cryptogamie
Bryologie
2020 • 41 • 9

Anthoceros tristanianus J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel (Anthocerotaceae, Anthocerotophyta) a new record for South America from the Colombian bryophyte flora

Gabriel Felipe PEÑALOZA-BOJACÁ,
Mateus Fernandes de OLIVEIRA & Adaíses Simone MACIEL-SILVA

art. 41 (9) — Published on 13 July 2020
www.cryptogamie.com/bryologie

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

Directeur de la publication/ *Publication director* : Bruno David,
Président du Muséum national d'Histoire naturelle

Rédacteur en chef / *Editor-in-chief* : Denis LAMY

Assistante de rédaction / *Assistant editor* : Marianne SALAÜN (bryo@cryptogamie.com)

Mise en page / *Page layout* : Marianne SALAÜN

Couverture / *Cover* :
Extraits d'éléments de la Figure 1 / Extracts of the Figure 1

Cryptogamie, Bryologie est indexé dans / Cryptogamie, Bryologie *is indexed in:*
– Biological Abstracts
– Current Contents
– Science Citation Index
– Publications bibliographiques du CNRS (Pascal).

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

Cryptogamie, Bryologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
***Cryptogamie, Bryologie** 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:*
Adansonia, Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae,* Cryptogamie sous-sections *Algologie, 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*) : 1290-0796 / ISSN (électronique / *electronic*) : 1776-0992

Anthoceros tristanianus J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel (Anthocerotaceae, Anthocerotophyta) a new record for South America from the Colombian bryophyte flora

Gabriel Felipe PEÑALOZA-BOJACÁ
Mateus Fernandes de OLIVEIRA
Adaíses Simone MACIEL-SILVA
Laboratório de Sistemática Vegetal, Departamento de Botânica,
Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais,
Av. Antônio Carlos, 6627, Pampulha, Belo Horizonte, 31270-901, MG (Brazil)
gpenaloza.bojaca@gmail.com (corresponding author)

Submitted on 5 September 2019 | Accepted on 15 May 2020 | Published on 13 July 2020

Peñaloza-Bojacá G. F., Oliveira M. F. de & Maciel-Silva A. S. 2020. — *Anthoceros tristanianus* J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel (Anthocerotaceae, Anthocerotophyta) a new record for South America from the Colombian bryophyte flora. *Cryptogamie, Bryologie* 41 (9): 105-110. https://doi.org/10.5252/cryptogamie-bryologie2020v41a9. http://cryptogamie.com/bryologie/41/9

KEYWORDS
Colombia Andes,
Eastern cordillera,
hornworts,
Montane forests,
neotropics
new record.

ABSTRACT
Anthoceros tristanianus J.C.Villarreal, J.J.Engel & Váňa is reported here for the first time in South America from the Colombian flora, increasing the number of *Anthoceros* Linnaeus species recognized in that country to five. We present a taxonomic description, diagnostic characters, information concerning the ecology and geographic distribution of the species, as well as brief comparisons with morphologically similar taxa.

MOTS CLÉS
Andes de Colombie,
est de la cordillière,
anthocérotes,
forêts de montagne,
néotropiques,
signalement nouveau.

RÉSUMÉ
Anthoceros tristanianus *J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel (Anthocerotaceae, Anthocerotophyta) récolté en Colombie, un signalement nouveau pour l'Amérique du Sud.*
Anthoceros tristanianus J.C.Villarreal, J.J.Engel & Váňa, récolté en Colombie, est une addition à la flore des Antocérotes d'Amérique du Sud. Une description taxonomique, les caractères diagnostiques et des données sur l'écologie et la distribution géographique de cette espèce sont présentés. *A. tristanianus* est brièvement comparé aux taxons semblables.

INTRODUCTION

Bryophytes are the second largest group of land plants, and comprise three distinct phyla: Marchantiophyta (liverworts), Bryophyta (mosses), and Anthocerotophyta (hornworts), which correspond to a total of approximately 25 000 species. Bryophytes are poikilohydric plants with the ability to tolerate desiccation and withstand wide ranges of temperatures, facilitating their colonization of many different environments (Gradstein *et al.* 2001; Goffinet & Shaw 2009; Glime 2013). Another important characteristic of bryophytes is their high capacity for dispersal, which is reflected in their broad and disjunct geographic distribution patterns (Shaw 2001; Patiño & Vanderpoorten 2018). Dispersal is facilitated by their small sexual (spores produced by sporophytes after fertilization) and asexual (such as gemmae and caducous propagules) diaspores (Longton 2006; Crawford *et al.* 2009; Kürschner & Frey 2013), which take advantage of wind as their main disperser (Zanatta *et al.* 2016; Patiño & Vanderpoorten 2018).

The phylum Anthocerotophyta is divided into five families, 12 genera, and 200 to 250 species distributed throughout the world (Duff *et al.* 2007; Villarreal *et al.* 2014; Söderström *et al.* 2016). Their spores vary from 18 µm in diameter in *Leiosporoceros* Hässel, to up to *c.*100 µm in the multicellular spores of *Dendroceros* Ness (Renzaglia *et al.* 2009; Villarreal *et al.* 2015). The genus *Anthoceros* Linnaeus (1753: 1139) includes 14 species in the Americas, which are most frequently reported in countries in the northern and central regions of that continent (Stotler & Crandall-Stotler 2010; Ibarra-Morales *et al.* 2015). Only three species are currently known from Columbia: *Anthoceros granulatus* Gottsche, *Anthoceros lamellatus* Steph., and *Anthoceros punctatus* L. (Gradstein & Uribe 2016). The distribution patterns of those species and the true diversity of the genus are not well known there, and the lack of complete records generates large gaps in our knowledge about the genus, and hornworts in general. The present study presents a new record of *Anthoceros tristanianus* J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel for Colombia, as well as for South America, and expands both its geographical and altitudinal distribution.

MATERIAL AND METHODS

The present study analyzed specimens collected by the first author in the municipality of Guicán department of Boyacá, Colombia, at 3920 m a.s.l. The specimens were examined using both light (LM) and scanning electron microscopy (SEM). Images were made using a Zeiss Axio Lab A1 light microscope equipped with an Axion Erc5 digital camera, or a FEG – Quanta 200 FEI Scanning Electron Microscope, housed at the Microscopy Center of the Federal University of Minas Gerais, Brazil.

RESULTS

Anthoceros tristanianus J.C.Villarreal, J.J.Engel & Váňa (Fig. 1)

In Memoirs of the New York Botanical Garden, Váňa & Engel 105: 33 (2013).

Type. — **Tristan Da Cunha**. Along small stream W. of the Settlement of Edinburgh, in open grassland, 30 m, *Gremmen 2005-T028* (holo-, herb. J. Váňa; see note below).

Specimens studied. — **Colombia**. Boyacá, Muncipio de Guican, Vereda San Antonio de la Cueva, Sendero Lagunillas-Pulpito, 11.VIII.2017. Roadside over exposed area on soil and rock, 6°23'50.53"N, 72°21'42.18"W, 3920 m a.s.l. collected by *G.F. Peñaloza-Bojacá*, *D. Sanín*, *M. Sundeu*, *W. Texto & B. Moncada 915, 926, 927, 928, 930* (COL, BHCB [198757: GFPB927, 198758: GFPB915]).

Description

Plants

Thallus dark green; 13.1-17 mm long and 3-6.2 mm wide; margins lobulated, dorsal lamellae absent. Schizogenous cavities scarce; transverse section of thallus 40-300 × 60-590 µm. One chloroplast per cell, without a pyrenoid; rhizoids hyaline to brownish. Monoicous. Androecia scattered over dorsal surface; antheridial chamber 0.34-0.46 mm in diameter; 3-8 antheridia per chamber (Fig. 1B); spherical; brownish; antheridial length 107.5-140 µm and jacket cells regularly arranged into four tiers. Involucre 2.2-6.8 mm long; lamellae absent (Fig. 1A). Sporophytes 1-3 per gametophyte. Capsule 2.2-35 mm long; dehiscent by two longitudinal valves; epidermal cells of capsule elongate; 7.5-17.5 × 52.5-132.5 µm, with thin to slightly thickened-walls; stomata abundant (Fig. 1C); assimilative tissue 3-6 cells thick in transverse section. Columella rigid and brownish with 16 cells in cross section. Pseudoelaters brownish to blackish at maturity; 1-4 cells; 47.5-137.7 µm long (n = 36 pseudoelaters measured from seven sporophytes). Spores dark brown to blackish at maturity; 40-75 µm in diameter (n = 112 spores from seven sporophytes; proximal surface with a distinct trilete mark; triangular areas with a central wart; ornamentation of scattered single papillae; up to 1 µm high (Fig. 1D); distal surface with spines single, bifid, or confluent; 1-4 µm long (Fig. 1E).

Distribution and ecology

This species was recently described from Tristan da Cunha in the South Atlantic, at approximately 30 m a.s.l. (Váňa & Engel 2013); it was subsequently reported in coniferous forests in two Mexican states, at above 2800 m (Ibarra-Morales *et al.* 2015). We report this species for Colombia in the Department of Boyacá, Guican Municipality, in an area of páramo vegetation, near streams, above 3920 m (Fig. 1F).

Affinities and differentiation

Currently only two species of the genus *Anthoceros* have been recorded with central warts in the triangular areas of the proximal spore surface. One of them is *Anthoceros tuberculatus,* Lehmann & Lindenberg (1838: 25), dioicous, chlo-

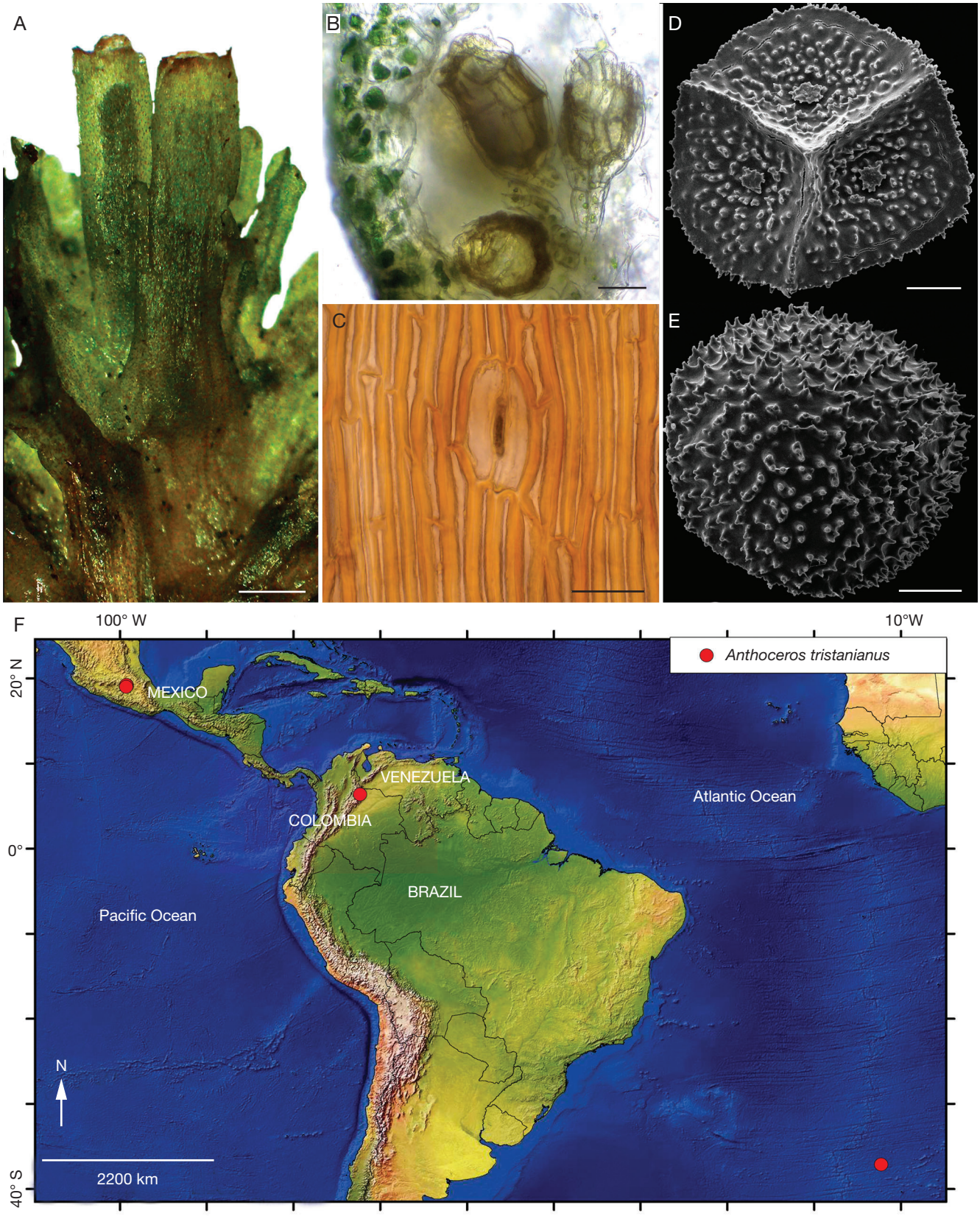

Fig. 1. — *Anthoceros tristanianus* J.C.Villarreal, J.J.Engel & Váňa in Váňa & Engel: **A**, Involucre; **B**, Antheridial chamber; **C**, Stoma on capsule wall; **D**, Spore, proximal surface; **E**, Spore, distal surface; **F**, Global distribution, Red circles indicate where the species has been reported. Scales bars: A, 1 mm; B, 35 µm; C, 40 µm; D, E, 10 µm.

TABLE 1. — Comparisons between the morphological characters of *Anthoceros* Linnaeus species reported for Colombia (Stephani 1917; Howe 1934; Hässel de Menéndez 1990; Ibarra-Morales *et al.* 2015; Gradstein 2018) and *Anthoceros tristanianus* J.C.Villarreal, J.J.Engel & Váňa.

Species	*A. tristanianus*	*A. lamellatus* Stephani	*A. punctatus* L.	*A. tuberculatus* Howe	*A. granulatus* Gottsche
Sexual system	Monoicous	Monoicous	Monoicous	Dioicous	Monoicous
Thallus size	13.1-17 mm long and 3-6.2 mm wide	8-21 mm long and 3-16 mm wide	5-15 mm long and 3-14 mm wide	–	–
Thallus morphology	Margins lobulated	Margins crenulate	Margins irregularly crenulate	Margins lobulated	Margins irregularly crenulate
Dorsal lamellae	Absent	abundant	abundant	abundant	Abundant on the margin
Epidermal plastid number	One	One	One	One	–
Pyrenoid	Absent	Present	Present	Present	–
Capsule	2.2-35 mm long	40-50 mm long	12-30 mm long	5.5- 80 mm long	40 mm long
Spore size (µm)	40-75	33-39	33-50	26-40	45
Proximal spore surface	With a distinct trilete mark, triangular areas with a central wart, ornamentation of scattered single papillae	Distinct trilete mark with a well-defined ridge, triangular areas smooth or with few verrucae	Distinct trilete mark with a well-defined ridge, triangular areas foveolate and covered by small verrucae	Distinct trilete mark with a well-defined ridge, triangular areas with a central wart	Trilete mark reduced or indistinct
Distal spore surface	Numerous bifid or confluent spines	Scattered bifid spines	bifid spines or tubercles	Bifid spines or tubercles	Blunt papillae

roplast with a central pyrenoid, spores smaller than 35 µm, and irregular crests or lamellae on the distal spore surface; the other is *A. tristanianus*, monoicous, chloroplast with no pyrenoid, spores 50-66 µm in diameter, and spines on the distal surface (Hässel de Menéndez 1990; Váňa & Engel 2013; Ibarra-Morales *et al.* 2015).

NOTE

Currently the Herbarium collections at the Charles University in Prague (PRC) has the largest collection of specimens (*c.* 40 000) studied by professor J. Váňa (https://botany.natur.cuni.cz/cevnate/prc/bryo.php).

DISCUSSION

The spores found in our specimens agree with the description of *A. tristanianus*: distal surface with numerous solitary spines and proximal surface with a distinct trilete mark, triangular areas with a central wart, and ornamentation of scattered, single papillae (Hässel de Menéndez 1990; Ibarra-Morales *et al.* 2015). Those spore characters are also found in specimens from Mexico and Tristan da Cunha. We highlight the sizes of the spores, which reach a maximum diameter of 66 µm in Mexico and Tristan da Cunha, and 75 µm in the Colombian Paramo specimens.

Ibarra-Morales *et al.* (2015) described three different hornwort morphotypes among the *A. tristanianus* specimens found in Mexico. The authors proposed that gametophytic and sporophytic traits varied among the morphotypes due to microhabitat conditions. Our specimens are similar to morphotype 1 recorded in Mexico, sharing traits such as a lobed margin, dorsal lamellae absent, up to nine antheridia per chamber, and capsule 35 mm long. Additionally, Colombian specimens show the same variations in capsule length (*c.* 12 mm) reported for plants from Tristan da Cunha.

In comparison with other species published for Colombia (*Anthoceros lamellatus* Stephani, *Anthoceros punctatus* L., *Anthoceros tuberculatus* Howe, and *Anthoceros granulatus* Gottsche; Table 1; Gradstein *et al.* 2016; Gradstein & Uribe 2016; Gradstein 2018), *A. tristanianus* can be differentiated by the size of its spores, the absence of dorsal lamellae, and the lack of a pyrenoid in the chloroplast.

Anthoceros tristanianus was first recorded on the island of Tristan da Cunha, and later on the American continent (Mexico, and now Colombia), suggesting a high capacity for long distance dispersal. That does not, however, eliminate the possibility of a relictual distribution, where widely distributed plants suffered later reductions in their original populations (including extinctions) during the Tertiary period, generating a disjunct distribution (Schofield & Crum 1972; Milne & Abbott 2002).

This new record increases the likelihood that this species has a wider distribution range in other South and Central American countries, such as Costa Rica (Villarreal J.C., pers. comm.). *Anthoceros agrestis* Paton and *Anthoceros punctatus* are other hornwort species having broad distributions as they are known from the American, European, Asian, and Oceania continents. That wide distribution range may be related to dispersal capacity linked to activities of humans, birds, and wind (Bisang 1992; Muñoz *et al.* 2004; Zanatta *et al.* 2016; Patiño & Vanderpoorten 2018). Small spores (i.e < 25 µm) should have an important role in the long-distance dispersal and shaping distribution of bryophyte species (Muñoz *et al.* 2004; Zanatta *et al.* 2016; Patiño & Vanderpoorten 2018). Additionally, ornamented diaspores of bryophytes (i.e. with papillae and spines) may be easily attached and transported in the plumage of birds, mammal

hair, and also humans (Heinken *et al.* 2001; Lewis *et al.* 2014; Patiño & Vanderpoorten 2018).

Morphological variations recorded in *A. tristanianus* may be related to its inherent ability to tolerate different environments – reflecting the spatially structured polymorphism often observed in bryophyte and fern species showing long-distance dispersal (Patiño *et al.* 2014; Patiño & Vanderpoorten 2018). The evolution of specialized races, or genetic specialization, is possibly less important, however, than physiological and morphological plasticity (Schneller & Liebst 2007; Patiño *et al*. 2014) in *A. tristanianus*.

Acknowledgements

This study was financed in part by: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-Brasil (CAPES)-Finance Code 001; Latin American and the Caribbean Macro Universities, the postgraduate Mobility Program 02-2017; Emerging Leaders in the Americas Program – ELAP (2018-2019); and the Rufford Foundation (Small Grants 2018-2019). This research was carried out with permission from the Cocuy National Park (record 001, 09-08-2017), ANLA (resolution 1342 of 11-2014). The first author thanks Dr Juan Carlos Villarreal (Université Laval), Dra. Bibiana Moncada (Universidad Distrital Francisco José de Caldas), and Dr Jaime Uribe Melendez (Universidad Nacional de Colombia) for their support and collaboration; and the Microscopy Center at the Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil (http://www.microscopia.ufmg.br) for the electron microscope images. We appreciate the comments made by the anonymous reviewers who helped strengthen the manuscript.

REFERENCES

Bisang I. 1992. — Hornworts in Switzerland-endangered? *Biological Conservation* 59: 145-149. https://doi.org/10.1016/0006-3207(92)90574-7

Crawford M., Linley K. J. & Garnock-Jones P. J. 2009. — Correlated Evolution of Sexual System and Life-History Traits in Mosses. *Evolution* 63 (5): 1129-1142. https://doi.org/http://dx.doi.org/10.1111/j.1558-5646.2009.00615.x

Duff J., Villarreal J. C., Cargill C. & Renzaglia K. S. 2007. — Progress and challenges toward developing a phylogeny and classification of the hornworts. *The Bryologist* 110 (2): 214-243. https://doi.org/10.1639/0007-2745(2007)110[214:PACTDA]2.0.CO;2

Glime J. M. 2013. — Meet the Bryophytes, *Bryophyte Ecology* Vol. 1.Michigan Technological University and the International Association of Bryologists:1-10.

Goffinet B. & Shaw A. J. 2009. — *Bryophyte Biology*. New York, United States, Cambridge University Press, 581 p.

Gradstein R. 2018. — Key to hornworts (Anthocerotophyta) of Colombia. *Caldasia* 40 (2): 262-270. https://doi.org/10.15446/caldasia.v40n2.71750

Gradstein R., Morales C., Negritto M. A. & Duckett J. G. 2016. — New Records of Liverworts and Hornworts from the Sierra Nevada de Santa Marta, Colombia. *Cryptogamie, Bryologie* 37 (4): 463-475. https://doi.org/https://doi.org/10.7872/cryb/v37.iss4.2016.463

Gradstein R. & Uribe M. J. 2016. — Anthocerophyta (Antocerotas), *in* Bernal R., Grandstein R. S. & Celis M. (eds), *Catálogo de plantas y líquenes de Colombia volumen I, Capítulos introductorios - líquenes a Lythraceae*. Bogotá, Universidad Nacional de Colombia (Sede Bogotá). Facultad de Ciencias. Instituto de Ciencias Naturales: 443-445.

Gradstein S. R., Churchill S. P. & Allen N. S. 2001. — Guide to the Bryophytes of Tropical America. *Memories of the New York Botanical Garden* 86: 1-577.

Hässel de Menéndez G. 1990. — Las especies de Anthoceros y Folioceros (Anthocerotophyta) de América del Norte, Sud y Central. La ornamentación de sus esporas y taxonomía. *Candollea* 41 (1): 201-220

Heinken T., Lees R., Raudnitschka D. & Runge S. 2001. — Epizoochorous dispersal of bryophyte stem fragments by roe deer (Capreolus capreolus) and wild boar (Sus scrofa). *Journal of Bryology* 23 (4): 293-300. https://doi.org/10.1179/jbr.2001.23.4.293

Howe M. 1934. — The Hepaticae (chiefly Riccia and Anthocerotaceae) of the Galapagos Islands and the Coasts and Islands of Central American and Mexico. *California Academy of Sciences* 21 (17): 199-210

Ibarra-Morales A., Muñíz M. E. & Valencia S. 2015. — The Genus *Anthoceros* (Anthocerotaceae, Anthocerotophyta) in Central Mexico. *Phytotaxa* 205 (4): 215-228. https://doi.org/10.11646/phytotaxa.205.4.1

Kürschner H. & Frey W. 2013. — Life strategies in bryophytes – a prime example for the evolution of functional types. *Nova Hedwigia* 96 (1): 83-116. https://doi.org/10.1127/0029-5035/2012/0071

Lewis L. R., Behling E., Gousse H., Qian E., Elphick C. S., Lamarre J. F., Bety J., Liebezeit J., Rozzi R. & Goffinet B. 2014. — First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. *PeerJ*: 1-13. https://doi.org/10.7717/peerj.424

Longton R. E. 2006. — Reproductive ecology of bryophytes: What does it tell us about the significance of sexual reproduction? *Lindbergia* 31 (1-2): 16-23

Milne R. I. & Abbott R. J. 2002. — The origin and evolution of tertiary relict floras. *Advances in Botanical Research* 38: 281-314. https://doi.org/10.1016/s0065-2296(02)38033-9

Muñoz J., Felicísimo Á. M., Cabezas F., Burgaz A. R. & Martínez I. 2004. — Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science* 304 (5674): 1144-1147. https://doi.org/10.1126/science.1095210

Patiño J. & Vanderpoorten A. 2018. — Bryophyte Biogeography. *Critical Reviews in Plant Sciences* 37 (2-3): 175-209. https://doi.org/10.1080/07352689.2018.1482444

Patiño J., Carine M., Fernández-Palacios J. M., Otto R., Schaefer H. & Vanderpoorten A. 2014. — The anagenetic world of spore-producing land plants. *New Phytologist* 201 (1): 305-311. https://doi.org/10.1111/nph.12480

Renzaglia K. S., Villarreal J. C., Duff R. J. & Goffinet B. 2009. — New insights into morphology, anatomy, and systematics of hornworts, *in* Shaw A. J. (ed.), *Bryophyte Biology*. Cambridge, Cambridge University Press: 139-172. https://doi.org/10.1017/CBO9780511754807.004

Schneller J. & Liebst B. 2007. — Patterns of variation of a common fern (Athyrium filix-femina; Woodsiaceae): population structure along and between altitudinal gradients. *American Journal of Botany* 94 (6): 965-971. https://doi.org/10.3732/ajb.94.6.965

Schofield W. B. & Crum H. A. 1972. — Disjunctions in Bryophytes. *Annals of the Missouri Botanical Garden* 59 (2): 174. https://doi.org/10.2307/2394752

Shaw A. J. 2001. — Biogeographic paterns and cryptic speciation in bryophytes. *Journal of Biogeography* 28 (2): 161-253

Söderström L., Hagborg A., Von Konrat M., Bartholomew-Began S., Bell D., Briscoe L., Brown E., Cargill D. C., Da Costa D. P., Crandall-Stotler B. J., Cooper E., Dau-

PHIN G., ENGEL J., FELDBERG K., GLENNY D., GRADSTEIN S. R., HE X., HENTSCHEL J., ILKIU-BORGES A. L., KATAGIRI T., KONSTANTINOVA N. A., LARRAÍN J., LONG D., NEBEL M., PÓCS T., PUCHE F., REINER-DREHWALD E., RENNER M., SASS-GYARMATI A., SCHÄFER-VERWIMP A., SEGARRA-MORAGUES J., STOTLER R. E., SUKKHARAK P., THIERS B., URIBE J., VÁŇA J., WIGGINTON M., ZHANG L. & ZHU R.-L. 2016. — World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828. https://doi.org/10.3897/phytokeys.59.6261

STEPHANI F. 1917. — Anthocerotaceae, *in* Georg & Librairies-Editeurs (eds), *Species hepaticarum: eine Darstellung ihrer Morphologie und Beschreibung ihrer Gattungen wie aller bekannten Arten in Monographien unter Berucksichtigung ihrer gegenseitigen Verwandtschaft und geographischen Verbreitung* Vol. 5. Geneva, Species Hepaticarum: 944-1022.

STOTLER R. & CRANDALL-STOTLER B. 2010. — A Revised Classification of the Anthocerotophyta and a Checklist of the Hornworts of North America , North of Mexico. *The Bryologist* 108 (1): 16-26. https://doi.org/10.1639/0007-2745(2005)108[16:ARCOTA]2.0.CO;2

VÁŇA J. & ENGEL J. 2013. — *The liverworts and hornworts of the Tristan da Cunha group of islands in the South Atlantic Ocean.* New York Botanical Garden Press, 148 p.

VILLARREAL J. C., CARGILL D. C., HAGBORG A., SODERSTROM L. & RENZAGLIA K. S. 2014. — A synthesis of hornwort diversity: Patterns, causes and future work. *Phytotaxa* 9 (1): 150. https://doi.org/10.11646/phytotaxa.9.1.8

VILLARREAL J. C., CUSIMANO N. & RENNER S. S. 2015. — Biogeography and diversification rates in hornworts: The limitations of diversification modeling. *Taxon* 64 (2): 229-238. https://doi.org/10.12705/642.7

ZANATTA F., PATIÑO J., LEBEAU F., MASSINON M., HYLANDER K., DE HAAN M., BALLINGS P., DEGREEF J. & VANDERPOORTEN A. 2016. — Measuring spore settling velocity for an improved assessment of dispersal rates in mosses. *Annals of Botany* 118 (2): 197-206. https://doi.org/10.1093/aob/mcw092

Submitted on 5 September 2019;
accepted on 15 May 2020;
published on 13 July 2020.