Received: 26 March 2019 | Revised: 30 May 2019 | Accepted: 27 June 2019
DOI: 10.1111/zsc.12377

ORIGINAL ARTICLE

Zoologica Scripta WILEY

The discovery of Neotropical *Lepidosira* (Collembola, Entomobryidae) and its systematic position

Rudy C. Nunes[1,2] | **Nerivânia N. Godeiro**[1] | **George Pacheco**[3] | **Shanlin Liu**[3,4] | **Marcus Thomas P. Gilbert**[3] | **Fernando Alvarez-Valin**[5] | **Feng Zhang**[6] | **Bruno C. Bellini**[1]

[1]Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte, Natal, Brazil

[2]Federal Institute of Education, Science and Technology of Piauí, Pedro II, Brazil

[3]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

[4]BGI-Shenzhen, Shenzhen, China

[5]Sección Biomatemática, Unidad de Genómica Evolutiva, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

[6]Department of Entomology, College of Plant Protection, Nanjing Agricultural University, Nanjing, China

Correspondence
Nerivânia N. Godeiro, Department of Botany and Zoology, Biosciences Center, Federal University of Rio Grande do Norte, Natal, RN, Brazil.
Email: nerivania@gmail.com

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 441451/2014-4, PQ2015 and 301498/2015-6; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: BEX 6891/15-2

Abstract

We herein present the first reliable record of *Lepidosira* from Neotropical Region. *Lepidosira neotropicalis* sp. n. from Brazil is described and illustrated in detail, including its complete mitochondrial genome. We perform a Bayesian phylogenetic analysis to place the new species within the Entomobryidae, and at the same time to test previous contrasting hypotheses on *Lepidosira* position within the Entomobryinae versus Seirinae for the first time. Phylogenetic analyses were based on one mitochondrial and two nuclear genes, Cytochrome Oxidase subunit I, 18S ribosomal RNA and 28S ribosomal RNA, respectively. *Lepidosira neotropicalis* sp. n. resembles *L. sundana* Yoshii and Suhardjono and *L. nigropunctata* (Nguyen) in dorsal chaetotaxy of abdominal segments I and II, but differs from all other species by the combination of head (dorsally and ventrally) and dorsal trunk chaetotaxy, plus empodial complex morphology. Our phylogenetic analyses support the placement of *Lepidosira* within Entomobryinae, as the sister group of *Lepidocyrtoides*. Overall, our revision enables a more objective diagnosis to *Lepidosira* and suggests that the genus is in need of a full revision due to its variable morphology, and lack of data needed to evaluate its monophyly. Finally, we provide an identification key for Neotropical genera of Entomobryinae.

KEYWORDS
Caatinga, Entomobryomorpha, genome, integrative taxonomy, mitochondrial, phylogeny

1 | INTRODUCTION

Entomobryinae *sensu stricto* (Collembola, Entomobryomorpha, Entomobryidae) currently presents a total of 12 genera recorded from the Neotropical Region: *Amazhomidia*, *Americabrya*, *Calx*, *Coecobrya*, *Desertia*, *Drepanosira*, *Drepanura*, *Entomobrya*, *Homidia*, *Lepidocyrtoides*, *Sinella* and *Willowsia*; with a total of 83 described species, summarized in Table 1 (Bellinger, Christiansen, & Janssens, 1996–2019; Jordana & Baquero, 2008; Mari-Mutt & Bellinger, 1990, 1996). Here, we consider the Entomobryinae as proposed by Zhang and Deharveng

(2015) and Zhang, Sun, Yu, and Wang (2015) studies, in which after integrating molecular and morphological evidence (mainly the S-chaetotaxy) disregarded the importance of the presence or absence of scales to separate the Willowsiini and Entomobryini. The genus *Lepidosira* has 54 described species. These are predominantly found in South and Southeast Asia and Oceania, although a few records also exist from Africa and even Antarctica (Bellinger et al., 1996–2019).

Schött (1925, p. 116) defined a broad and non-objective diagnosis for *Lepidosira*, which can be summarized to: "more or less *Seira*-like in appearance, with jointed tibiae and retractile terminal organ on Ant. IV. Scales of varying types but generally pointed, with long internal distinct striation." Womersley (1939, p. 201) complemented Schött's diagnosis with: antennae not annulated, mesothorax not overlapping head and claws "normal." Additionally, Salmon (1938, p. 349) proposed the genus *Urewera*, which was posteriorly considered as a junior synonym to *Lepidosira* (Soto-Adames, Barra, Christiansen, & Jordana, 2008; Womersley, 1939). In his description, Salmon (1938) diagnosed the new genus based solely on claw and scale morphology. Later, Salmon (1941, p. 376) extended the diagnosis of *Urewera* and added, among other features, an "Ant. IV generally with apical sensory knob," indicating this structure can be present or absent in members of the genus. In our bibliographic revision of the valid species of *Lepidosira*, we found that most of these diagnostic characters are quite variable (presence of annulations and apical bulb on Ant IV, and jointed tibiae), and furthermore, such data are not available for many species (Table 2). In fact, with the exception of the mesothorax not overlapping the head, all the diagnostic characters listed for *Lepidosira* look polymorphic and do not allow a precise delimitation of its members. For example, although some species of *Lepidosira* have a slightly projected mesothorax, it does not overlap the head as in *Lepidocyrtoides* taxa. This demonstrates the need for a revision and a detailed diagnosis of the genus that effectively encompasses all its members.

Most species descriptions within *Lepidosira* are poorly detailed and lack important data concerning dorsal chaetotaxy and other key taxonomic characters used in modern systematics. This lack of objective diagnostic characters and detailed species descriptions leads to mistaken descriptions in the genus. An example of this problem concerns the neotropical fauna. Until recently, there were three records of *Lepidosira* species from this region: *L. tapuia* Arlé & Guimarães, 1980 and *L. villasboasi* Arlé & Guimarães, 1981, both from Brazil, and *L. violaceapallipes* (Denis, 1931) sensu Christiansen & Bellinger, 2000, from Costa Rica, all three of which are poorly described. Cipola, Morais, and Bellini (2017) redescribed the two Brazilian species and transferred both to *Lepidocyrtoides*, based on the presence of a projected mesothorax overlapping head and manubrial plate with blunt macrochaetae, some of the few features that differentiate *Lepidocyrtoides* from other scaled Entomobryinae (Liu, Chen, & Greenslade, 2008; Yoshii & Greenslade, 1994; Yoshii & Suhardjono, 1992). Concerning *L. violaceapallipes*, this species was originally described as *Lepidocyrtinus domesticus f. violaceapallipes* Denis, 1931, and it was suggested as *Lepidosira* by Christiansen and Bellinger (2000, p. 42). Denis (1931, p. 142) focused his description only on colour pattern, and the single illustration of the description presented by the author is the habitus for the new species—no further distinguishable characteristics are available. Christiansen and Bellinger (2000) do not explicitly justify their decision, but simply mention that this species "may be" a *Lepidosira*. However, the real status of *L. violaceapallipes* was never confirmed, and the presence of *Lepidosira* in the Neotropical Region was discarded after the revision by Cipola et al. (2017).

The systematic position of *Lepidosira* within the Entomobryidae was also revised during recent decades. Yoshii and Suhardjono (1989) positioned the genus within the Seirini based on the morphology of scales and divided the tribe into *Lepidosira* and *Seira* groups based on mucro morphology (falcate in *Seira*-group and bidentate in *Lepidosira*-group). Soto-Adames et al. (2008) maintained this classification for Seirini, although the authors proposed other changes at subfamily and tribe levels. Posteriorly, Zhang and Deharveng (2015) provided an extensive systematic revision of Entomobryidae, transferring the *Lepidosira*-group from Seirinae to the Entomobryinae, based on distribution of tergal bothriotricha (2, 3, 2 on Abd. II–IV), mucro structure (bidentate) and chaetotaxy of tergal sens (22|122–3).

Here, we present and describe the first reliable record of *Lepidosira* from the Neotropical Region, specifically *Lepidosira neotropicalis* sp. n. from Sete Cidades National Park (Piracuruca municipality, Piauí State, Brazil). After an extensive bibliographic revision, a new diagnosis is proposed for the genus, excluding variable and uninformative characters. We also present the complete mitochondrial genome of the new species, which complements the 13 other mitogenomes published for springtails (Carapelli, Comandi, Convey, Nardi, & Frati, 2008; Faddeeva-Vakhrusheva et al., 2016, 2017; Wu et al., 2017). Additionally, we propose a hypothesis for the phylogenetic position of the new taxon among 19 species of Entomobryinae and six Seirinae, using one Lepidocyrtinae, three Orchesellinae, three Heteromurinae, two Isotomidae and one Tomoceridae as out-groups, to test the position of *Lepidosira neotropicalis* sp. n. among the Entomobryinae or Seirinae as suggested in different previous studies. Our analyses were based on one mitochondrial and two nuclear genes, Cytochrome Oxidase subunit I (COX1), 18SrRNA (18S) and 28SrRNA (28S), respectively. Finally, an identification key to the Neotropical genera of Entomobryinae is provided.

TABLE 1 Entomobryinae species recorded from the Neotropical Region

Genera	Species	Type locality
Amazhomidia	*duckeensis* Cipola and Bellini, 2016 (in Cipola, Morais, & Bellini, 2016)	Ducke reserve, Amazonas, Brazil
	guianiensis (Womersley, 1930) Cipola, Morais, & Bellini, 2018	Essequibo River, Moraballi Creek, Guyana
	thaisae Cipola and Bellini, 2018 (in Cipola et al., 2018)	Ducke reserve, Amazonas, Brazil
Americabrya	*arida* (Christiansen & Bellinger, 1980) Mari-Mutt & Palacios-Vargas, 1987	Rustlers Park, Arizona, USA
	epiphyta (Loring, 1984) Mari-Mutt & Palacios-Vargas, 1987	Rio Tambopata reserve, Madre de Dios Province, Peru
	matthewsi (Snider, 1981) Mari-Mutt & Palacios-Vargas, 1987	Parque Nacional Corcovado, Puntarenas Province, Costa Rica
Calx	*cubensis* Folsom, 1927	Tanamo, Cuba
	luthuli Rapoport & Rubio, 1968	Cerro el Pajonal, Antofagasta, Chile
	neryi Soto-Adames, 2002	Saint John, United States Virgin Islands, USA
	sabulicola (Mills, 1931)	Bryan, Texas, USA
Coecobrya	*tenebricosa* (Folsom, 1902) Gruia, 1998	Washington D.C., USA
Desertia	*semicolorata* (Handschin, 1928)	Chapultepec, Mexico
Drepanosira	*pulchra* Stach, 1960 (in Christiansen & Bellinger, 2000)[a]	Shahr-e Gholghola, Bamiyan, Afghanistan
Drepanura	*californica* Schött, 1891	California, USA
	delamarei Christiansen, 1963	Esquel, Colline Nord, Argentina
Entomobrya	*adustata* Börner, 1907	La Plata, Argentina
	aipatse Arlé, 1959	Alto Xingú, Mato Grosso, Brazil
	assuta Folsom, 1924	Geneva, New York, USA
	ataquensis Arlé, 1959	Serra da Mantiqueira, Minas Gerais/ São Paulo, Brazil
	atra (Nicolet, 1847) Brook, 1884	Chile
	atrocincta Schött, 1896	Hanford, California, USA
	bahiana Bellini and Cipola, 2015 (in Bellini, Cipola, & Godeiro, 2015)	Parque Nacional Chapada Diamantina, Bahia, Brazil
	bicolor Guthrie, 1903	Minneapolis, Minnesota, USA
	carbonaria Bonet, 1934	Argentina
	ciliata Börner, 1907	La Plata, Argentina
	citrensis Katz and Soto-Adames, 2015 (in Katz, Giordano, & Soto-Adames, 2015b)	Chassahowitzka National Wildlife Refuge, Florida, USA
	confusa Christiansen, 1958	Mount Evans, Colorado, USA
	corticola Jacquemart, 1975	Galápagos, Ecuador
	darwini Katz, Soto-Adames, and Taylor, 2016 (in Katz et al., 2016)	Santa Cruz Island, Galápagos, Ecuador
	decora (Nicolet, 1847) Brook, 1884	Chile
	egleri Arlé & Guimarães, 1978	Santo Antônio de Tauá, Pará, Brazil
	fasciata Denis, 1931	San José province, Costa Rica
	griseoolivata (Packard, 1873) Brook, 1884	USA
	inaequalis Denis, 1924	Curitiba, Paraná, Brazil
	infuscata Handschin, 1927	San José province, Costa Rica
	lavata Börner, 1907	La Plata, Argentina
	ligata Folsom, 1924	New York State, USA
	linda Soto-Adames, 2002	Saint Thomas, United States Virgin Islands, USA

(Continues)

TABLE 1 (Continued)

Genera	Species	Type locality
	litigiosa Denis, 1931	San José province, Costa Rica
	longipes Bonet, 1934	Argentina
	longiseta Soto-Adames, 2002	Saint John, United States Virgin Islands, USA
	mineola Folsom, 1924	Long Island, New York, USA
	multifasciata (Tullberg, 1871) Brook, 1884	Gotland, Sweden
	neotenica Katz & Soto-Adames, 2015b	Lawrence, Alabama, USA
	nivalis (Linnaeus, 1758) Ågren, 1904	European forests
	olivacea Rapoport, 1962b	Bahía Blanca, Buenos Aires province, Argentina
	paroara Arlé & Guimarães, 1978	Ananindeua, Pará, Brazil
	protrifasciata Denis, 1931	San José province, Costa Rica
	pseudodecora Rapoport, 1962a	Bahía Blanca, Buenos Aires province, Argentina
	pulchra Schäffer, 1897	Ushuaia, Tierra del Fuego, Argentina
	secca Christiansen, 1963	Arroyo del Puma, Los Alerces, Argentina
	simulans Denis, 1931	San José province, Costa Rica
	spectabilis Reuter, 1890	Brazil
	suzannae Scott, 1937	Santa Cruz, California, USA
	triangularis Schött, 1896	San Francisco, California, USA
	trifasciata Handschin, 1927	San José province, Costa Rica
	tupiana Arlé, 1939	Petrópolis, Rio de Janeiro, Brazil
	uambae Arlé, 1959	Alto Xingú, Mato Grosso, Brazil
	unostrigata Stach, 1930	Flix, Tarragona, Spain
	variocolorata Thibaud & Najt, 1989	near Latacunga, Cotopaxi province, Ecuador
	venezolana Díaz & Najt, 1995	Páramo de Mucubají, Venezuela
	virescens Schäffer, 1897	Viña del Mar, Valparaiso, Chile
	walkeri Christiansen, 1963	Nahuel Huapi, Patagônia, Argentina
	wasmanni Handschin, 1924	Blumenau, Santa Catarina, Brazil
	wheeleri Folsom, 1921	Kartabo, Guiana
	xanthoderma Rapoport & Izarra, 1962	González Chaves, Buenos Aires province, Argentina
Homidia	*socia* Denis, 1929	Fuzhou, Fujian, China
Lepidocyrtoides	*bicolorangelus* Cipola and Bellini, 2017 (in Cipola et al., 2017)	Parque Nacional do Viruá, Roraima, Brazil
	caeruleomaculatus Cipola and Bellini, 2017 (in Cipola et al., 2017)	Rio Preto da Eva, Amazonas, Brazil
	colormutatus Cipola and Bellini, 2017 (in Cipola et al., 2017)	Ducke reserve, Amazonas, Brazil
	tapuia (Arlé & Guimarães, 1980) Cipola et al., 2017	Parque Nacional da Tijuca, Rio de Janeiro, Brazil
	villasboasi (Arlé & Guimarães, 1981) Cipola et al., 2017	Parque Nacional do Xingu, Mato Grosso, Brazil
Lepidosira	*neotropicalis* sp. n.	Parque Nacional de Sete Cidades, Piauí, Brazil
Sinella	*avita* Christiansen, 1960	Crittenden and Livingston, Kentucky, USA
	barri Christiansen, 1960	Perry, Tennessee, USA
	curviseta Brook, 1882	Huddersfield, West Yorkshire, England
	hexophthalma Rapoport & Rubio, 1968	Cerro el Roble, Santiago, Chile
	laevis Denis, 1931	San José province, Costa Rica
	sexoculata (Schött, 1896) Mills & Rolfs, 1933	Sonora, Mexico

(Continues)

Genera	Species	Type locality
Willowsia	*buski* (Lubbock, 1870) Shoebotham, 1917	British Isles
	jacobsoni (Börner, 1913) Stach, 1965	Semarang, Java, Indonesia
	mexicana Zhang, Palacios-Vargas, & Chen, 2007	Oaxaca city, Oaxaca, Mexico
	nigromaculata (Lubbock, 1873) Shoebotham, 1917	British Isles
	pyrrhopygia Katz, 2017	Kissimmee Prairie Preserve State Park, Florida, USA

Note: Data extracted from Mari-Mutt and Bellinger (1990, 1996), Mari-Mutt, Bellinger, and Janssens (1996–2019), Bellinger et al. (1996–2019), Abrantes et al. (2012) and directly from the original descriptions.

[a] Doubtful record as *Drepanosira*.

2 | MATERIAL AND METHODS

2.1 | Taxa sampling

Specimens of *Lepidosira neotropicalis* sp. n. were collected in Sete Cidades National Park, in the transitional zone between Caatinga and Cerrado biomes, Piauí state, Northeastern Brazil (Figure 1); from top soil and leaf litter samples, using entomological aspirator. Most specimens were preserved in 70% ethanol, but specimens used for DNA extraction were preserved in 100% ethanol. All material was deposited in the Collembola Collection of Biosciences Center of Federal University of Rio Grande do Norte, Brazil (CC/UFRN).

2.2 | Microscopy and imaging

Specimens were preserved in 70% ethanol, clarified with a mixture of 100% hydrochloric acid and a saturated solution of potassium dichromate, washed in Arlé's liquid and mounted on glass slides in Hoyer's medium, following mostly the procedures described by Arlé and Mendonça (1982). Most specimens in 70% ethanol and on glass slides were photographed using a stereomicroscope Nikon SMZ1500 and a microscope Nikon Eclipse N*i*U, respectively, both attached to a Nikon DS-Ri1 camera, and using NIS-Elements AR v.4.51.00 software. For Figure S2, specimens were photographed in glass slides, using a microscope Leica DM750 attached to a Leica MC170 HD camera, and using LAS v.4.12 software. Photographs were digitally corrected using Corel Photo-Paint X8. For the morphological analysis and drawings, it was used a Leica DM750 microscope with an attached drawing tube. Figures were improved, assembled and labelled with CorelDraw X8 software.

2.3 | Terminology, abbreviations and symbols

The terminology used in the morphological description follows mainly: Gisin (1967) to labial chaetotaxy; Fjellberg (1999) to labial palp papillae; Cipola, Morais, and Bellini (2014) to labral chaetotaxy; Mari-Mutt (1979) to dorsal head chaetotaxy as modified by Soto-Adames (2008); Szeptycki (1972) to S-chaetotaxy; Szeptycki (1979) to dorsal chaetotaxy, with additions of Jordana and Baquero (2005), Soto-Adames (2008) and Zhang and Deharveng (2015).

Morphology abbreviations: **Abd.**—abdominal segment; **acc.**—accessory S-chaeta(e); **al**—anterolateral S-chaeta(e); **Ant.**—antennal segment; **as**—anterosubmedial S-chaeta(e); **b.c**.—basal chaetae; **l.p.**—lateral process; **mac**—macrochaeta(e); **mes**—mesochaeta(e); **mic**—microchaeta(e); **ms**—S-microchaeta(e); **p.c.**—proximal chaetae; **ps**—posterior S-chaeta(e); **sens**—ordinary S-chaeta(e); **Th.**—thoracic segment.

Symbols used in drawings to represent the dorsal chaetotaxy schemes are as follows: large empty circles for mac, large black circles for mes, black dots for mic, black chaetae-like drawings for sens or ms, large black circles with a cross line for pseudopores, long lines ending in a transversal bar for bothriotricha and a dash above any symbol for chaetae present or absent in different specimens of type series. Chaetae of uncertain homology are followed by a question mark (?).

2.4 | DNA extraction and sequencing

Genomic DNA was extracted from a whole individual of *L. neotropicalis* sp. n. and of the other newly sequenced species using the Cell and Tissue DNA kit (Thermo Scientific) following the manufacturer's protocol, with minor modifications. Specifically, the incubation time was increased to 48 hr, with an extra 15 µl of proteinase K was added after the first 24 hr. The KingFisher Duo Prime (Thermo Scientific) was used for automatized purification. An Illumina compatible sequencing library was prepared using the NEBNext kit 6070 (New England Biolabs) following the Illumina multiplex protocol of Meyer and Kircher (2010), using double indexed library adapters. Quantification and size estimation of the library was conducted on a Tape Station 2200 using a High Sensitivity DNA Analysis Kit (Agilent Technologies), and quantitative real-time PCR was performed to estimate the number of PCR cycles needed to amplify the library prior to sequencing using a Mx3000P (Strategene). The library was pooled with other samples then sequenced at the Danish National High-Throughput DNA Sequencing Centre on a fraction of a lane of an Illumina HiSeq 2000, using 80 paired-end cycles of a rapid run.

TABLE 2 Variation in diagnostic features of *Lepidosira* among the currently valid species

Species	Ant. IV annulations	Ant. IV apical organ	Jointed Tibiae	Additional references
L. angulata (Schött, 1917) Howard, 1969	–	Present	–	–
L. anomala Salmon, 1944	–	Present	–	–
L. arborea Salmon, 1944	–	Absent	No	Salmon (1944): plate 60, fig 132
L. australica (Schött, 1917) Greenslade & Majer, 1980	–	Present	No	Yoshii and Greenslade (1994): pp. 17–18, figs 9a, d
L. bifasciata (Salmon, 1944)	Yes	Present	–	–
L. bisecta (Salmon, 1944) Greenslade, 2012	–	Present	No	Salmon (1944): plate 61, fig 146
L. brunnea (Womersley, 1935) Greenslade, 1994	Yes	–	–	–
L. calolepis (Börner, 1913) Yayuk, 1989	Yes	Present	–	Yoshii and Suhardjono (1989): p. 42
L. congoia Salmon, 1956	–	Present[a]	–	–
L. faaroana (Carpenter, 1934) Greenslade, 2012	–	–	No	Carpenter (1934): p. 140, Figure 3a
L. fallaciosa Yoshii, 1989	–	Present	–	–
L. fuchsiata (Salmon, 1938) Greenslade, 2012	–	–	Yes	Salmon (1938): plate 35, Figure 1; Salmon (1941): plate 63, fig 390
L. gupta Howard, 1969	No	Present	Yes	–
L. javana (Börner, 1913) Yayuk, 1989	–	Present	No	Yoshii and Suhardjono (1989): pp. 40–41, fig 10a
L. laboriosa Greenslade, 1994	–	Present	–	Schött (1917): p. 45
L. longicornis (Schött, 1917) Yoshii & Greenslade, 1994	–	Present	–	–
L. magna (Salmon, 1937) Greenslade, 2012	–	–	Yes	Salmon (1941): plate 64, fig 397
L. minima Salmon, 1938	–	–	No	Salmon (1938): plate 36, fig 15; Salmon (1941): plate 65, fig 416
L. minuta Salmon, 1938	–	–	No	Salmon (1938): plate 36, fig 22
L. nigrocephala (Womersley, 1936) Yosii, 1960	Yes	Present	No	Womersley (1936): p. 481, fig 4a
L. nilgiri (Denis, 1936) Yosii, 1955	Yes	Indistinct	Yes	Denis (1936): p. 267, fig 17
L. obscura (Salmon, 1944) Greenslade, 2012	–	Present	No	Salmon (1944): plate 61, fig 139
L. okarita Salmon, 1938	–	Present	–	–
L. pigmenta Salmon, 1944	–	Absent	No	–
L. punctata Yosii, 1960	Yes	Present	No	Yosii (1960): p. 19, fig 9a
L. quadradentata (Salmon, 1941) Greenslade, 2012	–	–	No	Salmon (1941): plate 63, fig 387
L. rotorua Salmon, 1938	–	–	No	Salmon (1938): plate 36, fig 24
L. sagmaria (Schött, 1917) Schött, 1925	–	Present	–	Salmon (1941): p. 390
L. sexmaculata Salmon, 1938	–	Present	No	Salmon (1938): plate 37, fig 29; Salmon (1941): plate 65, fig 412
L. splendida (Salmon, 1941) Greenslade, 2012	–	Present	No	Salmon (1941): plate 63, fig 382
L. terraereginae (Ellis & Bellinger, 1973) Howard, 1969	–	Present	No	Salmon (1941): p. 389; Yoshii and Greenslade (1994): p. 16, fig 8a
L. unguserrata Salmon, 1970	–	Present	–	–
L. vicina Yoshii, 1989	No	Present	–	–

Note: Data extracted directly from the original descriptions; and from descriptions of species posteriorly synonymized with currently valid species, or providing additional information to the original descriptions, both cited in the "additional references" column. Valid species not included in the table have no available information about all the three characters. Unavailable information for isolated characters is marked with "–."

[a] According to Salmon (1956, p. 28), only males of *L. congoia* present the apical bulb.

2.5 | Sequence analysis and mitogenome assembly

The quality of the sequence was evaluated using FastQC software v0.11.8 (Andrews, 2018). AdapterRemoval v2 (Schubert, Lindgreen, & Orlando, 2016) was conducted to remove reads containing adapters and low-quality reads from the raw data. The mitogenome was de novo assembled and annotated using MitoZ v1.04 (Meng, Li, Yang, & Liu, 2019). The final mitogenome can be accessed at GenBank under the number MF716603. The circular mitogenome of *L. neotropicalis* sp. n. was visualized with Circos v0.69 (Krzywinski et al., 2009). During the same experiments, other Entomobryidae were sequenced: *Entomobrya* sp.2, *Lepidocyrtoides* sp., *Seira coroatensis* and *Tyrannoseira gladiata* to reinforce the phylogenetic analysis. The detailed mitogenomes of all sequenced species apart from *L. neotropicalis* sp. n. will be reported in an independent publication, which is currently in preparation.

2.6 | Ribosomal RNA genes assessment

Using the raw reads previously sequenced of *L. neotropicalis* sp. n., *Entomobrya* sp.2, *Lepidocyrtoides* sp., *Seira coroatensis* and *Tyrannoseira gladiata*, two nuclear genes (18S and 28S) were recovered using the following methodology: SicklePE v1.330 (Joshi & Fass, 2011) was used to clean the low-quality reads; the mapping was made using Bowtie2 v2.3.0 (Langmead & Salzberg, 2012), the reference sequences were *Orchesella flavescens* (Bourlet, 1839) Nicolet, 1847 and *Orchesella villosa* (Linnaeus, 1767) Dalla-Torre, 1895 for 18S, and *O. villosa* for 28S (KY382769.1, EU368606.1 and EF199972.2, respectively); the final assembly of paired-end reads was made with ABySS v2.0 (Jackman et al., 2017) (k-mer = 45).

2.7 | Phylogenetic inference

For the phylogenetic inference, the sequences of the complete nuclear genes 18S (1,265 bp) and region D1-3 of 28S (1,255 bp), and partial mitochondrial COX1 (641 bp) from 19 species of Entomobryinae and six Seirinae (ingroups), one Lepidocyrtinae, three Orchesellinae, three Heteromurinae, two Isotomidae and one Tomoceridae (outgroups) were downloaded from GenBank to complement those generated in this study (Table 3). All DNA sequences were aligned with the newly sequenced *L. neotropicalis* sp. n. by MAFFT v7 (Katoh & Standley, 2013). Bayesian Markov chain Monte Carlo (MCMC) analyses in BEAST v1.8.4. (Drummond, Suchard, Xie, & Rambaut, 2012) were performed using GTR model of evolution and gamma + invariant rate heterogeneity models, and base frequencies estimated. Simultaneous Markov chains were run for 15,000,000 generations, sampling every 1,500 steps. A total of 9,000 trees were sampled. Evaluation of effective sample size (ESS) values and state convergence were checked in Tracer v1.6.0 (Rambaut, Suchard, Xie, & Drummond, 2013), as well as the burn-in value, that was defined in 1,000 trees or 1,500,000 states. The consensus tree was generated using TreeAnnotator v1.8.4 (Drummond et al., 2012) and was visualized in FigTree v1.4.3 (Rambaut, 2014).

3 | RESULTS

3.1 | A new diagnosis proposed to the genus *Lepidosira*

Genus Lepidosira Schött, 1925: p. 116. Gender feminine; type species: *Lepidosira terraereginae* (Ellis & Bellinger, 1973) Howard, 1969, nom. nov. for *Lepidocyrtus (Lepidocyrtoides) coeruleus* Schött, 1917 (Bellinger et al., 1996–2019).

Urewera Salmon, 1938: p. 349. Gender feminine; type species: *Urewera fuchsiata* Salmon, 1938. Junior synonym of *Lepidosira* (Bellinger et al., 1996–2019; Soto-Adames et al., 2008).

3.1.1 | Diagnosis

Coarsely ribbed scales, apically pointed or rounded, present on antennae, head, body, manubrium and dens. Dorsal chaetotaxy of head and trunk polymacrochaetotic. 8 + 8 eyes. Tergal S-chaetotaxy, from Th. II to Abd. V as 2, 2 | 1, 2, 2, +, 3 for **sens**, and 1, 0 | 1, 0, 1, 0, 0 for **ms**. Abd. I with **ms** in the height of **acc.p6**, external to **m5**. Tergal bothriotricha on Abd. II–IV as 2 (**a5**, **m2**), 3 (**a5**, **m2**, **m5**), 2 (**T2**, **T4**). Abd. IV without lateral finger-shaped appendix in the reproductive females, linked to the segment by a distinct joint. Unguiculus without an external tooth. Manubrial plate without blunt chaetae. Mucro bidentate, with a basal mucronal spine.

3.1.2 | Remarks

We attempt to propose a new diagnosis to the genus maintaining most features originally used by Schött (1925) and complemented by Womersley (1939), but excluding the interspecific variable characters listed in Table 2. We included the number of tergal bothriotricha on Abd. II–IV and the S-chaetotaxy pattern characteristic to most Entomobryinae, established by Zhang and Deharveng (2015), which was observed in *L. vicina* by the same authors, and now in *L. neotropicalis* sp. n. We also included characters differentiating *Lepidosira* from *Lepidocyrtoides*, *Epimetrura*, *Lepidobrya* and *Lepidodens*, the only other genera of Entomobryinae with scales on body, manubrium and dens; mucro bidentate with mucronal spine; and lacking rows of spines on manubrium and dens (see Discussion topic).

3.2 | Description of the new species

Lepidosira neotropicalis Nunes and Bellini, sp. n. (http://www.zoobank.org/urn:lsid:zoobank.org:pub:37F86999-2D49-4C9C-8A8B-D852985D7CC5). The detailed description and comparison of the new species can be seen in the Appendix S1, and in the Figures S1–S10.

3.3 | Mitogenome analysis and features

A total of 14,327,173 raw reads were generated from the sequencing library. The assembled *L. neotropicalis* sp. n. mitogenome is 14,597 bp long, containing 37 genes (13 protein-coding genes—PCGs, 2 rRNA genes and 22 tRNA genes) (Table 4, Figure 2). The total GC content was 25.5%, with base composition of 39.2% A, 35.2% T, 10.5% G and 15.1% C. Nine PCGs (NAD2, COX1–3, ATP6, ATP8, NAD3, NAD6, CYTB) were located on the major J-strand, and four PCGs (NAD1, NAD4, NAD4L and NAD5) were located on the minus N-strand (Table 4, Figure 2). Two common start codons were observed: ATG (CYTB, ATP6, COX3, NAD4) and ATA (NAD6, NAD1–3), followed by ATT (COX1, COX2, NAD5), ATC (ATP8) and TTG (NAD4L). Ten genes contained a TAA stop codon, two had TAG, and one had incomplete stop codon T (NAD4) (Table 4). The size of the *L. neotropicalis* sp. n. mitogenome is similar to the previously published for other Collembola, ranging from 13,800 to 15,700 bp. The GC content is lower than average when compared with other collembolan mitogenomes (29.27%), although similar to *Folsomotoma octooculata* (Willem, 1901) Potapov, 2001 (25.5%) (Carapelli, Convey, Nardi, & Frati, 2014). This feature is commonly observed in mitogenomes of hexapods, which are AT-rich (Hassanin, Leger, & Deutsch, 2005).

The genes order of *L. neotropicalis* sp. n. presented in Figure 2 is the most common observed in Collembola. Despite the presumed long evolutionary history of major lineages of the group, the gene order remains identical to the presumed ancestral gene order state for the Pancrustacea group (Carapelli et al., 2008).

3.4 | Phylogeny

Phylogenetic analyses were performed with 10 taxa as outgroups in Lepidocyrtinae, Orchesellinae, Heteromurinae (all Entomobryidae), Anurophorinae (Isotomidae) and Tomocerinae (Tomoceridae) (Table 3). All genera of Entomobryinae *sensu stricto* for which genetic data are available in GenBank to complement our own sequence was included in the analyses (Zhang et al., 2014, 2016, 2015; Zhang, Ma, & Greenslade, 2017). Both genera of Seirinae were also included, to test for a possible relationship of *Lepidosira* with this taxon, as suggested previously (Soto-Adames et al., 2008). The Bayesian consensus tree is presented in Figure 3.

The monophyly of Entomobryinae *sensu stricto* was recovered with high node support (Figure 3). *Lepidosira* was recovered with high support as an ingroup of this subfamily, and as sister group to *Lepidocyrtoides* in a clade that is basal to the other Entomobryinae. *Entomobrya* and *Willowsia* were not recovered as monophyletic taxa, as seen in previous studies (Katz, Giordano, & Soto-Adames, 2015a, 2015b; Zhang et al., 2014, 2016, 2015; Zhang & Deharveng, 2015; Zhang, Ma, et al., 2017). Otherwise *Homidia* and *Sinella* appeared as natural groups, in agreement with all recent revisions to *Homidia* (Zhang et al., 2014, 2016, 2015; Zhang & Deharveng, 2015; Zhang, Ma, et al., 2017), and most to *Sinella* (Zhang et al., 2014, 2015; Zhang & Deharveng, 2015; Zhang, Ma, et al., 2017), but not all (Zhang et al., 2016). The monophyly of Seirinae was also recovered as recent studies suggested (Zhang et al., 2014, 2016, 2015; Zhang & Deharveng, 2015; Zhang, Ma, et al., 2017), including *Tyrannoseira*. In this first assessment, this last genus appeared as an ingroup of *Seira* (Figure 3).

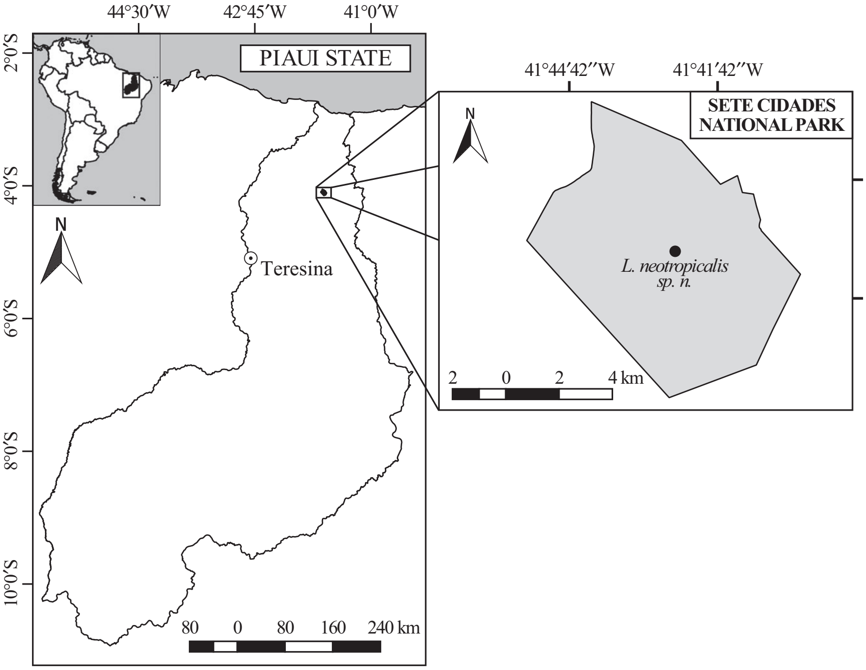
4 | DISCUSSION

4.1 | The diagnostic problem of *Lepidosira*

The diagnosis of *Lepidosira* was established in 1925 and complemented by Womersley (1939), at a time when only four species were described (currently there are 54). Indeed, it was because of this lack of knowledge concerning the potential diversity of species which could fit the diagnosis of *Lepidosira* that the original authors failed to provide more clear diagnostic characters. While the total number of species in the genus has significantly increased during the last century, no extensive taxonomic review has been undertaken, and thus, the initial diagnosis proposed is no longer representative of all species in the genus, and can neither effectively differentiate them from other genera.

Lepidosira, *Lepidocyrtoides*, *Epimetrura*, *Lepidobrya* and *Lepidodens* are the only genera of Entomobryinae *sensu* Zhang and Deharveng (2015) which combine the following features: scales on body, manubrium and dens; mucro bidentate with mucronal spine; and rows of spines lacking on manubrium and dens. *Epimetrura* is diagnosed by the presence of a finger-shaped appendage in the Abd. IV of reproductive females, connected to the segment by a distinct joint (Schött, 1925). *Lepidobrya* has no unpaired inner teeth in the unguis;

FIGURE 1 Geographical location of the sampled specimens of *Lepidosira neotropicalis* sp. n. Shapefiles downloaded from IBGE—Instituto Brasileiro de Geografia e Estatística (https://portaldemapas.ibge.gov.br/portal.php#homepage)



the unguiculus is truncated with a small external tooth; and the body scales are long, narrow and pointed (Womersley, 1937; Zhang, Greenslade, & Stevens, 2017), like the dental scales of *Lepidosira neotropicalis* sp. n. (Figure S10b). *Lepidodens* can be diagnosed by the unguiculus truncated; scales with basal ribs longer than distal ones; bothriotrichal complex with unmodified accessory mic; Abd. I with **ms** abnormally positioned at the height of the chaeta **m3** (Zhang et al., 2016). Despite its morphological resemblance with *Lepidosira* and *Lepidocyrtoides*, the genus *Lepidodens* was recovered in a distinct clade in our phylogeny (Figure 3), outside the *Lepidosira*-group.

In practical taxonomic terms, the principal diagnostic problem lies in the ability to differentiate between the *Lepidosira* and *Lepidocyrtoides* genera. The similarity between these two genera had already been observed at the beginning of the 20th century, and *Lepidosira* was proposed precisely to separate some "anomalous" species of *Lepidocyrtoides* (Schött, 1925; Womersley, 1939). Very few characters actually distinguish the two groups, the most reliable being the presence of blunt mac on the manubrial plate of the latter genus (Cipola et al., 2017). The occurrence of such blunt chaetae on the manubrial plate could be interpreted as an autapomorphy of *Lepidocyrtoides* or a plesiomorphy of *Lepidosira* + *Lepidocyrtoides* clade. Our review shows these chaetae, or very similar ones, can also occur in other parts of the body of *Lepidosira*, but never on manubrium and dens. This last finding suggests the presence of such modified chaetae could denote a common ancestor, which may have had blunt chaetae on different body parts. Another trend observed in both genera, that was probably also inherited from their common ancestor, is the enlarged Th. II. Traditionally, it is accepted that in *Lepidocyrtoides,* this projection is accentuated to the point of overlap with the head, about four times as long as Th. III according to Womersley (1939, p. 173), forming a hood-like structure; in *Lepidosira,* this projection is notably smaller, never overlapping the head (Liu et al., 2008; Yoshii & Suhardjono, 1992), as pointed out also by Womersley (1939, p. 201). For *Lepidosira australica*, *L. brunnea*, *L. calolepis*, *L. longicornis* and *L. nigrocephala*, Womersley (1939, pp. 173, 195) reports the length of Th. II as twice as long as Th. III, and for *Lepidosira neotropicalis* sp. n., the ratio Th. II: III ranges from 1.74 to 2.37:1. On the other hand, for five Neotropical and one Australian species of *Lepidocyrtoides*, Cipola et al. (2017) report a Th. II: III ratio ranging between 3.66 and 2.09:1. In the same way, Liu et al. (2008, Table 1) reports a Th. II: III ratio ranging between 4 and 1.43:1, for five Australian species of *Lepidocyrtoides*. In all cases, the inferior range overlaps the reported ratio of *Lepidosira*, thus, this character becomes useless for separating the two genera. Overall, dorsal chaetotaxy of Neotropical species of *Lepidocyrtoides* and *Lepidosira* also shows remarkable similarities, in particular, the presence of a high number of multiplets of centro-anterior mac on Th. II and centro-posterior mac on Abd. IV (Cipola et al., 2017).

Our revision suggests it is quite possible that one of the two genera (*Lepidosira* and *Lepidocyrtoides*) is an ingroup to the other. This is suggested by their overall morphological similarity, close phylogenetic relationship and overlapping circumglobal distribution. However, as was demonstrated

TABLE 3 List of taxa analysed in the present study, including collection locality, and GenBank accession numbers for each gene

Group	Species	Locality	18S	28S (D1–3)	COX1
Entomobryidae					
Entomobryinae	*Coecobrya tenebricosa*	France	KC236231	KC236272	KM978347
	Drepanura sp.	China	KC236233	KC236274	KM978349
	Entomobrya aino	China	KC236235	KC236279	KM978350
	Entomobrya multifasciata	France	KC236237	KC236276	KM978392
	Entomobrya proxima	China	KC236236	KC236279	KM978351
	Entomobrya sp.1	China	KC236234	KC236278	KM978352
	Entomobrya sp.2	Brazil	MK246434*	MK246429*	MF716608*
	Himalanura sp.	China	KC236243	KC236284	KM978357
	Homidia sichuanensis	China	KC236244	KC236285	KM978358
	Homidia sinensis	China	KC236245	KC236286	KM978359
	Homidia socia	China	KC236246	KC236287	KM978360
	Lepidosira neotropicalis sp. n.	Brazil	MK246432*	MK246427*	MF716603*
	Lepidocyrtoides sp.	Brazil	MK246433*	MK246428*	MF716598*
	Lepidodens similis	China	KC236266	KC236305	KM978396
	Sinella curviseta	China	KC236258	KC236300	KM978373
	Sinella longisensilla	China	KC236259	KC236299	KM978374
	Sinhomidia bicolor	China	KC236260	KC236301	KM978375
	Willowsia guangdongesis	China	KC236264	KC236306	KM978377
	Willowsia japonica	China	KC236265	KC236307	KM978378
	Willowsia nigromaculata	France	KC236263	KC236304	KM978379
Heteromurinae	*Dicranocentrus wangi*	China	KC236232	KC236273	KM978348
	Heteromurus major	France	KC236241	KC236282	KM978355
	Heteromurus nitidus	France	KC236242	KC236283	KM978356
Lepidocyrtinae	*Lepidocyrtus* sp. 1	China	KC236248	KC236289	KM978361
Orchesellinae	*Orchesella cincta*	France	KC236250	KC236290	KM978365
	Orchesellides sinensis	China	KC236251	KC236293	KM978363
	Orchesellides sp.	China	KC236226	KC236267	KM978364
Seirinae	*Seira coroatensis*	Brazil	MK246435*	MK246430*	MF716614*
	Seira delamarei	China	KC236255	KC236292	KM978370
	Seira barnardi	South Africa	KC236254	KC236296	KU508096
	Seira sp. 1	China	KC236257	KC236297	KM978371
	Seira sp. 2	South Africa	KC236256	KC236298	KM978372
	Tyrannoseira gladiata	Brazil	MK246436*	MK246431*	MF716599*
Isotomidae					
Anurophorinae	*Folsomia candida*	China	KC236239	KC236281	KM978353
	Folsomia quadrioculata	France	JN981027	KC236280	KM978354
Tomoceridae					
Tomocerinae	*Tomocerus ocreatus*	China	KC236262	KC236303	KM978376

Note: Numbers marked with an asterisk (*) are newly sequenced in the present study, with others extracted from the GenBank.

above, *Lepidocyrtoides* can be effectively differentiated from *Lepidosira* by the presence of blunt chaetae on manubrium and dens, something similar to what separates *Seira* (*Seira*) and *Seira* (*Lepidocyrtinus*).

4.2 | Phylogeny of Entomobryidae

Our analyses recovered the topology of derived Entomobryidae as: Lepidocyrtinae + (Entomobryinae + Seir

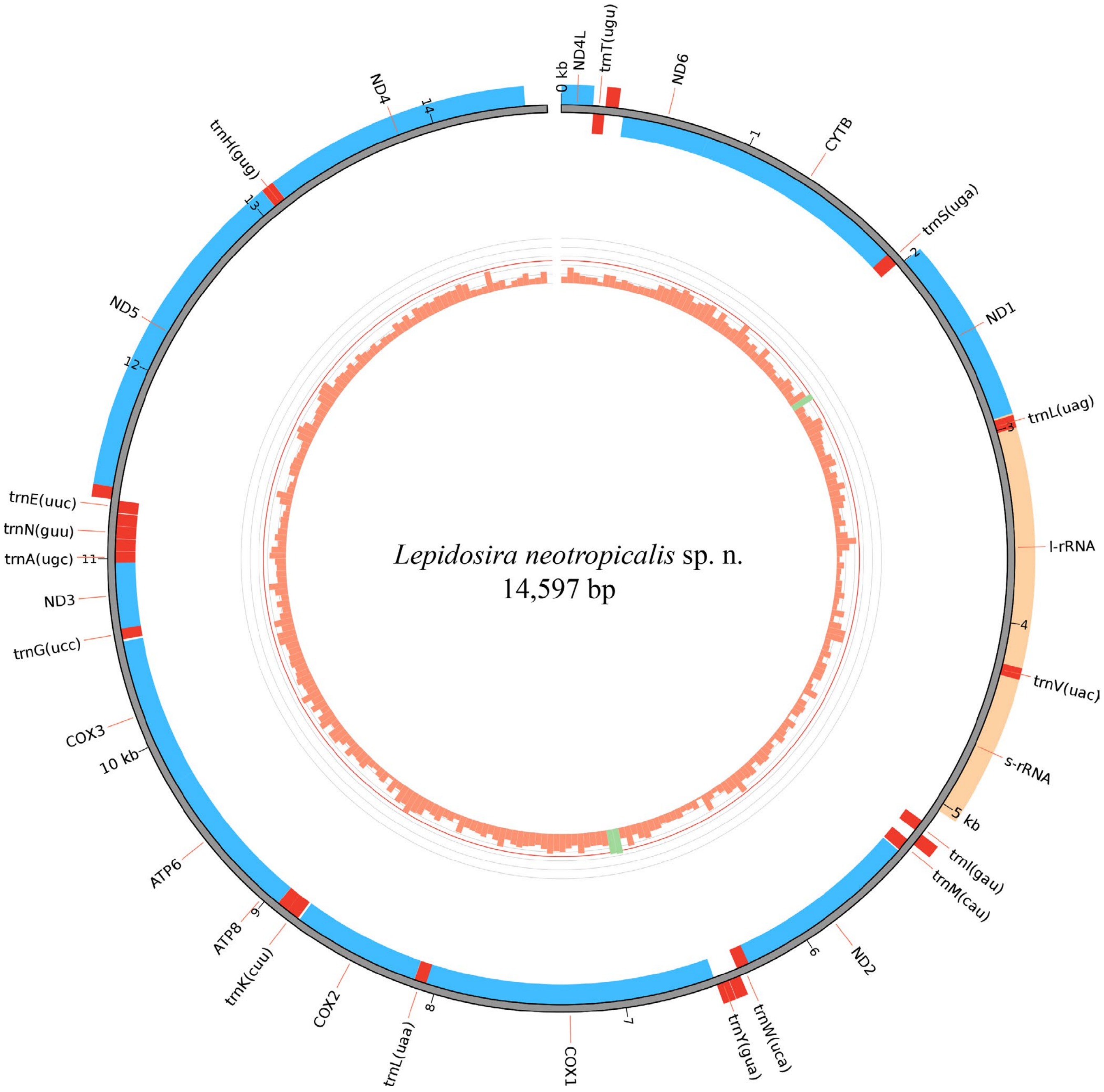


FIGURE 2 Mitochondrial genome of *Lepidosira neotropicalis* sp. n [Colour figure can be viewed at wileyonlinelibrary.com]

inae), consistent with the results of recent studies (Zhang, Ma, et al., 2017; Zhang et al., 2016, 2015). However, we identified Orchesellinae as the sister group of Heteromurinae, and Isotomidae as the sister group of Tomoceridae, both in disagreement with the same studies. Such disparate results are quite possibly due to the choice of genes in the analyses, since we could not use in this study the mitochondrial gene 16SrRNA (16S), which had been used in the previous studies. Also, the set of terminal taxa and outgroups (in number and identity of species) is different among these studies and may have weighed in the different topologies achieved here and in the cited studies. It is noteworthy all recent efforts concerning the Entomobryoidea phylogeny represent a work in progress and it is not entirely clear the relationships of Orchesellinae and Heteromurinae and the derived Entomobryidae (Entomobryinae, Lepidocyrtinae and Seirinae). Even so, this study did not aim to resolve the deeper relationships among the Entomobryidae taxa, but to understand the place of the new species (and *Lepidosira* as well) within the Entomobryinae.

Yoshii and Suhardjono (1989) included *Lepidosira* and similar genera (*Epimetrura*, *Lepidocyrtoides* and

TABLE 4 Location of features in the mitochondrial DNA of *Lepidosira neotropicalis* sp. n.

	Location (bp)				Codon
Gene	Start	Stop	Stand	Size (bp)	Start–Stop
NAD4L	2	163	N	161	TTG–TAA
trnT(ugu)	166	227	J	61	–
trnP(ugg)	228	295	N	67	–
NAD6	324	783	J	459	ATA–TAA
CYTB	784	1,916	J	1,132	ATG–TAA
trnS(uga)	1,915	1,985	J	70	–
NAD1	2,003	2,948	N	945	ATA–TAA
l-rRNA	2,940	4,279	N	1,339	–
trnL(uag)	2,949	3,013	N	64	–
trnV(uac)	4,213	4,276	N	63	–
s-rRNA	4,273	5,042	N	769	–
trnI(gau)	5,134	5,196	J	62	–
trnQ(uug)	5,193	5,260	N	67	–
trnM(cau)	5,258	5,328	J	70	–
NAD2	5,334	6,324	J	990	ATA–TAA
trnW(uca)	6,223	6,389	J	166	–
trnC(gca)	6,390	6,451	N	61	–
trnY(gua)	6,453	6,518	N	65	–
COX1	6,519	8,058	J	1,539	ATT–TAA
trnL(uaa)	8,054	8,118	J	64	–
COX2	8,118	8,799	J	681	ATT–TAA
trnK(cuu)	8,810	8,880	J	70	–
trnD(guc)	8,880	8,941	J	61	–
ATP8	8,941	9,103	J	162	ATC–TAA
ATP6	9,096	9,777	J	681	ATG–TAA
COX3	9,776	10,565	J	789	ATG–TAA
trnG(ucc)	10,576	10,636	J	60	–
NAD3	10,633	10,981	J	348	ATA–TAG
trnA(ugc)	10,980	11,040	J	60	–
trnR(ucg)	11,041	11,104	J	63	–
trnN(guu)	11,106	11,172	J	66	–
trnS(gcu)	11,173	11,239	J	66	–
trnE(uuc)	11,243	11,306	J	63	–
trnF(gaa)	11,309	11,372	N	63	–
NAD5	11,371	13,075	N	1,704	ATT–TAG
trnH(gug)	13,076	13,140	N	64	–
NAD4	13,140	14,485	N	1,345	ATG–T

Acanthocyrtus) in Seirini, based on scale morphology (with roughly striate surface) and manubrium ventral chaetotaxy (with rounded scales). This classification was used until recently, and the wide morphological revision of Entomobryomorpha provided by Soto-Adames et al. (2008) supported Yoshii and Suhardjono (1989) view of Seirini. It was only in 2015 that Zhang and Deharveng (2015) provided a phylogenetic analysis of the ingroups of Entomobryidae based on molecular data (original data presented in Zhang et al., 2014), and they observed that Seirini (promoted by that study to Seirinae) and Entomobryini (also promoted to Entomobryinae) could be separated by: mucro shape (falcate in the former, basally bidentate in the later); tergal sens (Th. II to Abd V 11|022–3 in Seirinae and 22|122–3 in

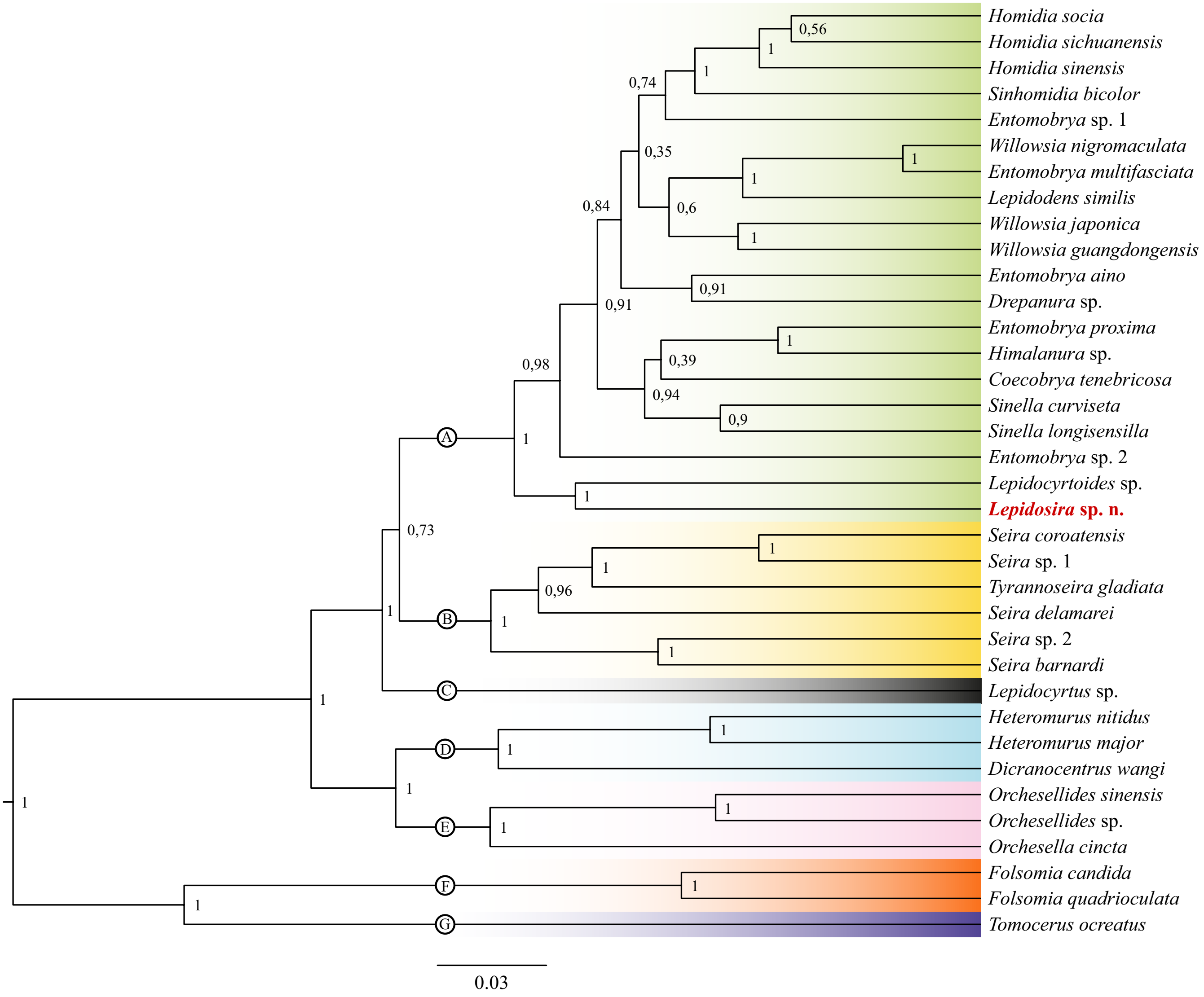


FIGURE 3 Phylogenetic position of *Lepidosira neotropicalis* sp. n. among 19 species of Entomobryinae (green—A), six Seirinae (yellow—B), one Lepidocyrtinae (grey—C), three Heteromurinae (blue—D), three Orchesellinae (pink—E), two Isotomidae (orange—F) and one Tomoceridae (purple—G). Numbers at the nodes indicate values of Bayesian posterior probabilities. For further details about specimens and GenBank accession numbers, see Table 3 [Colour figure can be viewed at wileyonlinelibrary.com]

Entomobryinae); and bothriotrichal formula of Abd. II–IV (2, 3, 3 in Seirinae vs. 2, 3, 2 in Entomobryinae). In 2014, another study (Zhang et al., 2014) also showed that Entomobryinae could present scales, excluding the significance of presence/absence of scales to separate Entomobryinae from other subfamilies of Entomobryidae. Posterior studies reinforced this point of view (Zhang et al., 2014, 2016, 2015). Although Zhang and Deharveng (2015) did not include any *Lepidosira* species in their molecular analyses, the new diagnostic features presented by the authors for all Entomobryinae allowed them to exclude the entire *Lepidosira*-group from Seirinae and enclose all their genera among the Entomobryinae. We are able, for the first time, to use molecular data to corroborate Zhang and Deharveng's (2015) argument for including *Lepidosira* and *Lepidocyrtoides* in Entomobryinae (Figure 3). Also, both *Lepidosira neotropicalis* sp. n. and neotropical species of *Lepidocyrtoides* (Cipola et al., 2017) fit the current diagnoses to Entomobryinae (Zhang & Deharveng, 2015; Zhang et al., 2016, 2015).

The finding of *Lepidosira* as the sister group of *Lepidocyrtoides* in our analyses (Figure 3) agrees partially with Yoshii and Suhardjono's (1989) definition of the *Lepidosira*-group, and other previous notes on the similarities of both genera (Schött, 1925; Womersley, 1939). On the other hand, the position of *Epimetrura*, *Acanthocyrtus* and other possibly related taxa as *Amazhomidia* within the Entomobryinae remains unclear. Further studies including species of these genera plus other species of *Lepidosira* and

Lepidocyrtoides, in particular from outside the Neotropical Region, are needed to verify how wide is actually the *Lepidosira*-group. The extensive array of morphological variation seen in the *Lepidosira* taxa (Table 2), even with regards to the dorsal chaetotaxy (see remarks of the new species in the Appendix S1), suggests this taxon could be poly or paraphyletic. Also, as discussed before, the similarities of *Lepidocyrtoides* and *Lepidosira* species, at least concerning the neotropical ones, suggest *Lepidocyrtoides* could be an ingroup of *Lepidosira* or vice-versa. Only a detailed revision of the genus and further phylogenetical analyses could bring further clarity to this discussion. Finally, the maintenance of the basal condition of *Lepidosira* + *Lepidocyrtoides* (*Lepidosira*-group) among the Entomobryinae (Figure 3), with inclusions of other taxa could permit in the future the division of Entomobryinae into new tribes.

4.3 | General comments about the Neotropical fauna of *Lepidosira* and Entomobryinae

Concerning the dorsal chaetotaxy, the few simplified schemes presented by some authors allow us to speculate that most species of *Lepidosira* from Oceania and Asia have a reduced chaetotaxy pattern compared to *L. neotropicalis* sp. n. (e.g., Yosii, 1960, pp. 18–19, figs 8b, 9b; Yoshii & Greenslade, 1994, pp. 16, 18–21, figs 8–11; Yoshii, 1989, pp. 241–242, figs 4j, 5f; Yoshii & Suhardjono, 1989, pp. 39, 41, 43, figs 9g, 10l, 11h; Nguyen, 2005, pp. 12–13, figs 6–7). The most obvious reduction can be seen at Abd. I–II, that is totally devoid of mac in most species described by the authors previously cited, or have a very reduced number of mac. Only *L. sundana* Yoshii & Suhardjono, 1989, *L. alba* (Nguyen, 2005) Zhang, Chen, & Deharveng, 2011 and *L. nigropunctata* (Nguyen, 2005) Zhang et al., 2011 have a dorsal chaetotaxy that shows some resemblance with *L. neotropicalis* sp. n., mainly on Abd. I–II, but differing in the other segments.

Concerning the Neotropical diversity of Entomobryinae, several genera were recorded for the first time in recent years from this region, in part as a consequence of collections in unexplored or little-known areas, and by revision of old material deposited at reference collections (e.g., *Amazhomidia*, *Lepidocyrtoides* and now *Lepidosira*). In Brazil, entire biomes with high indices of diversity and endemism, such as "Cerrado" and "Pantanal," and most of the Amazon rainforest, have yet to be extensively surveyed for Collembola. This scenario indicates that the subfamily diversity is much bigger than actual records, and the vast majority of this fauna still needs to be properly described.

Identification key to the Neotropical genera of Entomobryinae *sensu stricto*.

1	Body scales present	**7**
1′	Body scales absent	**2**
2	Mucro bidentate	**3**
2′	Mucro falcate	**5**
3	Dental spines present; mucro with subapical tooth much larger than apical one	***Homidia***
3′	Dental spines absent; mucro with subapical and apical teeth usually subequal	**4**
4	8 + 8 eyes	***Entomobrya***
4′	0 + 0 to 6 + 6 eyes	***Sinella***
5	Mucronal spine present	**6**
5′	Mucronal spine absent	***Calx***
6	Eyes present (8 + 8)	***Drepanura***
6′	Eyes absent (0 + 0 to 2 + 2)	***Coecobrya***
7	Mucro bidentate	**9**
7′	Mucro falcate	**8**
8	Mucronal spine present	***Drepanosira***
8′	Mucronal spine absent	***Desertia***
9	Dental scales present	**12**
9′	Dental scales absent	**10**
10	Dental spines present; prelabral chaetae bifurcate	***Amazhomidia***
10′	Dental spines absent; prelabral chaetae simple	**11**
11	Non-ciliated scales, with two distinct longitudinal ribs	***Americabrya***
11′	Ciliated scales, without two distinct longitudinal ribs	***Willowsia***
12	Manubrial plate with blunt macrochaetae	***Lepidocyrtoides***
12′	Manubrial plate without blunt macrochaetae	***Lepidosira***

ACKNOWLEDGEMENTS

The authors thank to Dr. Iuri G. Baseia and Gleyce M. Silva by the aid with the imaging equipment and the staff of the Danish National High Throughput Sequencing Centre for technical assistance. The senior author thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq—Brazil) for the financial support (Universal, Process # 441451/2014-4; PQ2015, Process # 301498/2015-6) and the corresponding author was supported by a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES—Brazil) scholarship (PDSE, Process # BEX 6891/15-2).

ORCID

Nerivânia N. Godeiro https://orcid.org/0000-0002-1669-6124

Marcus Thomas P. Gilbert http://orcid.org/0000-0002-5805-7195

Feng Zhang https://orcid.org/0000-0002-1371-266X

Bruno C. Bellini https://orcid.org/0000-0001-7881-9436

REFERENCES

Abrantes, E. A., Bellini, B. C., Bernardo, A. N., Fernandes, L. H., Mendonça, M. C., Oliveira, E. P., … Zeppelini, D. (2012). Errata Corrigenda and update for the "Synthesis of Brazilian Collembola: an update to the species list." ABRANTES et al. (2010). *Zootaxa*, *3168*, 1–21.

Ågren, H. (1904). Lappländische Collembola. *Arkiv för Zoologi*, *2*, 1–30.

Andrews, S. (2018). *FastQC: a quality control tool for high throughput sequence data* (version 0.11.8) [software]. Retrieved from http://www.bioinformatics.babraham.ac.uk/projects/fastqc

Arlé, R. (1939). Collemboles nouveaux de Rio de Janeiro. *Annais da Academia Brasileira de Ciências*, *11*, 25–32.

Arlé, R. (1959). Collembola Arthropleona do Brasil oriental e central. *Arquivos do Museu Nacional*, *49*, 155–211.

Arlé, R., Guimarães, A. E. (1978). Novas espécies de *Entomobrya* Rondani, 1861, do estado do Pará (Collembola, Entomobryomorpha). *Boletim do Museu Paraense Emilio Goeldi, Nova Série, Zoologia*, *89*, 1–18.

Arlé, R., & Guimarães, A. E. (1980). Sobre o gênero *Lepidosira* Schött, 1925, com descrição de uma espécie nova do Rio de Janeiro (Collembola). *Revista Brasileira de Biologia*, *40*, 409–414.

Arlé, R., & Guimarães, A. E. (1981). Descrição de *Lepidosira villasboasi*, sp. n., do Alto Xingu (Collembola, Entomobryidae). *Revista Brasileira de Entomologia*, *25*, 155–159.

Arlé, R., & Mendonça, C. (1982). Estudo preliminar das espécies de *Dicranocentrus* Schött, 1893, ocorrentes no Parque Nacional da Tijuca, Rio de Janeiro (Collembola). *Revista Brasileira de Biologia*, *42*, 41–49.

Bellinger, P. F., Christiansen, K. A., & Janssens, F. (1996–2019). *Checklist of the Collembola of the world*. Retrieved from http://www.collembola.org

Bellini, B. C., Cipola, N. G., & Godeiro, N. N. (2015). New species of *Lepidocyrtus* Bourlet and *Entomobrya* Rondani (Collembola: Entomobryoideia: Entomobryidae) from Brazil. *Zootaxa*, *4027*, 227–242. https://doi.org/10.11646/zootaxa.4027.2.3

Bonet, F. (1934). Colémbolos de la República Argentina. *Eos*, *9*, 123–194.

Börner, C. (1907). Collembolen aus Ostafrika, Madagascar und Südamerika. In A. Voeltzkow (Ed.), *Reise in Ostafrika in den Jahren 1903–1905, 2* (pp. 147–178). Stuttgart, Germany: E. Schweizerbartsche Verlagsbuchhandlung.

Börner, C. (1913). Zur Collembolenfauna Javas. Das trochanteralorgan der Entomobryiden. *Overgedrukt uit het Tijdschrift voor Entomologie*, *56*, 44–61.

Bourlet, C. (1839). Mémoire sur les Podures. *Mémoires de la Société des Sciences de l' Agriculture de Lille*, *1*, 377–418.

Brook, G. (1882). On a new genus of Collembola (*Sinella*) allied to *Degeeria* Nicolet. *Journal of the Linnean Society of London (Zoology)*, *16*, 541–545. https://doi.org/10.1111/j.1096-3642.1882.tb02398.x

Brook, G. (1884). A revision of the Genus *Entomobrya*, Rond. (*Degeeria*, Nic.). *Journal of the Linnean Society of London (Zoology)*, *17*, 270–282. https://doi.org/10.1111/j.1096-3642.1884.tb02023.x

Carapelli, A., Comandi, S., Convey, P., Nardi, F., & Frati, F. (2008). The complete mitochondrial genome of the Antarctic springtail *Cryptopygus antarcticus* (Hexapoda: Collembola). *BMC Genomics*, *9*, 1–12. https://doi.org/10.1186/1471-2164-9-315

Carapelli, A., Convey, P., Nardi, F., & Frati, F. (2014). The mitochondrial genome of the antarctic springtail *Folsomotoma octooculata* (Hexapoda; Collembola), and an update on the phylogeny of collembolan lineages based on mitogenomic data. *Entomologia*, *190*, 46–55. https://doi.org/10.4081/entomologia.2014.190

Carpenter, G. H. (1934). Collembola from the Society Islands. *Bernice P Bishop Museum Bulletin*, *113*, 135–141.

Christiansen, K. (1958). The nearctic members of the genus *Entomobrya* (Collembola). *Bulletin of the Museum of Comparative Zoology*, *118*, 438–545.

Christiansen, K. (1960). The genus *Sinella* Brook (Collembola: Entomobryidae) in Nearctic Caves. *Annals of the Entomological Society of America*, *53*, 481–491.

Christiansen, K. (1963). Preliminary notes on the genus *Entomobrya* in South America with special reference to Patagonia. *Biologie de l'amérique Australe*, *2*, 149–168.

Christiansen, K., & Bellinger, P. (1980). *The Collembola of North America north of the Rio Grande, Part 3. Family Entomobryidae*. Grinnell, IA: Grinnell College. https://doi.org/10.1002/mmnd.19840310103

Christiansen, K., & Bellinger, P. (2000). A Survey of the Genus *Seira* (Hexapoda: Collembola: Entomobryidae) in the Americas. *Caribbean Journal of Science*, *36*, 39–75.

Cipola, N. G., Morais, J. W., & Bellini, B. C. (2014). A new species of *Seira* (Collembola: Entomobryidae: Seirini) from Northern Brazil, with the addition of new chaetotaxic characters. *Zoologia*, *31*, 489–495. https://doi.org/10.1590/S1984-46702014000500009

Cipola, N. G., Morais, J. W., & Bellini, B. C. (2016). A new genus of Entomobryinae (Collembola, Entomobryidae) from Brazilian Amazon with body scales and dental spines. *Zootaxa*, *4105*, 261–273. https://doi.org/10.11646/zootaxa.4105.3.3

Cipola, N. G., Morais, J. W., & Bellini, B. C. (2017). The discovery of *Lepidocyrtoides* Schött, 1917 (Collembola, Entomobryidae, Entomobryinae) from the New World, including three new species from Brazil and one from Australia. *Zootaxa*, *4324*, 201–248. https://doi.org/10.11646/zootaxa.4324.2.2

Cipola, N. G., Morais, J. W., & Bellini, B. C. (2018). New species, redescriptions and a new combination of *Acanthocyrtus* Handschin, 1925 and *Amazhomidia* Cipola & Bellini, 2016 (Collembola, Entomobryidae, Entomobryinae). *Zootaxa*, *4387*, 401–435. https://doi.org/10.11646/zootaxa.4387.3.1

Dalla-Torre, K. W. (1895). Die gattungen und arten der Apterygogenea (Brauer). *Programme K. K. Staats-Gymnasium Insbruck*, *46*, 23.

Denis, J. R. (1924). Sur les Collemboles du Muséum de Paris. *Annales de la Société Entomologique de France*, *93*, 211–260.

Denis, J. R. (1929). Notes sur les collemboles récoltés dans ses voyages par le Prof. F. Silvestri. *Bolletino del Laboratorio di Zoologia*

Generale e Agraria della R. Scuola Superiore d'Agricoltura in Portici, *22*, 166–180.

Denis, J. R. (1931). Collemboles de Costa Rica avec une contribution au species de l'ordre. *Contributo alla conoscenza de Microgenton di Costa Rica*, *2*, 69–170.

Denis, J. R. (1936). Report on Collembola. *Memoirs of the Connecticut Academy of Arts and Sciences*, *10*, 261–282.

Díaz, A., & Najt, J. (1995). Collemboles (Insecta) des Andes vénézuéliennes. *Bulletin du Muséum National d'histoire Naturelle*, *16*, 417–435.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Ellis, W. N., & Bellinger, P. F. (1973). An annotated list of the generic names of Collembola (Insecta) and their type species. *Monografieen van de Nederlandse Entomologische Vereniging*, *7*, 1–74.

Faddeeva-Vakhrusheva, A., Derks, M. F. L., Anvar, S. Y., Agamennone, V., Suring, W., Smit, S., … Roelofs, D. (2016). Gene family evolution reflects adaptation to soil environmental stressors in the genome of the collembolan *Orchesella cincta*. *Genome Biology and Evolution*, *8*, 2106–2117. https://doi.org/10.1093/gbe/evw134

Faddeeva-Vakhrusheva, A., Kraaijeveld, K., Derks, M. F. L., Anvar, S. Y., Agamennone, V., Suring, W., … Roelofs, D. (2017). Coping with living in the soil: The genome of the parthenogenetic springtail *Folsomia candida*. *BMC Genomics*, *18*, 493. https://doi.org/10.1186/s12864-017-3852-x

Fjellberg, A. (1999). The Labial Palp in Collembola. *Zoologischer Anzeiger*, *237*, 309–330.

Folsom, J. W. (1902). Collembola of the grave. *Psyche*, *9*, 363–367. https://doi.org/10.1155/1902/42417

Folsom, J. W. (1921). A new *Entomobrya*. *Zoologica, Scientific Contributions of the New York Zoological Society*, *11*, 237–238. https://doi.org/10.5962/bhl.title.38001

Folsom, J. W. (1924). New species of Collembola from New York State. *American Museum Novitates*, *108*, 1–12.

Folsom, J. W. (1927). Insects of the subclass Apterygota from Central America and the West Indies. *Proceedings of the United States National Museum*, *72*(2702), 1–16. https://doi.org/10.5479/si.00963801.72-2702.1

Gisin, H. (1967). Espèces nouvelles et lignées évolutives de *Pseudosinella* endogés. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, *301*, 5–25.

Greenslade, P. (1994). Collembola. In W. W. K. Houston (Ed.), *Zoological Catalogue of Australia. Protura, Collembola, Diplura* (Vol. 22, pp. 19–38). Melbourne, Australia: CSIRO Australia.

Greenslade, P. (2012). Collembola. In D. P. Gordon (Ed.), *The New Zealand inventory of biodiversity: A species 2000 symposium review. Animalia* (Vol. 1, pp. 237–243). Christchurch, CT: Canterbury University Press.

Greenslade, P., & Majer, J. D. (1980). Collembola of rehabilitated mine sites in Western Australia. In D. L. Dindal (Ed.), *Soil biology as related to land use practices* (pp. 397–408). Washington, WA: Environmental Protection Agency.

Gruia, M. (1998). Collembola of the karstic system from Movile. *Travaux de l'institut de Spéologie Émile Racovitza*, *37–38*, 167–174.

Guthrie, J. E. (1903). *The Collembola of Minnesota*. Minneapolis, MN: Geological and Natural History Survey of Minnesota. https://doi.org/10.5962/bhl.title.1701

Handschin, E. (1924). Neue myrmecophile und termitophile collembolenformen aus Süd Amerika. *Neue Beiträge zur Systematischen Insektenkunde*, *3*, 13–28.

Handschin, E. (1927). Collembolen aus Costa Rica. *Entomologische Mitteilungen*, *16*, 110–119.

Handschin, E. (1928). Collembola from Mexico. *Zoological Journal of the Linnean Society*, *36*, 533–552. https://doi.org/10.1111/j.1096-3642.1928.tb02181b.x

Hassanin, A., Leger, N., & Deutsch, J. (2005). Evidence for multiple reversals of asymmetric mutational constraints during the evolution of the mitochondrial genome of Metazoa, and consequences for phylogenetic inferences. *Systematic Biology*, *54*, 277–298. https://doi.org/10.1080/10635150590947843

Howard, G. W. (1969). A new species of *Lepidosira* Schött (Collembola: Entomobryidae). *Journal of the Australian Entomological Society*, *8*, 189–191. https://doi.org/10.1111/j.1440-6055.1969.tb00756.x

Jackman, S. D., Vandervalk, B. P., Mohamadi, H., Chu, J., Yeo, S., Hammond, S. A., … Birol, I. (2017). ABySS 2.0: Resource-efficient assembly of large genomes using a bloom filter. *Genome Research*, *27*, 768–777. https://doi.org/10.1101/gr.214346.116

Jacquemart, S. (1975). Collembola. *Natuur- en Vogelreservaten van Belgie*, *2*, 83–84.

Jordana, R., & Baquero, E. (2005). A proposal of characters for taxonomic identification of *Entomobrya* species (Collembola, Entomobryomorpha), with description of a new species. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, *76*, 117–134.

Jordana, R., & Baquero, E. (2008). *Coecobrya kennethi* n. sp. (Collembola, Entomobryomorpha) and presence of *Arrhopalites caecus* (Tullberg, 1871) from Ana Roiho cave (Maunga Hiva Hiva). *Rapa Nui-Easter Island. Euryale*, *2*, 68–75.

Joshi, N. A., & Fass, J. N. (2011). *Sickle: A sliding-window, adaptive, quality-based trimming tool for FastQ files* (version 1.33) [software]. Retrieved from https://github.com/najoshi/sickle

Katoh, K., & Standley, D. M. (2013). MAFFT Multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780. https://doi.org/10.1093/molbev/mst010

Katz, A. D. (2017). A new endemic species of *Willowsia* from Florida (USA) and descriptive notes on all New World *Willowsia* (Collembola: Entomobryidae). *Zootaxa*, *4350*, 549–562. https://doi.org/10.11646/zootaxa.4350.3.7

Katz, A. D., Giordano, R., & Soto-Adames, F. N. (2015a). Operational criteria for cryptic species delimitation when evidence is limited, as exemplified by North American *Entomobrya* (Collembola: Entomobryidae). *Zoological Journal of the Linnean Society*, *173*, 818–840. https://doi.org/10.1111/zoj.12220

Katz, A. D., Giordano, R., & Soto-Adames, F. N. (2015b). Taxonomic review and phylogenetic analysis of fifteen North American *Entomobrya* (Collembola, Entomobryidae), including four new species. *ZooKeys*, *525*, 1–75. https://doi.org/10.3897/zookeys.525.6020

Katz, A. D., Taylor, S. J., Soto-Adames, F. N., Addison, A., Hoese, G. B., Sutton, M. R., & Toulkeridis, T. (2016). New records and new species of springtails (Collembola: Entomobryidae, Paronellidae) from lava tubes of the Galápagos Islands (Ecuador). *Subterranean Biology*, *17*, 77–120. https://doi.org/10.3897/subtbiol.17.7660

Krzywinski, M., Schein, J., Birol, I., Connors, J., Gascoyne, R., Horsman, D., … Marra, M. A. (2009). Circos: An information aesthetic for comparative genomics. *Genome Research*, *19*, 1639–1645. https://doi.org/10.1101/gr.092759.109

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, *9*, 357–359. https://doi.org/10.1038/nmeth.1923

Linnaeus, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymids, locis*. Stockholm, Sweden: Laurentii Salvii. https://doi.org/10.5962/bhl.title.542

Linnaeus, C. (1767). *Systema naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymis, locis. Tom. I. Pars II. Editio Duodecima Reformata*. Stockholm, Sweden: Laurenti Salvii.

Liu, L., Chen, J. X., & Greenslade, P. (2008). A new species of the genus *Lepidocyrtoides* (Collembola: Entomobryidae) from Australia. *Zootaxa*, *1745*, 55–62. https://doi.org/10.11646/zootaxa.1745.1.5

Loring, S. J. (1984). *Janetschekbrya epiphyta*, new species from Peru (Collembola: Entomobryidae). *Revue d'écologie et de Biologie du Sol*, *21*, 563–566.

Lubbock, J. (1870). Notes on the Thysanura. Part IV. *Transactions of the Linnean Society of London*, *27*, 277–297. https://doi.org/10.1111/j.1096-3642.1870.tb00214.x

Lubbock, J. (1873). *Monograph of the Collembola and Thysanura*. London, England: Ray Society. https://doi.org/10.5962/bhl.title.11583

Mari-Mutt, J. A. (1979). A revision of the genus *Dicranocentrus* Schött (Insecta: Collembola: Entomobryidae). *Agricultural Experiment Station Bulletin*, *259*, 1–79.

Mari-Mutt, J. A., & Bellinger, P. F. (1990). *A catalog of the Neotropical Collembola, including Neartic areas of Mexico*. Gainesville, FL: Sandhill Crane Press.

Mari-Mutt, J. A., & Bellinger, P. F. (1996). Supplement to the Catalog of the Neotropical Collembola – August 1989 to April 1996. *Caribbean Journal of Science*, *32*, 166–175.

Mari-Mutt, J. A., Bellinger, P. F., & Janssens, F. (1996–2019). *Supplement to the Catalog of the Neotropical Collembola – May 1996 to 2019*. Retrieved from https://www.collembola.org/publicat/neotrcat.htm

Mari-Mutt, J. A., & Palacios-Vargas, J. G. (1987). *Americabrya*, a new genus of Entomobryidae (Collembola), with a redescription of *A. arida* (Christianson and Bellinger) based on Mexican specimens and descriptive notes for *A. epiphyta* (Loring). *Journal of the New York Entomological Society*, *95*, 99–108.

Meng, G., Li, Y., Yang, C., & Liu, S. (2019). MitoZ: A toolkit for animal mitochondrial genome assembly, annotation and visualization. *Nucleic Acids Research*, *47* (11), e63. https://doi.org/10.1093/nar/gkz173

Meyer, M., & Kircher, M. (2010). Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Protocols*, *6*, 1–10. https://doi.org/10.1101/pdb.prot5448

Mills, H. B. (1931). New Nearctic Collembola. *American Museum Novitates*, *464*, 1–11.

Mills, H. B., & Rolfs, A. R. (1933). Collembola from the State of Washington. *The Pan-Pacific Entomologist*, *9*, 77–83.

Nguyen, T. T. (2005). Seven new springtail species (Collembola: Entomobryidae) from Vietnam. *Sinh Hoc*, *27*, 8–17. https://doi.org/10.15625/0866-7160/v27n1.5246

Nicolet, H. (1847). Essai sur une classification des insectes aptères, de l'ordre des Thysanoures. (Séance du 25 Mars 1846). *Annales de la Société Entomologique de France*, *2*, 335–395.

Packard, A. S. (1873). Synopsis of the Thysanura of Essex County, Mass., with descriptions of a few extralimital forms [Collembola included]. *Fifth Annual Report of the Peabody Academy of Science for the Year 1872*, *8*, 23–51.

Potapov, M. (2001). Synopses on Palaearctic Collembola, volume 3. Isotomidae. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, *73*, 1–603.

Rambaut, A. (2014). *FigTree, a graphical viewer of phylogenetic trees (version 1.4.2) [software]*. Retrieved from http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A., Suchard, M. A., Xie, W., & Drummond, A. J. (2013). *Tracer MCMC trace analysis tool (version v1.6.0) [software]*. Retrieved from http://beast.community/tracer

Rapoport, E. H. (1962a). Colémbolos de Bahía Blanca (Argentina). III. *Publicaciones del Instituto de Edafologia e Hidrologia*, *2*, 2–24.

Rapoport, E. H. (1962b). Colembolos de Bahia Blanca (Argentina), IV. *Acta Zoologica Lilloana*, *18*, 443–455.

Rapoport, E. H., & Izarra, D. C. (1962). Colémbolos de Bahia Blanca (Argentina) V. *Physis*, *23*, 249–256.

Rapoport, E. H., & Rubio, I. (1968). Fauna colembólica de Chile II. *Acta Biologica Venezuelica*, *6*, 52–67.

Reuter, O. M. (1890). Collembola in caldariis viventia enameravit novasque species descripsit. *Meddelanden af Societas pro Fauna et Flora Fennica*, *17*, 17–28.

Salmon, J. T. (1937). Descriptions and notes so some New Zealand Collembola. *Transactions of the Royal Society of New Zealand*, *67*, 352–358.

Salmon, J. T. (1938). A new genus of Collembola in New Zealand and the genus *Lepidosira*. *Transactions of the Royal Society of New Zealand*, *68*, 349–361.

Salmon, J. T. (1941). The Collembolan fauna of New Zealand, including a discussion of its distribution and affinities. *Transactions of the Royal Society of New Zealand*, *70*, 282–431.

Salmon, J. T. (1944). New genera, species and records of New Zealand Collembola, and a discussion of *Entomobrya atrocincta* Schött. *Records of the Dominion Museum*, *1*, 123–182.

Salmon, J. T. (1956). Contributions à l'étude de la faune entomologique du Ruanda-Urundi (Mission P. Basilewsky 1953). LXXIX. Collembola. *Collembola. Annales du Musée du Congo*, *8*, 9–40.

Salmon, J. T. (1970). Some new records and new species of Collembola from India. *Transactions of the Royal Society of New Zealand*, *12*, 145–152.

Schäffer, C. (1897). *Apterygoten*. Hamburg, Germany: Hamburger Magalhaensische Sammelreise.

Schött, H. (1891). Beiträge zur Kenntniss kalifornischer Collembola. *Bihang Till K. Svenska Vet.-Akad Handlingar*, *17*(8), 1–25.

Schött, H. (1896). North American Apterygogenea. *Proceedings of the California Academy of Sciences*, *2*, 169–196.

Schött, H. (1917). Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia, 1910–1913. No 15, Collembola. Arkiv för. *Zoologi*, *11*(8), 1–60.

Schött, H. (1925). Collembola from Mount Murud and Mount Dulit in Northern Sarawak. *Sarawak Museum Journal*, *3*, 107–127.

Schubert, M., Lindgreen, S., & Orlando, L. (2016). AdapterRemoval v2: Rapid adapter trimming, identification, and read merging. *BMC Research Notes*, *9*, 88. https://doi.org/10.1186/s13104-016-1900-2

Scott, D. B. (1937). Collembola found under the bark of dead trees in California, with descriptions of two new species. *The Pan-Pacific Entomologist*, *13*, 131–135.

Shoebotham, J. (1917). Notes on the Collembola, part 4. The classification of the Collembola; with a list of genera known to occur in the British Isles. *Annals and Magazine of Natural History*, *8*, 425–436. https://doi.org/10.1080/00222931709486959

Snider, R. J. (1981). A new species of *Janetschekbrya* from Costa Rica (Collembola: Entomobryidae). *Entomological News*, *92*, 39–41.

Soto-Adames, F. N. (2002). Four New Species and New Records of Springtails (Hexapoda: Collembola) from the US Virgin Islands and

Puerto Rico, with Notes on the Chaetotaxy of *Metasinella* and *Seira*. *Caribbean Journal of Science*, *38*, 77–105.

Soto-Adames, F. N. (2008). Postembryonic development of the dorsal chaetotaxy in *Seira dowlingi* (Collembola, Entomobryidae): With an analysis of the diagnostic and phylogenetic significance of primary chaetotaxy in *Seira*. *Zootaxa*, *1683*, 1–31. https://doi.org/10.11646/zootaxa.1683.1.1

Soto-Adames, F. N., Barra, J. A., Christiansen, K., & Jordana, R. (2008). Suprageneric Classification of the Entomobryomorpha Collembola. *Annals of the Entomological Society of America*, *101*, 501–513. https://doi.org/10.1603/0013-8746(2008)101[501:SCOCE]2.0.CO;2

Stach, J. (1930). Apterygoten aus dem nordlichen und ostlichen Spanien gesammelt von Dr. F. Haas in den Jahren 1914–1919. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, *42*, 1–83.

Stach, J. (1965). On some Collembola of North Vietnam. *Acta Zoologica Cracoviensia*, *10*, 345–372.

Szeptycki, A. (1972). Morpho-systematic studies on Collembola. III. Body chaetotaxy in the first instars of several genera of the Entomobryomorpha. *Acta Zoologica Cracoviensia*, *17*, 341–372.

Szeptycki, A. (1979). *Morpho-systematic studies on Collembola. IV. Chaetotaxy of the Entomobryidae and its phylogenetical significance*. Kraków, Poland: Polska Akademia Nauk.

Thibaud, J. M., & Najt, J. (1989). Errata et addenda aux Collemboles (Insecta) de l'Équateur II et IV. *Bulletin du Muséum National d'histoire Naturelle*, *11*, 983.

Tullberg, T. (1871). Förteckning öfver Svenska Podurider. *Öfvers Kongl Vet-Akad Förhandlingar*, *28*, 143–155.

Willem, V. (1901). Les Collemboles recueillis par l'expédition antarctique belge. *Annales de la Société entomologique de Belgique*, *45*, 260–262.

Womersley, H. (1930). On the Apterygota collected in British Guiana by the Oxford University Expedition of 1929. *Annals and Magazine of Natural History*, *6*, 305–317. https://doi.org/10.1080/00222933008673218

Womersley, H. (1935). On some new species and records of Australian and New Zealand Collembola. *Transactions and Proceedings of the Royal Society of South Australia*, *59*, 207–218.

Womersley, H. (1936). Further records and descriptions of Australian Collembola. *Records of the South Australia Museum*, *5*, 475–485.

Womersley, H. (1937). Collembola (Springtails). *Reports of the Australian National Antarctic Research Expedition. 1929–1931*, *4*, 1–7.

Womersley, H. (1939). *Primitive insects of South Australia*. Adelaide, SA: Government Printer.

Wu, C., Jordan, M. D., Newcomb, R. D., Gemmell, N. J., Bank, S., Meusemann, K., … Buckley, T. R. (2017). Analysis of the genome of the New Zealand giant collembolan (*Holacanthella duospinosa*) sheds light on hexapod evolution. *BMC Genomics*, *18*, 795. https://doi.org/10.1186/s12864-017-4197-1

Yayuk, R. S. (1989). Revised check list of Collembola from Indonesia and its adjacent regions. *Acta Zoologica Asiae Orientalis*, *1*, 1–22.

Yoshii, R. (1989). On some Collembola of New Caledonia, with notes on the "Colour Pattern Species". *Contributions from the Biological Laboratory, Kyoto University*, *27*, 233–259.

Yoshii, R., & Greenslade, P. (1994). Reconnaissance of some Entomobryid Collembola of Australia. *Acta Zoologica Asiae Orientalis*, *3*, 1–22.

Yoshii, R., & Suhardjono, Y. R. (1989). Notes on the Collembolan Fauna of Indonesia and its vicinities. I. Miscellaneous notes, with special references to Seirini and Lepidocyrtini. *Acta Zoologica Asiae Orientalis*, *1*, 23–90.

Yoshii, R., & Suhardjono, Y. R. (1992). Notes on the Collembolan Fauna of Indonesia and its vicinities. II. Collembola of Irian Jaya and Maluku Islands. *Acta Zoologica Asiae Orientalis*, *2*, 1–52.

Yosii, R. (1955). Meeresinsekten der Tokara Inseln. VI. Collembolen nebst beschreibungen terrestrischer formen. *Publications of the Seto Marine Biological Laboratory*, *4*, 379–401. https://doi.org/10.5134/174510

Yosii, R. (1960). On some Collembola of New Caledonia, New Britain and Solomon Islands. *Bulletin of the Osaka Museum of Natural History*, *12*, 9–38.

Zhang, F., Chen, J. X., & Deharveng, L. (2011). New insight into the systematics of the *Willowsia* complex (Collembola: Entomobryidae). *Annales de la Société Entomologique de France*, *47*, 1–20. https://doi.org/10.1080/00379271.2011.10697692

Zhang, F., Chen, Z., Dong, R., Deharveng, L., Stevens, M. I., Huang, Y., & Zhu, C. (2014). Molecular phylogeny reveals independent origins of body scales in Entomobryidae (Hexapoda: Collembola). *Molecular Phylogenetics and Evolution*, *70*, 231–239. https://doi.org/10.1016/j.ympev.2013.09.024

Zhang, F., & Deharveng, L. (2015). Systematic revision of Entomobryidae (Collembola) by integrating molecular and new morphological evidence. *Zoologica Scripta*, *44*, 298–311. https://doi.org/10.1111/zsc.12100

Zhang, F., Greenslade, P., & Stevens, M. I. (2017). A revision of the genus *Lepidobrya* Womersley (Collembola: Entomobryidae) based on morphology and sequence data of the genotype. *Zootaxa*, *4221*, 523–536. https://doi.org/10.11646/zootaxa.4221.5.2

Zhang, F., Ma, Y., & Greenslade, P. (2017). New Australian Paronellidae (Collembola) reveal anomalies in existing tribal diagnoses. *Invertebrate Systematics*, *31*, 375–393. https://doi.org/10.1071/IS16073

Zhang, F., Palacios-Vargas, J. G., & Chen, J. X. (2007). The Genus *Willowsia* and its Mexican species (Collembola: Entomobryidae). *Annals of the Entomological Society of America*, *100*, 36–40. https://doi.org/10.1603/0013-8746(2007)100[36:TGWAIM]2.0.CO;2

Zhang, F., Pan, Z., Wu, J., Ding, Y., Yu, D., & Wang, B. (2016). Dental scales could occur in all scaled subfamilies of Entomobryidae (Collembola): New definition of Entomobryinae with description of a new genus and three new species. *Invertebrate Systematics*, *30*, 598–615. https://doi.org/10.1071/IS16005

Zhang, F., Sun, D. D., Yu, D. Y., & Wang, B. X. (2015). Molecular phylogeny supports S-chaetae as a key character better than jumping organs and body scales in classification of Entomobryoidea (Collembola). *Scientific Reports*, *5*, 1–12. https://doi.org/10.1038/srep12471

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Nunes RC, Godeiro NN, Pacheco G, et al. The discovery of Neotropical *Lepidosira* (Collembola, Entomobryidae) and its systematic position. *Zool Scr*. 2019;48:783–800. https://doi.org/10.1111/zsc.12377