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ABSTRACT
The genus *Phaeomegaceros* R.J.Duff, J.C.Villarreal, Cargill & Renzaglia (Dendrocerotaceae J.Haseg.), represented by the species *P. fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia is recorded for the first time in Mexico, North America, extending its distribution range considerably to the North. Recording distribution ranges could aid to better understand ecological and biogeographical patterns, and detailed population level descriptions of wide-range distributing hornworts could be helpful in determining intraspecific variation, which in turn would aid to define species limits, nowadays poorly understood in Anthocerotophyta Stotler & Crandall-Stotler. Anatomical and morphological characters of collected plants are described in details and illustrations in light microscopy and SEM are provided. *P. fimbriatus* can be distinguished from other Mexican hornwort species by spore ornamentation, antheridial number per chamber, number of layers of spore tissue in the sporophyte and presence of band-like thickenings in cells of gametophyte thallus. Mexican plants of *P. fimbriatus* presented smaller spores (28-36 µm in diameter, average 34 µm) than those previously reported (32-43 µm in diameter) for this species, which extends the species variation range of this character and might be pointing out geographical variation.

KEY WORDS
Hornworts, Anthocerotophyta, anatomy, distribution, biodiversity, Mexico, new record.

RÉSUMÉ

Anatomie et morphologie de Phaeomegaceros fimbriatus *(Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia (Anthocerotophyta), nouveau signalement pour l'Amérique du Nord.*

Le genre *Phaeomegaceros* R.J.Duff, J.C.Villarreal, Cargill & Renzaglia (Dendrocerotaceae J.Haseg.), representé par l'espèce *P. fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia est nouvellement signalé au Mexique, Amérique du Nord, élargissant ainsi considérablement sa distribution vers le nord. Les échelles de relevé de la distribution pourraient aider à mieux comprendre les modèles écologiques et biogéographiques, et des descriptions détaillées des populations d'anthocérotes à large distribution pourraient être utiles pour déterminer la variation intraspécifique, ce qui permettrait de mieux définir les espèces dont les limites sont aujourd'hui encore mal comprises chez les Anthocerotophyta Stotler & Crandall-Stotler. Les caractères anatomiques et morphologiques des spécimens récoltés sont décrits en détails (microscopie optique et à balayage). *P. fimbriatus* peut être distingué des autres anthocérotes mexicains par l'ornementation de la spore, le nombre d'anthéridies dans la chambre anthéridiale, le nombre de couches du tissu sporal dans le sporophye et la présence d'épaississements semblables à des bandes dans les cellules du thalle gamétophytique. Les spécimens mexicains de *P. fimbriatus* ont des spores plus petites (28-36 µm de diamètre, avec une moyenne de 34 µm) que celles rapportées précédemment (32-43 µm de diamètre) pour cette espèce. Ainsi la plus large variation de ce caractère pourrait être une variation géographique.

MOTS CLÉS
Anthocérotes, Anthocerotophyta, anatomie, distribution, biodiversité, Mexique, nouveau signalement.

INTRODUCTION

Hornworts are a small group of non-vascular plants with about 220 species that constitute the division Anthocerotophyta Stotler & Crandall-Stotler (Villarreal *et al.* 2010a, 2015; Söderstrom *et al.* 2016). Being one of the earliest diverging groups of land plants (Zhang *et al.* 2020), Anthocerotophyta might be key for understanding land plant evolution. Recent molecular studies have postulated bryophytes (hornworts, hepatics and mosses) as a monophyletic group, being hornworts sister to the hepatics + mosses clade (Setaphyta), and bryophyte clade sister to all tracheophtyes (One Thousand Plant Transcriptomes Initiative 2019; Li *et al.* 2020). Nevertheless, the diversity and systematics within Anthocerotophyta are poorly understood (Villarreal *et al.* 2010a).

Recent hornwort studies have focused on describing gross morphological characters of gametophyte, sporophyte and spores (Cykowska 2014; Ahayoun *et al.* 2015; Gupta & Asthana 2015; Brusa 2019; Guerra *et al.* 2019; Pócs *et al.* 2019). However, anatomical characters, which have been poorly documented, might be of taxonomic value (Cargill *et al.* 2005). The lack of documentation of these characters might be related to the deficiency of well-preserved specimens, incompletely sampled geographical areas, and the specialized equipment and techniques required for its analysis. Despite this problematic, detailed analysis of anatomy and morphology throughout hornwort diversity could be influential for defining phylogenetic relations and taxonomic boundaries, and could further provide valuable information for inferring character evolution within hornworts (Cargill *et al.* 2005).

Phaeomegaceros R.J.Duff, J.C.Villarreal, Cargill & Renzaglia (Dendrocerotaceae J. Hasegawa) is a genus of seven species of subtemperate and pantropical distribution (Duff *et al.* 2007; Villarreal *et al.* 2010a; Söderstrom *et al.* 2016). This genus is characterized by a solid thallus, absence of pyrenoids in the chloroplast, capsule with stomata and a central columella, and yellow to brownish spores with a vermiculated surface and distal depressions (Duff *et al.* 2007; Villarreal *et al.* 2010a). *Phaeomegaceros* was proposed by Duff *et al.* (2007) by including species formerly placed within the genus *Phaeoceros* L., which shares most of its diagnostic characters (Proskauer 1951; Duff *et al.* 2007; Villarreal *et al.* 2010a). Despite the morphological similarity between *Phaeomegaceros* and *Phaeoceros*, molecular phylogenetic studies have inferred that *Phaeomegaceros* is genetically more related to *Megaceros* Campbell, *Nothoceros* (Schuster) Hasegawa and *Dendroceros* Nees (Duff *et al.* 2007; Villarreal & Renner 2012; Villarreal *et al.* 2015).

Phaeomegaceros fimbriatus (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia is a dioicous species that has been reported from South America, the West Indies and the southern part of Central America (Hässel de Menéndez 1989; Hasegawa 2001; Dauphin 2005; Villarreal & Renzaglia 2006a; Duff *et al.* 2007; Villarreal *et al.* 2010a; Cykowska 2014). This is the first report of this genus and species in Mexico and North America, which considerably increases their distribution range to the north. Hornwort diversity in Mexico has been poorly documented (Stotler & Crandall-Stotler 2005; Delgadillo-Moya & Juárez-Martínez 2012; Ibarra-Morales *et al.* 2015), and this report is part of an ongoing effort to document the diversity of this key group of plants.

Traditional key taxonomic characters in Anthocerotophyta have been sporophytic traits (e.g., Hässel de Menéndez 1989, 1990), however nowadays anatomical and ultrastructural gametophyte characters are also providing a wealth of information useful for taxa delimitation (Villarreal & Renzaglia 2006b; Villarreal *et al.* 2017; Peñaloza-Bojacá *et al.* 2019). Villarreal & Renzaglia (2006a) described the anatomy and ultrastructure of the sporophyte of *Phaeomegaceros fimbriatus*; nevertheless, anatomical characters of the gametophyte

had not been yet studied in detail. Therefore, this study aims to contribute to the knowledge of anatomical and morphological characters of Anthocerotophyta, providing a detailed description of gametophyte of male and female plants and sporophyte, including light microscopy and SEM illustrations of the Mexican population of *Phaeomegaceros fimbriatus*. Furthermore, here is documented a novel distribution range of this species in North America, thus increasing the knowledge of Mexican bryoflora.

MATERIAL AND METHODS

Fresh samples of *Phaeomegaceros fimbriatus* collected in the state of Veracruz, Mexico (Fig. 1) were observed under a stereomicroscope to record morphological characters of both the gametophyte and the sporophyte. Slides were obtained by squash technique using fragments of the thallus and capsules to describe characters such as antheridial color and number per chamber, chloroplasts structure, morphology of epidermal cells of capsule and presence of stomata. For anatomical description and image capture, plants were fixed in FAA (formalin, acetic acid and ethyl alcohol). Samples were dehydrated in a graded ethanol series (30-100%), followed by a graded ethanol-xylol, xylol and paraplast-xylol series. Samples were kept in paraplast at 60°C for at least 24 hours. Afterwards, were embedded in paraplast and left to solidify at room temperature. The paraplast cubes were sectioned with a Leica RM2165 microtome. The sections were stained with safranin-fast green and were mounted on slides with synthetic resin and observed under a light microscope (Leica DMLS). For scanning electron microscopy (SEM), plants were fixed in FAA and dehydrated in a graded ethanol series (30-100%). Fragments of thallus and sporophyte were dissected and critical point dried using Bal-tec CPD 030 and sputter coated with gold in a Denton Vacuum Sputter Coater DESK-II. Images were digitally captured on a Jeol JSM 5310LV.

An anatomical and morphological description and illustration of *Phaeomegaceros* is provided. All observations and measurements are based on the plants collected for this study.

RESULTS

Family Dendrocerotaceae J.Haseg.
Genus *Phaeomegaceros* R.J. Duff, J.C. Villarreal, Cargill & Renzaglia

Phaeomegaceros fimbriatus (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia
(Figs 2-3)

The Bryologist 110: 241 (2007).

Anthoceros fimbriatus Gottsche. *Annales des Sciences naturelles, Botanique* sér. 5, 1: 187 (1864). — Isolectotype: Boquerón, Colombia 2800 m, *A. Lindig s.n.* (G).

Specimens examined. — **Mexico**. Veracruz: Tlapacoyan, Arroyo Tendido, road Teziutlán-Tlapacoyan, 19°55'26"N, 97°15'17"W, growing on shadded 85° slopes, elevation: 790 m, *A Mendoza s.n.* (FCME).13.XII.2011.

Taxonomic history

This species was originally described as *Anthoceros fimbriatus* Gottsche in 1864 from plants of Colombia (Gottsche 1864). In 1944, part of the type material of *P. fimbriatus* was lost with the destruction of Gottsche herbarium, fortunately there are still specimens cited in Gottsche original description in some herbaria (e.g., G, P, NY). In 1979, *A. fimbriatus* was transferred to the genus *Phaeoceros* (Gradstein & Hekking 1979) within the family Notothyladaceae (Milde) Müll. Frib. *ex* Prosk. Afterwards, a study that included molecular phylogenetic inferences of hornworts postulated that *P. fimbriatus* was genetically more related to Dendrocerotaceae than to Notothyladaceae, erecting a new genus, *Phaeomegaceros*, that included *P. fimbriatus* and other three species, and describing morphological features that supported the new genus (Duff *et al.* 2007). Nowadays, seven species constitute the genus *Phaeomegaceros* (Söderstrom *et al.* 2016).

When Gottsche (1864) described this species, he named two subspecies based on plant morphology. *Anthoceros fimbriatus* α *lindigianus* was described as possessing a wider frond, whilst *A. fimbriatus* β *schlimianus* was described as possessing a narrower and larger frond; both subspecies were collected on different localities in Colombia (Gottsche 1864). Regarding variation between the two subspecies, Proskauer left a note on the isotype of *Anthoceros fimbriatus* var. β *schlimianus* (P) dated January 24th 1969, stating that "The present material differs from the lectotype of *P. fimbriatus* in being slightly more delicate and having slightly smaller antheridia and spores. Nevertheless, I consider the plants conspecific" (PC0104738). The information documented by Proskauer provides more evidence on intraspecific variation in *P. fimbriatus* and adds to Gottsche observations of differences between both populations; however the characters described by both authors are qualitative appreciations on thickness and sizes, thus impeding from comparing this data with more populations of *P. fimbriatus* without revisiting the types. In 1989, Hässel de Menéndez synonymized both subspecies with *Phaeoceros fimbriatus* based mainly on spore characters. A morpho-molecular revision of the types of both subspecies could provide valuable information on the extent of the differences between both taxa.

Description of Mexican plants

Dioicous plants, growing on soil in rosettes. Thallus yellow-green to green, irregular surface with small dorsal protuberances. Margins of plant are irregularly crenulate. Female plants reach up to 16 mm in length and 8 mm in width (Fig. 2A), meanwhile male plants reach up to 10 mm in length and 8 mm in width. Thallus is solid and 9-14 (161-493 µm) cells thick. Thallus cell walls present band-like thickenings (Fig. 2B). One chloroplast per cell without a central pyrenoid. Rhizoids hyaline to brown reddish stained and unbranched. Plants frequently with ventral unstalked tubers

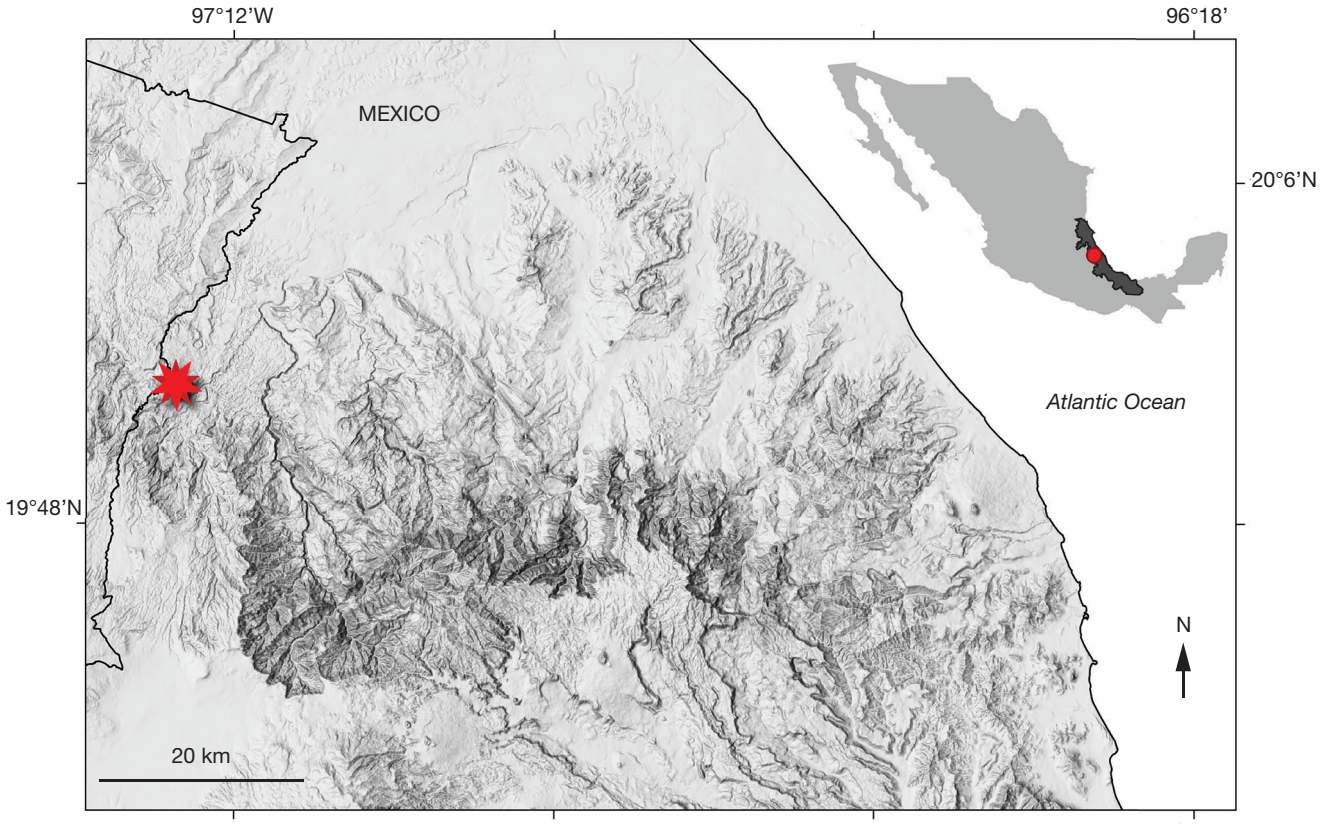

FIG. 1. — Map of the collection site of male and female plants of *Phaeomegaceros fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia, in the state of Veracruz, México. Collection site is indicated with a **red star**.

(Fig. 2C). Antheridial chamber with 1 (-2) antheridium per cavity (Fig. 2D-F), bright yellow to orange, 199-284 µm wide, irregular jacket cells arrangement. Archuegonia not observed. Involucres are erect and cylindrical, up to 4 mm long, solid, 6-10 cells thick (72-327 µm), surface irregular with small protuberances (Fig. 2G).

Sporophyte foot with abundant irregular placenta, haustorial cells penetrating the gametophyte (Fig. 2H). Up to three sporophytes per plant. Capsules erect, up to 55 mm long, opening by two valves becoming twisted with drying. Epidermal layer of capsule one cell thick in transverse section (Fig. 2J) with individual stomata scattered (4-5 stomata per mm^2), stomata 66-80 (-96) × 35-57 µm. Epidermal cells pale yellow, slightly thick, rectangular and elongate. Assimilative layer 6-8 cells thick (61-148 µm) in transverse section (Fig. 1J). Central columella rigid and brown (present along the sporophyte to the tip), up to 26 cells in transverse section (Fig. 1I-K). Sporogenous layer 1-3 tetrads thick (Fig. 1J). Pseudoelaters elongated, pale brown at maturity, thick-walled, 1-5 celled and 45-185 µm in length (Fig. 1L). Spores bright yellow at maturity, 28-36 µm in diameter (Figs 1L; 2). Distal surface with 5-6 depressions surrounding a central depression, depressions 4.5-7 µm in diameter, rest of the surface finely vermiculated (Fig. 2A, B). Proximal surface with distinct trilete mark, triradiate ridge covered with abundant vermiculae on either side of the dehiscence line (Fig. 2C). Triangular faces of the proximal surface with fine vermiculate-like pattern, confined to central section of each face are button-like verrucae up to 1 µm in diameter (Fig. 2C, D).

REMARKS

Morphological and anatomical variation of gametophyte characters within *Phaeomegaceros fimbriatus* is here discussed and compared with other species within the genus *Phaeomegaceros* (Table 1).

Thallus thickness is a variable character within *Phaeomegaceros*, having *P. foveatus* (J. Hasegawa) J.C.Villarreal and *P. hirticalyx* (Steph.) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia the most slender gametophyte thickness, while in the rest of the species a wide range of intraspecific variation has been documented (Table 1). Mexican plants of *P. fimbriatus* are within the slender-intermediate thickness documented for *P. fimbriatus* (Villarreal *et al.* 2010b). Regarding plant size, Cykowska (2014) reported plants forming rosettes of 0.8 to 3 cm diameter in *P. fimbriatus* from Bolivia; Mexican plants range from 0.8 to 1.6 cm in large, placing them within the previously reported range. It is noteworthy that in the Mexican material, male plants were generally smaller (0.8-1 cm long) than female plants (0.8-1.6 cm long).

The dorsal outgrows observed over the surface of the thallus are small scale-like pappillate and uniseriate projections rarely exceeding six cells long, giving the thallus surface a velvet-like appearance in Mexican plants. Within *Phaeomegaceros*, dorsal outgrows have been reported in *P. fimbriatus* (Villar-

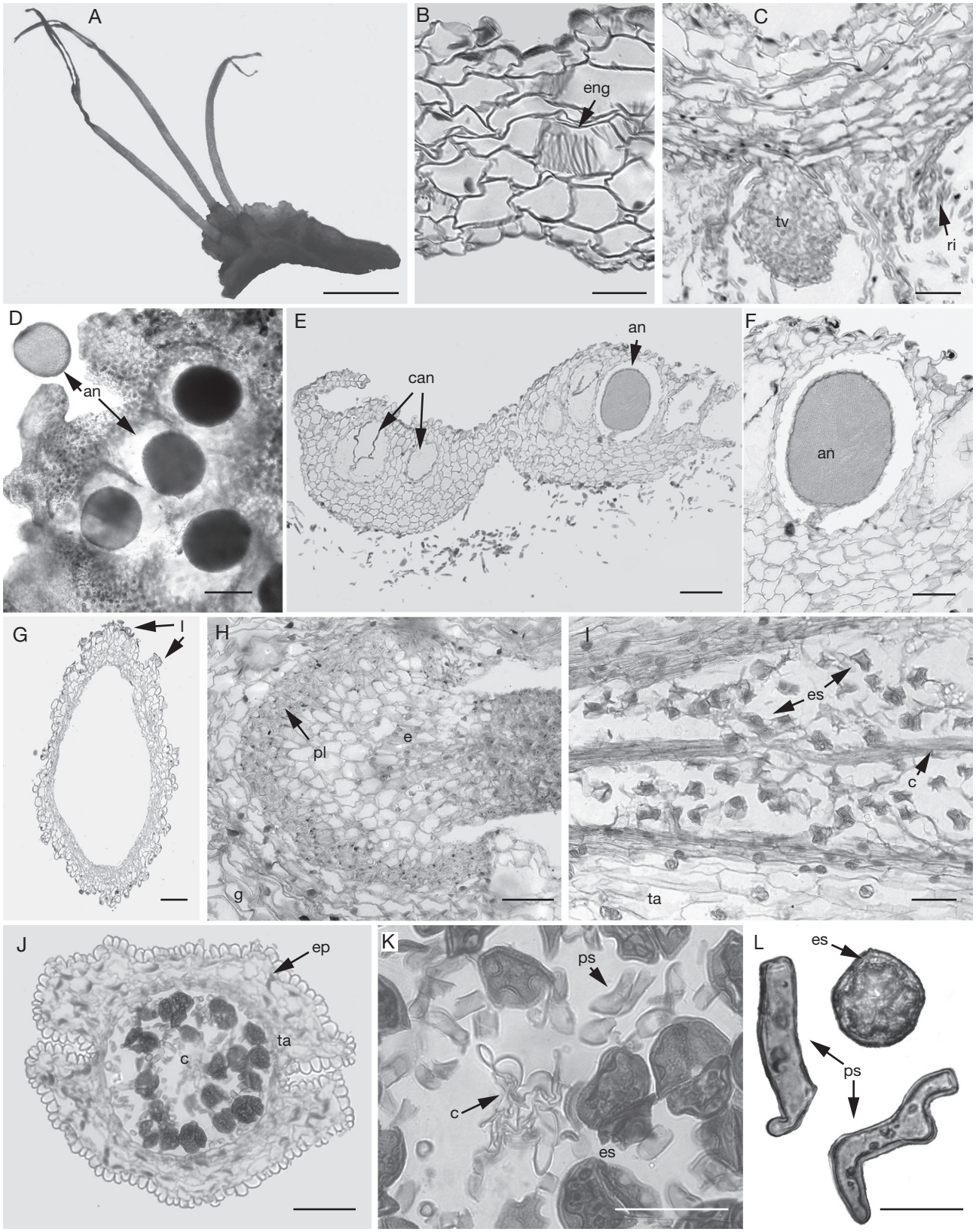

FIG. 2. — *Phaeomegaceros fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia: **A**, female plant; **B**, transverse section of gametophyte thallus with band-like thickenings (eng) in cell walls; **C**, transverse section of gametophyte thallus with ventral tuber (tv) surrounded by rhizoids (ri); **D**, dorsal surface of a male plant with an antheridium (an) in each antheridial chamber; **E**, transverse section of a male plant with numerous antheridial chambers (can) and an antheridium (an); **F**, close up on antheridium (an); **G**, transverse section of involucre (i) with numerous lamellae (l); **H**, longitudinal section of the sporophyte foot (e) with placenta (pl); **I**, longitudinal section of sporophyte capsule with assimilative tissue (ta), spores (es) and central columella (c); **J**, transverse section of sporophyte with epidermis (ep), assimilative tissue (ta) and central columella (c); **K**, close up of spores (es), pseudoelaters and central columella (c); **L**, spores (es) and pseudoelaters (ps). Scale bars: A, 5 mm; B, I, K, 50 µm; C, F, H, J, 100 µm; D, E, G, 200 µm L, 30 µm.

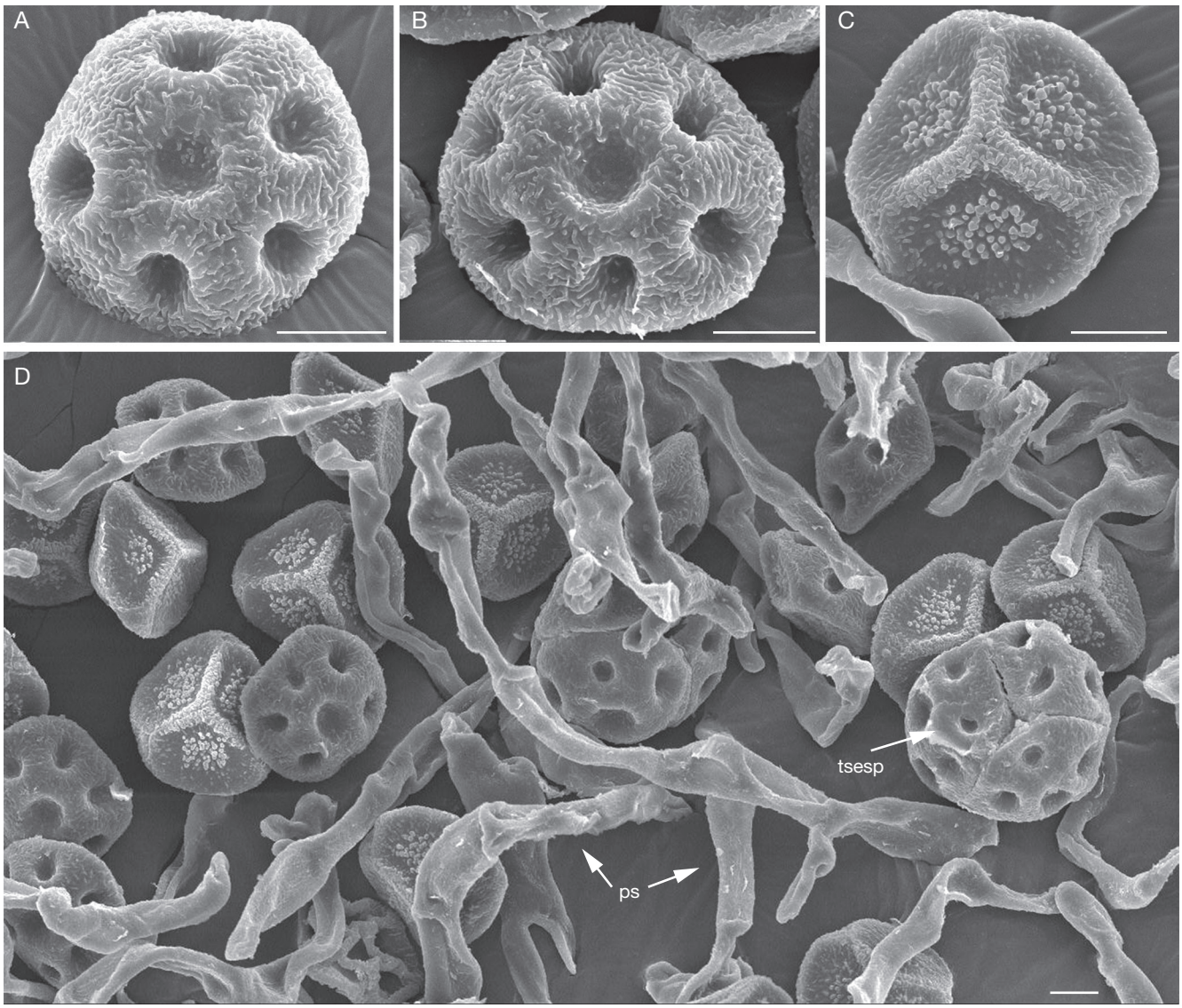

Fig. 3. — Spores of *Phaeomegaceros fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia under scanning electron microscopy: **A**-**B**, distal face variation of the spores: **A**, five depressions surrounding a central depression on distal face of spores; **B**, six depressions surrounding a central depression on distal face of spores; **C**, proximal face with button-like verrucae confined to the center of triangular areas; **D**, spore tetrads (tesp) and pseudoelaters (ps). Scale bars: 10 µm.

real *et al.* 2010b), *P. hirticalyx* (Hasegawa 1986; Campbell & Hasegawa 1993) and *P. squamuliger* (Spruce) J.C.Villarreal (Campbell & Hasegawa 1993; Villarreal *et al.* 2010b), while apparently absent in the rest of the taxa (Hasegawa 2001; Villarreal *et al.* 2010b). Intraspecific variation of this character has been documented; Villarreal *et al.* (2010b) described *P. squamuliger* subspecies *hasselii* J.C.Villarreal, Cargill & Goffinet based mainly on the absence of dorsal outgrows, once considered a defining character of *P. squamuliger*, and on distal spore ornamentation. The bases of this variation are still unknown. Dorsal outgrows are described in *P. fimbriatus* as usually present (Villarreal *et al.* 2010b), being absent in Bolivian plants (Cykowska 2014). The dorsal outgrows observed in Mexican plants resemble more those described in *P. hirticalyx* (Hasegawa 1986, 1988; Campbell & Hasegawa 1993) than the ones reported in *P. squamuliger* subspecies *squamuliger* (Campbell & Hasegawa 1993). Within Mexican hornwort flora, similar dorsal outgrows have been documented in *Leiosporoceros dussii* (Steph.) Hässel; Hasegawa (1988) considered that this character, along with some spore and pseudoelater characters pointed out that *L. dussii* and *P. hirticalyx* were very close related taxa; nevertheless, taxonomic revisions have supported previous proposals that place *L. dussi* in a monotypic genus (Hässel de Menéndez 1986) and not closely related to *P. hirticalyx* (Duff *et al.* 2007). Dorsal outgrows in Mexican hornworts are also common in species of the genus *Anthoceros* L. (Ibarra-Morales *et al.* 2015), which is characterized by thallus with schizogenous cavities, antheridia with 4-tiered jacket, several antheridia per chamber and black spores, which clearly differentiate them from *P. fimbriatus*.

Antheridial number and size has been a relatively homogenous character within *Phaeomegaceros* (Table 1). All of the species within the genus present one antheridia per chamber except for *P. hirticalyx*, where up to four antheridia per

TABLE 1. — Morphological characters of *Phaeomegaceros* R.J.Duff, J.C.Villarreal, Cargill & Renzaglia reported (Campbell 1982; Campbell & Hasegawa 1993; Hasegawa 2001; Villarreal *et al*. 2010b; Váňa & Engel 2013; Cykowska 2014; this study).

Species	***P. coriaceus*** **(Steph.) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia**	***P. fimbriatus*** **(Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia**	***P. foveatus*** **(J.Hasegawa) J.C.Villarreal**	***P. hirticalyx*** **(Steph.) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia**	***P. plicatus*** **(Mitt.) J.C. Villarreal, J.J. Engel & Váňa**	***P. skottsbergii*** **(Steph.) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia**	***P. squamuliger*** **(Spruce) J.C.Villarreal**	
							subsp. *squamuliger*	subsp. *hasselii* J.C.Villarreal, Cargill & Goffinet
Thallus length	Up to 40 mm	8-30 mm	Up to 9 mm	25 mm	–	–	–	Up to 40 mm
Thallus width	Up to 2 mm	Up to 8 mm	–	3-10 mm	–	–	–	(3) 6-10 mm
Thallus thickness	(3) 10-12 (16) cells	161-700 µm 7-16 cells	150-400 5-10 cells	280-500 µm 8-13 cells	400-800 µm (9) 10-20 cells	450-725 µm 10-15 cells	(250)400-700(1000) µm 8-20 cells	(250) 400-600 (1000) µm 8-25 cells
Dorsal outgrows	Epidermal pappillated cells	Small pappillate, uniseriate projections	Absent	Small laciniate scales, papillate projections, uniseriate filaments	Absent	–	Triangular in cross section, wider at their bases	Absent
Tubers	–	Absent/Present: Ventral unstalked	Absent	–	Short, finger like, ventral	–	–	–
Antheridia number	1	1(-2)	1	Up to 4	1	1	1	1
Antheridia size	Up to 300 µm long	199-284 µm	200-220 µm	–	–	–	–	240-275 µm
Spore diameter	45-50 µm (Maximum diam)	28-43 µm	38-46 µm	32-39 µm	45-59 µm	37-51 µm	45-55 µm	45-61 µm

chamber have been reported (Campbell & Hasegawa 1993). Regarding antheridial size, antheridia of about 200 µm have been documented in most species, ranging up to 275 µm in *P. squamuliger subsp. hasselii* (Table 1). Mexican plants of *P. fimbriatus* presented a wide range of variation within this character (199-284 µm), thus expanding the species variation range previously documented for this character (Table 1).

The presence of tubers in *Phaeomegaceros* has been reported in *P. plicatus* (Mitt.) J.C.Villarreal, J.J. Engel & Váňa (Váňa & Engel 2013), as short finger-like tubers. The tubers observed in Mexican plants are dark green, small (≤0.5 mm long), unstalked, subglobose to elongated, usually slightly narrower at the tip and wider at the base, sometimes bifurcated, somehow resembling those previously described in *P. plicatus*, a species that has been reported to distribute in Tristan da Cunha and Chile (Váňa & Engel 2013). The presence of tubers in *Phaeomegaceros* might be ecology related, since tubers are perennating structures that allow plants to survive long dry summers or diverse unfavorable conditions (Doyle & Stotler 2006; Crandall-Stotler *et al.* 2008), other tuber producing genera (e.g., *Paraphymatoceros* Hässel and *Phymatoceros* Stotler, W.T. Doyle & Crandall-Stotler) in Anthocerotophyta show mainly a north temperate distribution (Villarreal *et al.* 2010a, 2015). In *Phaeomegaceros*, this character has been documented only in austral taxa and the Mexican population here reported grows near the border of the Neartic and the Neotropical regions of Mexico, in a temperate climate region, which might indicate a climatic pattern. Within Mexican hornwort diversity, tubers are present in some species of *Phaeoceros* (e.g., *P. carolinianus, P. laevis*).

DISCUSSION

This study provides the first record for the genus *Phaeomegaceros* with the species *P. fimbriatus* in North America. *Phaeomegaceros fimbriatus* is known to distribute from Costa Rica to Bolivia and the West Indies (Hässel de Menéndez 1989; Hasegawa 2001; Dauphin 2005; Villarreal & Renzaglia 2006a; Duff *et al.* 2007; Villarreal *et al.* 2010a; Cykowska 2014). In this study it was found in the state of Veracruz, Mexico, growing on hillsides and forming rosettes of both male and female plants. This species presents the largest known distribution range within *Phaeomegaceros* in the American continent (Fig. 4).

Recording the distribution of dioicous species is relevant for understanding biogeographic and dispersal patterns in hornworts. The colonization and establishment of dioicous species populations within Anthocerotophyta is an interesting phenomenon, since it requires at least two spores to germinate and develop into male and female mature gametophytes growing a short distance from each other and with enough water availability for sperm to fertilize the egg (Villarreal & Renner 2013).

Regarding morphological and anatomical differentiation, *Phaeomegaceros fimbriatus* shares some macroscopic characters with other Mexican hornworts, such as species of *Phaeoceros*, e.g., solid thallus (Fig. 1B, C, E), erect capsule with stomata and central columella (Fig. 1I-K), and yellow spores. Nevertheless, *Phaeomegaceros fimbriatus* can be differentiated from species of *Phaeoceros* by distal spore ornamentation, being spiny to bumpy in *Phaeoceros,* whereas depressions or dimples are present in *Phaeomegaceros* (Figs 1L; 2) (Duff *et al.* 2007; Villarreal *et al.* 2010a); several layers of tetrads in the capsule are present in *Phaeomegaceros* (Fig. 1J), while *Phaeoceros* only

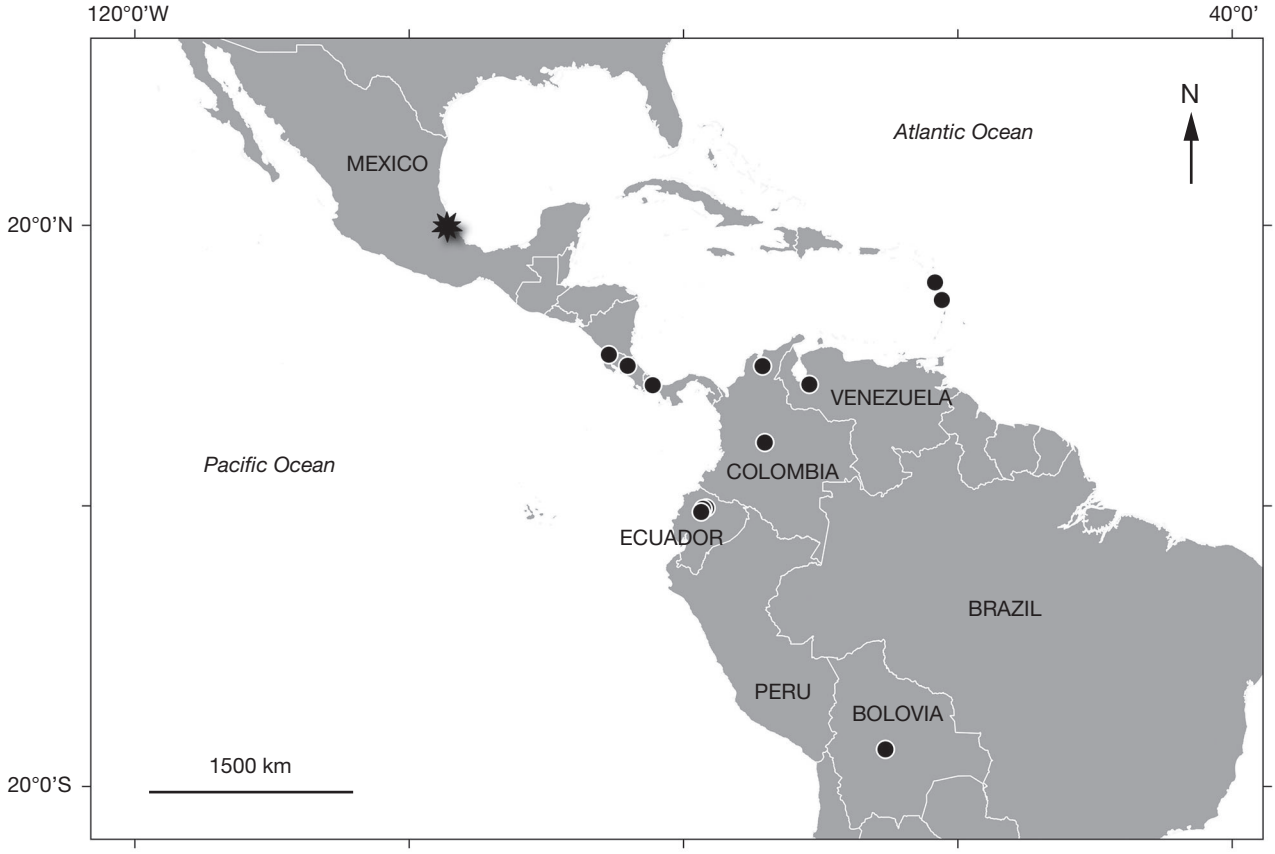

Fig. 4. — Map of *Phaeomegaceros fimbriatus* (Gottsche) R.J.Duff, J.C.Villarreal, Cargill & Renzaglia records. **Black dots** represent previously known distribution records (Hässel de Menéndez 1989; Hasegawa 2001; Dauphin 2005; Villarreal & Renzaglia 2006a; Duff *et al*. 2007; Villarreal *et al*. 2010b; Cykowska 2014), and **black star** represents the new record in Mexico.

shows one row of tetrads (Villarreal *et al.* 2010a); furthermore, the presence of one antheridium on each antheridial chamber separates this species from *Phaeoceros* species, which presents two or more antheridia per chamber. Regarding anatomical characters, the presence of band-like thickenings in the gametophyte cells (Fig. 2) is a valuable taxonomical character that is not shared with *Phaeoceros* species, however, appears to be characteristic of the Dendrocerotaceae family (Proskauer 1960; Duff *et al.* 2007; Villarreal *et al.* 2010a).

Spore ornamentation differentiates *Phaeomegaceros fimbriatus* from the rest of the species of *Phaeomegaceros*. Morphologically, the most closely related species, *Phaeomegaceros foveatus* (Hasegawa) Villarreal, is found in Southeast Asia and differs from *P. fimbriatus* by having a central depression in each of the triangular areas of the proximal face of the spores (Hasegawa 2001), *P. fimbriatus*, in contrast, shows centrally confined verrucae in each of the proximal triangular areas (Fig. 2C, D).

Mexican plants of *P. fimbriatus* collected presented smaller spores (28-36 µm in diameter, average 34 µm) than those previously reported, since southern Central-American and most of South American populations show larger spores (32-43 µm in diameter) (Hässel de Menéndez 1989; Villarreal & Renzaglia 2006a; Cykowska 2014), which extends the species variation range of this character, and might suggest geographical variation. A population of plants originally documented as *P. fimbriatus* from Paramo, Venezuela (Villarreal & Renzaglia 2006a) has not been considered within the species variation range because is currently being described as a new species (Villarreal J.C., pers. comm.), Paramo plants present larger spores (45-61 µm), higher number of spore distal depressions, smoother and thicker gametophyte (Villarreal & Renzaglia 2006a). Further population sampling, morphoanatomical characterization and molecular data are needed to test these hypotheses on spore size and the biogeographical distribution seen in *P. fimbriatus*.

A complete treatment of hornwort diversity in Mexico is lacking, records of these species in the country remain scattered in the literature, meanwhile most of the collections date back at least four decades. Delgadillo-Moya & Juárez-Martínez (2012) estimated Mexican hornwort diversity in nine species and three to four genera; however, they stated the need to stablish clearer limits between taxa and urged to increase collecting efforts within the country. About seven genera and more than 15 species are cited in the literature for Mexico (Hässel de Menéndez 1988, 1990; Schuster 1992; Stotler & Crandall-Stotler 2005; Villarreal *et al.* 2012; Ibarra-Morales *et al.* 2015; Escolástico-Ortíz & Juárez-Martínez 2018), nonetheless, a careful herbaria revision, as well as field exploration are critical to estimate more accurately Mexican hornwort diversity.

Detailed population level descriptions of wide-range distributing hornworts could be helpful to determinate intraspecific variation, which in turn would aid to define species limits in one of the most neglected groups of plants. On the other hand, recording distribution ranges will contribute to better understand ecological and biogeographical patterns, alongside to define conservation priority areas.

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