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Springtails (Collembola, Hexapoda) from Montebello Lakes, Chiapas, Mexico

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ABSTRACT
Springtails are mostly terrestrial organisms, relatively rare in truly aquatic environments; a few are neustonic while others are found in humid caves, surfaces, and crevices of marine coastal zones. We have found them in the benthic zone of 4 deep lakes, Bosque Azul, Dos Lagos, Ensueño, and Tziscao of Lagunas de Montebello National Park in Chiapas. We recovered 43 specimens belonging to 13 species from the samples, all of which except *Americabrya arida* were first records for the state of Chiapas; the most abundant were *A. arida* and *Lepidocyrtus lanuginosus*. Species richness of each lake varied between 1 and 12; density varied between 15 ± 25 and 133 ± 118 org m^{-2}, and biomass varied between 0.02 and 4.3 ± 4.4 and 0.02 μg m^{-2}. Tziscao showed the highest abundance (35 individuals), species richness (12 species), and density (133 ± 118 org m^{-2}), and Bosque Azul showed the highest average biomass (4.3 ± 4.4 μg). Together, 96% of the organisms were collected during summer when lakes were thermally stratified (warm monomixis); 44% of the organisms were recovered from deep anoxic samples (>20 m). Springtails were found living in warm waters in conditions varying from well oxygenated to anoxic, a slightly basic pH range (7.1–8.3), and a high range of electric conductivity (219.7–1716.0 μS cm^{-1}) values. Sediments were mainly composed of sands and mud (silt and clay) with a wide organic matter range (15.4–51.2%) and sedimentary carbonates (6.0–98.3%). Of the 43 specimens, 17 were adults (12 males and 5 females) and 26 were immature, both with gut content composed mostly of *Cladosporium* hyphae and conidia. These are the first records of submerged Collembola inhabiting the deep benthic zones of Mexican lakes.

KEYWORDS
aquatic springtails; biomass; density; habitat; species richness

Introduction

The aquatic environment is not a typical habitat for springtails (Collembola), which are usually found in soil, leaf litter, vegetation, including canopies and other humid environments such as caves, in high quantities. Usually they are highly abundant in the terrestrial part of terrestrial–aquatic ecotones (e.g., *Denisiella lithophila*; Snider 1988) but can also be incidentally found in the aquatic regions (Deharveng et al. 2008). However, neustonic collembolans have also been found in epicontinental aquatic bodies, in caves, and even in crevices and sand in marine littoral zones, but they have rarely been found in submerged plants and bottom sediments at depths >20 m (Christiansen and Snider 2008).

The morphological adaptations that allow collembolans to inhabit aquatic environments, particularly the neustonic habitat, have been poorly elucidated. These organisms have been shown to consist of a hydrophobic integument that allows them to float and remain in the surface film of the waterbody. In some cases, their legs have elongated unguis and empodial appendages (nail and empodium), furcula with hydrophobic setae, and a large mucro with large lamellae that allows them to move and jump across the water surface (Christiansen 1965).

Although some species of Onychiuridae, Tomoceridae, Entomobryidae, and Hypogastruridae can survive under water for a few days, evidence that their entire life cycle occurs in the aquatic environment is lacking (Deharveng et al. 2008). Thibaud (1970) tested some species of Hypogastruridae and found that the animals could move and survive under water up to 36 d as adults but were unable to molt.

Collembola is a key group that supports the phylogenetic relationships within the hexapods, so aquatic species have garnered interest as a way to address how the clade transitioned to terrestrial environments. Glenner et al. (2006) posited that hexapods could be derived from

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the Crustacea. D'Haese (2002) using rDNA 28S analysis showed that the aquatic condition of *Podura aquatica* (Poduridae/Collembola), a representative aquatic species, is not ancestral but derived, and it has evolved independently several times, which is interesting. Several species previously unknown in aquatic environments may yet be encountered in this habitat. This lack of knowledge about Collembola might be related to their small size and relatively low economic importance. The review by Deharveng et al. (2008) lists 109 marine species, 414 epicontinental species, and 2 species that may be associated with both marine and epicontinental environments worldwide. From the epicontinental environment, 285 species inhabit caves, 103 are neustonic, and 26 are cryophilic (inhabitants of permanent glaciers or ice sheets).

Little is known about the ecology of aquatic Collembola (Christiansen and Snider 2008), and most of the existing data come from marine littoral zones (i.e., Christiansen and Bellinger 1988, King et al. 1990, Soto-Adames and Guillén 2011). Although these species live in cracks or "spray" zones on rocky coasts as well as in beach gravel, they are in constant contact with water and can even be submerged, although not permanently, as a result of changes in the tides. Consequently, few records and even fewer studies exist for these aquatic hexapods in lake benthic zones.

In Mexico, a little more than 1000 species of 24 families of Collembola are known, but the number could be as many as 3600 because information is lacking for many states (Palacios-Vargas 2013). The most representative families are Entomobryidae, Neanuridae, Isotomidae, and Hypogastruridae, and the states where most surveys have been conducted are Estado de México, Veracruz, Distrito Federal, Morelos, Hidalgo, Jalisco, and Guerrero. In the state of Chiapas, 30 species have been reported, 7 of which are considered to characterize this biogeographic province: *Ceratophysella tolteca*, *Schoettella novajaniae*, *Brachystomella montebella*, *Palmanura lacandona*, *Thalassaphorura hera*, *Pseudodicranocentrus circulatus*, and *Trogolaphysa toroi* (Palacios-Vargas 2013). The National Commission for the Knowledge and Use of Biodiversity (CONABIO) dataset has 60 unpublished records (Cruz-Leal, UNAM, pers. comm.), however, and only 26 records of species are associated with aquatic environments in Mexico (although nearly 90 records might exist, including unpublished), most of which are from marine littoral zones (Table 1).

In our preliminary limnological study of Montebello, Chiapas, we found Collembola in the sediments of both the littoral zone and the deep zone (>20 m) of 4 lakes. This study resulted in 13 new records of Collembola associated with aquatic environments as well as information about their habitat and ecology.

Methods

Parque Nacional Lagunas de Montebello (PNLM) is in the south-southeast region of Chiapas bordering Guatemala.

Table 1. Species list of Collembola reported from aquatic environments in Mexico.

	Species	Locality	Habitat	Reference
1	*Archisotoma gourbaultae*	México	Marine shoreline	Thibaud and Palacios-Vargas 2001b
2	*Ballistura schoetti*	Ciudad del México	Water surface	Palacios-Vargas 2013
3	*Brachystomella baconaoensis*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
4	*Cryptopygus axayacatl*	Guerrero, Quintana Roo	Marine shoreline	Palacios-Vargas and Thibaud 2001, Thibaud and Palacios-Vargas 2001a
5	*Folsomides parvulus*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
6	*F. onychiurina*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
7	*Friesea cubensis*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
8	*Isotogastrura ahuizotli*	Baja California Sur	Marine shoreline	Palacios-Vargas and Thibaud 1998
9	*I. atuberculata*	Guerrero	Marine shoreline	Palacios-Vargas and Thibaud 2001
10	*I. veracruzana*	Veracruz	Marine shoreline	Palacios-Vargas and Thibaud 1998
11	*Isotomodes fiscus*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
12	*Mesaphorura matilei*	Guerrero	Marine shoreline	Thibaud and Palacios-Vargas 2000
13	*M. subitalica*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
14	*M. yosii*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
15	*Micranurida* cf. *furcifera*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
16	*Onychiurus pseudojusti*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
17	*Pseudachorutes* cf. *parvulus*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
18	*P.* cf. *subcrassoides*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
19	*Paraxenylla lapazana*	Baja California	Marine shoreline	Palacios-Vargas and Vázquez 1988
20	*Pseudostachia xicoana*	Guerrero	Marine shoreline	Palacios-Vargas and Thibaud 2001
21	*Sminthurides* sp.	Ciudad del México	Water surface	Palacios-Vargas 2013
22	*Sminthurides* sp.	Colima	Water surfaced	Palacios-Vargas 1997
22	*Stachorutes maya*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a
23	*Willemia psammophila*	Guerrero	Marine shoreline	Palacios-Vargas and Thibaud 2001
24	*W. arenicola*	Guerrero, Baja California	Marine shoreline	Palacios-Vargas and Thibaud 2001, Palacios-Vargas and Vázquez 1988
25	*W. bellingeri*	Baja California	Marine shoreline	Palacios-Vargas and Vázquez 1988
26	*Xenylla* cf. *bellingeri*	Quintana Roo	Marine shoreline	Thibaud and Palacios-Vargas 2001a

With a surface area of 64.25 km², the PNLM belongs to 2 municipalities: La Trinitaria and La Independencia. The extreme coordinates are 16°4′40″–16°10′20″N, 91°37′40″–91°47′40″W (CONANP 2007), at an altitude of 1200–1800 m a.s.l. (Durán-Calderón et al. 2014).

PNLM has >50 lakes (Fig. 1) that cover ~16% the park's surface area. The lakes display an ample array of morphometric characteristics with both large and small, shallow and deep waterbodies (Alcocer et al. 2016). Climate is wet temperate with cool and long summers and an average temperature of 17.3 °C. The rainy season extends from May to December with an annual mean precipitation of 1800 mm (García 2004).

Based on preliminary studies (e.g., Alcocer et al. 2016), 4 deep lakes were selected for this study, all varying in their maximum proportions and all exceeding 20 m in mean depth (Table 2, Fig. 2). The 4 lakes are warm-monomictic with a winter circulation–mixing period, remaining stratified the rest of the year. During the stratification period, the bottom waters (hypolimnion) become anoxic.

Our 2 sampling collections, October 2015 and March 2016, corresponded to the seasonal hydrodynamics of deep tropical lakes, the stratification and mixing periods, respectively. Stratification represents a period of harsh conditions for benthos because anoxic hypolimnia develop; meanwhile mixing represents a favorable period by reoxygenating the whole water column, allowing aerobic benthic organisms to establish and develop.

We established a transect from the middle of each lake to the shore with 4 sampling points at different depths along the bathymetric profile. For each site, sampling station depth was recorded with 95% precision using a Garmin echo-sounder (model GPSMap 526S Sounder; Table 3).

The following physicochemical variables were registered *in situ* with a water quality multiprobe monitoring instrument Hydrolab DS5: temperature (±0.10 °C accuracy, 0.01 °C resolution), dissolved oxygen (±0.2 mg L^{-1} accuracy, 0.01 mg L^{-1} resolution), electric conductivity (0.001 mS cm^{-1} accuracy, 0.0001 resolution), pH (0.2 accuracy, 0.01 resolution), and oxidation–reduction potential (ORP; ±20 mV accuracy, 1 mV resolution).

Sediment samples were collected using an Ekman dredge (15 × 15 × 15 cm), and the texture of the sediment was determined by laser diffraction using a Beckman Coulter LS 230 (range 0.04 at 2000 µm, resolution <20 mm). The organic matter content was determined by combustion (loss on ignition [LOI] = calcination at 550 °C for 4 h), and the sedimentary carbonate contents were determined by digesting carbonated compounds using 30% hydrochloric acid (García- Bazán 1990).

Collembolans were obtained with the same Ekman dredge. Samples were collected in each lake with 3 replicates at the 4 depths during both periods (stratification, circulation) totaling 96 samples (3 × 4 × 4 × 2). Each sample was passed through a 250 µm sieve to eliminate sediments and to retain the organisms, which were fixed and stained

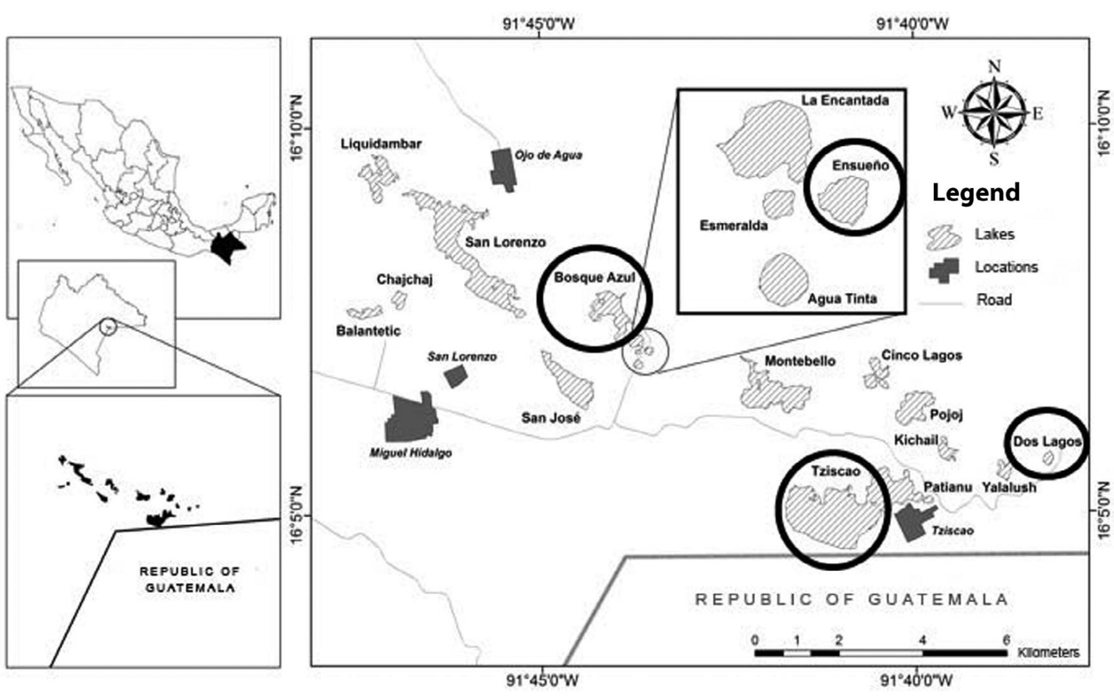

Figure 1. Location of the Parque Nacional Lagunas de Montebello (PNLM) lakes, Mexico. Lakes sampled are circled (modified from Alcocer et al. 2016).

Table 2. Location and morphometry of the studied Montebello lakes, Mexico (Alcocer et al. 2016).

	Dos Lagos	Ensueño	Tziscao	Bosque Azul
Latitude N	16°5′35″–16°5′45″	16°7′2″–16°7′8″	16°4′31″–16°5′34″	16°7′12″–16°7′53″
Longitude W	91°38′8″–91°38′17″	91°43′29″–91°43′36″	91°39′54″–91°41′44″	91°43′44″–91°44′21″
Altitude (m a.s.l.)	1427	1430	1490	1458
Maximum length (km)	0.34	0.22	3.20	1.32
Maximum width (km)	0.23	0.19	1.48	0.82
Surface (ha)	5.2	2.7	306.6	52.5
Maximum depth (m)	42	35	86	58
Mean depth (m)	25.2	21.6	28.9	20.0
Volume (m^3)	1 320 000	580 000	88 520 000	10 500 000

using a mix of 96% ethanol and Bengal Rose to increase the contrast between the live tissue and other materials. The organisms were then counted and identified at the Laboratory of Ecology and Systematics of Microarthropods at the Science Department of the National Autonomous University of Mexico (UNAM) following techniques recommended by Palacios-Vargas and Mejía-Recamier (2007). Keys used and actual systematic status were from Bellinger et al. (1996- 2017). Collembolans were quantified to estimate their density (org m^{-2}), and their biomass contribution was determined by estimating dry weights based on body length using the formula proposed by Hódar (1996):

$$W(mg) = 0.0024\, L\, (mm)^{3.676},$$

where W equals dry weight (mg), and L equals body length (mm).

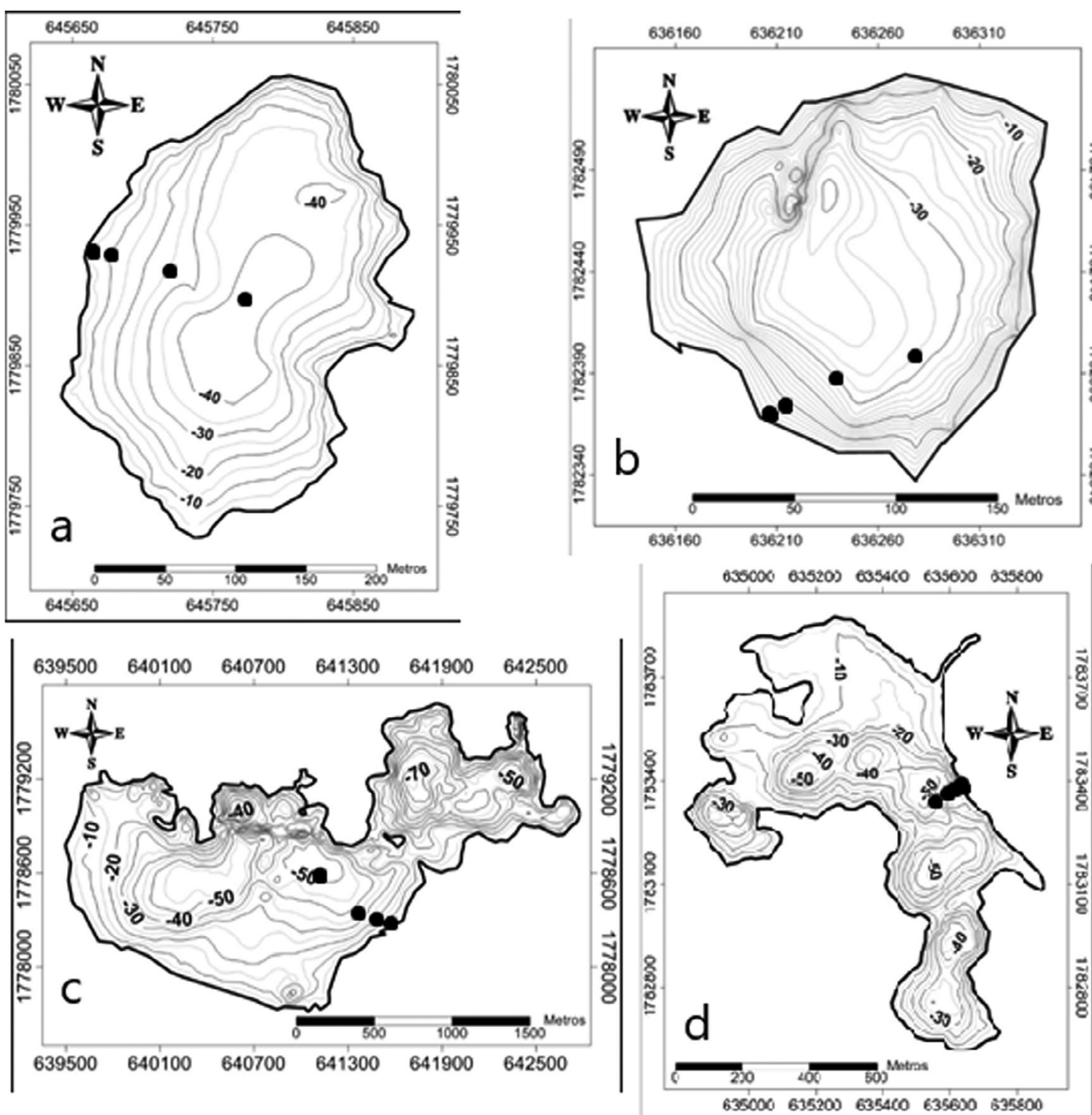

Figure 2. Bathymetric charts of the studied Montebello lakes, Mexico. Sampling stations are indicated with black dots. (a) Dos Lagos, (b) Ensueño, (c) Tziscao, (d) Bosque Azul (modified from Alcocer et al. 2016).

Table 3. Depth of the 4 sampling stations at each Montebello lake, Mexico.

Lake/Station	1	2	3	4
Dos Lagos	43 m	25 m	6 m	0.5 m
Ensueño	35 m	30 m	6 m	0.3 m
Tziscao	53 m	32 m	15 m	1 m
Bosque Azul	47 m	35 m	16 m	1 m

Results

From the 96 samples analysed, 43 organisms were recovered belonging to 6 families, 11 genera, and 13 species. The most common were *Americabrya arida* and *Lepidocyrtus lanuginosus*, with 10 individuals each; *Salina* cf. *beta* and *Willowsia mexicana* were the least common with only 1 individual each (Table 4). In Tziscao, 35 individuals belonging to 12 species and 6 families were found (species richness [S] = 12), and in Bosque Azul, 5 individuals were found from 3 species (S = 3). In Dos Lagos, 2 individuals from the same genus but different species were found (S = 2), and in Ensueño, only 1 individual was found (S = 1; Table 5). Of the 43 organisms, 26 individuals were immature and 17 were adults (12 males and 5 females).

Eight taxa (*Ceratophysella boletivora*, *C. sigillata*, *Clavisotoma laticauda*, *Desoria trispinata*, *Proisotoma minuta*, *Salina* cf. *beta*, *Tomocerus* sp., and *W. mexicana*) were exclusive to one lake. We recovered 41 individuals (≈96%) during the stratification period (Tables 4 and 5) and, by contrast, only 2 (≈4%), one in Ensueño and another in Dos Lagos, during the circulation period, both of which belonged to the same species, *Sminthurides* sp.2, which is known for its epineustonic habit.

The highest average density was found in Tziscao with 133 ± 118 org m^{-2}, followed by Bosque Azul with 25 ± 30 org m^{-2}, where individuals were only recovered during the stratification period. In Tziscao, the deepest sampling point had the highest average density (237 ± 68 org m^{-2}), and the lowest density was found in the littoral site (15 ± 25 org m^{-2}). By contrast, in Bosque Azul, the littoral and deepest points had the same density (30 ± 51 and 30 ± 26 org m^{-2}). The average density in Dos Lagos during the circulation period was 15 ± 25 org m^{-2}, the same as that found during stratification because only one individual was collected in each period. In Ensueño, the density results were 15 ± 25 org m^{-2} during circulation and none during stratification. Most abundant was *L. lanuginosus* (267 org m^{-2}), which was found in the deepest station in Tziscao, while 10 other species had densities of 44 org m^{-2}, which was lower than that at other stations (Table 5).

Bosque Azul had the highest average biomass, 4.278 ± 4.438 µg, followed by Tziscao with an average of 3.162 ± 0.881 µg. In Tziscao, the deepest point also exhibited the highest biomass, 3.912 ± 3.882 µg, and the lowest, 2.159 µg, was observed at the littoral point, where only one individual was found. At 16 m in Bosque Azul, *A. arida* had the highest biomass of 9.391 µg, and the lowest values were associated with *Sminthurides*. In particular, one individual was recovered from Dos Lagos at 25 m and had a biomass value of 0.020 µg.

Because of the different lake depths, the 2 stations closest to the shore were always defined as shallow (<20 m), whereas those located farthest from the shore were defined as deep (≥20 m). Note that not all deep stations were anoxic, such as the stations at 32 and 35 m in Tziscao and Ensueño. In addition, not all shallow stations were oxygenated, as was the case for the 16 m station in Bosque Azul (Table 5).

Most Collembola (29 individuals) were recovered from the deep stations (≥20 m), and only 14 were collected from the shallow stations (<20 m). Furthermore, of the 29 individuals from deep stations, 18 were immatures, 8 were adult males, and only 3 were females; from the 14 individuals collected at shallow stations, 8 were immatures, 4 were males, and 2 were females. In Dos Lagos and Ensueño, however, no individuals were found at the shallow stations. In Tziscao, 24 individuals were recovered from 2 of the deepest stations (53 and 32 m), and only 11 were recovered from the 2 shallowest. In Bosque Azul, 2 individuals were recovered from the deepest station (47

Table 4. Composition and abundance (*n*: number of organisms) of the collembolans sampled from the Montebello lakes, Mexico.

Family	Species	*n* Stratification	*n* Circulation
Entomobryidae	*Americabrya arida* Christiansen et Bellinger, 1980	10	0
	Lepidocyrtus lanuginosus Linnaeus in Gmelin, 1788	10	0
	Willowsia mexicana Zhang, Palacios-Vargas et Chen, 2007	1	0
Hypogastruridae	*Ceratophysella boletivora* Packard, 1873	3	0
	C. sigillata Uzel, 1891	1	0
Isotomidae	*Ballistura libra* Christiansen and Bellinger, 1980	4	0
	Clavisotoma laticauda Folsom, 1937	1	0
	Desoria trispinata Mac Gillivray, 1896	5	0
	Proisotoma minuta Tullberg, 1871	2	0
Paronellidae	*Salina* cf. *beta* Christiansen and Bellinger, 1980	1	0
Sminthurididae	*Sminthurides* sp.1	2	0
	Sminthurides sp.2	0	2
Tomoceridae	*Tomocerus* sp.	1	0
Total		41	2

Table 5. Collembola species found in the sampled Montebello lakes. (* = springtail found in anoxic waters). (+ = sampled organisms during the lake circulation, *Z* = depth, *n* = abundance, Imm = immatures, m = males, f = females).

Lake	Z (m)	Species	*n* Imm	*n* Adults m/f	Density org m−2 (SD)	Biomass µg m−2 (SD)
Dos Lagos	25	*Sminthurides* sp.1	0	1/0	15 (25)	0.02
	43*	*Sminthurides* sp.2+	0	1/0	15 (25)	0.07
Ensueño	35	*Sminthurides* sp.2+	0	0/1	15 (25)	0.38
Tziscao	1	*D. trispinata*	0	1/0	15 (25)	2.16
	15	*A. arida*	1	1/0	148 (156)	3.89 (3.44)
		C. boletivora	1	0		
		C. sigillata	0	1/0		
		D. trispinata	2	0		
		L. lanuginosus	2	0		
		B. libra	0	0/1		
		W. Mexicana	1	0		
	32	*A. arida*	4	0	133 (77)	2.69 (2.32)
		D. trispinata	1	1/0		
		L. lanuginosus	1	0		
		C. laticauda	0	1/0		
	53*	*L. lanuginosus*	5	0/1	237 (68)	3.91 (3.88)
		B. libra	0	2/0		
		C. boletivora	1	0/1		
		P. minuta	1	1/0		
		A. arida	0	1/0		
		Salina cf. *beta*	1	0		
		Sminthurides sp.1	1	0		
		Tomocerus sp.	1	0		
Bosque Azul	1	*A. arida*	1	0	30 (51)	1.41 (1.21)
		B. libra	0	0/1		
	16*	*A. arida*	0	1/0	15 (25)	9.39
	47*	*A. arida*	1	0	30 (26)	2.03 (1.54)
		L. lanuginosus	1	0		

m), and 3 were found at the shallow stations. Furthermore, in all lakes, 9 species were recovered from the deep stations (*A. arida*, *B. libra*, *C. boletivora*, *C. laticauda*, *L. lanuginosus*, *P. minuta*, *S.* cf. *beta*, *Sminthurides* sp.1, and *Sminthurides* sp.2), and only 6 were recovered from the shallow stations (*A. arida*, *B. libra*, *C. boletivora*, *C. sigillata*, *L. lanuginosus*, and *W. mexicana*).

By contrast, 20 individuals were recovered from anoxic stations—16 in Tziscao, 3 in Bosque Azul, and 1 in Dos Lagos—of which 12 were immatures, 6 were males, and 2 were females. At the oxygenated stations we recovered 14 immatures, 6 males, and 3 females. We found 9 species in oxygenated stations (*A. arida*, *B. libra*, *C. boletivora*, *L. lanuginosus*, *P. minuta*, *S.* cf. *beta*, *Sminthurides* sp.1, *Sminthurides* sp.2, and *Tomocerus* sp.) and 9 in anoxic stations (*A. arida*, *B. libra*, *C. boletivora*, *C. laticauda*, *C. sigillata*, *L. lanuginosus*, *Sminthurides* sp.1, *Sminthurides* sp.2, and *W. mexicana*).

Broadly, 19 individuals were found at deep and anoxic stations, 13 in shallow and oxygenated stations, 10 in oxygenated and deep stations, and only 1 in an anoxic and shallow station. *A. arida* was present at 3 stations from Tziscao and 3 from Bosque Azul, and its abundance was higher in deep oxygenated stations (4 individuals) but similar between the deep anoxic and shallow oxygenated stations (2 individuals). By contrast, *L. lanuginosus* was more abundant in deep anoxic stations (7 individuals) compared to other stations, and 9 of the 10 individuals were found in Tziscao.

The physicochemical characteristics of the water and sediment where the collembolans are found were recorded (Table 6). Tziscao, where most of the organisms were found, had the highest temperature and oxidation–reduction potential values, the lowest electric conductivity values, and moderate dissolved oxygen and pH levels. In particular, at 53 m, where the highest abundance, density, and biomass were found, the temperature (17.8 °C), dissolved oxygen concentration (0.0 mg L^{-1}), pH (7.1), and carbonate content (56.3%) were the lowest compared to the other points in the same lake.

In general, collembolans were found in warm waters between 17.5 and 24.0 °C in both oxygenated (8.8 mg L^{-1}) and anoxic conditions, with slightly basic pH between 7.1 and 8.3 and within a wide range of electric conductivity from 220 to 1716 µS cm^{-1}. Most individuals were concentrated in a lower conductivity range (220–275 µS cm^{-1}). The sediments in which springtails were found had carbonate contents that varied from 6.0 to 98.3% and a high proportion of organic matter between 15.4 and 51.2%, which characterizes them as organic sediments.

Discussion

In terms of the taxonomic richness of aquatic collembolans, Deharveng et al. (2008) mentioned 103 neustonic species in their global review, and Deharveng and Lek (1995) cited 73. In Mexico, 26 have been formally reported (Palacios-Vargas and Vázquez 1988, Palacios-Vargas and Thibaud 1998, 2001, Thibaud and Palacios-Vargas 2000, 2001a, 2001b, Palacios-Vargas 2013), so in this context, the 12 taxa found in the Montebello Lakes represent considerable species richness. Deharveng and Lek (1995) recognized that only 16% (12) of the 103 species are truly

Table 6. Environmental characteristics where collembolans were sampled. (Str = stratification, Cir = circulation, Water [T: temperature, DO: dissolved oxygen, K_{25}: electric conductivity, ORP: oxidation–reduction potential] and sediment [CO_3: carbonates, OM: organic matter]).

			T	DO	K_{25}		ORP	CO_3	OM	Sand	Silt	Clay
Lake	Season		°C	mg L^{-1}	µS cm^{-1}	pH	mV	%	%	%	%	%
Dos Lagos	Str	X	20.2	2.5	820	7.4	201	47.8	30.6	63.6	34.1	2.2
		(SD)	(2.4)	(3.2)	(385)	(0.3)	(70)	(11.6)	(11.3)	(23.5)	(22.5)	(1.1)
		Min–max	18.6–23.7	0.0–7.1	344–1283	7.2–7.9	96–247	34.9–62.8	16.6–43.3	40.8–88.9	10.4–55.9	0.7–3.3
Dos Lagos	Cir	X	18.8	3.6	900	7.4	131	64.8	40.0	63.8	34.7	1.5
		(SD)	(0.8)	(3.8)	(590)	(0.4)	(148)	(22.4)	(8.6)	(22.6)	(21.7)	(1.0)
		Min–max	18.1–20.0	0.0–8.2	342–1716	7.1–8.1	−91–217	52.5–98.3	32.0–51.2	43.2–95.1	4.5–54.6	0.4–2.4
Ensueño	Cir	X	19.4	7.3	289	8.0	161	24.2	21.8	14.5	59.3	26.2
		(SD)	(0.4)	(0.9)	(2)	(0.2)	(73)	(13.0)	(4.0)	(14.8)	(4.8)	(16.9)
		Min–max	19.2–20.0	6.5–8.4	288–291	7.8–8.2	89–232	7.9–39.2	15.4–26.6	2.0–35.2	52.4–63.3	4.8–45.6
Tziscao	Str	X	20.7	3.3	244	7.6	213	61.4	27.2	27.6	64.7	7.7
		(SD)	(3.2)	(3.8)	(23)	(0.4)	(20)	(6.2)	(13.6)	(15.0)	(14.1)	(3.2)
		Min–max	17.8–24.0	0.0–8.8	220–275	7.1–8.1	186–35	56.3–70.0	17.1–47.1	11.3–43.6	52.5–82.2	3.9–11.1
Bosque Azul	Str	X	18.9	1.5	531	7.8	51	48.1	32.2	30.8	64.1	5.1
		(SD)	(2.5)	(2.9)	(24)	(0.4)	(107)	(28.4)	(8.7)	(12.2)	(11.0)	(1.3)
		Min–max	17.5–22.7	0.0–5.9	505–559	7.5–8.3	−9–212	6.0–66.5	22.7–43.8	14.3–43.7	52.7–79.1	3.5–6.6

hydrophilic. Moreover, of the 26 aquatic species previously reported in Mexico, only 3 have been collected on the surface of the water (epineuston), and the rest are from marine littoral zones. Therefore, the richness of 12 taxa reported in this work is high. These are the first records of collembolan associated with lakes in Chiapas, but they are also the first global documentation showing that Collembola can be found alive at depths greater than 20 m in epicontinental waters.

The second interesting finding is that of all collembolans, only *Sminthurides* is epineustonic (Folsom and Mills 1938). The other species live in environments such as leaf litter, moss, and the forest canopy, so finding them in the benthic zones of lakes is surprising. Two other genera and one species have been reported in aquatic environments: *Ceratophysella*, *Desoria*, and *Lepidocyrtus lanuginosus* from river habitats and the French Pyrenees (Deharveng and Lek 1995).

Because of their water repellent cuticles, collembolan can be moved by water and dispersed with floods, a phenomenon that favours generalist species that can reach new habitats and establish easily (Deharveng and Lek 1995). Although this feature would prevent collembolans from being immersed in water, thus preventing them from reaching the deep benthos, eggs from the surroundings could be washed into the lakes and reach the benthic zone. Once in the benthic zone, eggs hatch under water, and when animals are exposed to air, the wax layer forms and they cannot resubmerge. Like *Anurida maritima*, which possesses a plastron supported by minor tubercles resistant to wetting by pressure and surfactants (King et al. 1990), many soil dwellers subject to periodic flooding (Zinkler and Rüssbeck 1986) probably retain a layer of air over the body, across which they continue to respire, even when totally submerged (Hopkin 1997). Eggs may also be adapted for prolonged submergence in water (Tamm 1984, 1986, Zeh et al. 1989).

Of the 13 species found in the present study, only *A. arida* had been previously reported from the State of Chiapas (Palacios-Vargas 1997). It was the most abundant species in this study, which is typical of terrestrial environments such as leaf litter and has even been found in epiphytes and mosses. In the study by Cutz-Pool et al. (2010), individuals of *A. arida* and *W. mexicana* were found in epiphytic mosses from the ground level up to 2 m in height, inferring that their vertical distribution could reach the tree canopy, as found in other members of these families and other genera (Palacios-Vargas et al. 1998, Palacios-Vargas and Castaño-Meneses 2003). This study found both species at great depths in the lakes of Chiapas.

Finally, the bottom of the lakes does not seem to be attractive for collembolan colonization. At first glance, one could conclude that our results may be due to sample contamination, as has been reported by Deharveng and Lek (1995) for riparian collembolans, but our sampling methodology allows us to reject this assumption. In all cases, the samples were taken at vegetation-free sites, and most of the specimens (29,≈67%) were collected from the deepest stations in the lakes, which were ~100–500 m offshore. In addition, contamination was unlikely during the displacement of the dredge along the water column, and the samples were screened away from vegetation and immediately stored in containers. Finally, the organisms were in good condition and showed no signs of decay; based on Bengal Rose (a vital stain) staining, they were alive at the time of collection. The samples were composed of mature (17) as well as immature (26) individuals; their guts ranged from totally filled to totally emptied, and the items we could identify in the gut content were hyphae and conidia of *Cladosporium* sp. (Fungi: Ascomycota: Davidiellaceae).

We report 12 new records of collembolans from Montebello lakes, increasing the taxonomic richness of this group in the State of Chiapas with the addition of the following taxa: *Ballistura libra*, *Ceratophysella boletivora*, *Ceratophysella sigillata*, *Clavisotoma laticauda*, *Desoria trispinata*, *Lepidocyrtus lanuginosus*, *Proisotoma minuta*, *Salina* cf. *beta*, *Sminthurides* sp.1, *Sminthurides* sp.2, *Tomocerus* sp., and *Willowsia mexicana*.

We present the first report of collembolans found in the deep benthos of lakes (i.e., >20 m). Although the aquatic environment and anoxic conditions are not particularly common habitats for collembolan, these results suggest that they must have adaptations that allow them to survive in these environments.

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References

Alcocer J, Oseguera LA, Sánchez G, González CG, Martínez JR, González JR. 2016. Bathymetric and morphometric surveys of the Montebello Lakes. Chiapas. J Limnol. 75:56–65.

Bellinger PF, Christiansen KA, Janssens F. 1996–2017. Checklist of the Collembola of the world; [cited Jan 2017]. Available from: http://www.collembola.org

Christiansen KA. 1965. Behavior and form in the evolution of cave Collembola. Evolution. 19:529–537.

Christiansen KA, Bellinger P. 1988. Marine littoral Collembola of North and Central America. B Mar Sci. 42:215–245.

Christiansen KA, Snider RJ. 2008. Aquatic collembolan. In: Merrit RW, Cummins KW, Berg MB, editors. An introduction to the aquatic insects of North America. 4th ed. Dubuque (IA): Kendall/Hunt; p. 165–179.

CONANP. 2007. Programa de conservación y manejo Parque Nacional Lagunas de Montebello [Conservation and management program Lakes of Montebello National Park]. México. México DF: Secretaría de Medio Ambiente y Recursos Naturales; p. 17–36.

Cutz-Pool LQ, Castaño-Meneses G, Palacios-Vargas JG, Cano-Santana Z. 2010. Distribución vertical de colémbolos muscícolas en un bosque de *Abies religiosa* del Estado de México, México [Vertical distribution of moss springtails in an *Abies religiosa* forest from the State of Mexico, Mexico]. Rev Mex Biodivers. 81:457–463.

Deharveng L, D'Haese CA, Bedos A. 2008. Global diversity of springtails (Collembola; Hexapoda) in freshwater. Hydrobiologia. 595:329–338.

Deharveng L, Lek S. 1995. High diversity and community permeability: the riparian Collembola (Insecta) of a Pyrenean massif. Hydrobiologia. 312:59–74.

D'Haese CA. 2002. Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization aligment. P Roy Soc Lond B Bio. 269:1143–1151.

Durán-Calderón I, Escolero-Fuentes O, Muñoz-Salinas E, Castillo-Rodríguez M, Silva-Romo G. 2014. Cartografía geomorfológica a escala 1:50000 del Parque Nacional Lagunas de Montebello, Chiapas (México) [Geomorphological mapping at a scale 1:50000 of Lakes of Montebello National Park, Chiapas (Mexico)]. Boletín de la Sociedad Geológica Mexicana. 66:263–277.

Folsom JW, Mills HB. 1938. Contribution to the knowledge of the genus *Sminthurides* Börner. Bull Mus Comp Zool. 82:231–274.

García E. 2004. Modificaciones al Sistema de clasificación climática de Köppen [Modifications to the Köppen Climate Classification System]. 5th ed. México DF: Instituto de Geografía UNAM.

García-Bazan E. 1990. Determinación de materia orgánica [Organic matter determination]. In: Dirección General de Oceanografía Naval, editors. México DF: Manual operativo de geología marina [Operating manual for marine geology]. Secretaria de Marina; p. 96–118.

Glenner H, Thomsen PF, Hebsgaard MB, Sørensen MV. 2006. The origin of insects. Evolution. 314:1883–1884.

Hódar JA. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecol. 17:421–433.

Hopkin ST. 1997. Biology of the Springtails (Insecta: Collembola): interactions between Collembola and the abiotic environment. Oxford (UK): Oxford University Press; p. 98–112.

King PE, Pugh PJA, Fordy MR, Love N, Wheeler SA. 1990. A comparison of some environmental adaptations of the littoral collembolans *Anuridella marina* (Willem) and *Anurida maritima* (Guérin). J Nat Hist. 24:673–688.

Palacios-Vargas JG. 1997. La cutícula de los colémbolos acuáticos bajo el microscopio electrónico de barrido [The cuticle of aquatic springtails under the scanning electron microscope]. XXXV Congreso Nacional de Entomología; p. 101–104.

Palacios-Vargas JG. 2013. Biodiversidad de Collembola (Hexapoda: Entognatha) en México [Biodiversity of Collembola (Hexapoda: Entognatha) in Mexico]. Rev Mex Biodivers. 85(Suppl):220–231.

Palacios-Vargas JG, Castaño-Meneses G, Gómez-Anaya JA. 1998. Collembola from the canopy of a Mexican tropical deciduous forest. Pan-Pacific Entomol. 74:47–54.

Palacios-Vargas JG, Castaño-Meneses G. 2003. Seasonality and community composition of springtails in Mexican forests. In: Basset Y, Novotny V, Miller SE, Kitching RL, editors. Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy. Cambridge (UK): Cambridge University Press; p. 159–169.

Palacios-Vargas JG, Mejía-Recamier BE. 2007. Técnicas de Colecta, Preservación y Montaje de Microartrópodos [Collecting, preservation and mounting techniques of microarthropods]. México DF: Las Prensas de Ciencias, Fac. Ciencias, National Autonomous University of Mexico.

Palacios-Vargas JG, Thibaud JM. 1998. Two new mexican *Isotogastrura* (Collembola: Isotogastruridae). Can Entomol. 130:195–199.

Palacios-Vargas JG, Thibaud JM. 2001. Three new species of littoral Collembola of genera *Willemia*, *Cryptopygus* and *Isotogastrura* (Hypogastruridae, Isotomidae, Isotogastruridae). Rev Fran Entomol. 23:161–168.

Palacios-Vargas JG, Vázquez MM. 1988. Three new species of littoral Collembola (Hypogastruridae) from Baja California Sur. Mexico. J Kansas Ent Soc. 61:433–440.

Snider RJ. 1988. *Denisiella lithophila*, a new species from a granite outcrop in Georgia (Collembola: Sminthuridae). Fla Entomol. 71:124–129.

Soto-Adames FN, Guillén C. 2011. Two new species of the marine littoral springtail genus *Spinactaletes* (Collembola: Actaletidae) from Costa Rica. Bull Mar Sci. 87:463–483.

Tamm JC. 1984. Surviving long submergence in the egg stage: a successful strategy of terrestrial arthropods living in flood plains (Collembola, Acari, Diptera). Oecologia. 61:417–419.

Tamm JC. 1986. Temperature-controlled underwater egg dormancy and postflood hatching in *Isotoma viridis* (Collembola) as forms of adaptation to annual long term flooding. Oecologia. 68:241–245.

Thibaud JM. 1970. Biologie et écologie des collemboles Hypogastruridae édaphiques et cavernicoles [Biology and ecology of edaphic and cavernicolous springtails Hypogastruridae]. Mem Mus Nat Hist Nat. 61:83–201.

Thibaud JM, Palacios-Vargas JG. 2000. Une nouvelle espèce du genre *Mesaphorura* des sables littoraux du Mexique (Collembola, Onychiuridae) [A new species of the *Mesaphorura* genus of littoral sands of Mexico (Collembola, Onychiuridae)]. Rev Fran Entomol. 22:146–148.

Thibaud JM, Palacios-Vargas JG. 2001a. Collemboles interstitiels des sables littoraux du Mexique (Collembola) [Interstitial springtails from littoral sands of Mexico (Collembola)]. Rev Fran Entomol. 23:181–184.

Thibaud JM, Palacios-Vargas JG. 2001b. Révision du genre *Archistoma* Linnaniemi, 1912 (Collembola: Isotomidae) [Review of genus *Archistoma* Linnaniemi, 1912 (Collembola: Isotomidae)]. Ann Soc Entomol Fr. 37:347–356.

Zeh DW, Zeh JA, Smith RL. 1989. Ovipositors, amnions and eggshell architecture in the diversification of terrestrial arthropods. Q Rev Biol. 64:147–168.

Zinkler D, Rüssbeck R. 1986. Ecophysiological adaptations of Collembola to low oxygen concentrations. In: Dallai R, editor. Second International Seminar on Apterygota. Siena (Italy): University of Siena; p. 123–127.