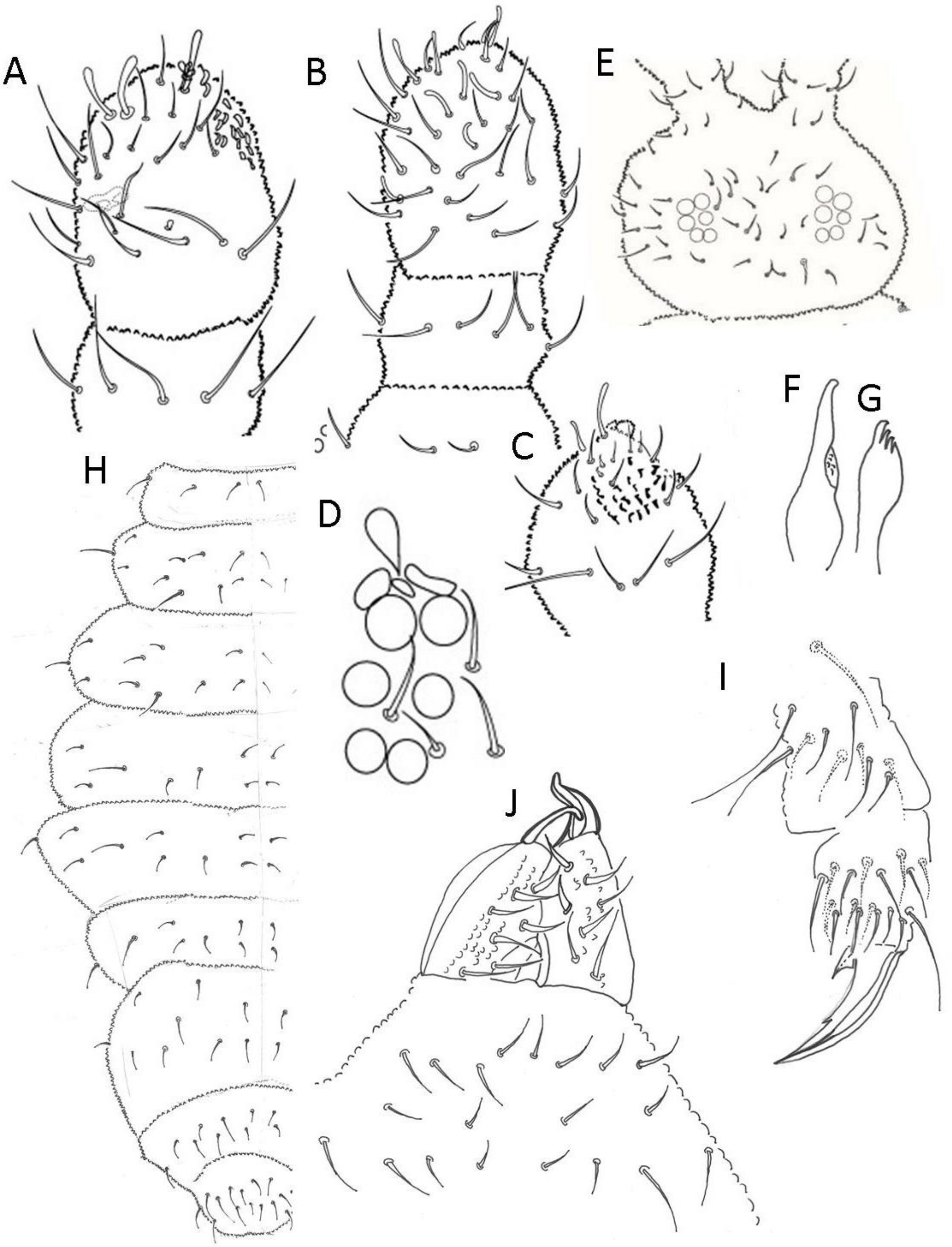

Figure 3.12 ***Microgastrura parvaboletus*** **sp.n.** A. Antenna ventral view B. Antenna dorsal view C. Ventral file of modified setae in Ant. IV D. Eyes and OPA E. Head dorsal view F. Mandible G. Maxilla H. Body dorsal view I. Leg J. Furcula.

3.11.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter and soil at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, soil, 815 m.a.s.l., 18.XI.2014, M.M.Rivera. Paratypes: 3 females, 2 males on slide Puerto Rico, Luquillo, Luquillo Mountains, Río Grande, *Dacryodes excelsa* forest type, leaf litter, 518 m.a.s.l., 11.III.2015. C.M.Ospina. 2 females, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, soil, 815 m.a.s.l., 18.XI.2014, M.M.Rivera. 1 males on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, leaf litter, 987.6 m.a.s.l., 04.XI.2014, C.M.Ospina. 1 immature on slide Puerto Rico, Luquillo, Luquillo Mountains, Yunque Peak, *Tabebuia rigida* forest type, leaf litter 1044.8 m.a.s.l., 9.XI.2014, C.M.Ospina.

3.11.4. Discussion

The new species is the first in the genera with 30 to 40 “trumpet” setae in Ant. IV and the presence of 4 spiniform setae plus three acuminate setae in dens. Additionally, have the unique combination of the characters: six sensillas on Ant IV, unguiculus trapezoidal with a filament reduced.

Between the *Microgastrura* species *M. jamaicensis* is the one with more “trumpet” setae (about 40 to 56) but is different to the new species in the presence of nine sensillas in Ant. IV; the apical vesicle in Ant. IV is trilobed, additionally the species from Jamaica have an acuminated unguiculus and five setae spiniform and two acuminated in dens (Massoud and Bellinger 1963), character that occurs in other four species of the genus: *M. massaudi, M. salgae, M. cantabrica* and *M. duodecimoculata*.

The new species is name after the shape of their sensillas in the sensorial organ in Ant. III, this shape appear in *M. nanacatlica,* but this differ of *M. parvubavoletus* in the presence of four apical teeth, the unguiculus with a fine and long filament. Their manubrium has four pairs of setae and the dens have three distal spiniform setae.

The comparison of characters of *Microgastrura* species are detailed in the table 3.7.

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Table 3.7 Comparison of the main characters of *Microgastrura* species

	Ant.IV				Unguiculus		# dens setae	
Species	"Trumpet" setae	sensillas	apical vesicle	Mandible teeth	filament	shape	Spini-form	Acumi-nate
cantabrica	8	7	simple		reduced		5	2
duodecimoculata	7-8	10	simple		small	knife	5	2
jamaicensis	40 - 56	9	trilobed	6	reduced	acuminate	5	2
massoudi	20-22	8-11?	simple	3-5	reduced	trapezoid	5	2
minutisima	few that 20	6-7		1	develop	lamellate		7
nanacatlica	10	7	simple	1	develop	lamellate	3 - distal	4
parvaboletus **n.sp**	30-40	6	simple	4	reduced	trapezoid	4	3
selgae	7-8	10	simple		small	trapezoid	5-7	2
sensilata	few that 20				small	trapezoid		
sofie	8-10	8	simple	1	fine	lamellate	3 - distal	4

3.12. *Xenylla* sp1. n.Ospina et al 2018

3.12.1. Genus *Xenylla* Tullberg 1869

The genus *Xenylla* was created by Tullberg to place the species *X. maritima* and *X. brevicauda* (Tullberg 1869). *Xenylla* is a cosmopolitan genus with 134 species described (Bellinger et al. 2018), 24 of them have been reported for the Neotropical Region (Mari Mutt and Bellinger 1990a). In Puerto Rico the following species have been reported: *X. grisea* Axelson, 1900; *X. malayana* Salmon, 1951; *X. portoricensis* da Gama, 1976; *X. welchi* Folsom, 1916 and *X. yucatana* Mills, in Pearse,1938 (Ospina Sánchez et al. 2018).

The diagnosis of the genus include the Hypogastruridae having well developed molar plate, lacking post antennal organ and having eyes (Christiansen and Bellinger 1980a). Claw usually with an inner tooth and empodial appendage absent. Furcula short with distinct separated joints, or the mucro is not separated from the dens and form jointly with the dens a mucrodens. Sometimes the mucrodens is reduce pretty strongly, rarely up to zero (Stach 1949).

3.12.2. Morphological description

Length 444µm (n = 3).

Color: Individuals in alcohol dark gray. Body granulation strong, setae comprising in setae smooth and acuminated, sensillas are 3.5 the length of the common setae (Fig. 3.13).

Head: Antenna shorter (0.6) than diagonal head. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with a single apical vesicle and one subapical organite; five subcylindrical thin sensilla and 14 long setae; dorsoexternal microsensillum absent (Fig. 3.13B); Ant III sense organ with two small rounded sensilla inside a fold of the tegument, two subequal subcylindrical guard sensilla; ventral microsensillum absent; Ant. II with 12 setae; Ant. I with six setae (Fig. 3.13C). Eyes 5+5 in a pigmented patch. Postantennal organ (PAO) absent. Chewing mouthparts typical of the genus. Buccal cone rounded; labral chaetotaxy formula 4/445. Labium as in figure 3.13D. Head dorsal quetotaxy as in figure 3.13A, with c1, c2, c3 and d1 setae, with L3 longer than L1, and L1 longer than the others; setae a0 absent. Ventrally with a1, m1, m3.and p1 (Fig. 3.13D).

Body: Ordinary body setae smooth, distributed as in figure 1.14A. Sensory setae (s) well differentiated, 3.5 larger than the normal setae. Dorsally Th I with 3+3 setae; Th.II with setae la1, la2, m3 and p3; seta a2 displaced posteriorly compared with seta a1; setae p2 displaced apically compared with seta p1; Th. III differ from Th. II in the absence of m3; Abd. III with 4+4 setae between the sensillae in posterior row; Abd. IV with p3 and m3, setae s in p5; Abd. V with seta a2; Presence of two anal spines (3 µm) on weakly developed papillae. Ventrally Th II and III without pair of medial setae; Abd. II with p1, p2 and p6, without a6; Abd. III with m3 and p2 absent; Abd IV with three medial setae (vestige of furcula), setae a1 displace and m1 present (Fig. 3.13E).

Female genital plate with six circumgenital setae and 1+1 eugenital setae (Fig. 3.13E). Male genital plate not seen. Anal valve with 14+14 setae and 2+2 hr (3.13E).

Tibiotarsi I-III, respectively, with 19, 19, 18 setae, being two long acuminate tenent hairs of them. Ungues measuring 10µm, without inner tooth; unguiculus absent (Fig. 1.14F).

Collophore with 4+4 setae (Fig. 1.14E), tenaculum and furcula absent.

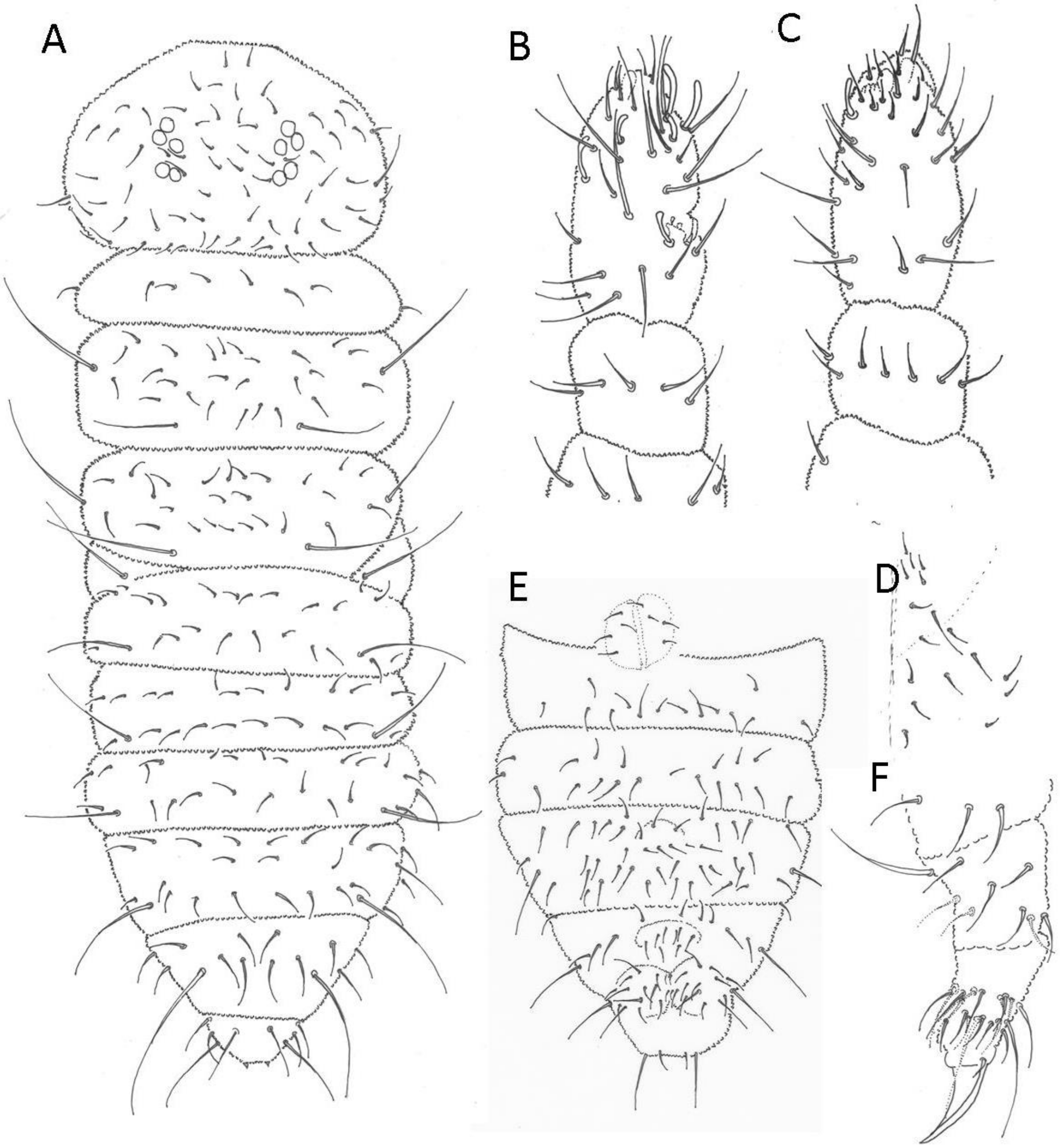

Figure 3.13 ***Xenylla*** **sp1. n.**A. Head and Body dorsal view B. Antenna dorsal view C. Antenna ventral view D. Head ventral view E. Abd II-VI ventral view F. Leg II.

3.12.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in epiphyte mosses at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, mosses, 815 m.a.s.l., 19.II.2015.

C.M.Ospina. Paratypes: 1 male, 1 female on slide Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail 1, *Cyrilla racemiflora* forest type, mosses, 815 m.a.s.l., 19.II.2015. C.M.Ospina.

3.12.4. Discussion

The new species is easily differentiated from another Xenyllas because de absence of furcula and tenaculum with the combination with the follow characters: Sensillas at least three times larger than the other body setae, presence of 5 bunt setae in Ant. IV, absence of setae a0 in head and the presence of tenet hairs acuminated.

Within the described species of *Xenylla, X. acauda* Gisin, 1947 is the only with absence of furcula but it differs from the new species for the presence of two dorsal clavate tenet hair (Stach 1949) and the five blunt setae in Ant. IV and the presence of weakly unilaterally serrate setae on the last two abdominal segments (Christiansen and Bellinger 1980a). The body chaetotaxy differ dorsally in the presence of setae a0 in head, que absence of La2 and presence of m3 in Th. II and III (Christiansen and Bellinger 1980a). Other species with five blunt setae in Ant. IV are *X. canadiensis* Hammer, 1953 that have a reduce furcula but no absent and *X. simberloffi* da Gama, MM, 1974 that have fully development furcula, like the other species of *Xenylla* previously reported in Puerto Rico.

3.13. ***Xenylla*** sp2. n.Ospina et al 2018

3.13.1. Morphological description

Length 409µm (n = 2).

Color: Individuals in alcohol dark gray. Body granulation strong. Body setae comprising in setae smooth and acuminated, Sensillas are 5 to 1 the length of the common setae (Fig. 3.14).

Head: Antenna shorter (0.5) than diagonal head. Ant. III and IV fused dorsally, ventral separation well marked. Ant. IV with a single apical vesicle; five subcylindrical thin sensilla and 14 long setae; dorsoexternal microsensillum absent (Fig. 3.14B); Ant III sense organ with two small rounded sensilla, two subequal subcylindrical guard sensilla; ventral microsensillum absent (Fig. 3.14C); Ant. II with 12 setae; Ant. I with six setae. Eyes 5+5 in a pigmented patch. Postantennal organ (PAO) absent. Chewing mouthparts typical of the genus; Labral chaetotaxy formula 4/5/3/3. Labrum as in figure 1.15D. Head dorsal quetotaxy as in figure 1.15A, with c1, c2, c3 and d1 setae, with L3 longer than L1, and L1 as long as the others; setae a0 and p3absent. Ventrally with a1, m1, m3 and p1 (Fig.3.14F).

Body: Ordinary body setae acuminated and smooth, with unilaterally serrate setae in Abd. IV, V and VI, distributed as in figure 3.14A. Sensory setae (s) well differentiated, 5 and 2.5 larger than the normal setae. Dorsally Th I with 3+3 setae; Th.II with setae la1, la2, m3 and p3 Th. III differ from Th. II in the absence of m2; Abd. III with 4+4 setae between the sensillae in posterior row; Abd. IV with p3, setae s in p5, m3 absent; Abd. V with seta a2; Abd. VI with two anal spines (2 µm) on weakly developed papillae. Ventrally Th II and III without pair of medial setae; Abd. II with p1, p2 and p6, without a6; Abd. III with m1 and m3, p2 absent; Abd IV with setae a1 and m1 present, m3 absent (Fig. 3.14F).

Male genital plate with 10 circumgenital setae and 1+1 eugenital setae (Fig. 3.14F). female genital plate not seen. Anal valve with 12+12 setae and 1+1 hr (Fig. 3.14F).

Tibiotarsi I-III, respectively, with 20, 18, 18 setae, being two of them long spatulate tenent hairs, per leg. Ungues measuring 10µm, without inner tooth; unguiculus absent (Fig.3.14G).

Collophore with 4+4 setae, tenaculum with 3+3 teeth and furcula reduce with one setae (Fig. 3.14H).

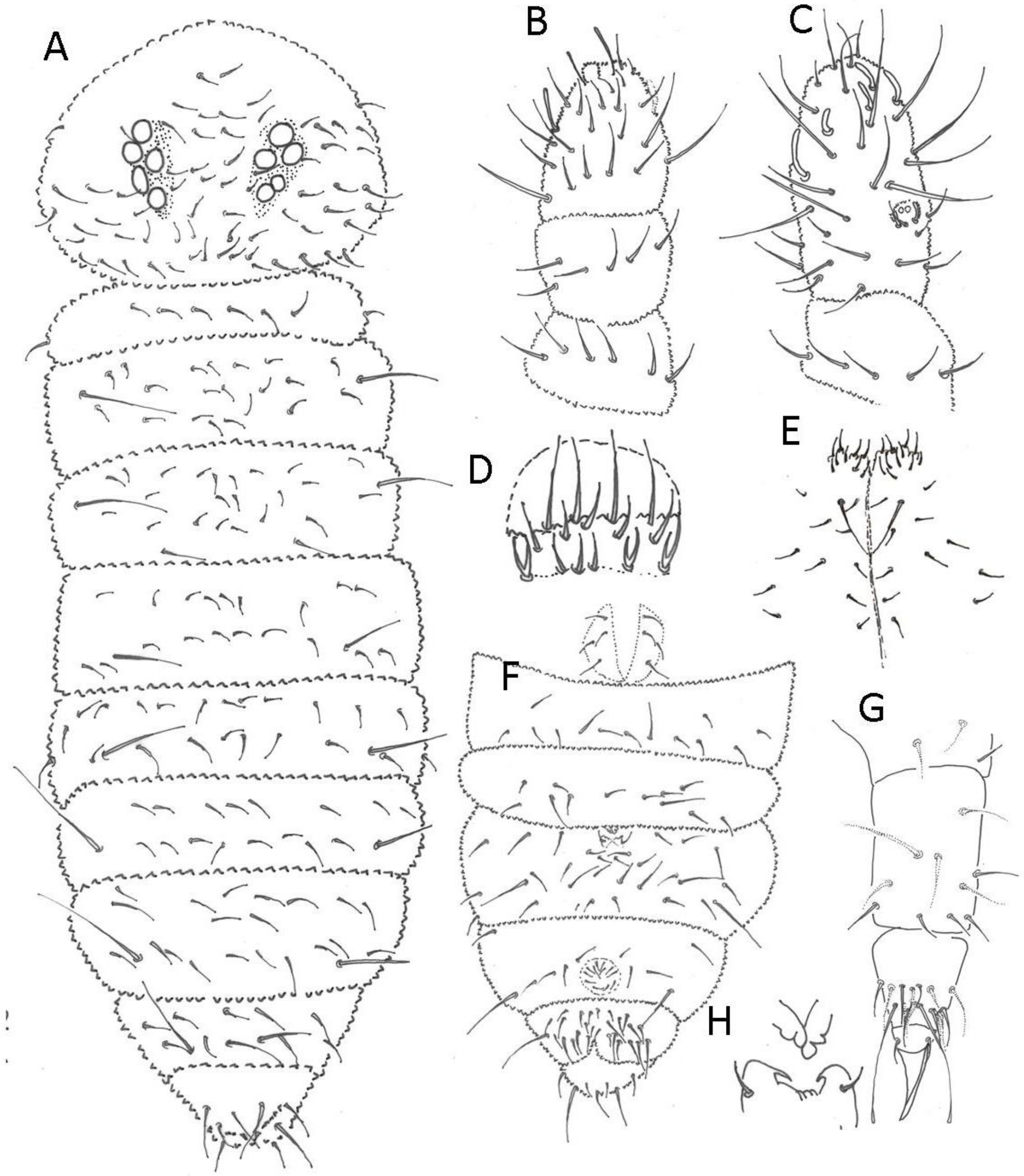

Figure 3.14 ***Xenylla*** **n.sp2** A. Head and Body dorsal view B. Antenna dorsal view C. Antenna ventral view D. Labrum E. Head ventral view F. Abd II-VI ventral view G. Leg H. Furcula.

3.13.2. Material Examined

All specimens were extracted using Berlese funnels from samples collected in epiphyte mosses at the Luquillo Mountains, Puerto Rico. Holotype: male, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Sabana 4B, *Dacryodes excelsa* forest type, epiphyte 300 m.a.s.l., 26.XI.2014

C.M.Ospina. Paratypes: 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Sabana 4B, *Dacryodes excelsa* forest type, epiphyte 300 m.a.s.l., 26.XI.2014

3.13.3. Discussion

The new species differ from another *Xenyllas* because the reduction of furcula and tenaculum with the combination with the follow characters: Sensillas between two and five times larger than the other body setae, presence of 5 bunt setae in Ant. IV, absence of setae a0 in head and tenet hairs spatulate.

The new species is close to *X. boerneri* Axelson, 1905, it differ in the chaetotaxy, dorsally for the absence of setae c2 and presence of a0 in head; the absence of setae p5 in Abd. I-III; ventrally in the presence of setae in Th. II-III, and the absence of a5 in Abd II (Jordana 1997). Another species with a reduced furcula is *X. canadensis* but it differ in the presence of two tenacular teeth, a small inner tooth and the clear separation of dens and mucron in lateral view (Christiansen and Bellinger 1980a).

Xenylla sp.n2. differ from Xenylla sp.n1 beside in the absence of a vestigial furcula. Additionally by the absence of spatulate tenet hairs and serrate setae in the last abdominal segments. In the chaetotaxy differ in the absence m3 in Th. III and the position of ss in p4 (vs p5) in Abd I-IV.

3.14. ***Thalassaphorura smilodontus*** sp. n.Ospina et al 2018

3.14.1. Genus *Thalassaphorura* Bagnall, 1949

The genus *Thalassaphorura* was created by Bagnall, 1949 to place species like *Onychiurus thalassophilus* Bagnall, 1937 that exhibits simple vesicles in the postantennal organ (PAO). So far 65 species have been described. In the Neotropical Region nine species are known: *T. cryptopyga* (Denis 1931) reported in Brazil, Costa Rica and the Lesser Antilles*; T. encarpata* (Denis 1931) from Argentina, Brazil, Costa Rica and Mexico; *T. hera* Christiansen & Bellinger

1980 *, T. hoguei* and *T. lagunensis* described from Mexico; *T. pavicornis* and *T. sensilata* Thibaud and Massoud 1980 reported in the Lesser Antilles; *T. subcadaverinus* reported in Costa Rica, Chile Guatemala, Mexico and Puerto Rico and *T. yolandae* Izarra 1971 from Venezuela (Palacios Vargas and Díaz 1995). This new species is the first of the genus described from Puerto Rico and the second species of the genus reported for the Island.

The diagnosis of the genus include the postantennal organ oval, with numerous simple vesicles perpendicular to the long axis; antennal basis more or less indicated; clubs of AIIIO smooth, ribbed or granulated; Ant. IV with S-chaetae differentiated or not, ms close to the second row of chaetae, and no bulb on Ant. IV; labral chaetae formula 4/1,4,2; no multiplication of dorsal pseudocelli, 3 (rarely 4 or 2) pseudocelli in the antenno-basal group, 3–4 (rarely 2 or 5) pseudocelli per half-tergum on Abd. IV, 3 (rarely 4 or 2) pseudocelli per half tergum on Abd. V (1–3 in a posterior-internal group, one in a posterior-lateral group); chaeta d0 on head present, rarely absent; Th. I usually with pseudocelli; Abd. VI with one or two axial chaetae (a0 or m0, or both); anal spines present or absent; distal whorl of tibiotarsal chaetae as 6, 7 or 9, no clavate tenent hairs; furcal rudiment as a finely granulated area with 4 small dental chaetae in two rows posteriorly, one manubrial row of chaetae present posteriorly to dental chaetae (Sun et al. 2013).

3.14.2. Morphological description *Thalassaphorura smilodontus* n.sp

Length 340 µm (n = 7).

Color: Individuals in alcohol white; Body subcylindrical with large granules and smooth and acuminates setae.

Head: Antenna shorter (0.7) than diagonal head. Ant. III and IV distinctly segmented; Ant. IV without apical vesicle; subapical organite present; four slender blunt setae present (Fig. 3.15A). Ant. III sensory organ composed of 4 papillae, 4 guard chaetae, 2 sensory rods and 2 smooth clubs, the inner bigger than the outer (Fig. 3.15B). Ant. II with 12 chaetae. Ant. I with 8 chaetae. Antennal base well marked. Eyes absent; PAO in a deep narrow furrow composed of 12-14 simple vesicles in two rows. Head dorsal quetotaxy as in figure 3.15C; setae d0 present. Labium quetotaxy as in figure 3.15D, with papilla B and D thick and pointy. Labral chaetotaxy 4/432 Head ventrally with 3+3 post labial chaetae along ventral groove (Fig. 3.15D).

Body: Ordinary body setae smooth, distributed as in Figure 3.15C. Dorsal Pseudocelli on the body distributed as: 32/233/33332. Anal spines absent.

Unguiculus short, about 0.3 times as long as inner edge of unguis, Unguis without teeth. (Fig. 3.15E). Ventral tube with 3+3 basal and 8+8 distal setae. Furcula reduced to a field of fine granulation with 4 small dental setae arranged in 2 rows posteriorly; only one manubrial row of chaetae present posteriorly to dental chaetae (Fig. 3.15F).

Etymology. The Ancient Greek meaning of Smilodon as σμίλη (smilē), a scalpel or two-edged knife, and οδόντος (odontús), tooth. In reference of the labium papillae thick and pointy.

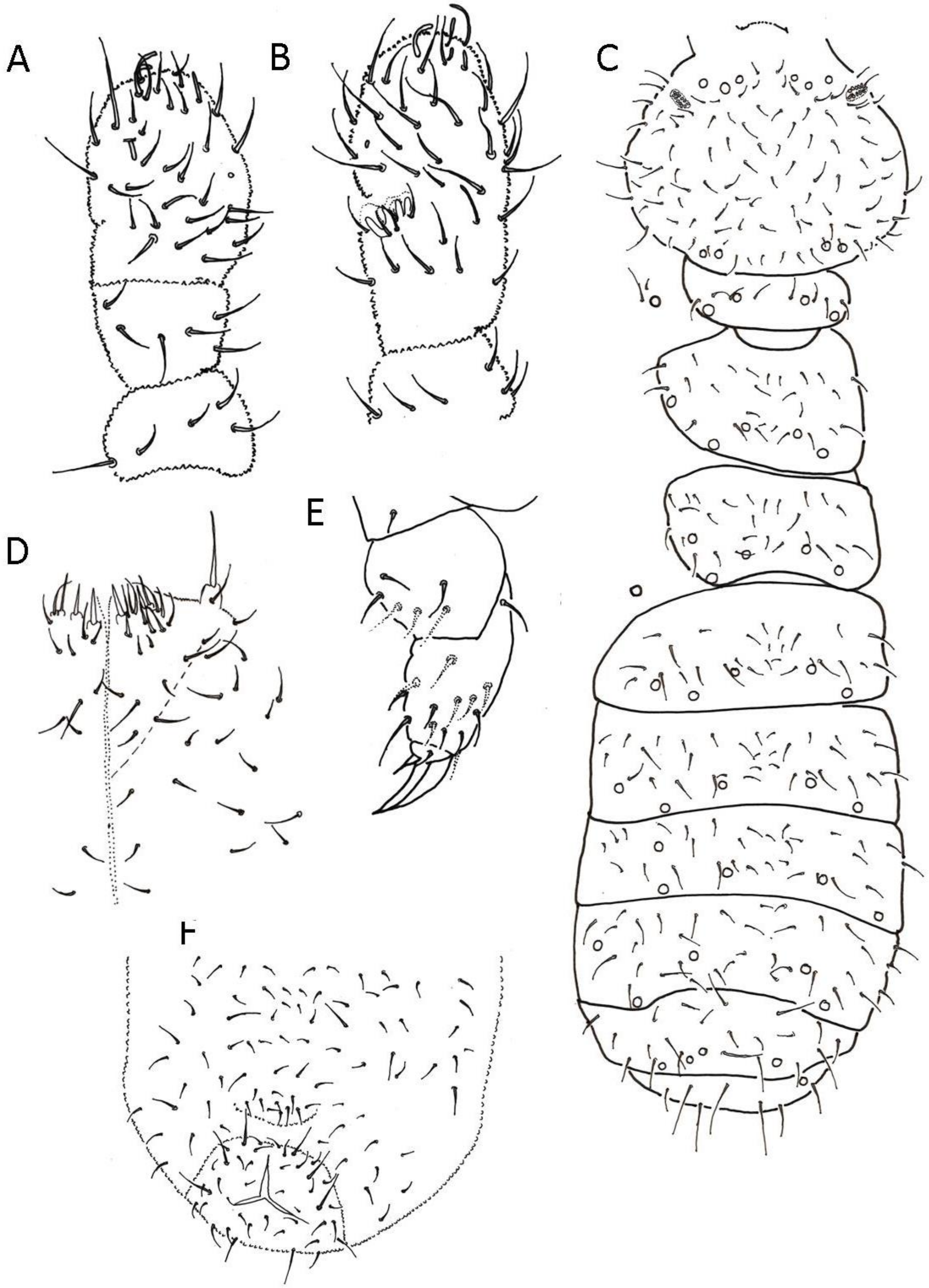

Figure 3.15 ***Thalassaphorura smilodontus* sp.n.** A. Antenna dorsal view B. Antenna ventral view C. Head and body dorsal view D. Head ventral view E. Tibiotarso I F. Abd. III-VI ventral view.

3.14.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in leaf litter at the Luquillo Mountains, Puerto Rico. Holotype: female, on slide, Puerto Rico, Río Grande, Luquillo Mountains, El Verde, *Dacryodes excelsa* forest type, 433.2 m.a.s.l., 11.III.2014 C.M.Ospina Paratypes: 2 female on slide , Puerto Rico, Río Grande, Luquillo Mountains, El Verde, *Dacryodes excelsa* forest type, 433.2 m.a.s.l., 26.XI.2014 C.M.Ospina. 1 immature on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail II, *Cyrilla racemiflora* forest type, 795 m.a.s.l., 25.VIII.2014 C.M.Ospina. 1 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail I, *Cyrilla racemiflora* forest type, 815 m.a.s.l., 25.VIII.2014 C.M.Ospina. 2 females 1 male on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail I, *Cyrilla racemiflora* forest type, 815 m.a.s.l., 19.VIII.2015. C.M.Ospina.

3.14.4. Discussion

This new species have the unique combination of characters: apical bulb in Ant. III absent, Sensorial Organ in Ant III with four guard setae and four sense clubs; OPA with 12 to 14 simple vesicles and the absence of anal spines. Within the *Thalassaphorura* species reported in the region, the only known without apical bulb is *T. hera*, this species differ from the new species in the distribution of psedocelli (21/122/11122), the presence of 3 guard setae in the sensorial organ in Ant.III and the presence of anal spines (Christiansen and Bellinger 1980a). The species *T. sensilata* is similar to the new species in pseudocelli distribution and in the number of guard setae in the sensorial organ in Ant.III, but differ in the presence of 5 sense clubs, the OPA is compound by 20 vesicles, additionally it species have anal spines and lanceolate sensilla in the las abdominal segments (Thibaud and Massoud 1980). *T. smilodontus* sp.n. seem a close species of *T. cryptopyga*, they share the pseudocelli distribution, the absence of unguiculus tooth and anal spines, the species have a similar number of vesicles in OPA (11-14 for *T. cryptopyga)* but differ in the presence of an apical bulb in Ant IV, the presence of a short and slender unguiculus (REF!!). The species *T. yolandae* have the same psedocelli distribution and number of guard setae and sense clubs in sensorial organ in Ant. III; but differ in the presence of 22-24 vesicles in OPA, the absence of unguiculus and the presence of anal spines (Cutini de Izarra 1971)

3.15. *Isotomurus degrade* sp.n. Ospina et al 2018

3.15.1. Genus *Isotomurus* Börner, 1776

This genus was created by Börner to place the species *Podura palustris* described by Müller in 1776. This cosmopolitan genus has 70 species described (Bellinger et al. 2018), however there are few species reported for the Neotropical Region: *I bimus* Christiansen and Bellinger 1980; *I. palustris* Müller 1776; *I. retardatus* Folsom 1937; *I. sensillatus* Winter 1963*; I. tricuspis* Börner 1906 and *I. yamaquizuensis* Winter 1963 (Mari Mutt and Bellinger 1990b). The genera was reported in Puerto Rico, but without identified species (Mari Mutt 1976).

The diagnosis of the genus include an habitus Stach (1947). Body tergites are clothed with numerous short setae and several long macrochaetae; thin trichobothria are found on abdomen (Abd.) II, III and IV, whereas the mucro is always quadridentate with a mucronal seta ‘usually present’ (Carapelli et al. 2001). This genus has different color patterns; Stach (1947) described *I. palustris* as comprising several forms with different pigmentation patterns: some have a uniform pattern (such as the forms *prasina* and *fucicola*), whereas others have a longitudinal median stripe (forms *unifasciata* and *maculata*).

3.1.5.2. Morphological description

Length µm (n = 9).

Color: Individuals in alcohol light blue been darker in the last abdominal segments, some specimens have a violet transverse bands across anterior portion in all body segment. Body setae comprising acuminate setae, macrochaetas and trichobothria in the Abd II-IV.

Antennae typical of the *palustris* group, relative lengths of the antennal segments I : II : III : IV are 1:1.6:1.8:2.6. Eyes 8+8 in a pigmented patch; Postantennal organ (PAO) with a rounded vesicle (Fig. 3.16A), Post Antennal Organ larger that the closer eye (1.4).Maxillary palp bifurcate (Fig. 3.16B) with four sub global hairs.

Trichobothria are distributed in abdominal segments as: II: III: IV 2:2:3. Unguis without inner teeth, Unguiculus present (Fig. 3.16C). Lateral vesicles of collophore with 4-8 setae (Fig. 3.16D); tenaculum corpus with 2-6 setae (Fig. 3.16E). Furcula well developed; mucro with a basal setae and 4 dorsal tooth (Fig. 3.16F), basal lamella and ventral teeth absent.

Etymology. Degrade is a Spanish word to refer to a color gradient where the tone is getting darker, in allusion to the color of the new species.

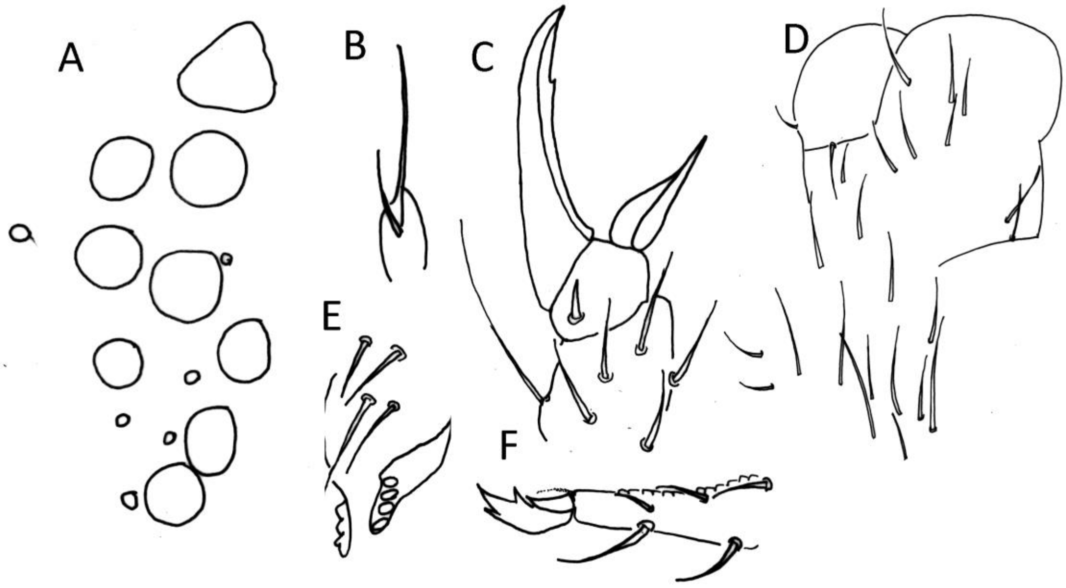

Figure 3.16 ***Isotomurus degrade*** **sp.n.** A. PAO and eyes B. Maxillary palp C. Leg II D. Collophore E. Tenaculum F. Mucro

3.15.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in soil, leaf litter and epiphyte at the Luquillo Mountains, Puerto Rico. Holotype: Male, on slide, Puerto Rico, Luquillo, Luquillo Mountains Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 11.II.2015 C.M.Ospina. Paratypes: 1 Immature, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Este, *Tabebuia rigida* forest type, epiphyte 987.6 m.a.s.l., 04.XI.2014 C.M.Ospina. 3 males on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, epiphyte, 994 m.a.s.l., 19.V.2015, C.M.Ospina. 1 male on slide , Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, soil, 994 m.a.s.l., 19.V.2015, M.M.Rivera. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, epiphyte, 994 m.a.s.l., 19.VIII.2015, C.M.Ospina. 2 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Pico del Oeste, *Tabebuia rigida* forest type, epiphyte, 994 m.a.s.l., 11.II.2015, C.M.Ospina. 1 male on slide, Puerto Rico, Luquillo,

Luquillo Mountains, Toro Trail II, *Cyrilla racemiflora* forest type, leaf litter, 795 m.a.s.l., 25.VIII.2014, C.M.Ospina. 1 female on slide, Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail II, *Cyrilla racemiflora* forest type, epiphyte, 795 m.a.s.l., 18.XI.2014, C.M.Ospina. . 1 male on slide , Puerto Rico, Luquillo, Luquillo Mountains, Toro Trail II, *Cyrilla racemiflora* forest type, leaf litter, 795 m.a.s.l., 19.II.2015 C.M.Ospina. 1 female, on slide, Puerto Rico, Luquillo, Luquillo Mountains, Sabana 4B, *Dacryodes excelsa* forest type, leaf litter 300 m.a.s.l., 05.VI.2015, C.M.Ospina.

3.15.4. Discussion

This new species has the absence of coloration pattern; additionally has 4 to 8 disto-lateral setae in the Collophore, 2-6 setae on corpus tenaculum and the absence of basal lamella in mucro.

The other species reported in the region have other coloration patterns. *I. bimus* has transversal bands, additionally differs from the new species in the presence of 5-8 disto--lateral setae in ventral tube and 8-12 setae on collophore (Christiansen and Bellinger 1980a). *I. palustris* has longitudinal bands and patches of color, the PAO is small to the nearest eye and the presence of 3 disto lateral setae in ventral tube and 10-22 setae on collophore (Müller 1776). *I. retardatus* has longitudinal bands of color, the PAO is small to the nearest eye and the presence of 8-12 disto-lateral setae in ventral tube and 12-18 setae on collophore (Folsom 1937).

3.16. *Entomobrya flavum* sp.n. Ospina et al 2018

3.16.1. Genus Entomobrya Rondani, 1861

The genus *Entomobrya* was created by Rondani, 1861, who place *Degeeria muscorum* Nicolet, 1842 as a type. To date 274 species have been described (Bellinger et al. 2018); 49 in the Neotropical region and 17 for the Caribbean area (Mari Mutt and Bellinger 1990a, 1996). In Puerto Rico the species *E. linda* and *E. longiseta* was described by Soto-Adames (2002a).

This genus include the Entomobryinae with 6+6 or more eyes, the fourth abdominal segment 3 or more times as long as the third, and greatly enlarged setae on the body (Christiansen and Bellinger 1980a). Mucro two-toothed and with basal spine; Body clothed with five types of setae: 1.Flexed, 2.Pubescent 3. Lasiotrichia 4. Similar to type 1, but half in size and usually limited to last abdominal segments and 5. are the common setae of the body (Christiansen 1958).

3.16.2. Morphological description

Length to 0.61 mm.

Color pattern: Largest adults background pale yellow with distinctive pattern formed by dark purple bands. Antennae light purple, Ant. I-II lighter than Ant. III-IV; distal end of Ant. III-IV with dark purple bands. Head pale yellow, eye patch dark brown. Legs lighter than trunk; femur III with lateral purple bands on distal third. Th II-III with thin dark lateral band. Yellow background pigment most intense dorsally on Th. III, Abd.I and Abd. III. Abd. IV with paired short diagonal bands near middle of segment, and paired dots on latero-posterior margin. Abd IV with short lateral band on the second third. Abd V and VI with lateral dots that do not reach the midline (Fig.3.17A). Ventral side of abdomen lighter, with little dark specks, tightly spaced near manubrium, but becoming more separated and lighter colored towards the ventral tube, they are dense near to the manubrium, and they are becoming more diffuse ending in the ventral tube.

Head: Antennae 1.9x cephalic diagonal. Apical papilla on Ant. IV bilobed. Sense organ of Ant. III with 2 short blunt sensilla in a common depression; 1 dorsal and 2 ventral short blunt sensilla also present (Fig. 3.17B). Macrochaetotaxy and distribution of type 5 setae as in Fig. (done). Head dorsally with two types of macrochaetae: most common type truncate, but anterior-most pair, those along antennal base and along inner margin of eye patch acuminate. Eye patch with 3 ciliate setae (2 macrochaetae and 1 type 5 seta) and 8+8 eyes; A-B subequal and larger than C-F, which is subequal to each other; G and H small. Prelabral setae ciliate, all labral setae smooth; labral intrusion U-shaped; labral papillae smooth, inner papillae blunt projecting mounds, lateral papilla elongate, not projecting. Subapical setae of outer maxillary lobe (Fig.3.17C) smooth and subequal in length to apical seta; sublobular plate with 3 appendages. Lateral process of labial papilla E (Fig.3.17C) thick, slightly curved and reaching tip of papilla. Labial chaetotaxy <u>M1EL1L2</u>, A1-5; all setae on posterior row coarsely ciliate, r absent, all anterior setae smooth. Postlabium with 6 ciliate setae along cephalic groove, all other postlabial setae ciliate and variable in distribution (Fig.3.17C).

Body: All ciliate trunk microsetae of type 5. Th. II macrochaetae truncate and subequal in length, collar with 1 row of macrochaetae; zones M, Pm and Pl each with one macroseta (m4, p3 and p5, respectively); zone L with 7 macrochaetae. Th. III zones M, Pm and Pl with 3 (a4, m5, a6), 1 (p3) and 2 (p5, p6) truncate macrosetae, respectively; posterior margin with 5+5 long acuminate setae with enlarged sockets may be confused with macrosetae. Abd. I with 1 macroseta. Abd. II with macrosetae m3 and m5, and smooth sensilla as; Abd. III with macrosetae m3, pm6 and p6; smooth sensilla as present, d2 absent. Abd. IV with 2 inner acuminate macrosetae, anterior setae short, posterior one long and ,acuminate 6-7 smooth microsetae between pseudopores and bothriotricha, 6 lateral macrosetae, and 9 posterior setae.

Trochanteral organ with 9-10 short conic setae (Fig. 3.17D). Distal inner tibiotarso with a protuberance. Unguis with 3 internal teeth (Fig. 3.17E): basal paired teeth subequal and inserted on basal ¼ of inner edge; unpaired tooth minute, inserted on distal half of inner edge.

Unguiculus truncate, anterior lamella sharply pointed. Smooth seta opposite to tenent hair 2/3 length of inner edge of unguis and subequal to unguiculus. Tenent hair spatulate and 2x inner tibiotarsal smooth seta. Tibiotarsus with rounded protuberance on distal end, at base of unguiculus.

Anterior face of collophore with 6 ciliate setae and one smooth and larger setae.

Dorsal manubrial plaque (Chen and Christiansen 1993) with 1 ciliate setae and 2 smooth setae. Dens proximal end dorsally with 1 long clubbed seta. Dens 2x longer than manubrium. Apex of dens beyond crenulation with 1+1 ciliate setae. Mucronal teeth subequal (Fig. 3.17F); mucronal spine smooth and reaching well onto basal tooth. Male genital plate not seen.

Etymology. The species name *flavum* is a Latin word for yellow, refers to the principal color of the specimens.

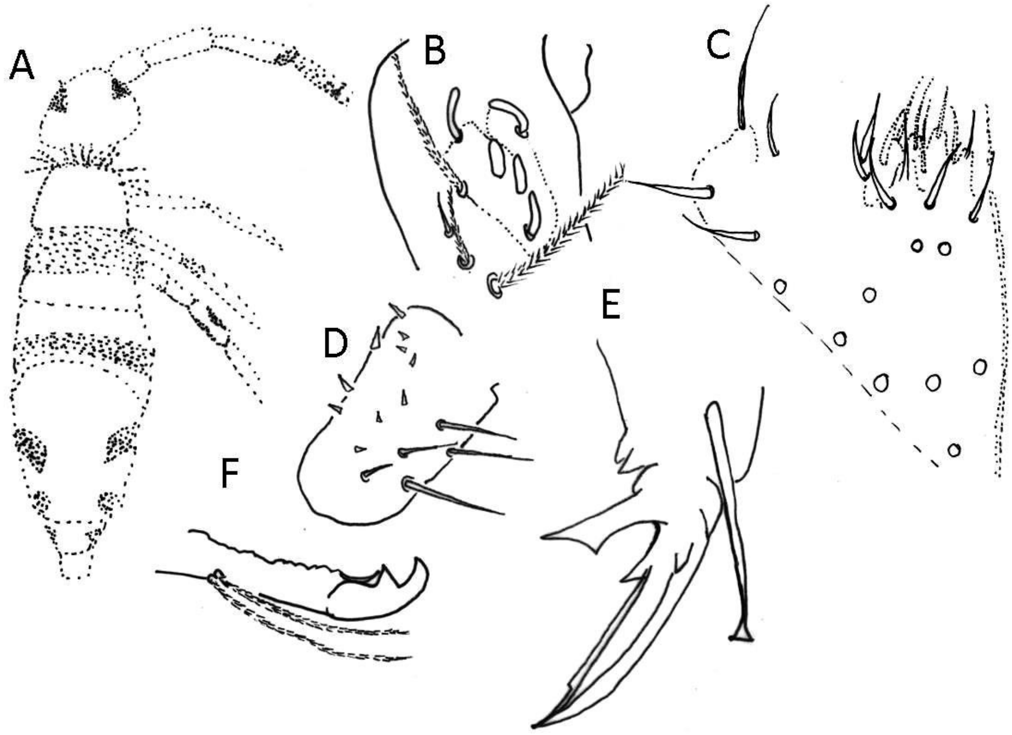

Figure 3.17 ***Entomobrya flavum*** **sp.n.** A. Coloration pattern B. Sense organ in Ant. III C. Head ventral view D. Trochanteral organ in femur E. Foot F. Mucro.

3.16.3. Material Examined

All specimens were extracted using Berlese funnels from samples collected in mosses growing in a tree; at least a 1m over ground, in some localities at the Luquillo Mountains, Puerto Rico. Holotype: Female, collected in *Cyrilla racemiflora* forest type, Pico del Este, Luquillo, PR. 27.V.2015. Paratypes: 1female, 1 male collected in *Cyrilla racemiflora* forest type, Pico del Este, 27.V.2015; 1 male , collected in *Cyrilla racemiflora* forest type, Pico del Este, 19.II.2015; 1male collected in *Tabebuia rigida* forest type, Yunque Peak, 11.II.2015 and 1 immature collected in *Tabebuia rigida* forest type, Pico del Oeste, 19.V.2015.

3.16.4. Discussion

This new species is differentiable from other described species given their coloration pattern, the foot complex, specially their strongly truncate unguiculus. Additionally, *E. flavum* n.sp has a reduced quetotaxy in their body. Few Neotropical species have unguiculus strongly truncate and reduction or the number of teeth in the ungus. *E. litigiosa* Denis, 1931 has sharp lateral teeth and very clear external tooth, has two odd and an internal pair teeth; the unguiculus is strongly truncate and with crenulations; the internal apex have a flat protrude hard to see; the coloration pattern goes to complete purple to margins of pigment in the segment divisions and in the half of the Abd IV (Denis 1931).

Some Neotropical species has background yellow and purple to blue dark pigment*: E. atrocinta* Schott, 1896, *E. confusa* Christiansen, 1958, *E. ligata* Folsom, 1924, *E. mineola* Folsom, 1924, and *E. triangularis* Schott, 1896. In *E. atrocinta* Ant III and IV are lightly pigmented. First two antennal segments apically ringed with dark pigment; antennal bases with narrow connecting band and wide dark band running laterally from posterior border of eyepatch; all legs bases darkened, mesothorax marrow lateral margin dark, reminder of the body pale; the apical antennal bulb of the fourth segment trilobed and ungus with seven teeth (Christiansen

1958). *E. confusa* is uniformly pigmented except for the two apical segments and the posterior margin of the body segments which are slightly darker, dorsum of head is pale with dark V-shape mark, legs and furcula which are pale except for extreme bases; ungus with seven teeth an unguiculus acuminate not ciliated (Christiansen 1958). *E. ligata* has in a dark apical ring on the first and second segments, moderate dark roughly triangular patch running posterior from beneath hind angle of eyepatch, the Abd 4 with transverse band expanded laterally forming a broad H-shaped mark; ungus with seven teeth and unguiculus acuminate, more strikingly tapered at extreme apex, sparsely ciliated for median two thirds of internal edge (Christiansen 1958). *E. mineola* the pattern is purple to black in the form of irregular mediolateral dark patches and lateral marginal dark borders (Christiansen and Bellinger 1980a). *E. triangularis* have several coloration patterns, one of them is similar, except for the pattern in the head, and in Abd where the pattern in the middle of the segment has a triangle pattern, the external differentiated seta is long and stout, ungus with seven teeth and unguiculus is acuminate (Christiansen and Bellinger 1980a).

The *Entomobry*a species described from Puerto Rico *E. linda* and *E. longiseta* differ in size, coloration pattern, ungus, unguiculus and quetotaxy. *E. linda* has a background color white or light yellowish orange. Antenna dark brown, thorax and abdomen with dark brown bands and Abd 4 with a curved lateral longitudinal band and an irregular transversal band; apical papilla of Ant 4 unilobed Abd. 1 with **m3** a truncate macrochaeta; 8 acuminate mesochaetae with large socket. Abd. 2 with macrochaetae **m3** and **m5**; **m3** slightly truncate apically, shape of **m5** central posterior setae shorter than **m3;** Abd. 4 with 2 long tapered acuminate macrochaetae between bothriotrichal complex and pseudopore, and 7 lateral macrochaetae:3 latero-posterior macrochaetae acuminate, 4 latero-anterior macrochaetae strongly truncate and slightly longer than half length of internal macrochaetae; Abd. 4 with 10-12 posterior setae; 10-11 smooth setae between bothriotrichal complex and pseudopore; ungus with 4 teeth and unguiculus acuminate, posterior membrane with at most 3 weak teeth (Soto-Adames 2002a).

E. longiseta, was collected in the same localities of the new species, is uniformly blue black; apical papilla on Ant 4 unilobed; ventral side of head with 4-5 ciliated setae along cephalic groove; Th. 3 with 4 anterior and 3 posterior truncate macrochaetae, and 1 smooth seta; lateral macrochaetae longer than internal; 4+4 long posterior acuminate setae with enlarged bases; Abd. 1 with 3 large setae, but only **m3** truncate; Abd. II with 2 truncate macrochaeta and 2 smooth setae; 1 large seta similar to lateral seta on Abd. I present beyond lateral smooth seta; 2 medial setae on posterior row almost as long as **m3**, but sockets not modified. Abd. III with 3 truncate macrochaetae and 3 smooth setae; **d2** short and conic; Abd. IV with 2 acuminate internal macrochaetae, 9-11 smooth microchaetae between pseudopores and bothriotricha, 10 lateral macrochaetae, and 14 posterior setae. Unguis with 4 teeth and unguiculus lanceolate, anterior lamella slightly curved (Soto-Adames 2002a).

***3.17. Lepidocyrtus paracaprilesi* form epiphyte**

Lepidocyrtus Bourlet, 1839 is a large and cosmopolitan genus, with more than 300 species and seven subgenera. In Puerto Rico 14 *Lepidocyrtus* species had been reported (Mari Mutt 1986, 1988). The form found in epiphyte habitats are the same as *L. paraprilesi*, described for Mari Mutt (1988), just differ in the coloration pattern (the new form is totally white) and the number of teeth in the unguis (Fig 3.18A-B)

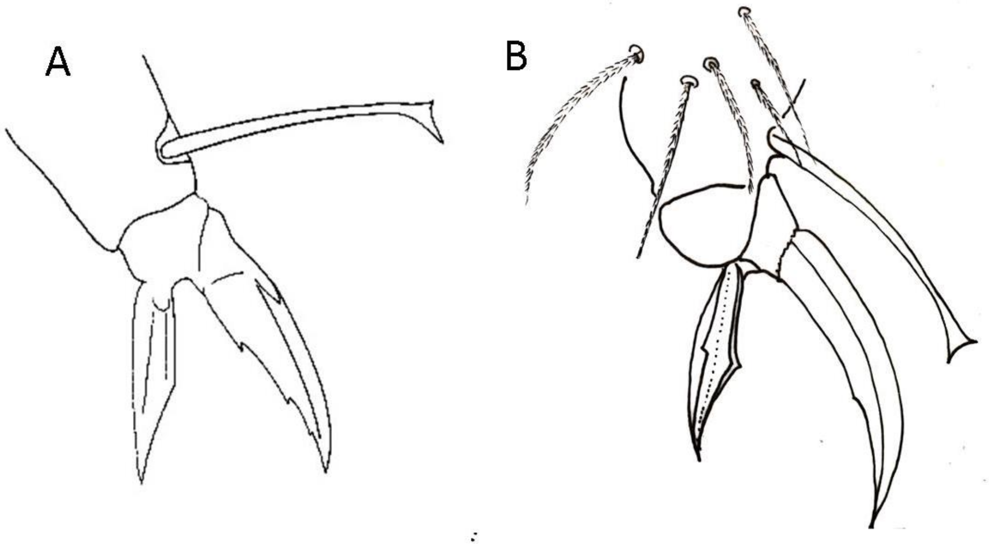

Figure 3.18 ***Lepidocyrtus paracaprilesi*** **form epiphyte**. A. Typical claws of L. paracaprilesi (Mari Mutt 1986) B. Claws of the new form.

3.18 *Campylothorax sabanus* form epiphyte

Campylothorax Schött, 1893 is a tropical genus, with nine species distributed in the Neotropics and Africa. In Puerto Rico, the species *C. sabanus* was reported by Wray in 1953. The form found in epiphyte has the same chaetotaxy of *C. sabanus* but differ in the reduction number of teeth in the unguis (Fig. 3.19) and in the coloration pattern. *C. sabanus* is easy to recognize due to this W coloration pattern in abdomen. The epiphyte form has a purple-dark coloration in all body.

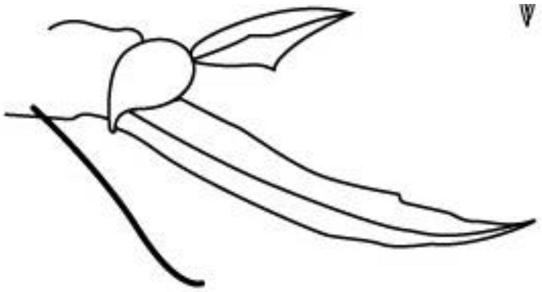

Figure 3.19. Foot complex of Campylothorax sabanus form epiphyte

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Chapter 4 : Distribution of Collembola traits along microhabitats in a tropical forest environment

1. Introduction

Soil biology is challenged to understand the specific role of organisms and how they are organized in the niches along soil resources. Knowledge of soil species could be a cumbersome task because their small size and large biodiversity (Anderson 1975, André et al. 1994). Some authors suggest there is redundancy in soil diversity, so the use of functional groups in a broad sense could provide enough information about niche partioning in soil (Naeem 1998), while others claim that knowledge of individual soil species is crucial for the understanding of the whole functioning of soil (Bengtsson 1998, Wolters 2001, Bardgett and van der Putten 2014). In this study we analyze the relationship between Collembola species traits, abundance and environmental variables on three microhabitats in a tropical forest. Through this analysis we are looking for a better understanding of species assemblages and their distribution along forest microhabitats.

It is estimated there is more than 4.8 million of arthropods species living in forest ecosystems (Ødegaard 2000). Yet this number could be extrapolated to 10 million when animals of less than 200μ are included (André et al. 1994). This great increase in species estimates could be attributed to the lack of knowledge of small arthropods (May 1988, 1992, André et al. 1994, Eisenhauer et al. 2017). To face the difficulty in the identification all the species present in soil, many studies use functional groups divisions, abundance or species richness parameter to understand their role in ecosystems (Bengtsson 1998, Wolters 2001).

Groups of soil fauna separate by size are useful to understand their role in soil ecosystems. In a broad sense, they can by separated as mesofauna (<2mm) that participates as regulators in microorganisms activities. The macrofauna (>2mm), this fauna create microhabitats for other soil biota by reworking the soil (Wallwork 1970, Brussaard 1998). Other classifications include their participation in ecosystems process as microorganism, micropredators, litter transformers and ecosystem engineer (Lavelle 1996). Recent studies, identified collembolans to species level, as well as categorized them into functional groups (Potapov et al. 2016). Identification to species level make comparisons among species within functional groups possible, and can help in determining how different species respond to environmental factors (Ponge and Salmon 2013, Potapov et al. 2016, Coyle et al. 2017).

The relationship between soil diversity and ecosystem function has been discussed but not definitely resolved. There are two principal hypotheses that assume a positive link: the “rivet” and the “redundant species” hypothesis (Wolters 2001). The first hypothesis suggest that each species has a unique effect on the ecosystem while the second hypothesis suggests that only a minimum number of species is necessary for ecosystem functioning (Naeem et al. 1995).The most concluding studies supporting the redundant hypothesis came from microcosms arrays, using three or five species and their combinations (Cragg and Bardgett 2001).

Other experimental studies that evaluated the relationship between soil species richness and ecosystem functioning to support the redundant species hypothesis but they did not demonstrate improved function at higher levels of species richness (Brussaard 1998, Schwartz et al. 2000, Frouz et al. 2015), often because these results are based on the presence of and abundance of particular functional groups, which may consist of related species, higher taxa or even mixture of phyla (Bengtsson 1998, Bardgett and van der Putten 2014). However, studies conducted in the field have given new insights into the functional importance of belowground communities. For example a field experiment set up across a gradient of sites from the subarctic to the tropics showed that reductions in decomposer functional diversity consistently slowed rates of litter decomposition and carbon and nitrogen cycling (Cragg and Bardgett 2001).

The rivet hypothesis considers that in each ecosystem every species plays a unique and essential role, so it is possible that a few species will be necessary to maintain the ecosystem functioning (Bengtsson 1998, Wolters 2001), but a more complex community with a number of substitutable species could build more stable ecosystem (Andrén et al. 1995). According to this hypothesis changes in belowground community composition, rather than species diversity, are of most importance for ecosystem functioning (Andrén et al. 1995).

Even though recognition of the functional importance of soil organisms on biogeochemical processes has increased, the understanding of the impact of species loss belowground still has many gaps in knowledge (Wolters 2001, Bardgett and van der Putten 2014). The most common metric reported for faunal studies is total abundance (Bengtsson et al. 2005); however this information not always reveals the most important trends in faunal responses and could give erroneous correlations between diversity and function (Coyle et al. 2017). Taxonomic and functional trait-based approaches have been demonstrated to have more precision in these correlations, unfortunately, these information in lacking for many groups of soil fauna (Janion-Scheepers et al. 2016).

The study of traits can provide an opportunity to understand the relationships among ecological function, niche occupancy and species composition (Barbaro and Van Halder 2009, Ozinga et al. 2009, Vandewalle et al. 2010, Widenfalk et al. 2016). Nevertheless, the lack of suitable taxonomic data, especially for soil invertebrates make difficult to visualize how to species with similar traits are assembled through several habitats (Salmon et al. 2014). Species traits may reflect how an organism respond to the environment and their effect on the ecosystem processes (de Bello et al. 2010) such as the role of litter community supporting nutrient cycling in soils (da Silva et al. 2016), because the overall species response to habitat constraints involves trade-offs (Lasky et al. 2014).

Collembola is an excellent group to study the relations between traits and function because they respond to a variety of environmental and ecological factors (Hopkin 1997), particularly to changes in microclimatic conditions and microhabitat configuration like moisture (Verhoef and Van Selm 1983), litter quality and humus type (Hasegawa 2002). Collembolans also play a relevant role in litter decomposition and nutrient cycling in the soil system at the local scale (Hopkin 1997), while these processes may be influenced by species distributions and collembolan community patterns throughout landscape mosaics (da Silva et al. 2012, Ponge and Salmon 2013, Heiniger et al. 2014, da Silva et al. 2016).

Traditionally, Collembola have been separated according the morphological characteristics commonly found in certain microhabitats. The classification was first proposed by (Gisin 1943), late reviewed by Christiansen (1964,Table 4.1) and then modified by Rusek (1989). This classification was based on a microhabitat, rather than in morphological characters or phylogenetic relationships (Petersen 2002). More recently, studies on autecology in Collembola show adaptations of a species or group of species in a specific environment, generally associated with humidity, temperature, CO_2 concentration, pH and feeding habits (Rusek 1998, Ponge 2003, Salmon and Ponge 2012). These adaptations are morphological, ethological and physiological (Salmon and Ponge 2012, Table 4.2).

Table 4.1 Collembolan Life Forms (Christiansen 1964)

Category	Characteristics	Normal Ecological Distribution
Epigeon	Eight eyes, well-pigmented ; antennae and furcula long	Plant growth
Hemiedaphon	Antennae moderately long ; eyes and pigment well developed	
• neustonic	Lamellate mucro ; modified unguis	Water surface
• normal	Normal mucro; few clavate or pointed tenent hairs	Surface. ground litter
• xeromorph	Normal mucro; cuticle often rigid; numerous clavate tenent hairs	Moss, bark, BN
Euedaphon	Eyes reduced ; antennae short; pigment absent or limited to eyes	Deeper layers of soil, caves, and soil cavities
Troglomorphs	Eyes and pigment absent; antennae long; unguis modified as in neustonic	Caves
Synoecomorphs	Eyes and pigment absent; mouth parts modified; furcula and legs well developed: and unusual scales and setae	Ant and termite nests

According to synecological studies, some species assemblages are found exclusively in a single microhabitat. In an Australian tropical forest *Australonura quarta* Greenslade and Deharveng 1990, and *Folsomides* sp. were found exclusively in forest floor litter while *Lepidosira* sp. 2 and *Lepidobrya* sp. were found exclusively in canopy litter (Rodgers and Kitching 1998). On the other hand, studies in epiphytes population did not show strong evidence of exclusive Collembola species in those habitats, even though in the description of *Deuterosminthurus delatorrei* noted that this species is associated with epiphytes in Mexico, (Palacios-Vargas and González 1995). Also *Pseudoisotoma sensibilis* (Tullberg) and *Sminthurinus quadrimaculatus* (Ryder) are abundant in bromeliads in Mexico (Palacios-Vargas and Gómez-Anaya 1993), but this species could move through microhabitats (Cutz-Pool et al. 2010).

Table 4.2 Ecological groups (Salmon and Ponge 2012)

Habitat	Characteristics	Strata
Grassland and epigeic	Big size, high mobility, protection against desiccation by round shape or cuticular clothing, avoidance of predation by scape using the furcula and color signaling, and sexual reproduction	Vegetation and leaf liter
Woodland and endogeic	Small size, small locomotor appendages, poor protection from desiccation, avoidance of predation by toxic excreta (pseudocella), and parthenogenesis.	Soil
Concealed environments	Short furcula, dark color, stocky body, and eyes present but in limited number, small size	Bark and associated mosses and lichens

Additionally to these classifications, other traits have been used to correlate morphology with niche occupancy in Collembola species, i.e. foot complex and feeding strategy (Christiansen 1988, Potapov et al. 2016). The foot complex is a studied character used as evidence of adaptation to substrates, where the hardness of them allows more teeth in the unguis but less modification in unguiculus (Christiansen 1965, 1988). Other modifications include the capitation (Christiansen 1988) and the number of the tenant hairs in epiphyte inhabitant species (Gisin 1967).

Collembola is known as generalist feeders (Christiansen 1964, Hopkin 1997, Rusek 1998). They are also able to switch between different foods sources depending on the environmental condition or food quality and availability (Endlweber et al. 2009). Nevertheless, it has been shown that epidaphic and euedaphic collembolans have distinct differences in feeding strategy suggesting trophic niche differentiation varying with the specific soil habitat (Chamberlain et al. 2006, Endlweber et al. 2009, Ngosong et al. 2011, Sechi et al. 2014). For example, in the upper litter layers collembolans may consume microalgae, but in lower litter strata they are feeding detritus and fungal mycelium (Ponge 2000).

Table 4.3 Grouping the collembolan orders and families into functional leagues, according to habitats and consistent differences in the $\delta^{13}C$ and $\delta^{15}N$ values.

Habitat layer/life form	Order, family	Functional league	Typical $\Delta^{13}C$‰	Typical $\Delta^{15}N$,‰	Presumed ecosystem function
Upper litter layers (atmobiotic and epedaphic life forms, and hemiedaphic species of Neanuridae)	Epigeic Symphypleona - Dicyrtomidae - Katiannidae - Sminthuridae Epigeic Entomobryomorpha - Tomoceridae - Entomobryidae - Isotomidae (epigeic species)	Epigeic plant and Microorganisms consumers	2 to 3	-1 to 2	Control microbial communities, affect the dynamics of the first stages of litter decomposition
	Epigeic Poduromorpha - Hypogastruridae - Neanuridae	Epigeic animal and microorganisms consumers	4 to 6	3 to 6	Regulate the population densities of microorganisms and microbivores; possibly affect wood decomposition rates
Lower litter layer and mineral soil (hemiedaphic and euedaphic life forms)	Edaphic Entomobryomorpha - Isotomidae (hemiedaphic and euedaphic species)	Hemiedaphic Microorganism consumers	3 to 5	2 to 3	Control microbial communities, affect the physical structure and mineralization rates of litter
	Edaphic Poduromorpha - Onychiuridae	Euedaphic Microorganism consumers	3 to 5	4 to 7	Affect nutrient uptake by roots, regulate the microbial community in the rhizosphere and soil organic matter decomposition

The most recent classification of functional traits in Collembola by Potavov et al (2016), was based on the signal of the stable isotope signals, where the $\delta^{13}C$ and $\delta^{15}N$ values are reflecting a shift in available food across different habitat layers and matching the vertical isotopic gradient of soil organic matter. Considering stable isotope compositions, as well as the taxonomic identity and life form of species, they outlined four collembolan functional guilds that use different types of food and perform different ecosystem functions (Table 4.3).

Considering there are gaps in the understanding of soil fauna diversity and functioning, in this study I ask if there is separation in the composition of the Collembola communities along microhabitats. Then use traits attributes of each species analyze how there are related within a microhabitat and are influenced by environmental conditions as elevation, temperature and rainfall, expecting a group of traits attributes can be defined for each microhabitat. Based on these morphological adaptations, correlation with the microhabitat characteristics and species clustering we propose a classification of functional groups along a tropical montane environment in Puerto Rico.

2. Methodology

Samples were taken the Luquillo Experimental Forest, in plots located in tabonuco *(Dacryodes excelsa)*, palo colorado (*Cyrilla racemiflora)* and elfin (*Tabebuia rigida)* forests that belong to the mountains environments. These samples were collected during August 2014 and August 2015. Three sampling locations were selected within the three forests (Table 4.4). Samples were collected from five individuals of the most common tree species according to Gould et al. (2006). Only mid-sized trees were selected from the tree inventory (González et al. unpublished data). In each tree two samples of soil, leaf litter and mosses adhered to the trunks was collected (Figure 1). Additional environmental data (temperature, rainfall and elevation) were providing for the US forest service (González et al., unpublished data, Table 4.4).

A total of 1124 samples were collected form the Luquillo mountains, represent 450 leaf litter, 450 soil and 224 mosses samples. Arthropods were extracted using Berlese funnels (González and Barberena 2018), until the sample arthropods extraction was complete (four to seven days); then collected collembolans were separated in morphospecies and counted using dissection microscopy. Following, five or more individuals for each morphospecies were prepared in slides for contrast face-microscopy examination (Figure 4.2). After species identification, we registered the total abundance by species. Additionally, all the individuals on slides were described in terms of their traits (Table 4.5). The traits were coded as binary variables as 0 when is absent and 1 when it is present, and were coded as presented in Table 4.5.

Table 4.4 Forest type, dominant tree species, sampling localities (Gould et al. 2006) and environmetal characteristics including, average daily mean temperatures in °C, site elevation in meters and precipitation in millimeters (mm). (González et al., unpublished data).

Forest type	Dominant tree sp	Locality	Elevation m.a.s.l.	Temperature °C	Rainfall mm
Tabonuco	*Dacryodes excelsa*	El verde	518.2	23	101.15
		Río Grande	433.2	22.29	108.81
		Sabana 4 Bisley	300.6	25.78	100.99
Palo Colorado	*Cyrilla racemiflora*	Toro Trail 1	759.3	21.67	125.51
		Toro Trail 2	815.3	20	89.28
		Pico del Este	795.3	20.3	89.28
Elfin	*Tabebuia rigida*	Pico de Este	1044.8	19.5	137.45
		Pico de Oeste	994.4	20.48	154.36
		Yunque Peak	987.6	19.58	154.49

Figure 4.1 Sampling locations according to microhabitats are show for the *Cyrilla racemiflora* (Palo Colorado) forest. Four samples were collected for each microhabitat. A. Soil sampling using 10 cm soil cores. B. Litter sampling 10 cm^2 by hand and C. Epiphyte mats sampling 10 cm^2 by hand. Photos by Maria Rivera and Claudia Ospina.

Initially using Past (Hammer et al. 2001), a SIMPER analysis was performed with the species abundance to evaluated the contribution of each species of the variability in the Collembola assemblages. Also a Non-metric multidimensional scaling (NMDS) was performed as an indirect gradient analysis approach which produces an ordination based on a distance or dissimilarity matrix and showing the species organization across the habitats. Using the morphological traits attributes matrix, we performed a Canonical correspondence analysis and a cluster analysis to visualize the distribution of traits along the three microhabitats.

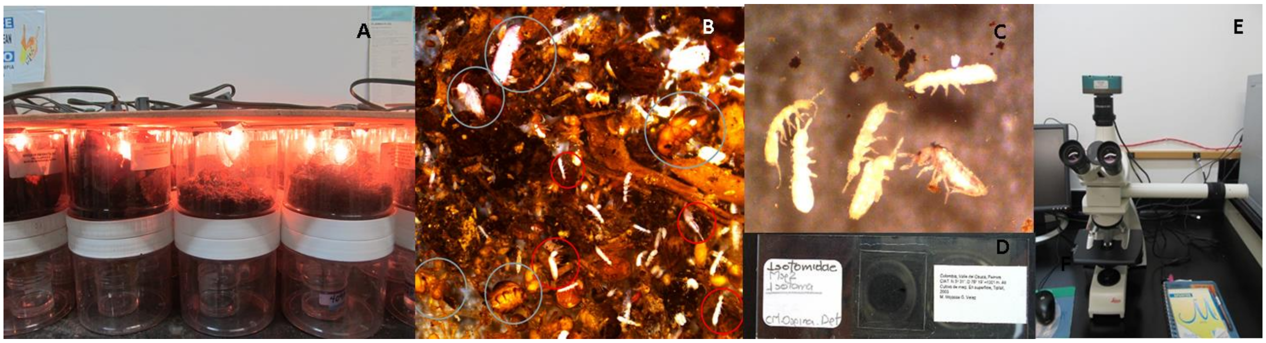

Figure 4.2 Laboratory process. A. Arthropods extraction using Berlese Funnel trap for seven days, B. Separation of Collembola from other arthropods via stereoscopy, C. Separation of Collembola morphospecies via stereoscopy, D. Slide of Collembola mount to identify species and E. Contrast Phase Microscopy for Collembola identifications. Photos by Claudia M. Ospina Sanchez.

For the correlation analysis between environmental variables and traits, we used QRL analysis performs with R ade4 package (Dray and Dufour 2007). Initially three tables were constructed: Table L for abundance of species (9 sites X 56 spp.); R for environmental variables (9 sites X 19 variables) and Q for traits attributes (56 spp. X 41 attributes). Then a separate analysis of each table was performed. Correspondence analysis was applied to the species table. For traits data, all variables are quantitative and thus we applied a principal component analyses. The environmental table contains both quantitative and categorical variables. In this case, we used the Hill Smith function that allows considering a mix of different types of variables. Finally, R, L, and Q tables were linked both by their m rows (sites) and k columns (species), and the ordination of the L-species table represents the link between the R-environment table and the Q-trait table (Dolédec et al. 1996).

As a complementary analysis we performed the fourth-corner method that allows evaluating the significance of bivariate associations between one single trait and one single environmental variable. We used model 6 (Dray and Legendre 2008) for randomization procedures, this model performs two separate tests using models 2 and 4 and combine the results by keeping the higher p-value produced by the two permutation tests (Model 2: Permute the n samples (i.e. rows of R or L) and Model 4: Permute the p species (i.e. rows of Q or columns of L).

Table 4.5 Traits and attribute traits evaluated for species collected in the Luquillo Mountains during august 2014 and 2015.

Trait related	Trait	Attribute	Code in graphs
Habitat	Color	Color pattern	CO-Pat
		Two color	CO-two
		One color	CO-one
		No color	CO-Abs
	Body shape	Slender	BS-Sle
		Stocky	BS-Sto
		Spherical	BS-Sph
	Mounth part	Chewing	MP-Che
		Modified	MP-Mod
	Ungus teeth	One	UT-One
		Two	UT-Two
		Absent	UT-Abs
	Unguiculus	Modified	UN-Mod
		Normal	UN-Nor
		Absent	UN-Abs
	Tenet hairs	Capitate or Spatulate	TH-Cap
		Acuminate	TH-Acu
		Absent	TH-Abs
Sensorial	Antenna	Shorter that head	ANT-Sho
		Larger that head	ANT-Lon
	Pseudocella	Present	PS-Pre
		Absent	PS-Abs
	Post-antennal organ	Compound	PAO-Com
		Simple	PAO-Sim
		Absent	PAO-Abs
	Sensorial setae	Development	SS-Dev
		Absent or poorly develop	SS-Abs
	Trichobothria	Present	TR-Pre
		Absent	TR-Abs
Mobility	Eyes	Complete (8+8)	EY-Com
		Reduce	EY-Red
		Absent	EY-Abs
	Scales	Present	SC-Pre
		Absent	SC-Abs
	Legs	Short	LE-Sho
		Long	LE-Lon
	Furcula	Develop	FU-Dev
		Reduce	FU-Red
		Absent or vestigial	FU-Abs

3. Results

A total of 56 Collembola species were identified in this study across 15 sampling dates, taken in soil, leaf litter and mosses at three forest types at the LEF. In soil microhabitats 40 of these species were found; the species *Isotomiella* sp. and *Oncopodura arecibena* were exclusive for this microhabitat and represent the 5% of the species. In leaf litter microhabitat 51 Collembola species were found; 18% of them are exclusive for this microhabitat: *Microanurid*a n.sp, *Neotropiella silvestrii*, *Hyleaenura infima*, *Brachystomella doucromata, Lepidocyrtus caprilesi*, *Lepidocyrtus dispar* A, *Troglolaphysa geminata*, *T. luquillensis* and *Arrhopalit*es sp1. For mosses microhabitats 38 species were identified, 13% corresponding to exclusive species: *Xenylla* n. sp1, *Xenylla* n. sp2, *Entomobrya flavum* n.sp, *Lepidocyrtus dispar* f.epifita and *Lepidocyrtus paracaprilesi.*

According to SIMPER analysis the species that most contribute to the dissimilarity is *Isotomiella minor* with a mean of 48.7 in soil and 141 in leaf litter. On the other hand, *Dicranocentrus marias* was the species that most contribute to this difference in mosses with a mean of 107 (Appendix 1). In the comparison of the tree microhabitats, the ANOSIM analysis show significant differences between the Collembola communities between the microhabitat (Bonferroni corrected p-value: 0.0002) and high separation between them (R: 0.3436). The NMDS show that leaf litter and soil Collembola communities are similar, but that is not is the case with the mosses communities (Figure 4.3).

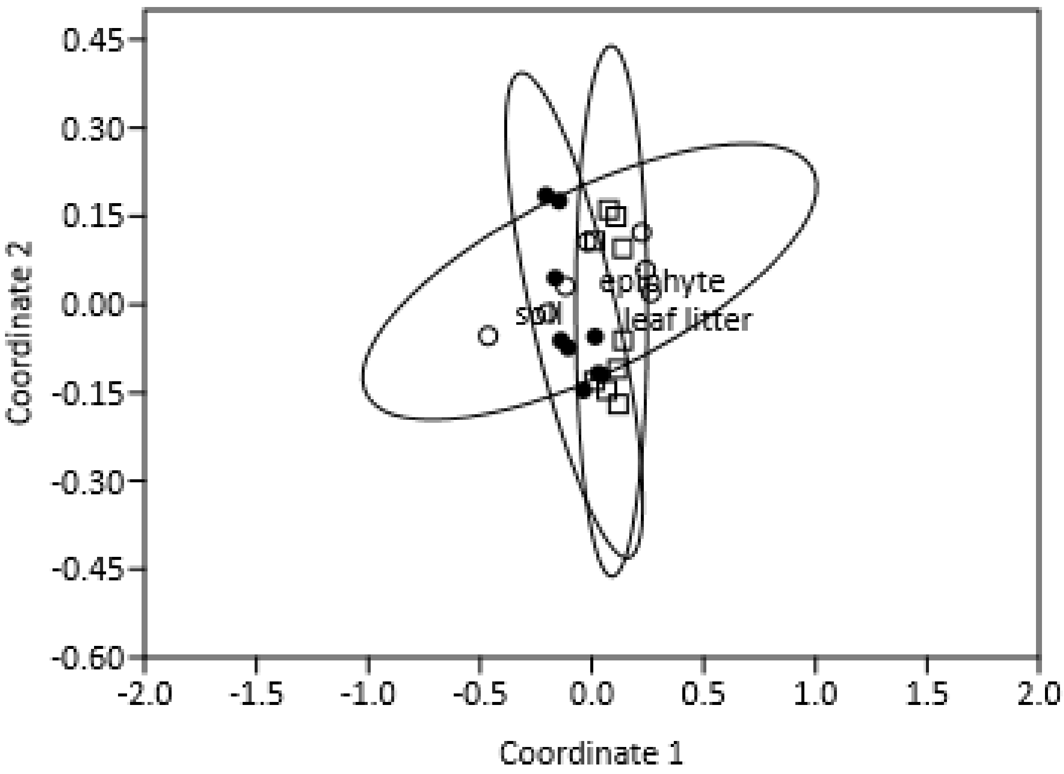

Figure 4.3 NMDS of the abundance of each species among microhabitats. •Soil, Epiphyte ▫Leaf litter. Bray&Curtis distance, 95% ellipses. ANOSIM Bonferroni corrected p= 0.0002, R: 0.3436.

According to the traits attribute matrix the species found in the Luquillo Experimental Forest can be clustered in two large groups: High and low mobility. Inside each of these groups, species can be separated according to the microhabitat. In the group of low mobility species, the larger groups belong to species found in mosses; while in the group of high mobility, most of the species belong to leaf litter inhabitants (Figure 4.4).

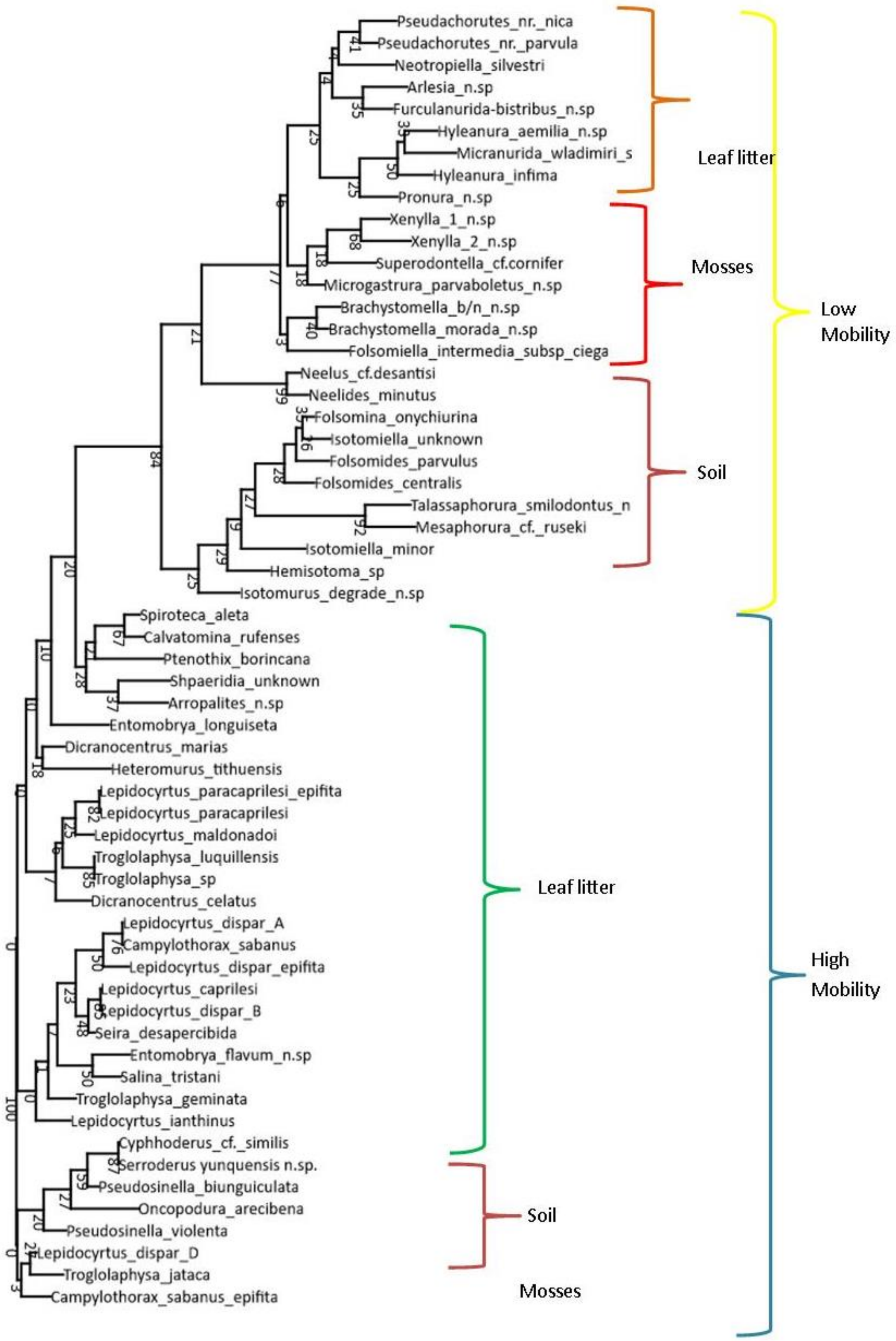

Figure 4.4 Cluster Analysis bases on morphological traits attributes using Neighbor cluster join, Distance Euclidean and 999 permutations.

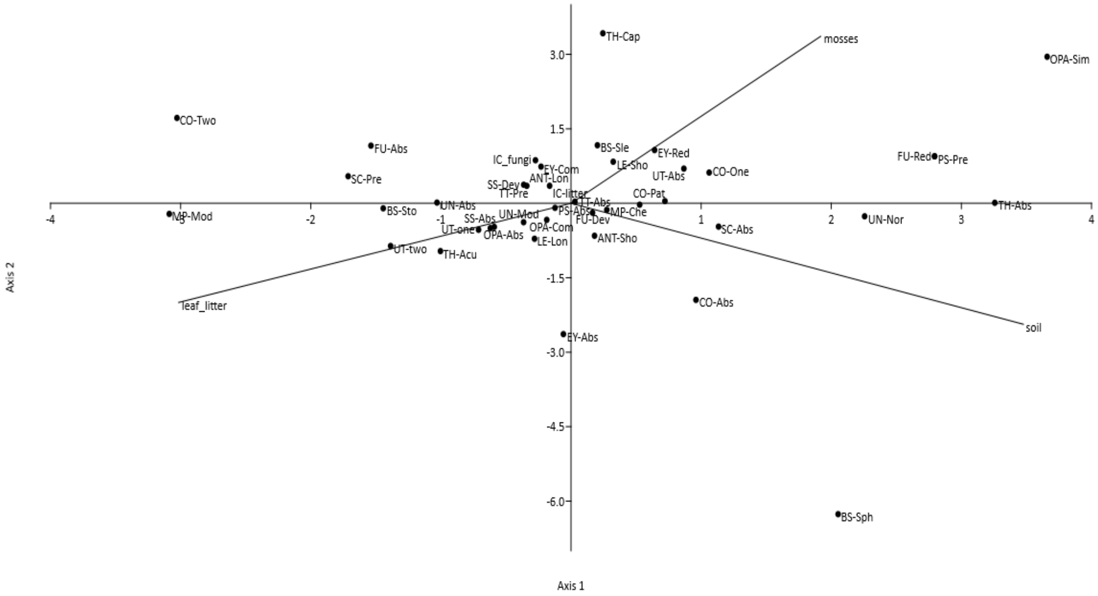

Figure 4.5 Canonical correspondence analysis of the traits attributes. The environmental variables are the presence and absence of the species in mosses, leaf litter and soil. Ax1 Eigenvalue 0.037264, %71.49. Ax2 Eigenvalue 0.014451, % 27.72. See table 5 for codes of traits attributes.

Canonical Correspondence Analysis (CCA) with species trait attributes as dependent variables and species habitats as independent variables, showed that traits were significantly differentiated by habitats (number or permutations = 999). The first two canonical components of CCA explain the 98% of the variability (71% and 27% for F1 and F2, respectively). The projection of trait attributes in the Axis1–Axis2 plane is shown in Figure. 4.5. Both species and trait attributes were distributed along two dimensions. Species with a tenet hair capitate, eyes complete and antennas long were distributes along to the positive side of Axis 1; these traits appear related with species habitat in mosses but with high mobility. In this part the attributes with a large correlation were OPA simple (0.70), Tenet Hair absent (0.62), furcula reduce and pseudosella present (0.53 each). On the negative side to the component, species with tenet hair acuminated, eyes absent and antenna short were related with soil habitats. On this side the attributes with the highest correlation were present to two color in body (-0.58) and modified mount pieces (-0.59). The second canonical component Axis2 was linked to species with mount parts modified, two color on body and furcula absent (as habitat traits); corresponding to the leaf litter for negative values. In the positive, side eyes complete and scales present (as movement traits) correspond to mosses. For the Axe 2 the highest correlation was 0.41 for the capitate tenet hairs and -0.31 for the absence of eyes.

Table 4.6 Results of RLQ analyses

RQL axes	EIgenvalue	Covariance	Correlation	Projected inertia (%)
1	12.2383656	3.4983375	0.6475254	87.2902
2	0.8353729	0.9139874	0.3593365	5.9583

The RLQ Analyses show high correlation rates between variables, more that 90% of the inertia was found in the Axes 1 and 2 (Table 4.6). The highest correlation between environmental variables and RLQ in the Axe 1 were, for the positive side all the elfin forest sites (Pico del Este an Oeste and Yunque Peak), elevation and rainfall with the mosses microhabitat. For the negative side of the same Axe highest correlations were found in Tabonuco forest and their sites (El Verde, Río Grande and Sabana 4 Bisley). The temperature also shows high correlation on the negative side of the Axis 1. For the Axis 2 the highest correlation in the positive side was for elfin forest type and soil microhabitat, while in the negative side Pico del Este (colorado) showed the highest correlation (Table 4.7).

The first two axes accounted for the most of the variance (Table 4.8). According to RLQ correlation ratios, the Axe 1 is related with the characters of mobility. At the positive side the high mobility traits: presence of color, compound eyes, scales and long legs; at the negative side the low mobility traits: no color, eyes, scales and trichobotrias absent and short legs have the higher ratios (Table 4.8, Figure 4.6). In the Axis 2, the traits related with habitat had the higher ratios, at the positive side traits associated with species found in soil: scales absent, leg short and OPA simple had the higher ratios, while on the negative side traits associated with open habitats: Scales present, body shape sphaeric, unguiculus modified, long legs and OPA absent had the highest correlation ratios (Table 4.8, Figure 4.6). The best correlation ratios for traits on the axis were obtained for the trichobotrias, OPA type, longitude of legs and coloration (Table 4.8)

Table 4.7 Correlations between environmental variables and RQL axes for Collembola in the Luquillo Mountains

Variable		**Axe 1**	**Axe 2**
Forest type	Elfin	0.18370373	**1.1436732**
	Palo Colorado	-0.5057572	0.06507543
	Tabonuco	**-1.1624136**	-0.37411113
Site	Pico del Este (elfin)	**1.1391406**	-0.59975774
	Pico del Oeste	**1.1150557**	**1.16837880**
	Yunque Peak	**1.2225771**	-0.72563782
	Pico del Este (colorado)	-0.1618920	**-1.25119598**
	Toro Trail 1	-0.4308017	-0.41924211
	Toro Trail 2	**-0.6599169**	0.85288051
	El verde	**-1.1351727**	-0.51698837
	Río Grande	**-1.0901694**	0.14780816
	Sabana 4 Bisley	**-1.4082877**	-1.62478674
Microhabitat	Mosses	**1.1138220**	0.38147422
	Leaf litter	-0.4988339	-0.54173894
	Soil	**-0.8361427**	**1.02061153**
	Elevation	**0.9054379**	0.24703622
	Temperature	**-0.7228656**	-0.30249048
	Rainfall	**0.8542691**	0.12954680

Highest correlations values are indicated in bold

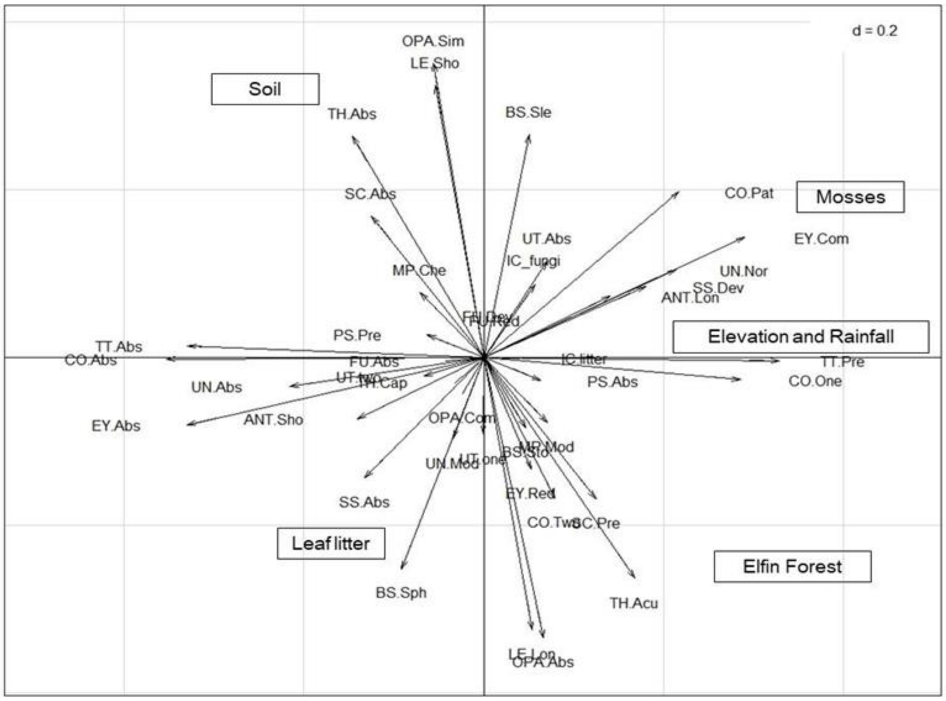

Figure 4.6 RLQ scores of morphological traits attributes, in boxes, the highest correlated environmental variables for each quadrant. See table 5 for codes of traits attributes.

Table 4.8 Correlation ratios between trait attributes and RLQ axes for Collembola from the Luquillo Mountains.

Traits attributes	**1**	**2**
IC_fungi	0.00484608	0.38595633
IC.litter	-0.05102419	0.25299304
CO.Abs	**-0.86305797**	0.16268261
CO.One	**0.61526692**	-0.08547526
CO.Two	0.09545386	-0.40688117
CO.Pat	0.46064373	0.19661066
UT.one	0.19846718	-0.32698619
UT.two	0.22373646	-0.36630857
UT.Abs	-0.22837883	0.38822950
UN.Abs	**-0.66213579**	0.19219886
UN.Nor	0.42383688	0.19675445
UN.Mod	0.19705702	**-0.47598467**
TH.Acu	**0.50859685**	**-0.71690168**
TH.Cap	0.19740322	-0.24132009
TH.Abs	**-0.58537403**	**0.81134342**
EY.Com	**0.78262682**	0.10212924
EY.Red	0.05172562	-0.38733241
EY.Abs	**-0.84419995**	0.09470891
FU.Dev	0.23886626	0.13456168
FU.Red	-0.13192017	-0.12920242
FU.Abs	-0.28059822	-0.03367118
SS.Abs	-0.36276644	-0.27323411
SS.Dev	0.10855209	0.11998968
SC.Pre	**0.59908148**	**-0.57017119**
SC.Abs	**-0.59908148**	**0.57017119**
MP.Che	0.05824125	0.25824731
MP.Mod	-0.05824125	-0.25824731
BS.Sle	0.18448583	**0.56072298**
BS.Sto	-0.07947784	-0.27161887
BS.Sph	-0.16019841	**-0.46605921**
ANT.Sho	-0.43536466	-0.23381057
ANT.Lon	0.43536466	0.23381057
PS.Pre	-0.27578596	0.03613106
PS.Abs	0.27578596	-0.03613106
LE.Lon	**0.46726691**	**-0.84465204**
LE.Sho	**-0.46726691**	**0.84465204**
TT.Pre	**0.87558113**	-0.28673803
TT.Abs	**-0.87850325**	0.30769344
OPA.Com	-0.22314082	-0.11297794
OPA.Sim	-0.35001656	**0.94696885**
OPA.Abs	0.44835410	**-0.90243125**

Highest correlation ratios are indicated in bold, traits and attributes are detailed in Table 5.

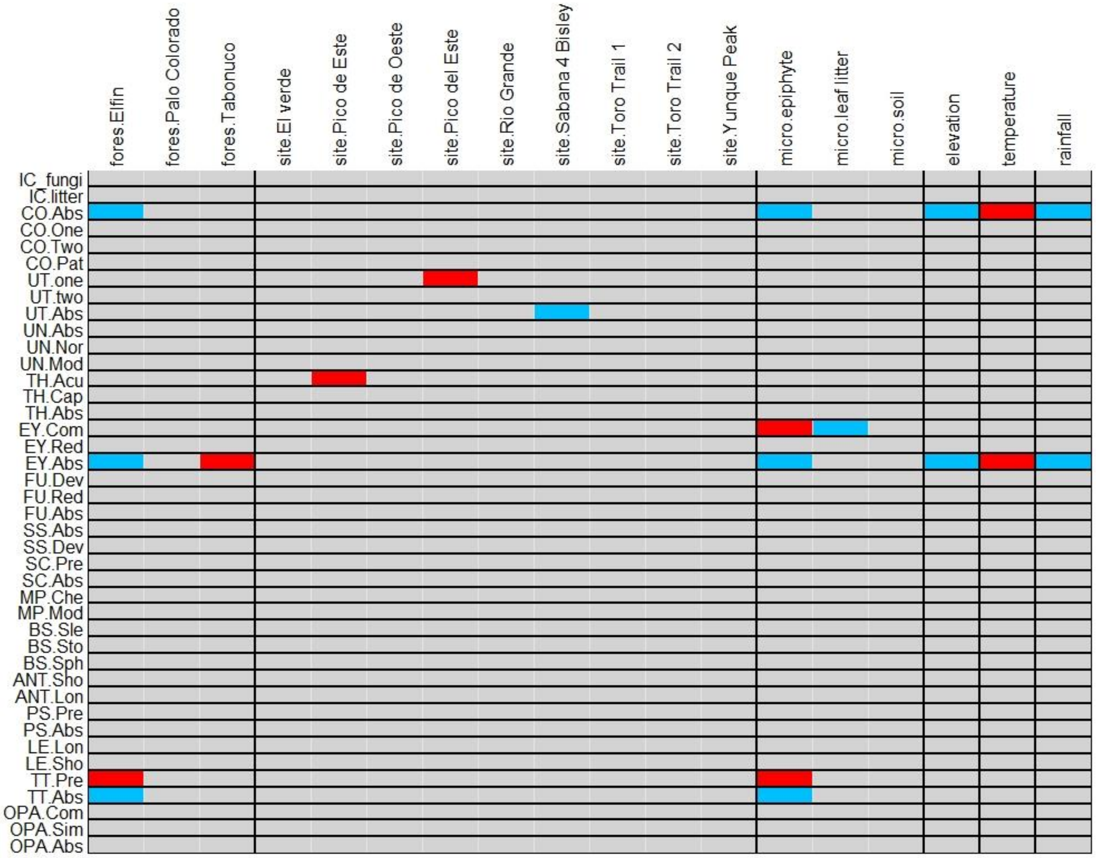

Figure 4.7 Fourth corner approximation. Blue cells correspond to negative significant relationships while red cells correspond to positive significant relationships. Model type 6, stat D2. See table 5 for codes of traits attributes.

Combined the data of habitat, abundance and traits, the fourth corner approximation shows significate correlation between the absence of color and forest type (p=0.015), sites (p=0.009), microhabitats (p=0.011), elevation (p=0.033), temperature (p=0.034) and rainfall (p=0.022). Similarly the reduction of eyes was significant for forest type (p=0.038), site (p=0.031), microhabitat (p=0.045), elevation (p=0.036), temperature (p=0.042) and rainfall (p=0.050). Other significate traits in elfin forest and mosses were the presence and absence of trichobotrias, where the presence was positive and the absence was negative correlated. Another significate traits related with habitat were the color pattern in Pico del Este (palo colorado forest type), the absence of unguiculus teeth in Sabana 4B (tabonuco forest) and the acuminated tenet hairs in Pico del Este (elfin forest type).

Using the information on the cluster analysis based on traits attributes and the high correlation traits in RLQ analysis and the significant correlation in the fourth corner analysis we propose a classification of Collembola functional groups along these tropical microhabitats (Table 4.9).

Table 4.9 Functional groups of Collembola in Tropical Forest

Mobility range	Microhabitat	Principal morphological traits	Type species
High • Long legs • Furcula develop • Eyes complete • Long antenna • Body slender or spherical • High abundance	Generalist: Wide mobility through microhabitats	-One color or with patter -Foot complex with unguis with teeth, unguiculus present modified and tenet hairs acuminated. -Eyes complete, OPA absent -Scales present	*Heteromurtrella tithuensis*
	From leaf litter to mosses: open environment group	-One, two color or with pattern. - Foot complex with unguis without teeth, unguiculus modified and tenet hairs acuminated - Eyes complete, OPA absent -Scales present	*Entomobrya longiseta*
	Below mobility Form leaf litter to soil (concealed environmental group)	-One color or color absent - Foot complex with unguiculus with teeth, unguiculus modified and tenet hairs acuminated -Eyes and OPA absent -Scales absent or absent -Trichobothria present	*Pseudosinella biunguiculata*
Low • Short legs • Small antenna • Furcula reduce or absent • Reduction of eyes • Low abundance • Body Stocky	Euedaphic (concealed environmental group)	-No color -Foot complex with unguiculus without teeth, unguiculus normal and tenet hairs acuminated or absent -Presence of pseudocelli -Presence of OPA -Eyes reduce 0 to 2	*Tallasaphorura smilodonta* *Hylaeanura aemilia sp.n.*
	Epidaphic (open environmental group)	-Color present or absent - Foot complex with unguis without teeth, unguiculus absent and tenet hairs acuminated -Eyes variable , OPA absent -Scales absent	
	Hemiedaphic (Xeromorph) (open environmental group)	- One color, mostly dark -Short furcula -Foot complex with unguis without teeth, unguiculus	*Xenylla* n.sp

absent and tenet hairs
capitate or acuminated
-OPA absent or present
-Buccal parts modified

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4. Discussion

In this study we use morphological characters as traits attributes to correlate with microhabitats characteristic of Collembola species with the purpose of classifing Collembola communities in to functional groups so to improve the knowledge of the role of Collembola in ecosystems. Due to the differences in ecological characteristics of each forest types and microhabitats evaluated, we expect communities with in a group of morphological traits attributes as adaptations of the specific environment. Our result demonstrate correlation between morphological traits and the distribution of Collembola species though microhabitats and other environmental variables.

According to our observations the Collembola species could be divided in two larger groups, one group with species with a high mobility traits attributes (Table 7) and large abundance. According the SIMPER, this group has a large contribution in the variability in the species composition along microhabitats. The species with this attributes can be considered key species (Brussaard 1997, Bengtsson 1998), and have an important contribution in the ecological functions as decomposer (Brussaard 1998, Gessner et al. 2010). According the redundant species hypothesis the presence of these species are enough to complete all major functions of decomposers in the soil; but there are other groups of species in less abundances, commonly called rare species and their function could be overlooked (Giller 1996, Brussaard 1997, Novotný and Basset 2000).

These rare species emphasize the differences in the Collembola communities in each microhabitat, showing particular traits attributes in a community. According to the present study, low abundant species are restricted to one microhabitat fulfill functions on the decompositions process (Andrén et al. 1995, Bengtsson 1998, Wolters 2001). Moreover, these rare species can act like replacement species when abundant species have the probability to be removed; keeping the relationship between species diversity and function (Frouz et al. 2015).

The differences in morphology traits attributes between the groups reflect the variability of microhabitats characteristic though strong short scale resources allowing a high level of niche partitioning (Takeda 1987, Berg and Bengtsson 2007). These microhabitats variations influence essentially every biochemical parameter as well as plant community, organic matter content, and subsequently, fauna (Potapov et al. 2016, Coyle et al. 2017). The potential effect of associated diversity in soil implies that redundant species may gain functional significance by interacting with functionally important species. Also, there are many niche unstudied in soil environments and every species should have their function (Andrén et al. 1995, Bengtsson 1998). Additionally, more diversity is the key for a resilient environments (Wolters 2001).

Collembola species present in this study were divided by the cluster analysis in two large groups: High and low mobility species. These groups are distributed along all the microhabitats and forest types. The high mobility species present characters related to open habitats and have the ability to disperse and colonize new areas (da Silva et al. 2012, Salmon and Ponge 2012): Well-developed locomotory organs (furcula, legs), longer antennae, and presence of sensorial organs sensitive to air movements and light. In this group we found the most abundant species, *Dicranocentrus marias* demonstrating their large adaptability of several environments and microhabitats.

On the other side, the low mobility species are characterized by short locomotory appendages, high number of defense organs (pseudocella), presence of post-antennal organs

(Salmon and Ponge 2012). These species should be live in concealed environments because they are badly equipped for jumping rapidly from a micro-site to another in a changing environment (Bauer and Christian, 1987). Generally, this species are soil-dwelling inhabitants, to the exception of small surface species that lives under protection of mosses and lichens (Ponge et al. 2006). We found species with low mobility traits in all three microhabitats, this variability is attributed to soils with thicker litter layers (da Silva et al. 2012), with higher resource availability and the preferred moisture conditions (Hopkin 1997, Berg and Bengtsson 2007, da Silva et al. 2016).

For the mosses microhabitat in the elfin forest, we found a community of low abundance and low mobility species like *Xenylla* n. sp1 and *X*.n.sp2. Some of their relevant traits like stocky body and short appendages are shared from the concealed environment species. However, they also have the presence of color in their body, eyes complete and presence of OPA; these traits are used protection for UV radiation and possibilities like escaping, offered by vision (Salmon and Ponge 2012). In mosses we also found species like *Entomobrya flavu*m sp.n. that in addition to the already mentioned characters also have large appendages, but this species was not found in other microhabitats.

In leaf litter microhabitats several exclusive species were found, but not all these species can be classified as low mobility ones. Species of *Arropalithes* are commonly associated with concealed environments (Heiniger et al. 2014), while most *Trogolaphysa* species are largely distributed along several environmental conditions, including caves (Mari Mutt 1987, Soto-Adames 2015), even these two species have long appendages.

The exclusive soil species have as common characters the absence of color and the presence of OPA, however *Oncopodura arecibena* exhibit another characters like long legs, developed furcula and presence of scales. These traits could be considered as high mobility but also are attributed as adaptations of synoecomorphs species. In our survey we found that the exclusive species in each microhabitat are not in the same cluster, this is a reflection of the many niches along the soil and their extensions (leaf litter and mosses) but their characteristics still unstudied (Bengtsson 1998, Eisenhauer et al. 2017).

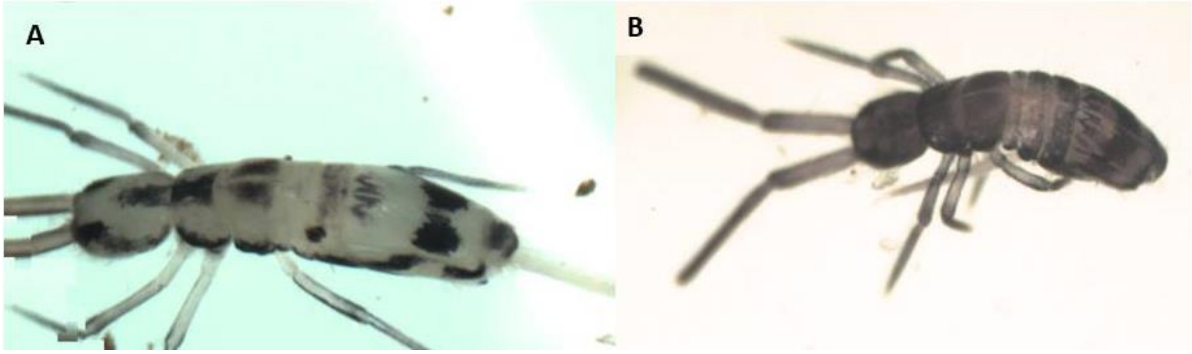

Figure 4.8 Coloration pattern in *Campylothorax sabanus*. A. Known W pattern. B. New coloration pattern, in individuals from mosses. Photos by Claudia M. Ospina Sanchez

According to the fourth corner analysis, the presence or absence of color was a significant character and the highest correlated with the microhabitats. The color pattern varies within metapopulations in the same area (Soto-Adames 2002). In this study we found *Campylothorax sabanus* in all the microhabitats, this species is easy to recognize for this W coloration pattern in the abdomen, but we also found a subspecies of *C. sabanus* with uniform dark color in abdomen and reduction of teeth in unguis. The dark subspecies was commonly found in mosses microhabitat (Figure 4.8). Moreover, we found three species with the same coloration patter that belongs to two families and three genera, these taxonomic difference usually is related more with the geographical origin (Frati et al. 1997, Jordana and Baquero 2005). Many Collembola species includes member with a different coloration pattern, but they keep the same chaetotaxy, which is the case of *Lepidocyrtus paracaprilesi* that have dark colored thorax; the form found in mosses is totally pale (Figure 4.9), but the chaetotaxy is still the same of the originally describe from; this change can be attributed to a taxa diverge during the speciation process, because pigmentation patterns seem to differentiate more rapidly than other morphological characters (Frati et al. 1997).

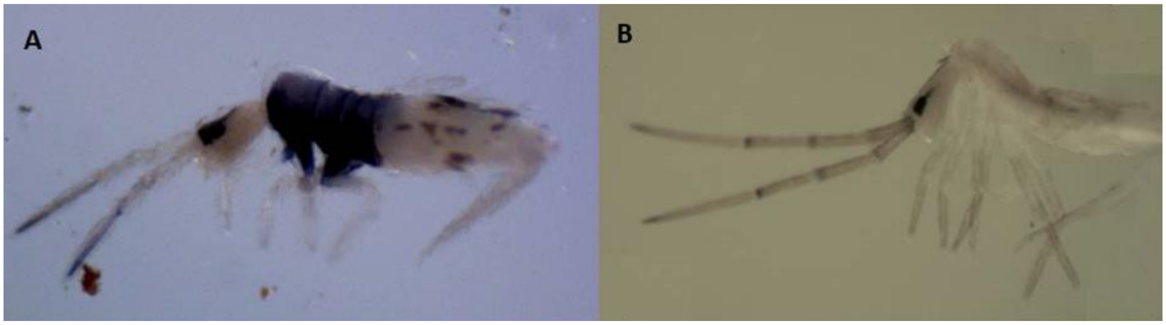

Figure 4.9 Coloration in *Lepidocyrtus paracaprilesi*. A. known Coloration darker in thorax segments, B. Coloration restricted to eye patch and end of the antennal segment.Photos by Claudia M. Ospina Sanchez.

Traditionally, the characters used to classify Collembola functional groups were color, body shape, length of their appendages and presence of sensorial organs (Christiansen 1964, Gisin 1967). In this analysis we also include the characters of the foot, according to the theory that food complex shows the adaptive changes for living in caves (Christiansen 1965). This adaptations occur because the hardness and water contents of the surface (Christiansen 1988). Our results show that this traits attributes in foot complex are related with the habitat (Table 4.7). We found that species in mosses had reduction of their unguis teeth with modifications in the “tenet hairs”, while species from leaf litter had not modification in “tenet hair” or in unguiculus and usually the unguis had teeth.

The food content trait does not show any significant relation, possible because we just make a distinction between fungi and litter. Currently there are many methods to identify the food content in macroarthropods. Potavop et al (2016) use the stable isotope signatures, found that collembolans can occupy different trophic levels. Ponge (2000) also found a strong relationship between food objects and habitat depth reveled in the gut content analysis. A deeper study of this food content must be considering for future studies because this give information about the microhabitat and the tropic niches adaptations (Potapov et al. 2016).

These results show that Collembola species explore many niches and can move through them. Other studies showing that one species in most cases the dominant is able to fill up the ecological functions in soils (Cragg and Bardgett 2001) but the contrary is found in field studies (Potapov et al. 2016). The importance of having many species that in theory belong to the same niche might be the possibility of replace in case that one species become less abundant or in cases where the diversity is low, the traits distribution results more important than species richness (Bardgett and van der Putten 2014). Additionally, there are species with less abundance and low mobility; this rare species play a different role that we do not test already and most to be known and protected in their environment.

Here we demonstrate with the examination of morphological traits, the mechanism that shape species distribution along microhabitats in a tropical forest (Ponge and Salmon 2013, Salmon et al. 2014, Widenfalk et al. 2016). Also, we showing the importance of using traits attributes over abundance, richness and other diversity functional measures (McGill et al. 2006). Differences on species composition through microhabitats were found, but the moving capacity that results in morphological adaptations was more important for classification. As conclusion, there are two types of populations, (low and high mobility), and their traits attributes variates between microhabitats. However, we need more evidence about the grade of mobility and the mechanisms to determinate the variation in community composition (Moore et al. 1988). Understanding the roles of the soil organisms would lead us to direct studies about the functioning of soil ecosystems. In consequence we would get a better predict in changes in land use or climate (Bardgett et al. 2005, McGill et al. 2006).

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Chapter 5 : Collembola populations along environmental gradients.

1. Introduction

In the tropics, the understanding of environmental influences on the regulation of soil diversity is still in development (Maunsell et al. 2013, Mori et al. 2013). The reasons for this bias include the difficulty in accessing sites representing complete altitudinal gradients, where suitable data do not yet exist (Olson 1994, Willig et al. 2013). Another reason for this delay is that arthropods present a methodological challenge because of their often extreme richness in tropical regions and associated difficulties in sorting and identification (Longino et al. 2002, Brehm et al. 2007). The Luquillo Experimental Forest (LEF) has a history of unique soil ecological studies (González and Barberena-Arias 2017, González and Lodge 2017) that include leaf litter decomposition rates (González and Seastedt 2001), structure and composition of vegetation (Gould et al. 2006), soil microbial biomass (Ruan et al. 2004), invertebrate communities in Bromelidae (Richardson et al. 2000, Richardson and Richardson 2013), arthropods in leaf litter (Richardson et al. 2005, Richardson et al. 2018) and studies looking at the effect of organisms on decay (González et al. 2014). These previous studies allow for significant advances in understanding the influences of environmental variables on soil arthropods. However, there is a lack of information about how environmental variables affect specific taxa.

Intra-taxonomic comparative studies of the altitudinal and latitudinal gradients represent a convenient natural system to investigate the effect of extent on mechanisms determining geographical and environmental variation in species richness (Rahbek 2005). Nevertheless, this approach remains largely unexplored (Kitching et al. 2011). In this study, Collembola are chosen as a soil-arthropod biodiversity indicator because of their high taxonomic diversity and their high abundance in all terrestrial habitats, especially in soils and leaf litter of several forests where they constitute one of the most numerous arthropods (Hopkin 1997, Greenslade 2007).

1.1. Climate variation

Arthropods are sensitive to changes in climate because of their ectothermic dependency and small size. One of the principal soil characteristics that influence distribution of soil arthropods is soil moisture because their survival can be negatively affected by both low and high soil moisture values (Adis and Junk 2002, Frouz et al. 2004). This effect of moisture is closely related to temperature. At higher temperatures, soils are more likely to desiccate because of faster evaporation, leading to soil drought that may have adverse effects on soil fauna (Frouz et al. 2004). In consequence, community diversity and abundance of arthropods should respond to regional gradients in temperature and precipitation (MacArthur et al. 1972, Schowalter and Ganio 1999, Progar and Schowalter 2002).

Soil moisture is a key variable of the climate system. It constrains plant transpiration and photosynthesis in several regions of the world, with impacts on the water, energy and biogeochemical cycles. Moreover it is a storage component for precipitation and radiation anomalies, inducing persistence in the climate system (Seneviratne et al. 2010). In several field studies, the distribution of springtails appeared to be influenced by humidity and clear correlations between density and soil water content have been found (Verhoef and Van Selm 1983).

1.2. Gradients

The structure and function of ecosystems change markedly along elevation gradients. Analysis of published data of species richness on altitudinal gradients shows that the most typical pattern is a hump-shaped, followed by a monotonic decreasing pattern (Rahbek 2005, Richardson et al. 2005). This pattern is related to a reduction of temperature as elevation increase and the assumed to correspond to a reduction in ecosystem productivity (Rahbek 2005, Sanders and Rahbek 2012). However, other patterns, including horizontal and then decreasing, or always increasing with elevation can also be found (Rahbek 2005, Richardson et al. 2005, Cutz-Pool et al. 2007). These differences are usually attributed to different plant responses to the direct effects of changing climatic conditions in montane gradients (Bardgett and Wardle 2010).

Although many studies of species richness and diversity along elevational gradients have been published, most of them are focused on plants and are conducted in temperate zones. In spite of the global majority of terrestrial organisms being tropical arthropods, knowledge of their richness patterns along altitudinal gradients is still very poor (Brehm et al. 2007). It was long believed that species richness of insects showed a monotonic decline along elevational gradients. However, the paradigm has changed and peaks at medium elevations are generally accepted as being the rule rather than the exception (Rahbek 2005, Richardson and Richardson 2013). Examples include groups such as butterflies and ants, which show a maximum diversity in tropical regions far below 1000 m (Brühl et al. 1999, Fisher 2002).

However, evidence is still limited because few insect studies have investigated complete elevational gradients. So far, only a few exceptions to an overall declining diversity of insects at elevations higher than 1000 m have been documented. Examples include arctiid and geometrid moths in Ecuador (Brehm et al. 2003) and Costa Rica (Brehm et al. 2007). This last study confirms that Geometrid moths have a predominantly montane distribution with exceptionally high species richness at elevations up to 2100 m. Richness at the lowest elevations is markedly lower, and also decreases towards higher elevations at the mountain summit (Brehm et al. 2007). Intra-taxonomic comparative studies of the altitudinal and latitudinal gradients represent a convenient natural system to investigate the effect of extent on mechanisms determining geographical variation in species richness (Rahbek 2005).

Altitudinal studies with Collembola indicate that as a group, they respond strongly to the physico-chemical and/or biological changes that occur with increasing elevation, even over a relatively small elevation range (Cutz-Pool et al. 2010, García-Gómez et al. 2011, Maunsell et al. 2013). Several distribution patterns have been detected for Collembola with respect to elevation (García-Gómez et al. 2009, Maunsell et al. 2013). More importantly, however, is the finding that these patterns might vary along microhabitats (Cutz-Pool et al. 2007, Maunsell et al. 2013).

Collembola species richness in leaf litter and soils was lower at high elevation than at low elevations (Maunsell et al. 2013). On the contrary, for Collembola communities of bark mosses, an increase of abundance with a decrease in richness in high elevation has been detected (Cutz-Pool et al. 2007), while both richness and abundance tend to diminish with elevation when the samples begin at high elevations (Cutz-Pool et al. 2010). In addition to these differences with altitude, Collembola assemblages showed some differences between sampling occasions (Cutz-Pool et al. 2007, Cutz-Pool et al. 2010, Maunsell et al. 2013). In a preliminary result from pitfall traps of tropical forest environments, the species richness was high at mid-elevation and then declined; however at high elevation an increase in the presence of endemic species was detected (Figure 5.1).

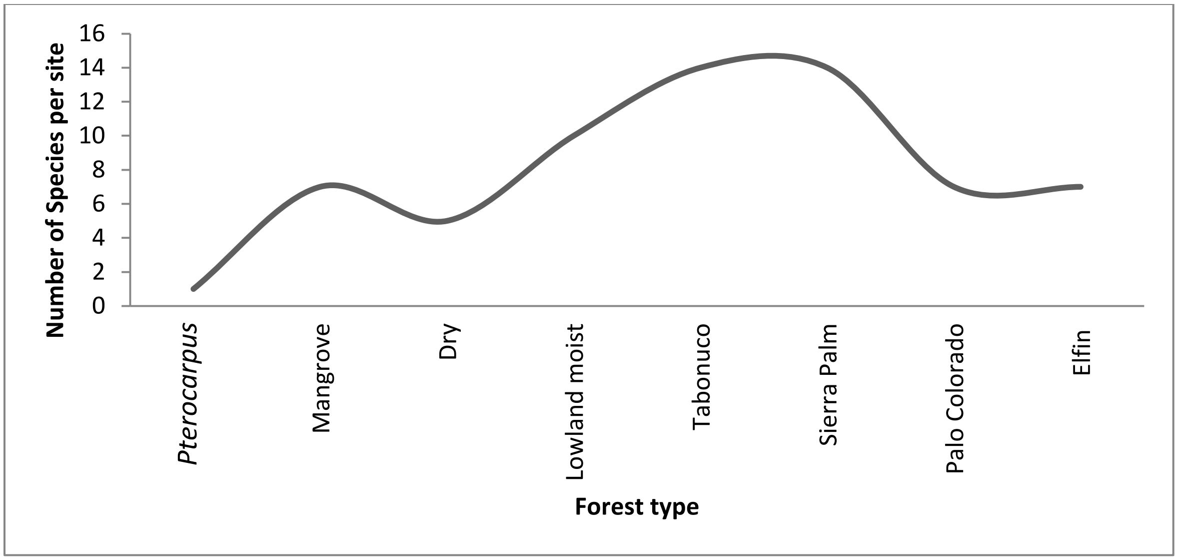

Figure 5.1 Preliminary Collembola community's evaluation for pitfall tramps. Survey at Mangrove, Dry, *Pterocarpus*, Lowland moist, Tabonuco, Sierra Palma and Palo Colorado Forests were taken in January of 2002. Elfin forest samples were taken between August and September 2003. These samples belong to 15 geographic areas represented by 8 forest types. A total of 2,646 specimens of Collembola were separated and 30 species and 13 families were identified.

The main objective in this chapter is to compare the Collembolan communities among tabonuco, palo colorado, and elfin forest types, evaluating the influence of environmental variables that can determine their assemblages. The three forests evaluated have sharp differences in temperature (in soil and air), humidity, and precipitation and vegetation type. I compared the Collembola species composition, richness and abundance within these three montane forests. I expected a peak of these measures in the middle elevation where the environmental conditions would be favorable for soil arthropods. Using non-parametric analysis, environmental parameters were evaluated to explain variations in Collembola assemblages along the elevational gradient. I expected that among the environmental variables evaluated, precipitation would largely explain the assemblage's variation because of its influence on temperature and moisture, influential conditions for Collembola species distribution.

2. Methodology

Samples were taken from the Luquillo Experimental Forest, in plots located in tabonuco *(Dacryodes excelsa)*, palo colorado (*Cyrilla racemiflora)*, and elfin (*Tabebuia rigida)* forest types that belong to mountain environments. These samples were collected during August 2014 and August 2015 (Table 5.1). Three sampling locations were selected within the three forests (Table 4.4). Samples were collected from five individuals of the most common tree species according to Gould et al. (2006). Only mid-sized trees were selected from the tree inventory (González et al. unpublished data, Table 1.1). In each tree, two samples of soil, leaf litter and mosses adhered to the trunks were collected. For soil samples, the soil was collected from the surface down to10 cm of depth using a soil core (10 cm in diameter) on the ground areas directly adjacent to the selected tree. For leaf litter, a 10 cm^2 sample with its entire depth was collected. For mosses, in the middle branches of each tree, 10 cm^2 of the contiguous pieces of live and dead mosses perched upon branches of trees were sampled with the entire depth of the collected moss material.

Table 5.1 Samples dates for Collembola survey during 2014 and 2015. In each date, the three localities for the forest type was sampled.

Forest type	1 (2014)	2 (2014)	3 (2015)	4 (2015)	5 (2015)
Elfin	06 August	04 November	11 February	19 May	29 July
Palo Colorado	25 August	18 November	19 February	27 May	18 August
Tabonuco	15 August	26 November	11 March	05 June	06 August

The same day of the collection, material collected in soil, litter and mosses were placed in plastic bags and transported to the lab for further processing. Here, the fresh weight was recorded and the arthropods were extracted using Berlese funnels (González and Barberena 2018) for four to seven days until the sample was dry. After the extraction, the dry weight of the samples was measured. The water content in the sample was calculated by the following formula (Arbea and Jordana 1990):

$$\text{Water Content} = \frac{\text{Fresh weight of sample} - \text{Dry weight of sample}}{\text{Dry weight of sample}}$$

The soil samples were sorted by hand into roots and soil (Figure 5.2A). The leaf litter samples were sorted by hand into three categories: organic matter, entire broad leaves and others (twigs, roots, etc. Figure 5.2B). The weight of these categories and total samples were registered as percentage, to characterize the physical composition of the microhabitat.

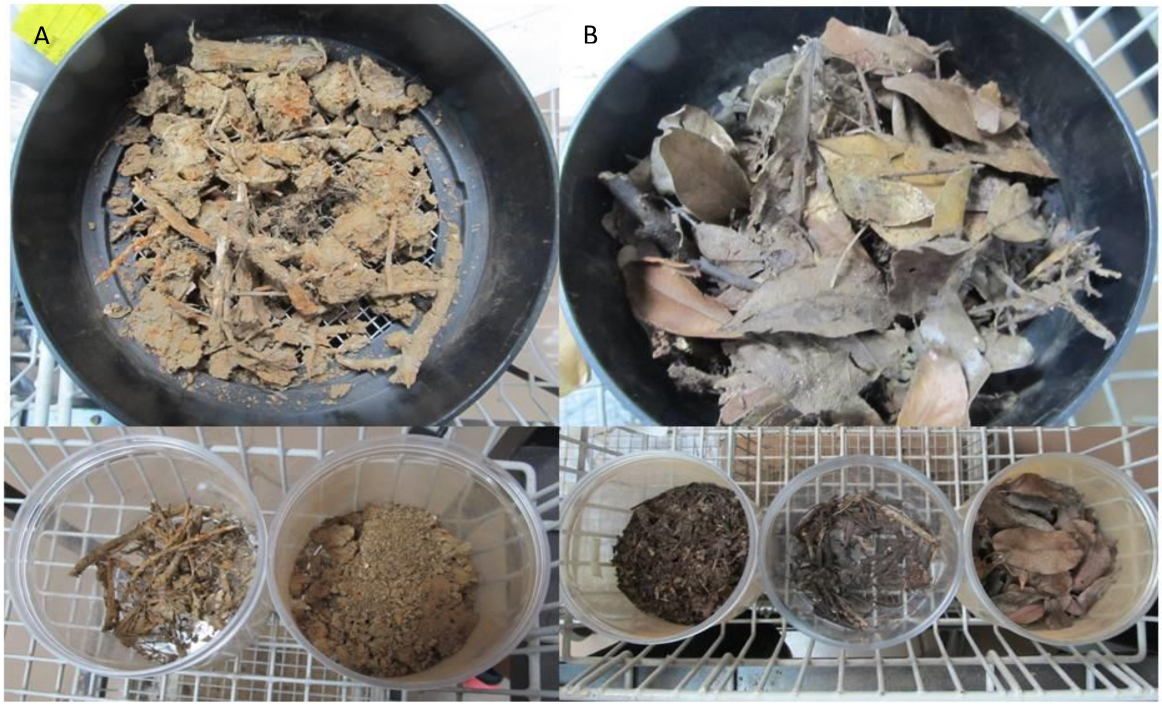

Figure 5.2 Substrate sample separation A. Soil samples were sorted into roots and soil B. Leaf litter samples were sorted into organic matter, entire broad leaves and others. Photos by Claudia M. Ospina Sanchez.

The arthropod samples were preserved in 96% ethanol and collembolans were separated, sorted in morphospecies and counted using dissection microscopy. Following, five or more individuals for each morphospecies were prepared in slides for contrast face-microscopy examination. After species identification, we registered the total abundance by species.

Additional environmental data (temperature, rainfall and elevation) for each plot sampled (locality) were provided by the USDA Forest Service (González et al., unpublished data, Figure

6.3). For air and soil temperature, I used the average hourly temperature for seven days after and seven days before the sample date. For precipitation, the average in millimeters measured two weeks before, the week of the sample, and the week after was used. Like other tropical environments, temperature declines with increasing elevation (Lessard et al. 2011, Purcell 2011). Also there is a tendency to show less seasonal variation in temperature with increasing elevation, but a strong seasonality in precipitation (Blanckenhorn and Demont 2004).

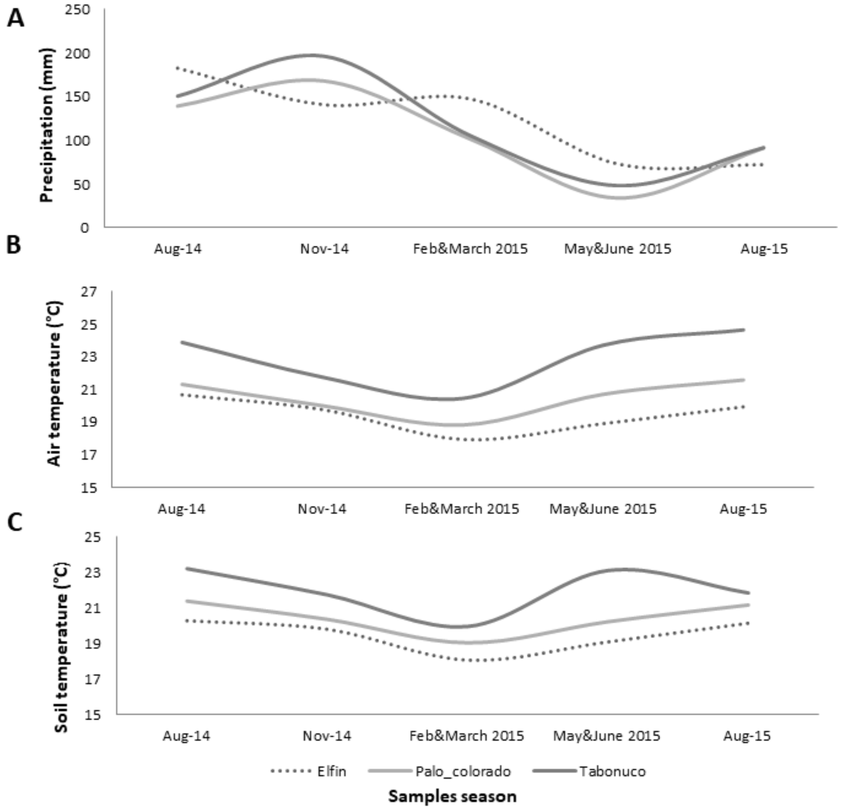

Figure 5.3 Environmental data from LEF. A. Average precipitation (in millimeters, mm), B. air temperature (in degrees Celsius, °C) and C. soil temperature (in degrees Celsius, °C) in three forest types. Data provided by the USDA Forest Service (González et al., unpublished data).

2.1. Statistical Analysis

The analysis of Collembola data and environmental variables was done in two parts. First using no parametric statistics, the correlation of environmental variables with Collembola abundance and richness in each forest type was performed. Then, I performed a biodiversity analysis using the abundance of each species in the forest type. To find hypothetical variables (components) which account for the variance in our multidimensional data (Davis and Sampson 1986) a principal components analysis (PCA) was performed through all the environmental (altitude, precipitation, air and soil temperature; % of humidity in leaf litter, soil and mosses; % litter in leaf litter samples, % roots in soil samples) and Collembola population variables (Number of species and individuals in soil, leaf litter and mosses samples), with a 95% bootstrapped confidence intervals. For the correlation of the environmental variables with the Collembola assemblages, I performed a Sperman (r') correlation analysis separately for each forest type. As a result of this correlation, a classification of values was given in a range of -1 to 1 and the significance value was $\alpha = 0.05$ using a Bonferroni correction for p-values.

To study the variation of species along the environmental variables, diversity index rarefaction curves and Similarity Percentage (SIMPER), and detrended correspondence analysis (DCA) were performed. SIMPER is a simple method for assessing which taxa are primarily responsible for an observed difference between groups of samples (Clarke 1993). The overall significance of the difference was assessed by ANOSIM. The similarity measure used was the Bray-Curtis. Community structure was ordinated using DCA, which is an eigenvector ordination technique based on reciprocal averaging. It is especially suited for analysis of ecological data sets based on samples and species (Hill and Gauch 1980), and is quite popular in ecological analyses, especially when sample units are collected along an environmental gradient (Progar and Schowalter 2002).

To analyze patterns of Collembola species diversity at multiple spatial scales, I used multiplicative diversity decompositions of effective numbers of species (so-called Hill numbers) in its unweighted form (Jost 2007). Hill numbers (qD) represent true diversities, as they obey the replication principle (Jost 2007, Tuomisto 2010). They are in units of 'species', and hence, they can be plotted on the same graph to construct diversity profiles that can be useful to characterize the species abundance distribution of a community and to provide complete information about its diversity (Chao et al. 2012). The Hill numbers or effective number of species is defined as:

$$D^q = \left(\sum_{i=1}^{s} p_i^q \right)^{1/(1-q)}$$

Where $\bar{p}i$ denotes the mean relative abundance of the *i*th species in the N communities (Jost 2007, Tuomisto 2010), and *q* is a parameter that determines the sensitivity of the measure to the relative abundances. Because this measure is undefined for q = 1, diversity of order 1 can be estimated as:

$$D^1 = exp\left(- \sum_{i=1}^{s} p_i^q \; log\, \bar{p}i\right)$$

When *q* = 0, diversity represents the species richness, which is not sensitive to abundances and so gives disproportionate weight to rare species (Jost 2006, 2007, Tuomisto 2010). When q = 1, diversity is equivalent to the exponential of Shannon's entropy index, and weighs each species according to its abundance in the community, without favoring rare or abundant species (Jost 2007). The Hill number of order 1 can be therefore interpreted as the number of 'typical species' in the community (Chao et al. 2012). Finally, if q = 2 (equivalent to the inverse Simpson concentration), abundant species are favored and rare species are discounted, and hence, this diversity can be interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2007, Chao et al. 2012).

To avoid discarding data, we performed the sample-size-based rarefaction and extrapolation (R/E) sampling curve for species richness that can be rarefied to smaller sample sizes or extrapolated to a larger sample size (Colwell et al. 2012). This method was better able to judge the magnitude of the differences in richness among communities, and ranked communities more efficiently, compared to traditional R/E from equal sample sizes (Chao and

Jost 2012). The sample-size-based R/E curve includes a rarefaction part (which plots ${}^{q}\ \widehat{D}(m)$ as a function of m < n), and an extrapolation part (which plots ${}^{q}\,\widehat{D}(n+m^{*})$ as a function of n + m*); both join smoothly at the reference point (n, S_{obs}), where S_{obs} denotes the observed species richness in the reference sample (Hsieh et al. 2016).

This analysis was performed using abundance data, with a confidence interval of 0.95 and bootstrap sample size of 500, using the main function iNEXT in R to compare diversity estimates of standardized samples (Hsieh et al. 2016).

The diversity index performed was N: Number of individuals of Collembola in each forest type, S: Number of species, H: Shannon diversity index, D: Dominance, 1-D: Simpson diversity index, and Exp(H)/S: Evenness. All indices were performed with PAST v 3.2.

3. Results

3.1. Environmental variables within Collembola populations

The values for humidity in mosses, leaf litter and soil samples show their highest values for elfin forests and decline with decreasing altitude. The percentage of litter in ground samples was highest in tabonuco and then declined with increasing altitude. The percentage of roots in soil samples was highest in palo colorado followed by elfin and tabonuco forests (Table 5.2).

Table 5.2 Mean values for the percentage of humidity in leaf litter (LL), soil (S) and mosses (M) for field samples. Percentage of litter in leaf litter samples and percentage of roots in soil samples for three forest types in LEF.

Forest type	LL % humidity	%litter	S % humidity	%roots	M % humidity
tabonuco	52.88	57.50	36.62	5.45	43.44
Palo colorado	64.97	50.55	45.93	8.06	64.83
elfin	80.73	40.61	61.15	7.77	79.72

The PCA returned a variance of 94.5 for the first component and 3.7 for the second, which represent altitude and precipitation, respectively. The 95%confidence ellipses show a separation of the Collembola assemblages in the three forest types (Figure 5.4). The PC1 shows a high positive correlation with altitude, % humidity in leaf litter and soil and a negative correlation with temperature in air and soil. The PC2 shows a high positive correlation with precipitation and % of humidity in soil, leaf litter and mosses.

The PCA analysis indicate altitude as an important component, to visualize the differences in between the three evaluated forest types, a correlation analysis was performed to help visualize the effect of the other variables for each forest type. For tabonuco forest, the number of individuals in leaf litter was correlated with soil (r’=-0.37) and air temperature (r’=-0.49), % humidity (r’= 0.49) and % litter (r’=0.33) in leaf litter samples. The number of species in leaf litter was correlated with soil (r’=-0.34) and air temperature (r’=0.39), and % humidity (r’=0.41) in leaf litter samples. The number of individuals in the soil was correlated with the number of individuals in leaf litter (r’=0.30). The number of species in soil was correlated with precipitation (r’=0.30). In soil and leaf litter, the number of individuals was correlated with the number of species (r’= 0.94 and 0.87). Other significate correlations are shown in Figure 5.5A.

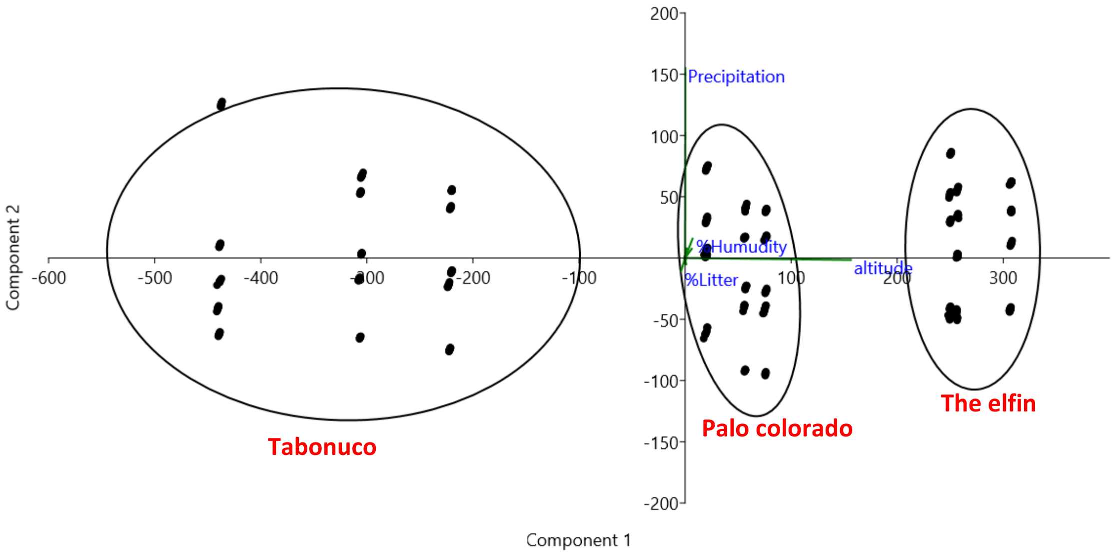

Figure 5.4 PCA of component 1 and 2 using forest type as group. The 'Biplot' show a projection of the original axes. The 95% bootstrapped confidence intervals are given for the eigenvalues for each group at gray colored area. The groups are red labeled.

In the palo colorado forest, the number of species in leaf litter was correlated with air temperature (r’= 0.34). The number of individuals and species in soil were correlated with the percentage of humidity in leaf litter (r’=0.30, 0.29) and the number of individuals (r’=0.31, 0.33) and species (r’=0.38, 0.41) in leaf litter. The number of individuals in mosses was correlated with air temperature (r’= -0.40) and the number of species in mosses was correlated with air temperature (r’= -0.49). In all of the microhabitats, the number of individuals was correlated with the number of species (r’= soil 0.86, leaf litter 0.93, mosses 0.90). The palo colorado forest correlations are shown in Figure 5.5B.

The elfin forest was the forest type with the least significant correlations (Figure 5.5C). Precipitation was correlated with the % litter in leaf litter samples (r’= -0.45) and % humidity in mosses (r’=0.41). The number of individuals and species in moss samples were negatively correlated with precipitation (r’= -0.37, -0.42) and air temperature (r’=-0.38,-0.33). In all of the microhabitats, the number of individuals was correlated with the number of species (r’= soil 0.99, leaf litter 0.94, mosses 0.81).

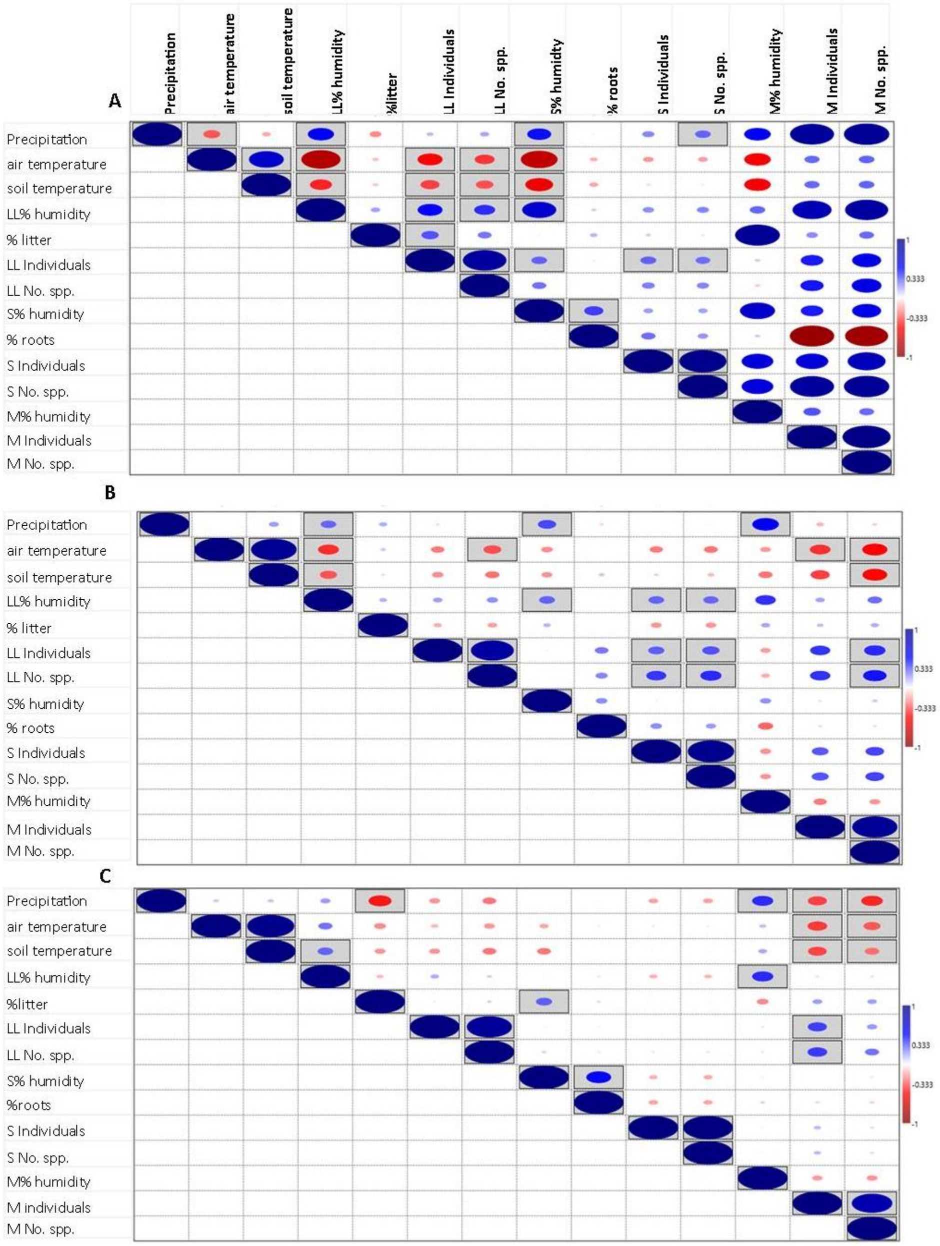

Figure 5.5 Sperman (rs) Correlation analysis for A. tabonuco B. palo colorado and C. elfin forests. The squares indicates significate correlation Bonferroni corrected (p<0.05) and the ellipse the size of the correlation. Blue denotes a positive and red negative correlation.

3.2. Diversity analysis

The rarefaction curves performed with Hill numbers show the effective numbers of species (q=-0) was highest for palo colorado followed by elfin and tabonuco forest. The elfin forest observed diversity did not reach the asymptote of the rarefaction curve, indicating it is possible to find more species in this forest type. The curves for q=1 and 2 showed the same shape, and indicated that diversity was again higher in palo Colorado followed by tabonuco and elfin (Figure 5.6).

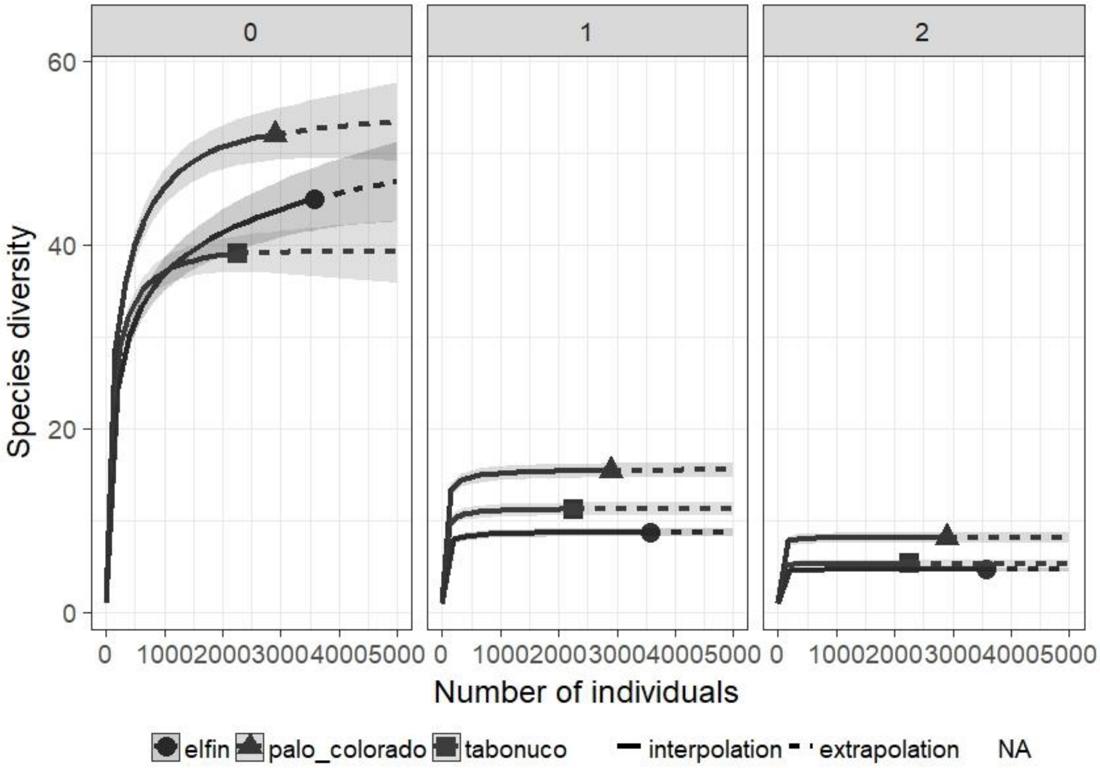

Figure 5.6 Rarefaction curves based on Hill numbers. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for the Collembola abundance data of three forest types by diversity order: q = 0 (species richness, left panel), q = 1 (Shannon diversity, middle panel) and q = 2 (Simpson diversity, right panel). The solid dots/triangles/squares represent the reference samples.

The comparison of the diversity between forest types shows high diversity in the elfin forest, drawing an ascendant pattern according to the altitudinal gradient. However, this pattern was different for each of the included diversity indices. The number of species (S), Shannon diversity (H) and Simpson diversity (1-D) showed a peak in the middle elevations, and dominance (D) showed a peak at high elevation, while evenness (Exp(H)/S) was similar in tabonuco and palo colorado and went down in the elfin forest.

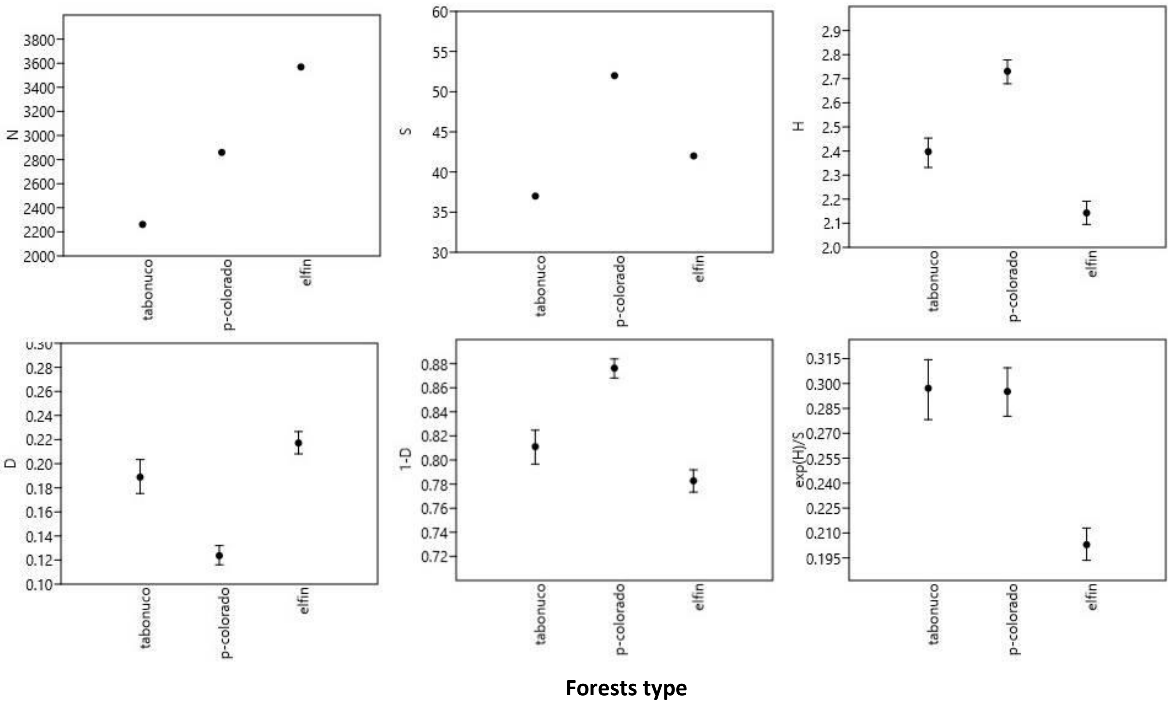

Figure 5.7 Diversity index by forest type. N: Number of individuals of Collembola in each forest type. S: Number of species. H: Shannon diversity index. D: Dominance. 1-D: Simpson diversity index. Exp(H)/S: Evenness. All indices were performed with PAST v 3.2.

The DCA was performed using the abundance of each species in each forest and microhabitat. This also shows a difference between forest types as indicated by a separation of groups for each forest type. Figure 5.8 shows the distribution of species along the gradient and the forest types: the species on the left are from lower elevations and moving to the right are the high elevation species. The species closer to the microhabitat-forest type points have a higher probability of being found in that habitat.

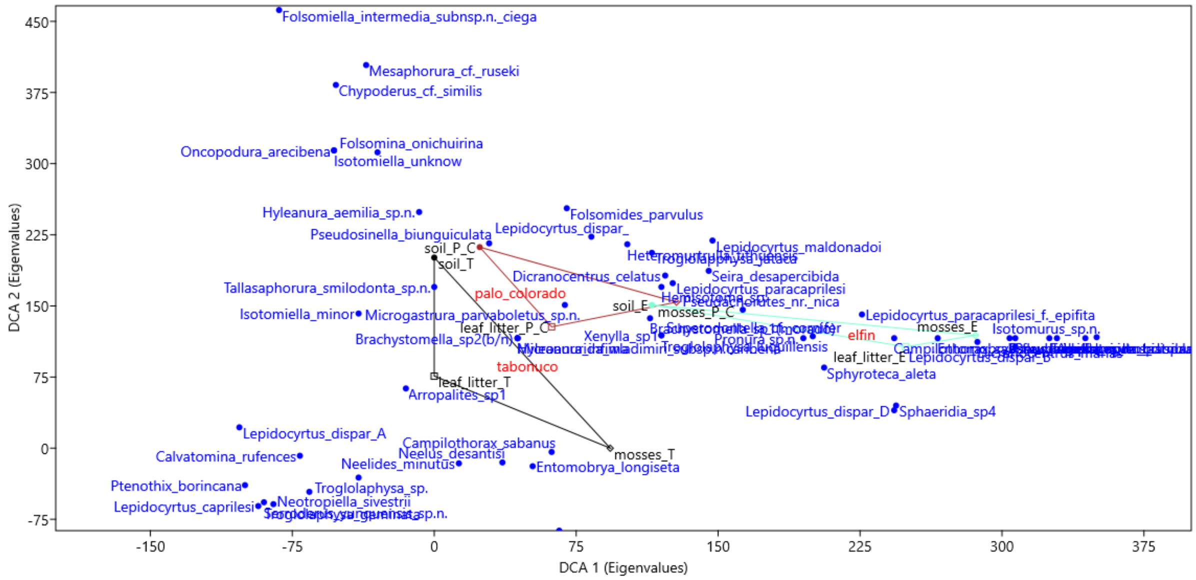

Figure 5.8 DCA based in species abundances of tabonuco, palo colorado and elfin forest types and their microhabitat sampled: soil, leaf litter and mosses in LEF. The ordination shows the distribution of species according to the altitudinal gradient.

The SIMPER analysis shows that the species *Isotomiella minor* had a contribution of 19.13 in the % of variation between the three forest types, but when tabonuco and palo colorado forests were compared its contribution was 62%. However, when the elfin was compared with the other forest types, the species *Isotomurus degrade* sp.n. had the largest contribution at 51.76% when compared with tabonuco and 54.58% when compared with palo colorado. According to ANOSIM (Bray-Curtis similarity index) the elfin forest is significatively different from tabonuco (p<0.01) and palo colorado (p=0.01), while tabonuco and palo Colorado are similar (p=0.24).

4. Discussion

In this study it was found that Collembola assemblages are significantly different among the evaluated forest types. The species composition, number of species, abundance and diversity are ll related to the environmental conditions that define each forest type. The distribution of the Collembola species along the altitudinal gradient was different. The diversity index varied, while the effective number of species and the abundance were higher in the elfin forest (higher elevation) followed by palo colorado (mid elevation) and tabonuco (lower elevation). The other diversity index (Shannon, evenness, dominance) showed the peaks at mid elevation.

4.1. Environmental factors

Because environmental changes in precipitation and temperature occur within very short geographical distances, a montane gradient allows for the exploration of how species composition, diversity and endemism are driven by gradual changes in local climate (Beniston et al. 1997, Hodkinson 2005, Maunsell et al. 2013). In this study, the altitudinal variation (300 – 1045 m a.s.l.) was a determining factor of Collembola assemblages. As a consequence, the forest with the highest percent humidity and lowest temperature (elfin forest) was favorable for Collembola abundance while the forest with the mid values (palo colorado) was the more favorable for Collembola diversity.

According to a PC analysis, the elevation was the variable that explained 94.5% of the variability in Collembola assemblages. Elevation is a factor that can explain other variables like climate, topographic conditions and vegetation that are simultaneously affecting the dynamics of the soil microclimate at a given site, and thus also Collembola dynamics (Hågvar 1982, Ponge et al. 1993, Kuznetsova 2006, García-Gómez et al. 2011, Raschmanová et al. 2015).

According to the correlation analysis, both the abundance and number of species of Collembola were related to climatic factors, especially to soil and air temperature in all the forest types. In this montane environment, precipitation tends to show strong seasonality (Gould et al. 2006), and along with temperature is the most significant environmental factor related to humidity in the substrate, and as a consequence to the number of Collembola individuals and species. Previous studies have demonstrated that Collembolan abundance and distribution patterns were significantly influenced by soil moisture content and soil temperature in soil and leaf litter systems of tropical forest environments (Takeda 1987, Badejo and Van

Straalen 1993, Wolters 2001, Castaño-Meneses et al. 2014). Collembola species are also sensitive to these conditions due to their small body size and exothermic nature (Palacios-Vargas et al. 2007, Weaver 2012). Although some biotic factors (interspecific interactions, food resources, phenology, life strategy and seasonal migration of species) can influence populations, studies have demonstrated that habitat characteristics and air temperature played a much more significant role in determining population abundance (Ferguson and Joly 2002).

In a temperate forest in Mexico, altitude and humidity played an important role in the establishment of different assemblages; the highest abundance of Collembola was recorded at the highest elevation (3.687 m a.s.l.), but the highest diversity was recorded at 3.250 m a.s.l. (García-Gómez et al. 2009). For the present study the highest abundance was also found at high elevations (elfin forests 994 m a.s.l), but the highest number of species was recorded at mid-elevation (palo colorado forest 795 m a.s.l). In a previous study (Richardson et al. 2005), the invertebrates in an LEF elevation gradient were found to be more abundant in the lower elevations, while there were no significant differences in diversity between the lower and intermediate elevations. These differences in the results point out the importance of separately evaluating the distribution of soil arthropod species.

The mid elevation Collembola assemblages show few correlations with environmental factors. Leaf litter and soil abundance and diversity of Collembola in palo colorado forest showed no correlation with the tested environmental variables, while assemblages with mosses were negatively related to precipitation and air temperature. However, local invertebrate species richness may be determined by some set of factors related to the rainfall regimen at middle elevations (Olson 1994). For future analyses, it will be important to consider other factors related to the vegetation composition and substrate chemical composition, which may influence decompositions rates, resource availability and the chemical tolerance of Collembola species (Butcher et al. 1971, Berg et al. 1998, Rzeszowski et al. 2017).

4.2. Abundance

A principal difference between assemblages is given by the difference in niche occupancies between the forest types. In tabonuco and palo colorado, the highest Collembola abundance was found in leaf litter, while in the elfin the highest abundance was found in mosses. As a result, an ascendant curve for abundance can be seen in Collembola assemblages at LEF. If the curves are visualized separately by microhabitats, those for leaf litter and soils reach their peaks at mid elevation, while that for mosses appears to continue rising past the highest elevations (Figure 5.9).

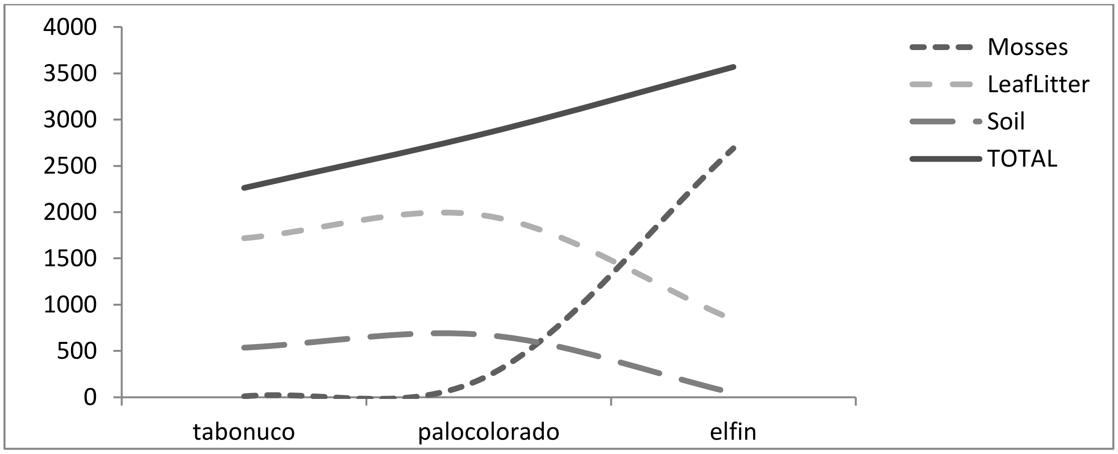

Figure 5.9 Abundance of Collembola collected through august 2014 – 2015 in three forest types in LEF, separated in the three microhabitats sampled.

The variation in abundance in Collembola assemblages is explained by the observation that at higher elevations (the elfin forest), more mosses adhered to threes and become a larger microhabitat for arthropods. Humidity and temperature were a determinate factor for arthropod abundance, with mosses and epiphytes capable of decreasing water loss through evaporation by almost 20% as well as lowering the temperature of their immediate surroundings (Stuntz et al. 2002). This creates a special microhabitat for arthropods in the canopy with fewer fluctuations in climate (Hölscher et al. 2004). As a consequence, the presence of large epiphytes within the canopy could, in some cases, double the abundance of arthropods within the canopy of a single tree (Stuntz et al. 2002, Weaver 2012). Additionally, higher elevations experience the lowest water stress (García-Gómez et al. 2011). Persistent cloud cover, fog stripping, and cool temperatures at higher elevations create conditions of high relative humidity and low evaporation rates (Hölscher et al. 2004).

4. 3. Diversity

According to the rarefaction curves using the Hill numbers and the diversity indices of Shannon and Simpson, diversity reached its peak at mid elevation. The elevational gradient in Luquillo mountains has been evaluated by many groups, and as a result the species richness in this gradient demonstrates monotonic decreases, monotonic increases, modal relationships, and invariant patterns. For tree species (Waide et al. 1998), litter invertebrates (Richardson et al. 2005), and gastropods (Willig et al. 2013), species richness declines with elevation. However earthworms reach their species richness peak at high elevations (González et al. 2007), while litter invertebrates along a palm forest transect are unequal in all elevations (Richardson et al. 2005). Invertebrates from bromeliads (Richardson and Richardson 2013), vascular epiphytes and vines (Brown et al. 1983) and vegetation (Gould et al. 2006) have a species richness peak at mid elevations. Nevertheless, these studies cannot be compared because of the variation in sampling methodology or the niche characteristics of biotas and the salient environmental characteristics to which they respond (Willig et al. 2013). The sampling plots used in the present study were also used for the study of distribution of arthropods in the LEF gradient by (Richardson et al.2005). They found that the richness of arthropod communities declines with increasing elevation. In the present study, richness reaches its peak at mid-elevations. This difference emerges from the taxonomic resolution of the studies. The Richardson (2005) study made a separation of principal groups as Acari, Formicidae, Collembola, Isoptera, Coleoptera, and Diptera. In my study, the focus was exclusively on Collembola species, demonstrating the importance of taxonomic resolution in better understanding soil arthropod assemblages.

In this study, comparisons of diversity components of dominance and evenness in Collembola species were performed. In palo colorado forest the dominance index was lower than at all other forest types, while the evenness and diversity were highest. The Collembola assemblages in palo colorado is characterized by an even distribution of a larger number of species, so there is no one dominant species. This species distribution may be related to a positive correlation between environmental factors like precipitation and humidity and Collembola populations. In some cases, Collembola diversity increases with humidity (Rusek 1998, Maunsell et al. 2013), but in this study, the Collembola assemblage show the highest diversity at mid elevation, while it is the highest elevation that has more humidity in the substrates. The high diversity in palo colorado forest could therefore be attributed to differences in climatic conditions and changes in vegetation type that create several microhabitats with more stable favorable conditions (García-Gómez et al. 2011).

Collembola in the tabonuco forest show intermediate dominance but high evenness and the lowest number of species, all indicating the presence of few abundant species. On the contrary, the elfin forest has an intermediate number of species, high dominance and lower evenness, indicating the presence of few abundant species and many species represented by few individuals (Figure 5.7, Table 5.3). In this case, the adaptation of some species to a particular resource or microhabitat may be an important factor in determining community structure than are climatic conditions (Richardson et al. 2005). It is important to note that the abundant species in elfin forest was *Dicranocentrus marias*, the larger species in the survey (up to 3mm). This increase in size with elevation was also observed by Willig et al. (2013) in gastropods from LEF.

Generally, size increases are explained by a negative relationship between developmental temperature and size among ectothermic animals in a non-resource-limited environment (Atkinson 1994, Smith et al. 2000). By contrast, a large number of small species (less than 1mm) are present in lower numbers, because these are generally thought to decrease in size as a result to resource limitations, often linked to seasonal resource availability, which restricts potential growth (Hill et al. 1998).

For the sampled forest sites in LEF, we found a large number of species at middle elevations. The palo colorado forest tends to support those species that are most restricted in elevational distribution, and as a consequence, those species that are least abundant (Table 5.3). In the palo colorado forest, ten species were exclusive, while elfin and tabonuco forest had five exclusive species, respectively (Table 5.3). On the other hand, the abundant species *Neelus desanty* and *Hemisotoma* sp. were evenly distributed along the gradient. Other abundant species such as *Dicranocentrus marias* increase their abundance while *Isotomiella minor* decreased according to the elevational gradient (Table 5.3, Figure 5.7 and 9).

Table 5.3 List of identify species and their total abundance at three forest type in LEF.

Species/Forest type	tabonuco	palo colorado	elfin
Furculanurida bistribus **sp.n**.	0	0	52
Microanurida wladimiri **subsp.n**.*caribena*	0	7	0
Arlesia **sp.n**.	0	0	106
Neotropiella sivestrii	16	3	1
Hyleanura infima	0	1	0
Hyleanura aemilia **sp.n**.	0	18	0
Pronura **sp.n.**	0	21	26
Brachystomella sp2(b/n)	0	29	0
Brachystomella sp1(morado)	8	28	18
Folsomiella intermedia **subnsp.n**. *ciega*	12	5	0
Microgastrura parvaboletus **sp.n**.	6	11	5
Superodontella cf. *cornifer*	0	6	4
Xenylla **sp.n**.1	0	5	0
Xenylla **sp.n.**2	3	0	0
Pseudachorutes nr. *nica*	0	5	7

Table 5.3 *List of identify species and their total abundance at three forest type in LEF (continuation)*

Species/Forest type	tabonuco	palo colorado	elfin
Pseudachorutes nr. *parvula*	0	2	49
Tallasaphorura smilodonta **sp.n.**	26	66	1
Mesaphorura cf. *ruseki*	30	49	2
Dicranocentrus celatus	3	82	40
Dicranocentrus marias	18	227	1032
Heteromurtrulla tithuensis	27	65	39
Isotomurus degrade **sp.n.**	2	25	1248
Hemisotoma sp.	192	383	282
Folsomides parvulus	31	96	21
Isotomiella minor	891	818	6
Isotomiella unknow	0	3	0
Folsomina onichuirina	107	207	3
Entomobrya longiseta	34	37	2
Entomobrya flavum **sp.n.**	0	11	21
Lepidocyrtus caprilesi	175	3	2
Lepidocyrtus dispar	52	44	26
Lepidocyrtus dispar A	4	0	0
Lepidocyrtus dispar B	9	12	119
Lepidocyrtus dispar D	10	17	57
Lepidocyrtus dispar f.epifita	0	2	39
Lepidocyrtus maldonadoi	14	10	19
Lepidocyrtus paracaprilesi	2	11	2
Lepidocyrtus paracaprilesi f. epifita	0	10	11
Seira desapercibida	8	71	32
Pseudosinella biunguiculata	6	17	5
Pseudosinella violenta	0	0	10
Oncopodura arecibena	0	1	0
Chypoderus cf. *similis*	19	32	1
Serroderus yunquensis **sp.n.**	11	1	0
Campylothorax sabanus	46	60	16
Campylothorax sabanus f.epifita	0	3	7
Troglolaphysa geminata	49	2	1
Troglolaphysa jataca	0	10	5
Troglolaphysa luquillensis	0	1	0
Troglolaphysa sp.	17	3	2
Sphaeridia sp4	20	17	123
Arropalites sp1	1	3	0
Sphyroteca aleta	15	23	50
Calvatomina rufences	26	8	0
Ptenothix borincana	33	2	0

Table 5.3 *List of identify species and their total abundance at three forest type in LEF (continuation)*

Species/Forest type	tabonuco	palo colorado	elfin
Neelus desantisi	269	230	63
Neelides minutus	70	57	14

In this survey, I cannot make conclusions regarding species turnover because the localities on the gradient are not along a linear transect. I can therefore only discuss ranges of altitude adaptation. The species with a large influence on the observed variability change through forests types. *Dicranocentrus marias* and *Isotomurus degrade* sp.n. were abundant in the elfin forest while there were few individuals of this species in tabonuco and palo colorado forest (Figure 5.9, Table 5.3). On the contrary, *Isotomiella minor* exhibited large numbers in tabonuco forest and decreased in abundance at the highest elevation. Finally, *Hemisotoma* sp. showed a high abundance in the three forests types, suggesting a possibility of survival when environmental conditions change.

Some species with low influence in the variation are exclusive to one forest type. This is the case of *Arlesia* **sp.n** and *Furculanurida bistribus* **sp.n.** in the elfin forests or *Hylaeanura aemilia* **sp.n.,** and *Xenylla* **sp.n.**1 in palo colorado forest (Figure 5.7). The mentioned species have low abundance but are important in the differentiation of the Collembola assemblages and show adaptations to climatic and biotic conditions that are different for each species (McCoy 1990, Olson 1994). Tropical species have been suggested to be more habitat specific and have narrower tolerance ranges to physical conditions because of the relative uniformity of local environmental conditions (Janzen 1967, Giller 1996, González and Seastedt 2001).

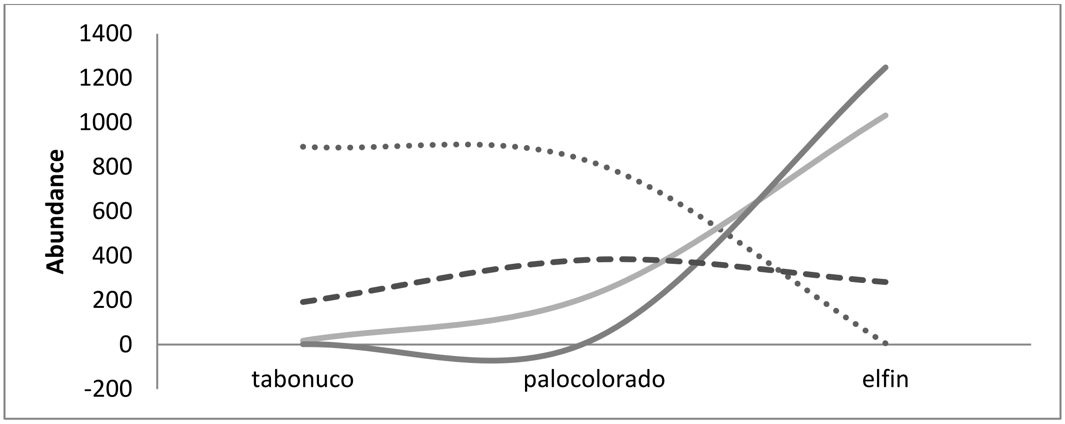

Figure 5.10 Changes in abundance for Collembola species with more contribution to the variation between three forest types at LEF according to SIMPER. Solid line light is for *Dicranocentrus marias*, and dark for *Isotomurus degrade* sp.n. The pointed line is for *Isotomiella minor* and discontinuous line for *Hemisotoma* sp.

As a way of maintaining more effective ecosystem function, it is necessary to obtain a deeper understanding of how species are distributed and where can their highest diversity by found (Weaver 2012). Collembola was present in a wide range of habitats throughout the montane forests at the LEF. My results show significant differences between Collembola assemblages among the forest types. These differences in species abundance and diversity could be explained by the environmental factors of altitudinal variation, soil and air temperature and humidity. Other environmental factors with lower correlation, such as precipitation, may also be affected by altitudinal variation. The Collembola species can be separated according to altitudinal ranges, similar to what has been described for vegetation (Gould et al. 2006). For a better understanding of Collembola assemblages, it is important to incorporate physicochemical properties of litter and soils in statistical analyses, due to the variability in these characteristics among forest types and their influence on plant species composition. This information will be useful in clarifying the extent to which the differences in abundance and biodiversity of Collembola depend on altitude, climate, plant composition or soil characteristics (Richardson et al. 2005, Willig et al. 2013).

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Chapter 6 Conclusions: Collembola assemblages in the montane environments of the Luquillo Experimental Forest in Puerto Rico.

Soil ecology is a relatively new and very active field of research (Lavelle 2009), and as all other ecological sciences, faces many challenges in studying rapidly changing environments (Andrén et al. 2008). One of the biggest challenges in many ecological fields is the identification of species (Anderson 1975, Eisenhauer et al. 2017). For soils, the number of species is ever higher because they are the natural habitat for millions of species of bacteria, saprophytic fungi, arbuscular mycorrhizal fungi, mites, springtails and earthworms that include broad functional groups widely used in studies of soil ecology (Andrén et al. 1995, Wardle 2006).

To simplify the composition of soil inhabitants, their separation into functional groups is often used (Wallwork 1970, Brussaard 1998). As a group, Collembola are detritivoric mesofauna (Hopkin 1997, Lavelle et al. 2006) but there is little recognition of the composition and function of specific assemblages (Potapov et al. 2016). The present works represent early steps in understanding these assemblages as well as the population dynamics of Collembola species in a tropical montane environment in Puerto RIco. As a consequence, my objective with this study was to understand the organization of Collembola species along a gradient of soils and their related microhabitats of leaf litter and mosses. My first step was identifying species; as there are many unknown species that require a description. As a second step, I studied the species distribution along habitats and microhabitats and looked for environmental variables that explained the observed distribution patterns.

1. Collembola diversity in Puerto Rico

The Collembola fauna of Puerto Rico are reasonably well known, but many recent reports are scattered in published literature and unpublished theses. The first goal of this dissertation was to present a summary of all springtail species identified from Puerto Rico, including new, previously unpublished and historical records. As a result I list 124 species in 59 genera and 17 families. Most species, 73, belong to the Entomobryidae family, but this work made a significant contribution to the inventory of Poduromorpha species with 17 new reports, as well as up to 52 species never before found in Puerto Rico for this order (Figure 6.1). In addition to the new reports, a database of the distribution of the species outside the island is provided. The dataset presented here is a work in progress and will be updated as ongoing taxonomic inventories are completed. The complete dataset is available via the Long Term Ecological Research –Luquillo web site: http://luq.lter.network/datacatalog

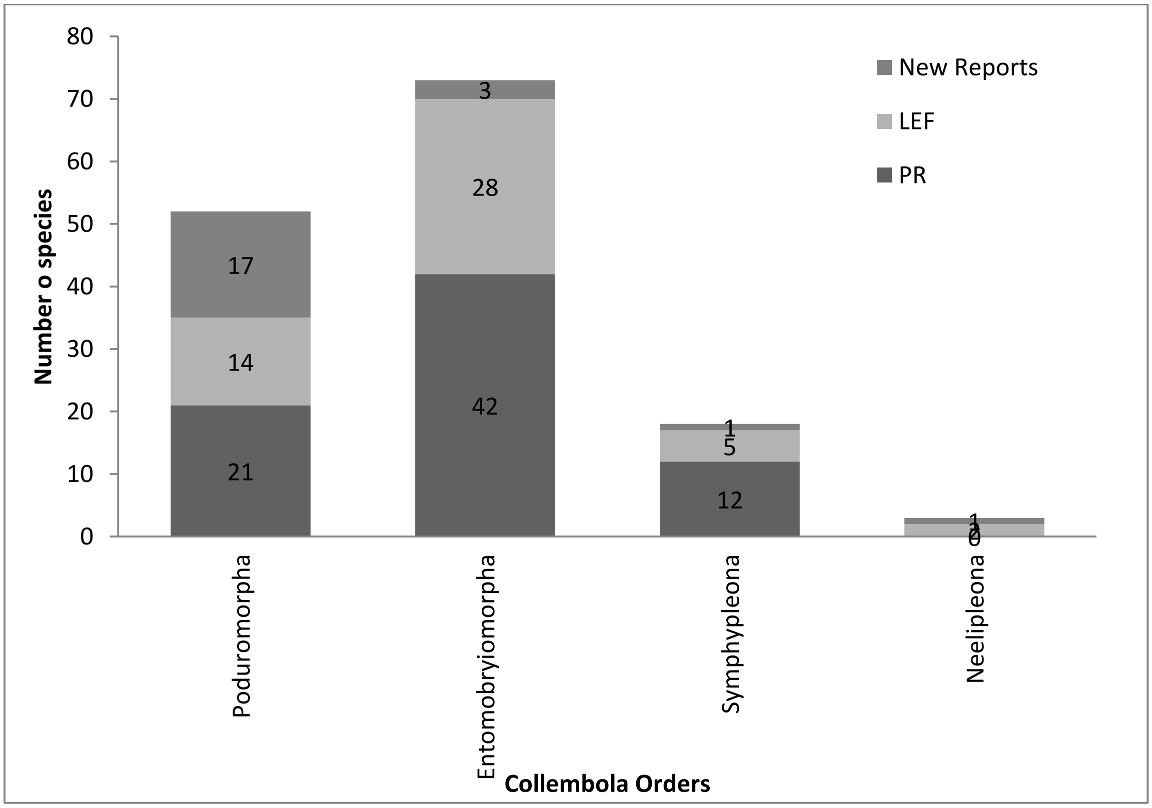

Figure 6.1 Number the species reported in Puerto Rico (PR), previous reports in Luquillo Experimental Forest (LEF) and new reports for the present survey.

In this study, the Collembola inventory in the Luquillo Mountains includes 16 families, 37 genera and 53 species and seven subspecies. Among them, 15 are new species in 12 genera.

Moreover, two are new subspecies for the species *Folsomiella intermedia* and *Micranurida wladimiri*. In total, 22 species are new reports from Puerto Rico. After this survey, the inventory of Collembola species identified in the Luquillo Experimental Forests totals 70 species in 44 genera and 15 families.

In Puerto Rico, the largest entomological collections are located at the "Museo de Entomología y Biodiversidad Tropical" (MEBT) and on the main campus of the University of Puerto Rico at Mayagüez campus (UPRM). Inside these entomological collections, Collembola is one of the better represented groups (Capriles 1996, Franz and Yusseff Vanegas 2009). The present inventory, besides being an important contribution for the description of Collembola in PR also shows that even well studied soil organismal groups need more recognition.

2. New Collembola species from the LEF

In this study, 15 new species in the genera *Pronura, Arlesia, Furculanurida, Hylaeanura, Pseudachorutes, Brachystomella, Xenylla, Microgastrura, Thalassaphorura, Isotomurus, Entomobya* and *Serroderus* have been described. Two new subspecies were described for the species, *Folsomiella intermedia* and *Micranurida wladimiri* (Table 6.1).

Table 6.1 Synthesis of the characteristics, distribution and ecological classification of the new species from LEF

Genera	Species	Diagnosis	Distribution	Ecological clasification
Pronura	sp.n.	No color, no eyes, one acuminated macrosetae, one thick macrosetae and one microsetae in Adb VI	Leaf litter at *Tabebuia rigida* and *Cyrilla racemiflora* forest type	Epiedaphic, low mobility
Arlesia	sp.n.	Color pattern, eyes 3+3, absent to the unguiculus internal teeth	Leaf litter at *Tabebuia rigida* forest type	Epiedaphic, low mobility
Furculanurida	*bistribus* sp.n	Color pattern, eyes 3+3, 3 setae in dens and the absent of internal tooth in the unguis	Leaf litter and mosses at *Tabebuia rigida* forest type	Hemiedaphic, low mobility
Hylaeanura	*aemilia* n.sp	No color, 2+2 eyes enlarge of the sensilla s3 in Ant IV, manubrium without setae	Soil and leaf litter at *Cyrilla racemiflora* forest type	Euedaphic, low mobility
Micranurida	*wladimiri* subsp. *caribeña*	No color, 2+2 eyes in a pigmented patch, PAO with seven vesicles disposed in a rosette	Leaf litter at *Cyrilla racemiflora* forest type	Epiedaphic, low mobility

Table 6.1 Synthesis of the characteristics, distribution and ecological classification of the new species from LEF (continuation)

Genera	Species	Diagnosis	Distribution	Ecological clasification
Pseudachorutes	n.sp1	Color purple, eyes 8+8, PAO with 5-6 vesicles, absent of teeth in the unguis and presence of one acuminate tenet hair	Leaf litter and mosses at *Tabebuia rigida* and *Cyrilla racemiflora* forest type	Hemiedaphic, low mobility
Pseudachorutes	n.sp2	Color pattern, eyes 8+8, OPA with 16-20 vesicles, ocular macrosetae, presence of an inner teeth in the unguis and one acuminated tenet hair	Leaf litter and mosses at *Tabebuia rigida* and *Cyrilla racemiflora* forest type	Hemiedaphic, low mobility
Brachystomella	n. sp1	Color pattern, eyes 8+8, bilobulate apical vesicle in Ant. IV, 6-7 setae in dens	Soil and leaf litter at *Cyrilla racemiflora* forest type	Euedaphic, low mobility
Brachystomella	n. sp2	Color purple, eyes 8+8, simple apical vesicle in Ant. IV, 5 setae in dens	Leaf litter at *Cyrilla racemiflora* and *Tabebuia rigida* forest type	Epiedaphic, low mobility
Folsomiella	*Intermedia* subsp.n. *ciega*	Color light blue, eyes 1+1 or 2+2, OPA with 7-8 vesicles, 5 setae in dens	Leaf litter at *Cyrilla racemiflora* and *Dacryodes excelsa* forest type	Epiedaphic, low mobility
Microgastrura	*parvaboletus* sp.n.	Color gray, eyes 6+6, 30 to 40 “trumpet” setae in Ant. IV and the presence of 4 spiniform setae plus three acuminate setae in dens.	Leaf litter and soil at *Cyrilla racemiflora* and *Tabebuia rigida* forest type	Epiedaphic, low mobility
Xenylla	n.sp1	Color gray, eyes 5+5, absence of furcula and tenaculum	Mosses at *Cyrilla racemiflora* forest type	Hemiedaphic, low mobility
Xenylla	n.sp2	Color gray, eyes 5+5, furcula reduce and tenaculum present	Mosses at *Dacryodes excelsa* forest type	Hemiedaphic, low mobility
Thalassaphorura	*smilodonta* n.sp	No color, no eyes, OPA with 12-14 simple vesicles in two rows	Leaf litter at *Cyrilla racemiflora* and *Dacryodes excelsa* forest type	Epiedaphic, low mobility
Isotomurus	*degrade* n.sp	Color light to dark blue, 4 to 8 disto- lateral setae in the Collophore, 2-6 setae on corpus tenaculum and the absence of basal lamella in mucro	Soil, leaf litter and mosses at *Cyrilla racemiflora, Tabebuia rigida* and *Dacryodes excelsa* forest type	Generalist, high mobility
Entomobrya	*flavum* n.sp	Color pattern, their strongly truncate unguiculus	Mosses at *Cyrilla racemiflora, Tabebuia rigida* and forest type	Open environment, high mobility
Lepidocyrtus	*paracaprilesi* Form epiphyte	Color white, one teeth in the unguis	Mosses at *Cyrilla racemiflora, Tabebuia rigida* and forest type	Open environment, high mobility
Campylothorax	*sabanus* Form epiphyte	Color dark purple.	Mosses at *Cyrilla racemiflora, Tabebuia rigida* and forest type	Open environment, high mobility
Serroderus	*yunquensis sp.n.*	No color, no eyes, mucro with 12 teeth	Leaf litter at *Cyrilla racemiflora* and *Dacryodes excelsa* forest type	Below mobility, high mobility

For the new species, 12 belong to Poduromorpha Order, denoting that this group needs more sampling, identification and phylogenetic resolution (Soto-Adames, personal communication). Using the proposed ecological classification in chapter four of the present dissertation, most of the new species had low mobility (Table 6.1), and as a consequence they are less abundant and hard to find. This would be an explanation for why these species were only found after my intensive sampling.

3. Collembolans along Microhabitats

In this study, morphological traits were correlated with microhabitat characteristics of Collembola. Additionally, Collembola species could be divided in two larger groups characterized as low and high mobility. Collembola assemblages change in each microhabitat, in abundance, number of species, and species composition (Figures 6.2-3).

Figure 6.2 Stacked area showing the percentage of the abundance in soil, leaf litter and mosses of each species classify as high mobility ecology group in the LEF samples.

An ecological classification of the Collembola species identified at LEF is proposed here (chapter 4), based on their morphological traits and their distribution among the microhabitats. Following this classification, species abundance was distributed according to their capacity to move (Figures 6.2-3). In the case of the low mobility group (Figure 6.3), there are rare species found in low abundances. These species emphasize the differences in the Collembola assemblages of each microhabitat, showing that particular traits characterize a community and fulfill decomposition functions (Andrén et al. 1995, Bengtsson 1998, Wolters 2001).

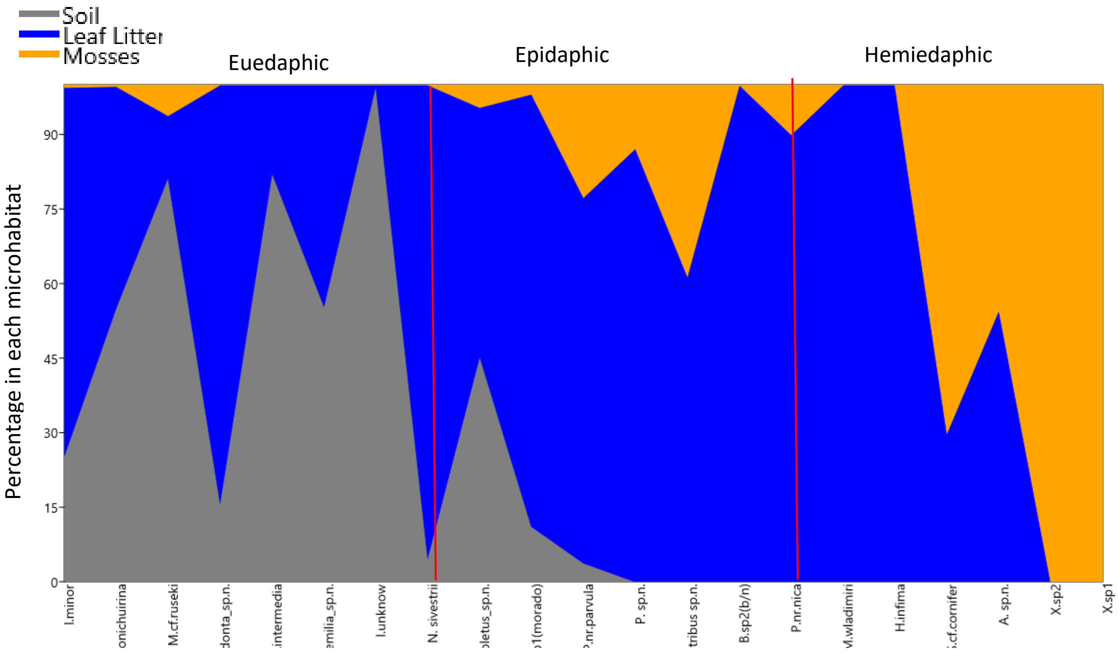

Figure 6.3 Stacked area showing the percentage of the abundance in soil, leaf litter and mosses of each species classify as low mobility ecology group in the LEF samples.

The general species distribution pattern (Figure 6.4) shows greater numbers for leaf litter microhabitats, where a large number of individuals and species were found. This habitat has better quality and quantity of available Collembola food resources (Yoshida and Hijii 2005), like decomposer fungi (Lodge 1997). Moreover, leaf litter becomes a stable environment when the soil is flooded or when wind is strong (Palacios-Vargas et al. 1998). Mosses were the second habitat preferred by Collembola in the LEF, confirming that mosses and epiphytes play an important role in sustaining the abundance and diversity of Collembola (Palacios-Vargas et al. 1998, Rodgers and Kitching 2011).

In general, the vertical distribution of Collembola follows that as soil depth increases, abundance and diversity decreases (Cutz-Pool et al. 2010). Some Collembola species are restricted to one stratum of the ecosystem (Hågvar 1982, Ponge 2000). Springtail communities are unique even if they show similar species composition among stratum. The differences in abundance of common species and, the characteristics of more specialized species, highlight the differences in vertical distribution of Collembola communities (Rodgers and Kitching 1998, Palacios-Vargas et al. 2007, Sanders and Rahbek 2012).

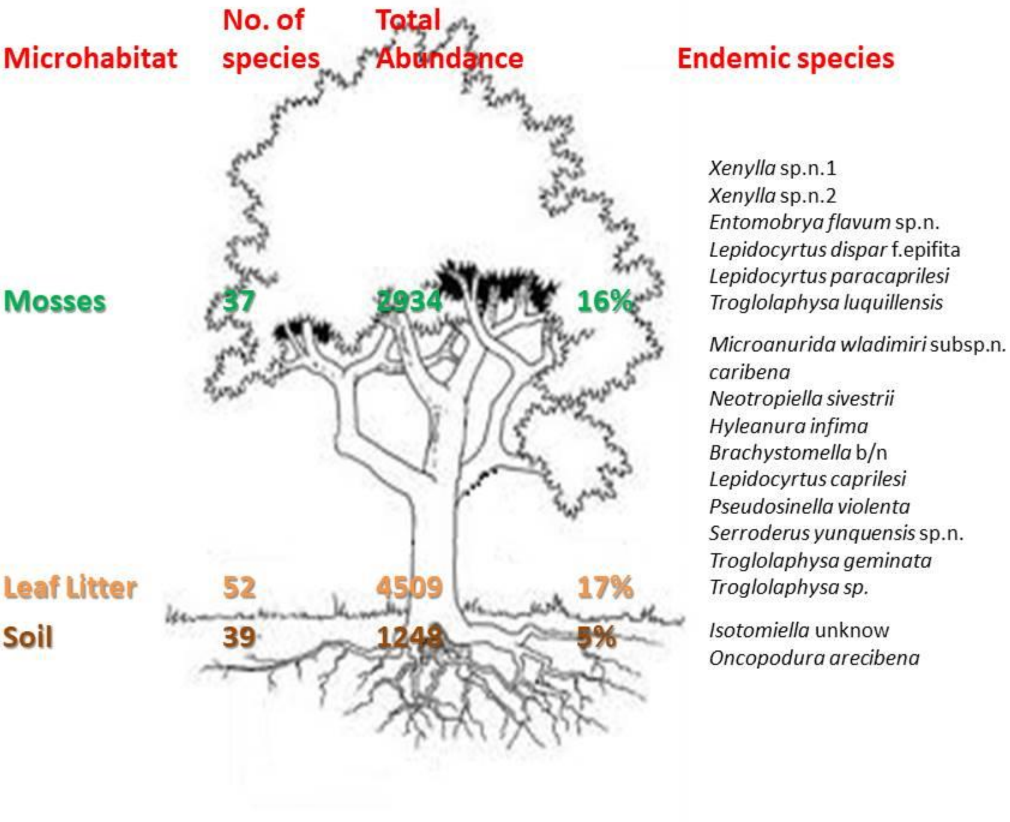

Figure 6.4 Distribution of number of species and individuals, percentage and list of endemic species of Collembola in soil, leaf litter and mosses sampled in LEF.

In examining morphological traits, it is possible to visualize the mechanisms that shape species distribution along microhabitats in a tropical forest (Ponge and Salmon 2013, Salmon et al. 2014, Widenfalk et al. 2016). Previous studies point out the importance of using trait attributes over abundance, richness and other diversity functional measures (McGill et al. 2006, de Bello et al. 2010, da Silva et al. 2016). My analysis shows differences in species composition through microhabitats, and that mobility capacity resulting from morphological adaptations was more important for the ecological classification. However, more evidence is needed concerning the relationship between the grade of mobility of a species and the mechanisms that determinate the variation in community composition (Moore et al. 1988). Understanding the roles of the soil organisms would lead us to direct studies about the function and conservation of soil ecosystems (Bardgett et al. 2005, McGill et al. 2006).

4. Distribution of Collembola along environmental gradients

For the comparison of Collembolan assemblages among forests types, I evaluated the influence of environmental variables that could best determinate their assemblage. The three forest types of tabonuco *(Dacryodes excelsa)*, palo colorado (*Cyrilla racemiflora)* and elfin (*Tabebuia rigida)* have sharp differences in temperature (in soil and air), humidity, precipitation and vegetation type. According to the results, the altitude, precipitation, temperature and humidity are parameters that explain variations in Collembola assemblages along the studied environmental gradient. According to PCA, the altitudinal variation is the parameter that most influences Collembola variation. The influences of other environmental parameters vary between the forest types.

The distribution of Collembola assemblages along the environmental gradient was plotted using our proposed ecological classification (Figures 6.5-6). The high mobility - upper group (Figure 6.5) was most abundant in the elfin forest, while the low mobility group, epidaphic, was most abundant in palo colorado forests. For the wide mobility group an even distribution along the three forest types observed, confirming their generalist nature and their adaptation ability. In the upper areas- mobility group, half of the species are evenly distributed while the other half prefers palo colorado and/or elfin forest. This is an expected distribution when considering that the tabonuco forest type does not have many epiphytes or mosses that serve as habitat for this species. Finally, the below areas- mobility group have their greatest abundance at tabonuco and palo colorado forests but few species and individuals in the elfin forest, demonstrating that the soil conditions in the latter are not favorable for collembolans.

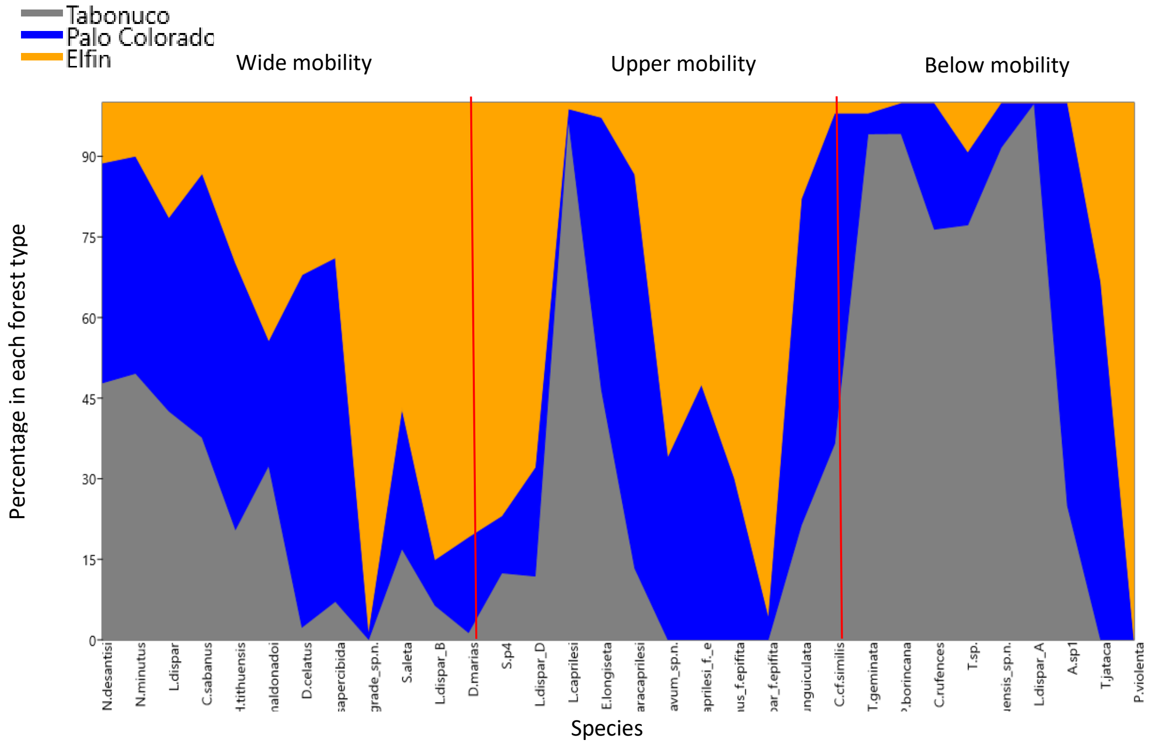

Figure 6.5 Stacked area showing the percentage of the abundance in tabonuco, palo colorado and elfin forests of each specie classify as high mobility ecology group in the LEF samples.

For the low mobility group, *Isotomiella minor* and *Folsomina onychiurina*, are cosmopolitan species that are distributed worldwide (Hopkin 1997, Ospina Sánchez et al. 2018), so these species are present in all three forest types at LEF. The euedaphic species show an even distribution, but with less abundance in the elfin forest. Moreover, the epidaphic and hemiedaphic species are scarce in the tabonuco forest. In palo colorado forests, we found good representation in terms of the number of individuals of epidaphic and hemiedaphic species. In elfin forests, we have less species but the largest abundance. The differences in Collembola assemblages and species morphological traits among the montane forest reflect the variation along the altitudinal gradient in terms of temperature and rainfall but also vegetation composition, and the degree of isolation that affects species distribution (Gould et al. 2006, da Silva et al. 2016).

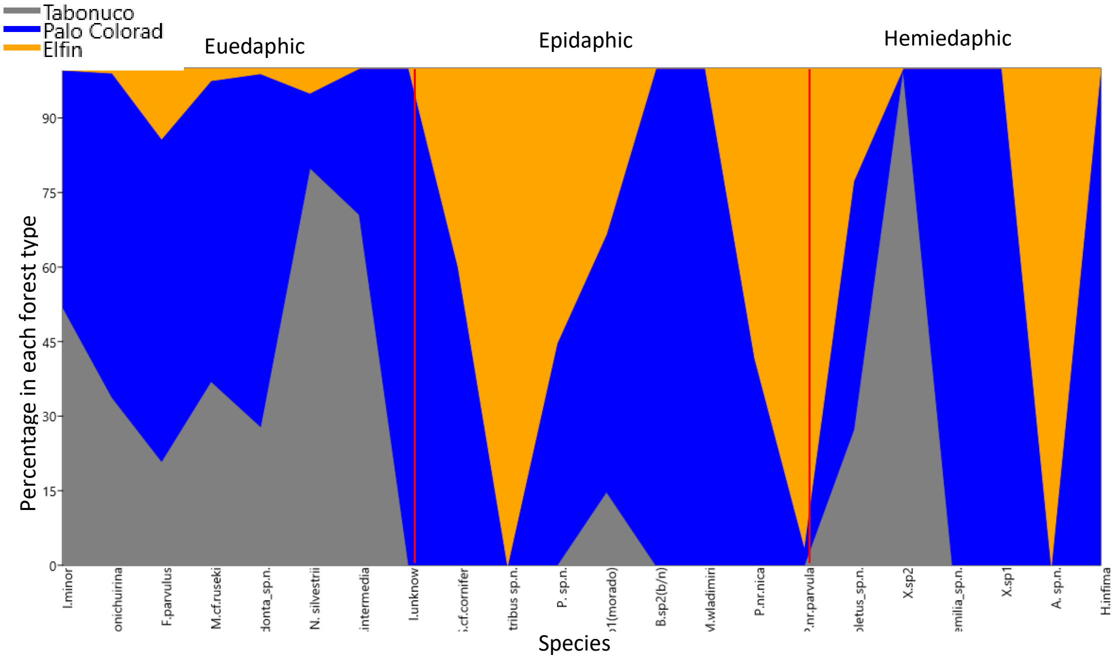

Figure 6.6 Stacked area showing the percentage of the abundance in tabonuco, palo colorado and elfin forests of each species classify as low mobility ecology group in the LEF samples.

In summary, 8691 individuals were collected, belonging to 16 families, 37 genera and 53 species and seven subspecies. For tabonuco and palo colorado forests, the largest abundance and number of species were found in the leaf litter microhabitat (Table 6.2), while in the elfin forest, the larger abundance was found in the mosses. The total abundance of Collembola was highest in the elfin forest but the largest number of species was found in palo colorado forest (Figure 6.7).

The mid elevation forests were the most diverse, with an even distribution of species and low dominance. Palo colorado forests seem most favorable for invertebrate survival (Richardson et al. 2000, Richardson et al. 2005).This forest has lower wind velocities than the elfin forest and higher rainfall than the tabonuco (Gould et al. 2006). Adaptation to increasing elevation appears to be species-based. Changes in humidity, temperature, rainfall, and food supply can determine growth rates and body size of arthropods (Richardson et al. 2005). The tabonuco forest in PR has longer dry periods, while Palo Colorado and dwarf forests are amenable habitats for species most vulnerable to desiccation (Richardson 1999).

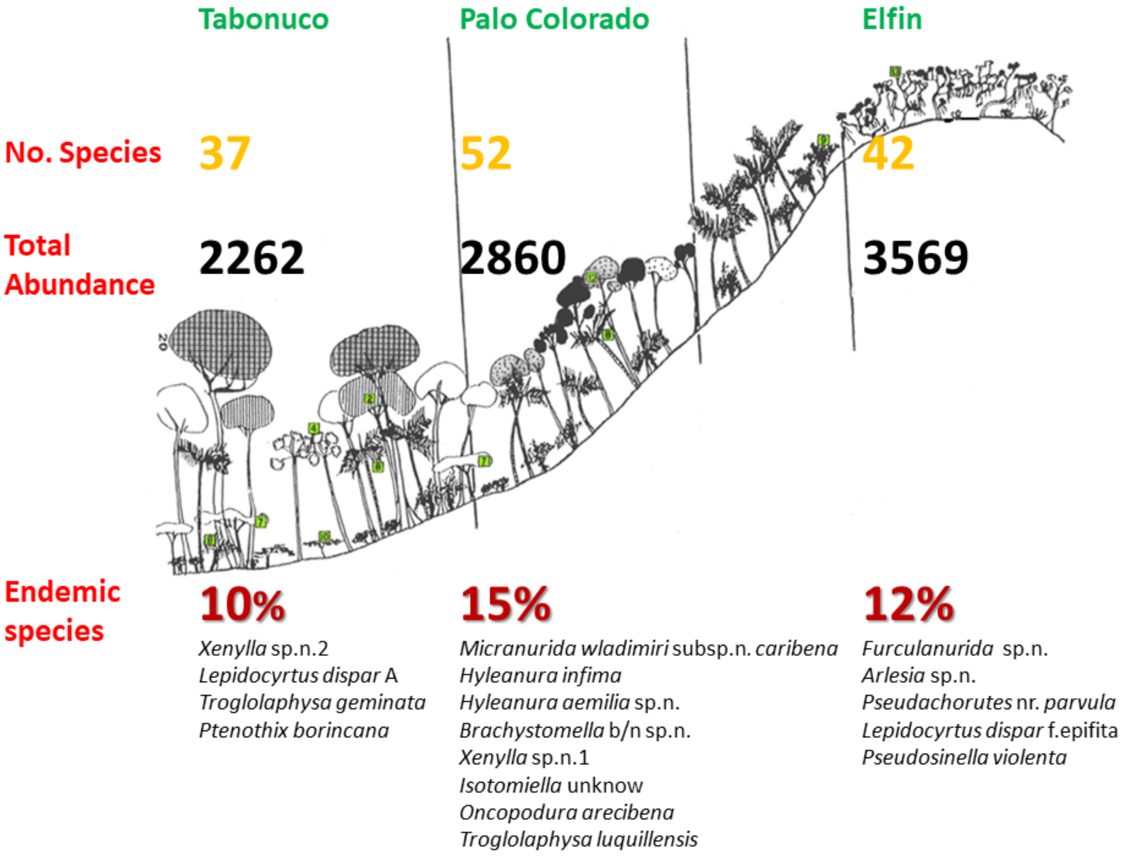

Figure 6.7 Distribution of number of species and individuals, percentage and list of endemic species of Collembola in tabonuco, palo Colorado and elfin forests types in LEF.

5. Perspectives

Collembolans have the ability to colonize many distinct environments. They are also one of the soil fauna groups with greater biomass contribution to soils (Hopkin 1997). These organisms are common detritivores and fungivores. These microarthropods are found throughout the vertical microhabitat structure of forests from aboveground (canopy and leaf litter suspended in epiphytes) to belowground parts (soil forest floor leaf litter and humic soils). They play important roles in the functioning of detrital food webs (Seastedt 1984, Petersen 2002) and participate actively in organic material degradation processes, nutrient recycling, and mineralization of useful elements for plants (Palacios-Vargas et al. 2000).

Variations in Collembolan communities have been related to various habitat factors, such as soil water condition, vegetation, and soil fertility (Hågvar 1982), as well as soil chemistry (Salamon and Alphei 2009) and the presence of other organisms (Salmon and Ponge 1999). Moreover, Collembola is a very diverse group in soil, litter, and vegetation, making it an efficient instrument for diversity studies in those habitats (Deharveng 1996). Although there have been many studies of the spatial distribution of collembolan in various microhabitats (Rodgers and Kitching 2011), few studies have examined patterns between the canopy and soil strata in relation to the vertical structure of chemical factors, mobility, or the changing conditions on the tropics.

5.1. Research gaps on chemical factor that influence the Collembola assemblages

Soil, vegetation and plant litter types are important habitat components in which the diversity of decomposer organisms may potentially influence ecosystem functioning (Wallwork 1970). The question of how mixing of litter from different plant species in turn influences decomposer processes has recently been attracting attention (Gartner and Cardon 2004, Schädler and Brandl 2005), and is apparent from several studies that diversity within major belowground groups to be unrelated to live plant diversity even when other community- and ecosystem level properties are related (Wardle 2006).

In the LEF studies, arthropods α-diversity declines with decreasing NPP at higher elevations (Richardson 1999). However, species richness is not related to litter quantity and quality or to nutrients in the forest ecosystem *per se* (Richardson et al. 2000, Yang et al. 2007). For the common cations, animal species richness increases as nutrient inputs per plant increase. Both animal diversity and plant nutrient inputs are significantly larger in the tabonuco and palo colorado forests than in the elfin forest, with nutrient inputs in the palo colorado being slightly higher than those in the tabonuco, due to of larger overall plant size (Richardson et al. 2000). Yet, the importance of nutrient composition on Collembola species assemblages is seldom mentioned in previous studies (García-Gómez et al. 2009), representing an important focal point for future work.

5.2. More sampling in mosses and epiphyte mats.

The canopy organic matter is composed of shoots and roots of vascular and non-vascular plants, abscised leaves of host trees, and epiphytes that have been intercepted by branches (Nadkarni et al. 2002). These mats are colonized by communities of meso- and microarthropods, fungi, and other microorganisms that are distinct from floor communities, and as a consequence, interact with whole-forest processes (Nadkarni et al. 2002). The canopy organic matter influences nutrient cycling by altering ecosystem nutrient pools, pathways, and rates of fluxes (Coxson and Nadkarni 1995).

Arthropods and epiphytes are significant biodiversity components of tropical forest canopies. These two biological elements share a link in forests via the presence of epiphyte mats—accumulations of living and dead plant material on the upper surfaces of branches (Yanoviak et al. 2003) that harbor a diverse but inconspicuous arthropod fauna. This material also provides habitat for other diversified invertebrate fauna, which includes many of the major groups of decomposers found in terrestrial soil (Nadkarni and Longino 1990). Entomologists have documented that the dead organic matter is inhabited by numerous species of invertebrates in both tropical and temperate forest canopy mats (Longino and Nadkarni 1990). This system is dominated by mites, springtails, ants, and minute beetles (Yanoviak et al. 2004, Yanoviak et al. 2007, Richardson and Richardson 2013). Many species are canopy specialists, which are never encountered on the forest floor (Nadkarni and Longino 1990, Paoletti et al. 1991). Additionally, recent studies have documented numerous forest types where canopy organic matter is abundant: tropical montane forests, temperate rainforests, elfin woodlands, and some lowland forests (Coxson and Nadkarni 1995). Our study recognizes these areas of canopy litter are important for ecosystems, demonstrating their large biodiversity and the need for more studies to understand and protect them.

5.3. Measuring the effect of climatic change on islands and Collembola assemblages

Litter moisture content clearly affects the distribution of arthropods in the forest during the dry and rainy seasons (Aerts 1997, Chernova and Kuznetsova 2000). Some of the variance in litter arthropod populations can be attributed to litter moisture content (Levings and Windsor 1984, Frith and Frith 1990). The abundance of soil inhabiting arthropods in tropical forests with a seasonal pattern of rainfall was observed to be lower during dry periods (Adis et al. 1987, Richardson et al. 2005). Changes in abundance are related to decreasing precipitation and litter and soil moisture contents (Levings and Windsor 1984). These factors also resulted in vertical migration of arthropod groups into the soil (Adis et al. 1987)

Factors such as seasonal changes in rainfall, severity of the dry season, litterfall moisture content and decomposition rates have all been shown to influence the annual and seasonal changes of litter faunas in tropical rain forests (Levings and Windsor 1984, Adis et al. 1987, González et al. 2007). Moisture availability would appear to be the most important of these factors (Frith and Frith 1990). In the LEF, there is a clear seasonality: a dry season begging in February and a wet season usually initiated in May and extending to November (Schowalter et al. 2014). It is relevant to evaluate the responses of Collembola populations over these changes in precipitation regimes to get an idea of how arthropod assemblages respond to seasonal environmental changes.

5.4. Study the biotic interaction of Collembola with other arthropods

Biotic drivers of soil biodiversity operate over a range of spatial and temporal scales. Soil organisms can be regulated both within and between taxa or functional groups (Wardle 2006). The interactions among taxa within the same trophic group are most likely to be regulated by competition or resource availability, although most groups are regulated to some extent by both factors (Wardle 2002). However, soil animal diversity generally does not show a hump-backed response to increases in disturbance intensity or resource availability (Wright and Coleman 1993), indicating that factors that maximize soil animal biomass or density do not promote dominance of competitive species that reduce subordinate species by competitive exclusion (Wardle 2006).

Regulation of major groups of soil biota through predation is widespread in soil food webs (de Ruiter et al. 1995) and there are many examples of regulation of densities of both soil animals and soil microbes by their consumers (Wardle 2002). Further, consumption of microbes by soil fauna is likely to be an important driver of soil microbial community structure. Fungal-feeding fauna show a distinct preference for some fungal taxa or hyphal types above others (Ferlian et al. 2015). Even this implies that identifying species and their relationships is relevant to understanding the biotic drivers of soil biodiversity. This so-called “diversity-functioning” issue is focused on determining whether organism diversity influences key ecosystem properties such as decomposition, nutrient flow rates, productivity, and resistance and resilience to disturbances.

5.5. Other considerations and future work

- Even though the use of morphological traits was useful in the segregation of functional groups of Collembola, it is necessary to evaluate the role of mobility within each species among microhabitats to determine this functional trait's importance in the context of disturbances and climate change. In the LEF, disturbances produced due to changes in the precipitation regimen include the hurricanes and flooding; and these could be determinant factors for microarthropods distributions.
- Multiple factors such as, pH levels, and other physical and chemical characteristics of the substrate can have a large influence on Collembola species distribution. Species with a restricted distribution may be responding to some of these factors. Therefore, it is important to characterize forest microhabitats, to evaluate their ability to support species and to determine how their differences influence the assemblages of Collembola. The soil characterization would be useful to describe the functioning of collembolans when these species are unique or whether contributing to redundancy in soils.
- The diversity index allows for comparisons among sites; however other community level indexes provide a better understanding of the distribution of species within sites. The similarity and evenness for Collembola assemblages should be included in future analysis because they can help understand how species abundance is distributed among the microhabitats and forest types, highlighting the importance of abundant and exclusive species.

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