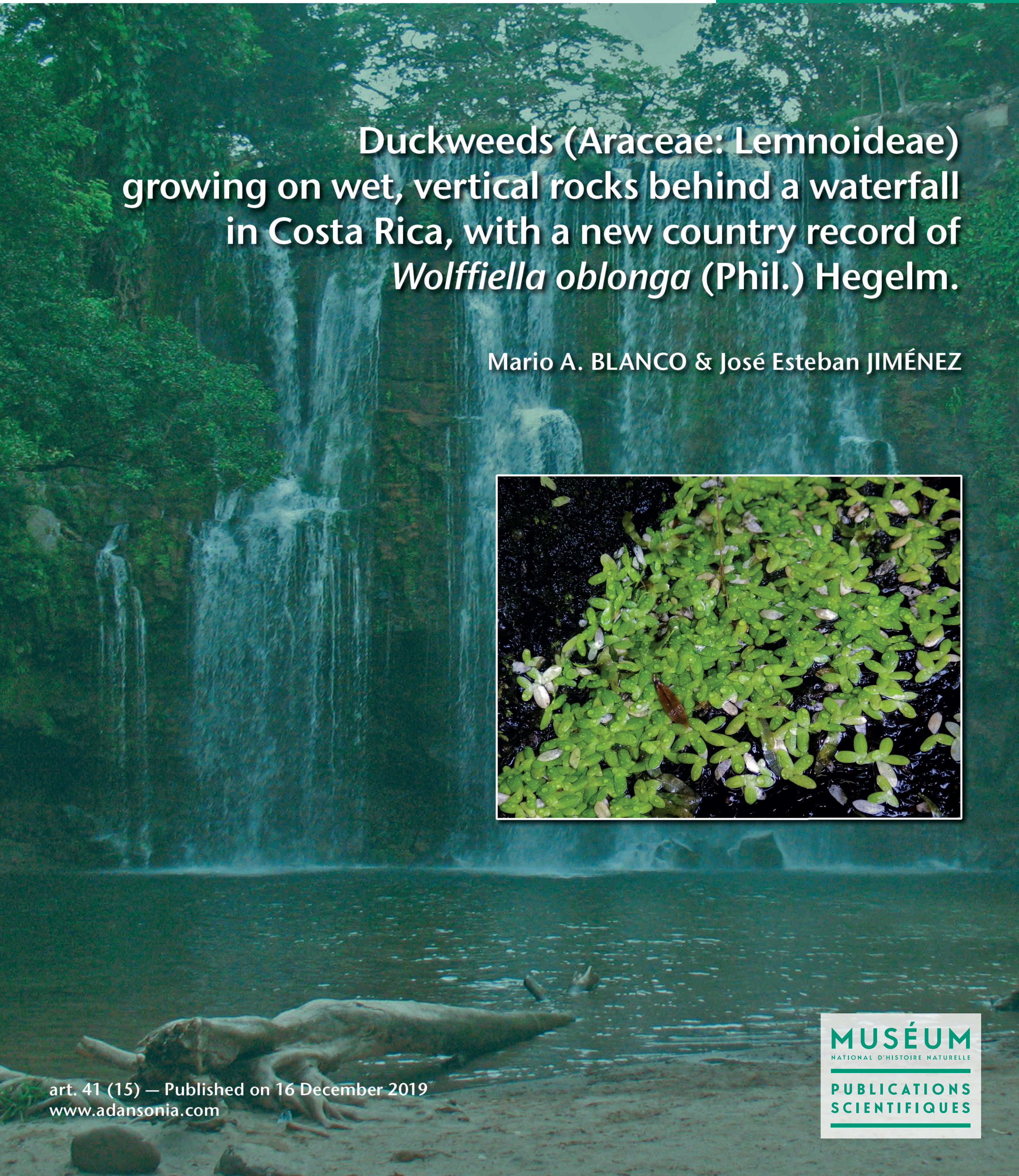
adansonia

2019 • 41 • 15



Duckweeds (Araceae: Lemnoideae) growing on wet, vertical rocks behind a waterfall in Costa Rica, with a new country record of *Wolffiella oblonga* (Phil.) Hegelm.

Mario A. BLANCO & José Esteban JIMÉNEZ

art. 41 (15) — Published on 16 December 2019
www.adansonia.com

MUSÉUM NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

Couverture / *Cover* :
Background: front view of the Llanos de Cortés waterfall; foreground: small colony of *Lemna valdiviana* Phil., clinging to the wet rock wall.

Adansonia est indexé dans / Adansonia *is indexed in:*
– Science Citation Index Expanded (SciSearch®)
– ISI Alerting Services®
– Current Contents® / Agriculture, Biology, and Environmental Sciences®
– Scopus®

Adansonia est distribué en version électronique par / Adansonia *is distributed electronically by:*
– BioOne® (http://www.bioone.org)

Adansonia est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Adansonia *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Geodiversitas*, *Zoosystema*, *Anthropozoologica*, *European Journal of Taxonomy*, *Naturae*, *Cryptogamie* sous-sections *Algologie*, *Bryologie*, *Mycologie.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-8571/ ISSN (électronique / *electronic*) : 1639-4798

Duckweeds (Araceae: Lemnoideae) growing on wet, vertical rocks behind a waterfall in Costa Rica, with a new country record of *Wolffiella oblonga* (Phil.) Hegelm.

Mario A. BLANCO
Herbario Luis Fournier Origgi (USJ), Escuela de Biología, Universidad de Costa Rica,
Apdo. 11501-2060, San José (Costa Rica)
and Jardín Botánico Lankester, Universidad de Costa Rica,
Apdo. 1031-7050, Cartago (Costa Rica)
mario.blancocoto@ucr.ac.cr (corresponging author)

José Esteban JIMÉNEZ
Research associate, Herbario Luis Fournier Origgi (USJ), Escuela de Biología,
Universidad de Costa Rica, Apdo. 11501-2060, San José (Costa Rica)
gaiadendron.jej@gmail.com

Submitted on 3 February 2019 | accepted on 1 July 2019 | published on 16 December 2019

Blanco M. A. & Jiménez J. E. 2019. — Duckweeds (Araceae: Lemnoideae) growing on wet, vertical rocks behind a waterfall in Costa Rica, with a new country record of *Wolffiella oblonga* (Phil.) Hegelm. *Adansonia*, sér. 3, 41 (15): 193-200. https://doi.org/10.5252/adansonia2019v41a15. http://adansonia.com/41/15

ABSTRACT
A large colony of duckweeds (Araceae: Lemnoideae) grows on the constantly wet, vertical wall of the rock shelter behind the Llanos de Cortés waterfall of the Potrero River, Guanacaste province, Costa Rica, the first such case ever documented. Its unique hygropetric environment is described. The colony covers several square meters distributed in several different patches, and consists almost entirely of *Wolffiella oblonga* (Phil.) Hegelm., with much fewer individuals of *Lemna valdiviana* Phil. and *L. aequinoctialis* Welw. This also constitutes the first case of the genus *Wolffiella* Hegelm. growing in a hygropetric manner (an extremely rare condition for duckweeds) and the first record of *W. oblonga* in Costa Rica.

KEY WORDS
Duckweeds,
Araceae,
Lemnoideae,
Waterfall rock shelter,
Hygropetric habitat,
Costa Rica.

RÉSUMÉ
Lentilles d'eau (Araceae: Lemnoideae) poussant sur des rochers verticaux et humides derrière une cascade au Costa Rica, avec un nouvel enregistrement pour le pays de Wolffiella oblonga *(Phil.) Hegelm.*
Une vaste colonie de lentilles d'eau (Araceae: Lemnoideae) se développe sur le mur vertical constamment humide de l'abri rocheux situé derrière la cascade Llanos de Cortés de la rivière Potrero, dans la province de Guanacaste, au Costa Rica. C'est le premier cas de ce type jamais documenté. Son environnement hygropétrique unique est décrit. La colonie couvre plusieurs mètres carrés répartis en plusieurs parcelles différentes et consiste presque entièrement en *Wolffiella oblonga* (Phil.) Hegelm., avec beaucoup moins d'individus de *Lemna valdiviana* Phil. et *L. aequinoctialis* Welw. Ceci constitue également la première espèce du genre *Wolffiella* Hegelm. poussant de manière hygropétrique (une condition extrêmement rare pour les lentilles d'eau) et son premier enregistrement au Costa Rica.

MOTS CLÉS
Lentilles d'eau,
Araceae,
Lemnoideae,
Abri rocheux de cascade,
environnement hygropétrique,
Costa Rica.

INTRODUCTION

The duckweeds comprise a cosmopolitan group (five genera with *c.* 38 species) of tiny floating aquatic plants, that includes the smallest angiosperms. Their highly reduced vegetative and reproductive structures have given rise to divergent interpretations about their homology (e.g., Engler 1889; Arber 1920; Lawalrée 1945; Hillman 1961; Daubs 1965; Landolt 1986; Grayum 1990; Les *et al.* 1997; Stockey *et al.* 1997; Landolt 1998a; Lemon & Posluszny 2000; Bogner 2009; Landolt & Schmidt-Mumm 2009; Armstrong 2011). Currently, the most widely accepted interpretation is that the basal part of the thalloid "frond" represents caulinar (stem) tissue, while the distal part is formed by foliar (leaf) tissue (Landolt 1998a); both regions intergrade into each other, and the entire upper surface of the frond (which may not be homologous with the adaxial leaf surface of most other plants) is photosynthetic. Species of three genera (*Landoltia* Les & D.J. Crawford, *Lemna* L. and *Spirodela* Schleid.) produce one to several, short, unbranched roots from the lower surface of each frond, and species of the other two genera (*Wolffia* Horkel ex Schleid. and *Wolffiella* Hegelm.) are rootless. The plants have sympodial growth, and new fronds (sympodial units) are produced from "budding pouches" (probably homologous with leaf sheaths) located toward the base of the mother frond; individual plants naturally divide in ramets of 2-7 fronds each. The highly reduced, achlamydeous flowers of duckweeds are produced either from these same budding pouches (in *Landoltia*, *Lemna* and *Spirodela*) or from dorsal "furrows" (in *Wolffia* and *Wolffiella*); there is some debate on whether the single gynoecium and adjacent 1-2 stamens belong to a single, perfect flower or represent independent, staminate and pistillate flowers of a single inflorescence (Landolt 1998a). The fruits develop partially or completely embedded in the frond tissue. Sexual reproduction appears to be unfrequent in many species; however, compared with other angiosperms, duckweeds show extremely rapid reproductive rates (Kutschera & Niklas 2014), which may be related to their high rates of molecular evolution (Nauheimer *et al.* 2012).

The extremely reduced structure of the duckweeds has posed a historical challenge for inferring their systematic affinities, and traditionally they were classified in their own family, the Lemnaceae. Many workers, however, recognized a close relationship with the Araceae based on morphological, embryological and fossil evidence (e.g., Engler 1889; Arber 1920; Hillman 1961; Daubs 1965; Landolt 1986; Stockey *et al.* 1997; Lemon & Posluszny 2000; Les *et al.* 2002; Bogner 2009; Landolt & Schmidt-Mumm 2009; Armstrong 2011; see Mayo *et al.* 1997 for a summary of alternative views). Phylogenetic analyses based on molecular data have confirmed this view, indicating that the duckweeds form a well-supported clade firmly nested within Araceae, although not closely related to the genus *Pistia* L. as previously assumed (Cabrera *et al.* 2008; Cusimano *et al.* 2011; Nauheimer *et al.* 2012, and references therein). Thus, most recent phylogenetic classifications treat the duckweeds as a subfamily of the aroids, a scheme followed by us.

Duckweeds occur almost exclusively as pleustophytes (i.e., floating at or just under the water surface, not attached to the underlying substrate; den Hartog & Segal 1964; Schuyler 1984), on permanent or seasonal lentic habitats (i.e., static or very slow-flowing bodies of water, like lakes and ponds), usually rich in nutrients and well exposed to the sun. They do not normally occur on lotic habitats (i.e., medium to fast-flowing waters, like rivers), where they would be carried away by the current. Rarely, duckweeds can grow on mud, provided that this substrate remains constantly wet (Landolt 1986: 140, 141). On very few occasions and under special conditions, duckweeds have been observed growing on wet rock walls or in the drip of waterfalls (Landolt 1986: 141, 142; 1998b; 2000; see below). Here, we document a remarkable first case of a large duckweed community growing on wet, vertical rocks behind a waterfall.

MATERIAL AND METHODS

Site description

The study site is the Llanos de Cortés waterfall (also spelled "Llanos de Cortéz", named after a nearby small village with the same name), located in Costa Rica, Guanacaste Province, Bagaces County (Cantón), Bagaces District (10°31.447'N, 85°17.926'W, datum WGS84, *c.* 70 m above sea level). This waterfall is part of the Potrero River, which originates *c.* 8 km to the North, NWN of the city of Bagaces, on the Southeastern flank of the Rincón de la Vieja Volcano on the Cordillera de Guanacaste. Circa 1 km downstream from the waterfall, the Potrero River joins the Piedras River, which in turn flows into the Blanco River, then into the Bebedero River (of the Bebedero River watershed), which empties into the Gulf of Nicoya on the Pacific coast. Unlike some seasonal creeks in the area, the Potrero River flows all year round.

The Llanos de Cortés waterfall is a ledge- or block-type, punchbowl waterfall, *c.* 24 m tall × 25.3 m wide (described as 75 m tall by Janzen 1976, an apparent error meaning either feet or the elevation above sea level; Fig. 1A). It falls into a large, semicircular pool (*c.* 30.5 m at its widest point, *c.* 2 m deep at its deepest point close to, but not immediately under, the waterfall). The face of the bedrock is irregular and not completely vertical, with a series of small ledges gradually projecting forward on the upper part of the waterfall. A small, closed canyon is formed immediately around the waterfall, which continues for several hundred meters downstream.

From the date of our first observations (July 2013) and until October 2017, a spacious undercutting or rock shelter *c.* 2-4 m high × 1-4 m deep was present at the base (whose contour is partially visible in Fig. 1A), evidently formed by sporadic partial collapses of the lower wall caused by splashback erosion of the bedrock. This shelter spanned the entire width of the waterfall base, and its rocky bottom was (and still is) above the waterline. On October 2017, the rock shelter suffered a substantial collapse of its roof during a period of intense precipitation caused by Hurricane Nate, and a smaller rock collapse happened on November 2018 (Rosbin Rojas, personal communication). At the time of this writing (January 2019), the rock shelter is much more exposed and irregular. The falling water loses contact with the vertical rock face at *c.* 5-7 m from the base and plunges directly onto rock boulders or the adjacent pool surface. The air inside the shelter is constantly saturated with water spray, and the entire rock surface of the shelter is permanently wet, forming a hygropetric or madicolous habitat (*sensu* Hynes 1970; Wantzen *et al.* 2008).

The waterfall faces almost due east, so it receives direct sunlight in the mornings during most of the year. We have not been able to measure the light environment inside the shelter, but before the partial collapse of its roof, it seemed comparable to that of a dense rain forest floor; little direct sunlight reached the vertical rock wall of the shelter. After the collapse, more direct sunlight reaches many parts of the shelter, partially filtered in places by the water curtain.

The region is markedly seasonal, with a dry season from December to April and a rainy season from May to November (with a maximum of precipitation occurring between September and October and a minor peak during June). The river volume varies seasonally, although no quantitative data are available. During periods of unusually high precipitation, the river volume increases dramatically and the waterfall projects forward and falls near the center of the pool; the last such episode happened in September 2018 (Rosbin Rojas, personal communication).

The surrounding vegetation is riparian forest in a matrix of tropical dry forest, cattle pastures and agricultural fields (especially rice). Janzen (1976) provided a description of the site and a microclimatic comparison between the riparian forest and the adjacent seasonally-dry forest. Sawyer & Lindsey (1971) characterized in detail the adjacent seasonally-dry forest (as Study Area 1A, Rio Potrero). Gómez-Solís (2017) described the vegetation of the nearby Lomas de Barbudal Biological Preserve, located 8 Km to the southwest of the waterfall.

The Llanos de Cortés waterfall is a popular local attraction, drawing dozens of visitors each day, especially during weekends. Since February 2018, it is administered by the Bagaces County municipality; swimming in the pool is allowed but approaching the waterfall or entering the rock shelter is prohibited.

Methods

Observations at the study site were made on 16th July 2013 (rainy season), 13th April 2014 (dry season), 21st July 2015 (rainy season, but toward the end of a prolonged dry spell due to the El Niño Southern Oscillation), and 22nd-23rd January 2019 (dry season).

Notes were taken on the relative size of the duckweed colonies in the shelter. The river was inspected both immediately above and for 300 m downstream from the waterfall, for the presence of duckweeds. Measurements of the waterfall shelter and the pool were made with a 50 m measuring tape. Duckweeds were inspected under a dissecting microscope, using several taxonomic treatments for identification (Daubs 1965; Landolt 1986; Davenport & Haynes 2001; Grayum 2003; Landolt & Schmidt-Mumm 2009; Armstrong 2011, 2012).

Herbarium specimens of the plants growing on or near the waterfall were prepared and deposited in the Herbarium of the Universidad de Costa Rica (USJ); when available, duplicates were sent to the Costa Rican National Herbarium (CR). Herbarium acronyms follow Index Herbariorum (Thiers 1997 and continuously updated).

RESULTS

Several patches of duckweeds were found growing on the vertical wet wall of the rock shelter behind the waterfall during all four visits, mostly located *c.* 0.5-1.5 m away from the free-falling water curtain. The patches were irregular in shape and variable in size (Fig. 1B); the largest one seen was *c.* 2 m^2, located 1-2.5 m above the rocky bottom of the shelter. Possibly more duckweeds occurred higher up (both within the shelter and on the wet rock face of the waterfall not in direct contact with the falling water), but the constant dripping makes it very hard to look up inside the shelter, and it is almost impossible to distinguish the tiny duckweeds from other plants and green algae that grow on the rock face higher up on the waterfall from more than 2 m away. The estimated visible area of rock wall covered by duckweeds inside the rock shelter during our first three visits was 7-11 m^2. During our fourth visit (after the partial collapses of the rock shelter) it was much reduced, *c.* 3-4 m^2.

The duckweeds were loosely adhered to the rock surfaces only by means of the permanent, thin film of water, never physically anchored (Fig. 1C, D, F). A splash of water could easily wash the duckweed colonies off the rock wall, but we never perceived such an event during several hours of cumulative observation.

The duckweed colonies were composed almost exclusively of *Wolffiella oblonga* (Phil.) Hegelm. (voucher: *Blanco et al. 4300*), the plants of which accumulated in dense mats of several layers in some places (Fig. 1C, D, E). Growing on top of the *W. oblonga* plants (and occasionally forming small pure patches directly on the wet rock) were far fewer, scattered plants of *Lemna valdiviana* Phil. (voucher: *Blanco et al. 4301*, Fig. 1D, F), and even fewer plants of *L. aequinoctialis* Welw. (mixed with *L. valdiviana* in *Blanco et al. 4301*). At first sight, these duckweeds (especially *W. oblonga*) were difficult to recognize as such, as they resemble green algal mats, thalloid liverworts, or even fern gametophytes. No flowers nor fruits were detected on several dozen duckweed plants of either species that were examined under a dissecting scope.

Small groups of *Lemna aequinoctialis* were seen stranded among aquatic plants and floating debris *c.* 150-250 m downstream from the waterfall, but none above.

Both *Marathrum foeniculaceum* Bonpl. (voucher: *Blanco et al. 4296*) and *Tristicha trifaria* (Bory ex Willd.) Spreng. (voucher: *Blanco et al. 4303*) (both Podostemaceae) grew abundantly on the boulders at the bottom of the waterfall during our first three visits, but not in the rock shelter. *Marathrum foeniculaceum* was much less abundant at the bottom of the waterfall during our fourth visit, apparently because many of the plants were buried by the recently collapsed rocks. This species also grows on the rocky river bed immediately above the waterfall and on the vertical, constantly wet rock wall of the waterfall (visible with binoculars).

DISCUSSION

The Llanos de Cortés waterfall is the only place in the world where duckweeds have been documented growing on wet rocks behind a waterfall. This phenomenon is even more remarkable because of the large size of the duckweed community found there, at least before the recent partial collapse of the rock shelter.

Duckweeds have been documented growing on wet rock walls or in the drip of waterfalls on very few occasions (Landolt 1986: 141-142; 1998b; 2000). *Lemna aequinoctialis* has also been collected growing on a permanently wet cement wall in Costa Rica (*Hammel et al. 20017*, CR, MO). For duckweeds to grow successfully in a hygropetric or madicolous environment, they require the presence of a permanent, thin film of water on the substrate, not being exposed to rain or water overflow (which could easily wash the tiny plants off as they cannot secure themselves to a solid substrate), and having sufficient illumination for the plants to survive. The rock shelter behind the Llanos de Cortés waterfall stays permanently wet because of the constant spray produced by the falling water. During periods of unusually high precipitation, the water comes out with such force that most of it loses contact with the rock from the upper edge of the waterfall. Thus, even when waterfalls are lotic habitats par excellence, this rock shelter behaves more as a static aquatic microhabitat, although very different from typical lentic habitats.

According to Landolt (1986: 142) only duckweeds with roots are capable of growing on wet, vertical rocks (heretofore, a few species of *Lemna* are the only duckweeds that have been documented growing hygropetrically; Landolt 1986, 1998b). However, duckweed roots lack a mechanism to anchor themselves to a substrate (much less solid rock), and thus roots do not represent an actual requisite for duckweeds to grow hygropetrically. The case presented here evidently shows that the rootless genus *Wolffiella* is also capable of growing in the same manner, and can form large colonies under the appropriate conditions.

Some duckweed patches in the rock shelter grew on parts with relatively low illumination. *Wolffiella oblonga*, by far the most abundant species in the rock shelter, belongs to a genus that commonly thrives in relatively dim light, submerged just under the surface in dense colonies, usually under the cover of other floating plants (including other duckweed genera; Hillman 1961; Armstrong 1992). The other two duckweed species present in the rock shelter (*Lemna aequinoctialis* and *L. valdiviana*), which normally grow in more exposed situations, are much less abundant and probably grow there at a relatively slow rate. They manage to stay on top of the dense colonies of *W. oblonga* thanks to their hydrophobic upper frond surface.

The dense colonies of *Wolffiella oblonga* in the rock shelter apparently have grown vegetatively, spreading on the rock surface as new fronds emerge from old ones and push each other, and by occasional short-distance dispersal by water splashing. Conceivably, short distance dispersal (i.e., within different parts of the rock shelter) can also occur when individual duckweeds temporarily adhere to moving snails, crabs, aquatic insects, or other small invertebrates of the hygropetric microhabitat. Possibly some displacement of the two species of *Lemna* occurs on the surface of the water film (the upper frond surface of these species is hydrophobic).

Duong & Tiedje (1985) showed that part of the nutritional needs of duckweeds growing in ponds is provided by their epiphytic nitrogen-fixing cyanobacteria. A similar situation likely occurs on the Llanos de Cortés rock shelter, where cyanobacteria grow on virtually every surface of the hygropetric habitat (including on the duckweeds themselves). The algal and invertebrate communities of the Llanos de Cortés waterfall are currently being studied by researchers at the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR, Universidad de Costa Rica).

It is unknown how these duckweeds first arrived at this unusual place, but conceivably they could have been carried by the river from suitable upstream habitats, or they could have been transported from other areas by aquatic birds seeking food or temporary refuge in the rock shelter. In any case, it is evident that the presence of duckweeds on the wet rock wall of the shelter is permanent and not an accidental, temporary situation.

The present report also constitutes the first record of *Wolffiella oblonga* in Costa Rica. This species has a wide latitudinal and elevational distribution in the tropics and subtropics of the New World (from California, Texas, Louisiana and Florida to Argentina and Chile, and from 3600 m down to sea level; Landolt 1986); thus, its occurrence in Costa Rica was expected (Grayum 2003).

Wolffiella oblonga can be difficult to recognize from *W. lingulata* (Hegelm.) Hegelm. (also expected in Costa Rica, Grayum 2003); the morphology of both taxa is somewhat variable and overlapping (Landolt 1986: 538; Crawford *et al.* 1997; Crawford *et al.* 2006; Armstrong 2011, 2012). However, *W. oblonga* can be distinguished from *W. lingulata* by its generally narrower (3-5 vs 4-10 mm) and flatter (vs recurved) fronds, a narrower budding pouch (angle 40-70° vs 80-120°), and a tract of elongated cells running along or

Fig. 1. — Llanos de Cortés waterfall and its duckweed community: **A**, front view of the Llanos de Cortés waterfall on July 2015, before the partial collapse of its rock shelter; the contour of the latter is partially visible behind the water curtain; **B**, permanently wet, vertical rock wall of the shelter behind the waterfall, covered by duckweeds (green); **C**, portion of duckweed mat with several layers of individual plants, mostly of *Wolffiella oblonga* (Phil.) Hegelm.; **D**, detail of duckeeds (mostly *W. oblonga*) clinging to the rock wall only by means of the permanent water film, but notice plants of *Lemna valdiviana* Phil. near both fingernails; **E**, four plants of *W. oblonga* as seen under the dissecting microscope; **F**, small colony of *L. valdiviana*, clinging to the wet rock wall. Scale bars: B, 1 m; C, 5 cm; D, F, 1 cm; E, 5 mm.

close to the lower edge of the pouch (vs running halfway between the median line and the lower edge of the pouch) (Landolt 1986; Armstrong 2011, 2012). The plants from the Llanos de Cortés waterfall fit well the above-mentioned description of *W. oblonga* (Fig. 1E). It has been suggested, on the basis of morphological, molecular and geographical evidence (both taxa have largely overlapping distributions and frequently occur in sympatry), that *W. oblonga* and

W. lingulata may not constitute distinct species after all (Kimball *et al.* 2003). In any case, *W. oblonga* has nomenclatural priority over *W. lingulata*.

It is curious that *W. oblonga* was first found in Costa Rica growing in such an atypical situation, and that neither *W. oblonga* or *Lemna valdiviana* have been found in the extensive seasonal marsh of Palo Verde National Park (PVNP), located *c.* 21 km to the SW of the Llanos de Cortés waterfall at near sea-level, in the adjacent Tempisque River basin. The aquatic macrophytes of the PVNP marsh have been studied in detail (e.g., Crow & Rivera 1986; Hernández-Esquivel 1990; Hernández-Esquivel & Gómez-Laurito 1993; Crow 2002), and four duckweed species have been recorded among them: *Lemna aequinoctialis* (voucher: *Blanco et al. 1958*, misidentified as *L. gibba* L. in Crow & Rivera 1986 and in Hernández-Esquivel & Gómez-Laurito 1993), *Spirodela intermedia* W. Koch (voucher: *Blanco et al. 1959*, newly reported here for the site), *S. polyrhiza* (L.) Schleid. (reported by Crow 2002, without citing a voucher) and *W. welwitschii* (Hegelm.) Monod (voucher: *Blanco et al. 1957*). In Costa Rica, *L. valdiviana* is rarely encountered at elevations below 600 m (Grayum 2003); the cool environment of the rock shelter probably provides the appropriate conditions for this species to occur at this relatively low elevation.

The abundance of two species of riverweeds (*Marathrum foeniculaceum* and *Tristicha trifaria*, of the Podostemaceae, a family of submerged rheophytic plants specialized on river rapids) indicates that the river is not contaminated or very little so (Philbrick & Novelo 1995). Furthermore, although the tolerance to pollutants of species of *Wolffiella* has been scarcely tested (Ziegler *et al.* 2016), there is anecdotic evidence that they are much less tolerant to turbid water, sewage and detergents than other duckweeds (Armstrong 1992). This is somewhat surprising as agricultural and cattle fields partially flank the Potrero River upstream from the waterfall, although recent aerial images show that substantial portions of its riparian forest still remain in place.

Janzen (1976) described the Llanos de Cortés waterfall as “perhaps the best remaining example of a moist canyon effect [caused by the blast of cool, hyper-humid air from the waterfall] in Guanacaste province”, and remarked that “its organisms are unique” (see Zartman & Pittillo 1998 for a discussion of the highly specific plant communities of spray cliffs around waterfalls). The existence of a large, permanent duckweed community in the rock shelter of the waterfall underscores the uniqueness of this site and the need for its protection. Janzen (1976) mentioned that “the increasing agricultural exploitation of the Bagaces–COMELCO region, and specifically the area immediately above the waterfall, is very likely to destroy both the water flow and the actual riparian forest itself [at this site]” (COMELCO stands for “Compañía Ganadera El Cortés, S.A.”). Fortunately, more than 40 years after Janzen´s dire predictions, the waters of the Rio Potrero still flow all year round and do not show visible signs of contamination at the site of the waterfall. The current prohibition for visitors to enter the rock shelter is a positive measure in favor of the conservation of this unusual duckweed colony and its delicate associated biotic community. The surrounding riparian vegetation already shows some signs of degradation due to the intensive visitation for recreational use that this site experiences.

Construction of a visitor complex adjacent to the waterfall by the Bagaces county municipality is planned for the immediate future (Sánchez-Herrera 2016). The project proposal aims to minimize its environmental impact, preserving much of the surrounding riparian forest. We suggest that measures be taken to protect and minimize potential damage to the unique rock shelter duckweed colony.

Acknowledgements

Fieldwork for this study was done during the field courses OET 2013-18 and OET 2015-18 (“*Sistemática de Plantas Tropicales*”) of the Organization for Tropical Studies, and during a field trip for the course “*Morfología de Flores y Frutos*” of the Universidad de Costa Rica. Students of these courses provided some assistance. Cindy Fernández, Darha Solano and Monika Springer (Escuela de Biología and Centro de Investigación en Ciencias del Mar y Limnología [CIMAR], Universidad de Costa Rica) also provided field assistance during the last visit to the site. Heiko Hentrich (formerly Swiss Orchid Foundation Herbarium [RENZ], University of Basel) and Mark Whitten (Florida Museum of Natural History Herbarium [FLAS], University of Florida) kindly provided critical literature. Irene Calderón Sanou (Université de Grenoble Alpes) kindly reviewed the French translation for the title and the abstract. Rosbin Rojas, coordinator of the Cataratas Llanos de Cortés Eco-Touristic Project, Municipality of Bagaces, provided much information, advice and logistical support during the last visit to the site. We thank Michael H. Grayum (Missouri Botanical Garden Herbarium [MO]) for a discussion about the proper spelling of the name *Spirodela polyrhiza* (as in the original spelling of its basionym, *Lemna polyrhiza* L.) vs the commonly used orthographical variation *S. polyrrhiza* (see Stearn 2004: 261). Revisions by Thierry Deroin (Muséum national d’Histoire naturelle, Paris [P]) and Wayne P. Armstrong (Palomar College Herbarium [PASM]) helped to improve the manuscript.

REFERENCES

Arber A. 1920. — The vegetative morphology of *Pistia* and the Lemnaceae. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 91 B: 96-103. https://doi.org/10.1098/rspb.1920.0002

Armstrong W. P. 1992. — Mudmidgets in California. *Fremontia* 20 (2): 15-21.

Armstrong W. P. 2011. — *Wayne Armstrong's Online Treatment of the Lemnaceae.* https://www2.palomar.edu/users/warmstrong/1wayindx.htm (last updated 8 September 2018)

Armstrong W. P. 2012. — *Wolffiella*, Mud-midget, *in* Baldwin B. G., Goldman D., Keil D. J., Patterson R., Rosatti T. & Wilken D. (eds), *The Jepson Manual: Vascular Plants of California, Second Edition, Thoroughly Revised and Expanded*. University of California Press, Berkeley: 1302, 1307.

BOGNER J. 2009. — The free-floating aroids (Araceae) – living and fossil. *Zitteliana* A48/49: 113-128. https://epub.ub.uni-muenchen.de/11980/ (last consultation on 10th, December 2019).
CABRERA L. I., SALAZAR G. A., CHASE M. W., MAYO S. J., BOGNER J. & DÁVILA P. 2008. — Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *American Journal of Botany* 95: 1153-1165. https://doi.org/10.3732/ajb.0800073
CRAWFORD D. J., LANDOLDT E., LES D. H. & TEPE E. 1997. — Allozyme variation and the taxonomy of *Wolffiella*. *Aquatic Botany* 58: 43-54. https://doi.org/10.1016/S0304-3770(97)00012-0
CRAWFORD D. J., LANDOLDT E., LES D. H. & KIMBALL R. T. 2006. — Speciation in duckweeds (Lemnaceae): Phylogenetic and ecological inferences. *Aliso* 22: 231-242. https://doi.org/10.5642/aliso.20062201.19
CROW G. E. 2002. — *Plantas acuáticas del Parque Nacional Palo Verde y el valle del Río Tempisque, Costa Rica / Aquatic plants of Palo Verde National Park and the Tempisque River valley, Costa Rica.* Editorial InBio, Santo Domingo de Heredia, 296 p.
CROW G. E. & RIVERA D. I. 1986. — Aquatic vascular plants of Palo Verde National Park, Costa Rica. *Uniciencia* 3: 71-78.
CUSIMANO N., BOGNER J., MAYO S. J., BOYCE P. C., WONG S. Y., HESSE M., HETTERSCHEID W. L. A., KEATING R. & FRENCH J. C. 2011. — Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *American Journal of Botany* 98: 654-668. https://doi.org/10.3732/ajb.1000158
DAUBS E. H. 1965. — A monograph of Lemnaceae. *Illinois Biological Monographs* 34: 1-118. https://biodiversitylibrary.org/bibliography/50203
DAVENPORT L. J. & HAYNES R. R. 2001. — Lemnaceae, *in* STEVENS W. D., ULLOA ULLOA C., POOL A. & MONTIEL O. M. (eds), Flora de Nicaragua, Tomo II, Angiospermas (Fabaceae-Oxalidaceae). *Monographs in Systematic Botany from the Missouri Botanical Garden* 85: 1211-1213.
DUONG T. P. & TIEDJE J. M. 1985. — Nitrogen fixation by naturally occurring duckweed-cyanobacterial associations. *Canadian Journal of Microbiology* 31: 327-330. https://doi.org/10.1139/m85-062
ENGLER A. 1889. — Lemnaceae, *in* ENGLER A. & PRANTL K. (eds), *Die natürlichen Pflanzenfamilien, nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen* II, 3. Verlag von Wilhelm Engelmann, Leipzig: 154-164. https://biodiversitylibrary.org/page/16792470
GÓMEZ-SOLÍS W. 2017. — Evaluación del componente forestal de la Reserva Biológica Lomas de Barbudal. *Revista Universidad en Diálogo* 7: 101-122. https://doi.org/10.15359/udre.7-1.6
GRAYUM M. H. 1990. — Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Garden* 77: 628-697. https://doi.org/10.2307/2399668
GRAYUM M. H. 2003. — Lemnaceae, *in* HAMMEL B. E., GRAYUM M. H., HERRERA C. & ZAMORA N. (eds), Manual de plantas de Costa Rica, volumen II: Gimnospermas y monocotiledóneas (Agavaceae-Musaceae). *Monographs in Systematic Botany from the Missouri Botanical Garden* 92: 618-622. https://biodiversitylibrary.org/page/773071
HARTOG C. DEN & SEGAL S. 1964. — A new classification of the water plant communities. *Acta Botanica Neerlandica* 13: 367-393. https://doi.org/10.1111/j.1438-8677.1964.tb00163.x
HERNÁNDEZ-ESQUIVEL D. A. 1990. — *Cambios anuales en la composición y distribución de la vegetación acuática en el humedal estacional de Palo Verde, Costa Rica.* Master's thesis, Programa Regional en Manejo de Vida Silvestre, Universidad Nacional, Heredia, 25 p.
HERNÁNDEZ-ESQUIVEL D. A. & GÓMEZ-LAURITO J. 1993. — *La flora acuática del humedal de Palo Verde*. Editorial Universidad Nacional de Costa Rica, Heredia, 131 p.
HILLMAN W. S. 1961. — The Lemnaceae, or duckweeds: a review of the descriptive and experimental literature. *The Botanical Review* 27: 221-287. https://doi.org/10.1007/BF02860083
HYNES H. B. N. 1970. — *The Ecology of Running Waters.* University of Toronto Press, Suffolk, 555 p.
JANZEN D. H. 1976. — The microclimate difference between a deciduous forest and adjacent riparian forest in Guanacaste province, Costa Rica. *Brenesia* 8: 29-33.
KIMBALL R. T., CRAWFORD D. J., LES D. H. & LANDOLDT E. 2003. — Out of Africa: molecular phylogenetics and biogeography of *Wolffiella* (Lemnaceae). *Biological Journal of the Linnean Society* 79: 565-576. https://doi.org/10.1046/j.1095-8312.2003.00210.x
KUTSCHERA U. & NIKLAS K. J. 2014. — Darwin-Wallace Demons: survival of the fastest in populations of duckweeds and the evolutionary history of an enigmatic group of angiosperms. *Plant Biology* 17: 24-32. https://doi.org/10.1111/plb.12171
LANDOLT E. 1986. — The family of Lemnaceae – a monographic study. Vol. 1. *Veröffentlichungen des Geobotanischen Institutes ETH, Stiftung Rübel, Zürich* 71: 1-566.
LANDOLT E. 1998a. — Lemnaceae, *in* KUBITZKI K. (ed.), *The Families and Genera of Vascular Plants. IV. Flowering Plants – Monocotyledons – Alismatanae and Commelinanae (except Gramineae)*. Springer Verlag, Berlin: 264-270. https://doi.org/10.1007/978-3-662-03531-3
LANDOLT E. 1998b. — *Lemna yungensis*, a new duckweed species from rocks of the Andean Yungas in Bolivia. *Bulletin of the Geobotanical Institute ETH* 64: 15-21.
LANDOLT E. 2000. — Contribution on the Lemnaceae of Ecuador. *Fragmenta Floristica et Geobotanica* 45: 221-237.
LANDOLT E. & SCHMIDT-MUMM U. 2009. — Lemnaceae. *Flora de Colombia* 24: 1-54.
LAWALRÉE A. 1945. — La position systématique des Lemnaceae et leur classification. *Bulletin de la Société royale de Botanique de Belgique/Bulletin van de Koninklijke Belgische Botanische Vereniging* 77: 27-38. https://www.jstor.org/stable/20791962
LEMON G. D. & POSLUSZNY U. 2000. — Comparative shoot development in the Lemnaceae. *International Journal of Plant Sciences* 161: 733-748. https://doi.org/10.1086/314298
LES D. H., LANDOLT E. & CRAWFORD D. J. 1997. — Systematics of the Lemnaceae (duckweeds): inferences from micromolecular and morphological data. *Plant Systematics and Evolution* 204: 161-177. https://doi.org/10.1007/BF00989203
LES D. H., CRAWFORD D. J., LANDOLT E., GABEL J. D. & KIMBALL R. T. 2002. — Phylogeny and systematics of Lemnaceae, the duckweed family. *Systematic Botany* 27: 221-240.
MAYO S. J., BOGNER J. & BOYCE P. C. 1997. — *The Genera of Araceae*. Royal Botanic Gardens, Kew, 370 p.
NAUHEIMER L., METZLER D. & RENNER S. S. 2012. — Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938-950. https://doi.org/10.1111/j.1469-8137.2012.04220.x
PHILBRICK C. T. & NOVELO A. 1995. — New World Podostemaceae: Ecological and evolutionary enigmas. *Brittonia* 47: 210-222. https://doi.org/10.2307/2806959
SÁNCHEZ-HERRERA L. 2016. — *Proyecto turístico en las Cataratas de Llanos de Cortés, Bagaces, Costa Rica*. Proyecto de graduación, Licenciatura en Arquitectura y Urbanismo, Escuela de Arquitectura y Urbanismo. Instituto Tecnológico de Costa Rica, Cartago, 315 p.
SAWYER J. O. & LINDSEY A. A. 1971. — *Vegetation of the Life Zones in Costa Rica*. Indiana Academy of Science, Indianapolis, 214 p.
SCHUYLER A. E. 1984. — Classification of life forms and growth forms of aquatic macrophytes. *Bartonia* 50: 8-11. https://www.jstor.org/stable/41609886
STEARN W. T. 2004. — *Botanical Latin. Fourth Edition*. Timber Press, Portland, 546 + xiv p.

Stockey R. A., Hoffman G. L. & Rothwell G. W. 1997. — The fossil *Limnobiophyllum scutatum*: resolving the phylogeny of Lemnaceae. *American Journal of Botany* 84: 355-368. https://doi.org/10.2307/2446009

Thiers B. 1997 (continuously updated). — *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff.* New York Botanical Garden, New York. http://sweetgum.nybg.org/science/ih/

Wantzen K. M., Yule C. M., Tockner K. & Junk W. 2008. — Riparian wetlands of tropical streams, *in* Dudgeon D. (ed.), *Tropical Stream Ecology*. Academic Press, London: 199-217. https://doi.org/10.1016/B978-0-12-088449-0.X5001-8

Zartman C. & Pittillo J. 1998. — Spray cliff communities of the Chattooga Basin. *Castanea* 63: 217-240. https://www.jstor.org/stable/4033977

Ziegler P., Sree K. S. & Appenroth J. 2016. — Duckweeds for water remediation and toxicity testing. *Toxicological and Environmental Chemistry* 98: 1127-1154. https://doi.org/10.1080/02772248.2015.1094701

Submitted on 3 February 2019;
accepted on 1 July 2019;
published on 16 December 2019.