

# Juan Carlos Villarreal A.

<http://villarreal-lab.ibis.ulaval.ca/>

## Current address:

Département de Biologie,  
Institut de biologie intégrative et des systèmes (IBIS),  
Université Laval, Québec (Québec), G1V 0A6, Canada  
**Email:** jcvil9@ulaval.ca

---

## AFFILIATIONS and EMPLOYMENT

- **Assistant Professor**, Université Laval: since 2015
  - **Canada Research Chair (Junior)**, Canada Government: 2020-2024
  - **Research Associate**, Smithsonian Tropical Research Institute (Panama): since 2020
  - **Regular member**, Center of Nordic Studies, Université Laval: since 2016
  - **Research Associate**, Royal Botanic Garden, Edinburgh, Scotland: since 2015
  - **Earl S. Tupper Fellow**, Smithsonian Tropical Research Institute: 2015-2017
  - **Sibbald Postdoctoral Fellow**, Royal Botanic Garden, Edinburgh: 2015
  - **Postdoctoral Fellow**, Munich Botanic Garden: 2012-2014.
- 

## EDUCATION

- Ph.D., University of Connecticut, (UCONN). Ecology and Evolutionary Biology. 2006-2011.  
Supervisors: Bernard Goffinet, Louise Lewis and Kent Holsinger.  
**Thesis:** Genetic and evolutionary consequences of a shift to asexuality in bryophytes.
  - M.Sc., Southern Illinois University–Carbondale, SIUC. 2003-2005  
Supervisor: Karen Renzaglia.  
**Thesis:** A comparative anatomical and ultrastructural study of two phylogenetically significant hornworts: *Leiosporoceros dussii* and *Phaeomegaceros fimbriatus*.
  - B.Sc., University of Panamá
- 

## SELECTED PEER-REVIEWED PUBLICATIONS:

A list is provided at the end of the CV. 6212 citations, h-index=32, i10-index: 52.

For citations: <https://scholar.google.ca/citations?user=R4DpS5oAAAAJ&hl=en>.

1. Marta Alonso–García\*, Raquel Pino–Bodas, **Juan Carlos Villarreal A.** 2022. Co–dispersal of symbionts in the lichen *Cladonia stellaris* inferred from genomic data. *Fungal Ecology* 60 : 101165.
2. Rahmatpour, N., D.A. Hauser, J.M. Nelson, P.Y. Chen, **J.C. Villarreal A.**, M.Y. Ho, F–W. Li. 2021. A novel thylakoidless isolate fills a billion year gap in the evolution of Cyanobacteria. *Current Biology* 31(13): 2587–2867. Cover of the journal.
3. Bell–Doyon, P., J. Laroche, K. Saltonstall, **J.C. Villarreal A.** 2020. Specialized bacteriome uncovered in the coralloid roots of the epiphytic gymnosperm, *Zamia pseudoparasitica*. *Environmental DNA* 2(4) : 418-428.

4. Alonso, M.\*, F. Grewe, S. Payette & **J.C. Villarreal**. 2021. Population genomics and genetic diversity of a reindeer lichen species in Eastern Canada lichen woodlands. *American Journal of Botany* 108(1) 159–171. Cover of the journal.
5. OneKP Initiative. 2019. A Phylogenomic View of Evolutionary Complexity in Green Plants. *Nature* 574, pages 679–685. *I have equal contribution in the second tier of authors, the first tier includes the PIs of the consortium.*
6. **Villarreal, J.C.**, Crandall-Stotler, B.J., et al. 2016. Divergence times and the evolution of morphological complexity in an early land plant lineage (Marchantiopsida) with a slow molecular rate. *New Phytologist* 209(4):1734-46. doi: 10.1111/nph.13716
7. Laenen, B., --**J.C. Villarreal**, --15 authors. 2014. Extant diversity of bryophytes emerged from successive post-Mesozoic diversification bursts. *Nature Communications*. 5: 6134. DOI: 10.1038/ncomms6134
8. Li, F.-W., **J.C. Villarreal**, --32 authors, D.W. Stevenson, K.M. Pryer. 2014. Horizontal gene transfer of a chimeric photoreceptor, neochrome, from bryophytes to ferns. **Proceedings of the National Academy of Sciences, USA** 111: 6672–6677, DOI: 10.1073/pnas.1319929111.
9. **Villarreal, J.C.** & S.S. Renner. 2012. Hornwort pyrenoids: carbon-concentrating mechanisms evolved and were lost at least five times during the last 100 million years. **Proceedings of the National Academy of Sciences, USA** 109: 18873–18878. DOI: 10.1073/pnas.1213498109

#### BOOK CHAPTERS AND TRIBUTE PAPERS - PEER REVIEWED

1. Hanson, D., K.S. Renzaglia & **J.C. Villarreal**. 2014. Diffusion limitation and CO<sub>2</sub> concentrating mechanisms in bryophytes. In *Advances in Photosynthesis and Respiration: Photosynthesis in Early Land Plants*, D.T. Hanson & S.K. Rice (eds). Vol. 37: 95-112 Springer, Dordrecht. DOI:10.1007/978-94-007-6988-5\_6.
2. Renzaglia, K.S., **J.C. Villarreal** & R.J. Duff. 2009. New insights into morphology, anatomy and systematics of hornworts. In *Bryophyte Biology II*, B. Goffinet & J. Shaw (eds.), pp 139-171. <http://dx.doi.org/10.1017/CBO9780511754807.004>
3. Duff, R.J., D.C. Cargill, **J.C. Villarreal** & K.S. Renzaglia. 2004. Phylogenetic relationships of the hornworts based on *rbcL* sequence data: novel relationships and new insights. *Monographs in Systematic Botany from the Missouri Botanical Garden* 98: 41-58.

#### BOOK REVIEWS AND CONFERENCE PROCEEDINGS

1. Budke, J.M., M. Renner, **J.C. Villarreal A.**, M. Stech. (Eds.) 2022. In celebration of Jeffrey Graham Duckett's unending curiosity and impactful contributions to bryology. *Bryophyte diversity and Evolution* 45(1).
2. **Villarreal, J.C.**, B. Goffinet, N. Fenton, M. Favreau, S. Schuette & M. von Konrat. 2021. [Proceedings of Bryophytes, lichens, and northern ecosystems in a changing world](#) (July 6-9, 2021). *Bryological Times* 152.
3. **Villarreal, J.C.**, L. Rochefort, C. Boismenu & M. Guéné-Nanchen. 2017. Future Arctic: from species to ecosystems. *Proceedings of the workshop Future Arctic*.
4. **Villarreal, J.C.** 2010. Before the vascular plants. Book review of "Syllabus of Plant Families A. Engler's Syllabus der Pflanzenfamilien. 3. Bryophytes and seedless vascular plants." 2009. Eds.: W. Frey, M. Stech & E. Fischer. *The Bryologist* 113: 431–434

---

## RECENT RESEARCH GRANTS

- **\$600,000 (CAD)**. Natural Sciences and Engineering Research Council of Canada. Chaire de recherche du Canada, niveau 2. “Genomics and metabolomics of the plant-microbial symbiosis”. **Role in project:** Experimental and functional genomics of the symbiosis between tropical plants (cycads) and microbes, especially leaf and root symbioses between bacteria and cycads. 2019-2024.
- **\$230,000 (CAD)**. Canadian Funds for Innovation, Fonds des leaders John-R. Evans. “Infrastructure grant”. 2020-2024.
- **\$710,000 (CAD)**. Sentinelle Nord. “Ecogenomics of mining areas for sustainable Canadian North (GENOSCAN)”. (PI. Damase Khasa, co-PI **J.C. Villarreal**). **Role in project:** Population genomics and microbial genomics of mining sites in Northern Canada. 2020-2023.
- **\$343,224 (CAD)**. Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) Mise en végétation écologique des sites miniers recouverts d'un matériau granulaire: développement d'une méthode efficace et peu coûteuse (PI Line Rochefort, co-PI **J.C. Villarreal**). **Role in project:** Microbial genomics of mining sites in Northern Canada, especially biological crusts and the role of cryptogams. 2019-2023.
- **\$168,000 (CAD)** NSERC. “Spatial and temporal diversity of the bryophyte Arctic flora and associated cyanobacterial and fungal biota”. **Role in project:** Population genomics and functional genomics of microbes associated with lichens and bryophytes. 2016-2022.
- **\$1,100,000 (US)**. National Science Foundation, USA. “Diversity, ecology, and genetics of hornwort-cyanobacterium symbiosis”. (P.I. Fay-Wei Li, J. Meeks, J. Sparks). **Role in project:** JCVA is an international collaborator, no direct funding is received. Cyanobacterial genomics and microscopy. 2019-2023.
- **\$65,976 (CAD)**. Natural Sciences and Engineering Research Council of Canada (NSERC). “Determining critical thresholds of landscape disturbance in boreal and mixed coniferous forests in eastern Canada” (P.I. Nicole Fenton, UQAT, co-PI **J.C. Villarreal**). **Role in project:** Population genomics of bryophytes in fragmented landscapes. 2018-2022.
- **\$100,000 (US)**. SENACYT. “Cicadófitas y sus simbioses: diversidad genética y química como potencial en la conservación de especies”. (PI. **J.C. Villarreal**). 2018-2021
- **\$149,144 (CAD)**. Canadian Funds for Innovation, Fonds des leaders John-R. Evans. “Infrastructure grant”. 2017-2020.
- **\$32,000 (CAD)** Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT). “Documenter la diversité génétique et chimique de gymnospermes tropicales”. 2017-2020.
- **€168,995** Deutsche Forschungsgemeinschaft (DFG). “Understanding the evolution of key traits in hornworts, the sister group to vascular plants”. (PI: S.S. Renner, co-PI: **J.C. Villarreal**, DFG does not allow post-doctoral researchers to be PI). 2012-2014.

---

## AWARDS

- **\$400** Hattori Prize Award, International Association of Bryologists (IAB): Best paper or series of papers published within the previous two years by a member of IAB. 2017
- **\$500** A.J. Sharp Award, American Bryological and Lichenological Society (ABLS) : Best student paper, BSA Meeting, Rhode Island. 2019
- **\$5000** Presidential Summer Graduate Research Award, UCONN. 2009.
- **\$500** Extraordinary Doctoral Travel Award, UCONN. 2009.

---

## FELLOWSHIPS

- **\$60,000 (US)** Earl's Tupper Fellowship, Smithsonian Tropical Research Institute, Panama. **Project:** Highly competitive postdoctoral fellowship to work on the functional genomics of the plant-cyanobacterial symbiosis. Including salary and research money. 2015-2018.
- **\$28880 (US)** Sibbald Fellowship, Royal Botanic Garden Edinburgh (RBGE). **Project:** Diversification of complex thalloids liverworts, including the model system *Marchantia polymorpha*. Including salary and research money. 2015.

---

## POST-DOCTORAL RESEARCHERS:

- **Marta Alonso García**, Université Laval. Financed by the SENECA foundation, Murcia and Sentinel North. **Project:** Lichen population genomics, microbiome, metatranscriptomics. Currently, Dr. Alonso works as research professional. 2018-2023.

## GRADUATE STUDENTS

- **Philip Bell-Doyon**, Université Laval: Doctoral student, 2020-2024.  
**Project:** Lichen metagenomics and metabolomics in old-growth forests. Metabolomics and genomics of the lichen symbiosis.
- **Dennis Escolástico**, Université Laval: Doctoral student. 2018 -2023.  
**Project:** Population genomics and microbial genomics and physiology of tundra mosses
- **Adriel Sierra**, Université Laval: Doctoral student. 2019-2023.  
**Project:** Population genomics and microbial genomics of fragmented forests of Amazonia
- **Laura Hjartarson**, Université Laval: Master student, 2020-2023  
**Project:** Metagenomics of biological crusts in Eastern Canada
- **Anthony Piot**, Université Laval: Doctoral student, co-supervision. 2017-2022.  
**Project:** Disruptive genetic variants in secondary wall deposition in poplar
- **Sandrine Toupin**, Université Laval: Master student. 2019-2021.  
**Project:** Transcriptomics of the root cyanobacterial symbiosis in cycads
- **Loïc Soumila**, Université Laval: Master student. 2019-2022

- **Project:** Metabolomics of gymnosperms
- **Philip Bell-Doyon**, Université Laval: Master student. 2019-2020  
**Project:** Soil metagenomics of old-growth forests
- **Catherine Chagnon**, Université Laval: Master student, co-supervision. 2018-2020  
**Project:** Effect of shrubification on lichen diversity and abundance in the Canadian tundra

#### EXTERNAL GRADUATE STUDENTS

- **Lilisbeth Rodríguez**, Universidad de Panama: master student. 2021-2023.  
**Project:** Phyllosphere metagenomics of tropical canopy epiphytes
- **Enrique Hernández-Rodríguez**, UQAT (Canada): doctoral student. 2018- 2023.  
**Project:** Effect of fragmentation on bryophyte diversity in the boreal forests
- **Gabriel Peñaloza-Bojacá**, Universidad de Minas Gerais, Brasil: doctoral student, co-supervision. 2017- 2022.  
**Project:** Hornwort diversification and symbiosis in the Neotropics
- **Adriel Sierra**, Instituto Nacional de Pesquisas da Amazonia, Brasil: master student, co-supervision. 2017- 2018.  
**Project:** Fragmentation in epiphyll diversity in the Amazon: a genomic approach

---

#### SELECTED INVITED SEMINARS in the last 10 years:

- 2022. Universidad de Panama, Panama
  - 2021. Smithsonian Tropical Research Institute, Panama
  - 2021. MADLAND, University of Marburg, Germany
  - 2021. Universidad Nacional de La Plata, Argentina
  - 2020. Universidad Militar de Nueva Granada, Colombia
  - 2020. Université de Québec en Abitibi-Témiscamingue, Canada
  - 2018. Concordia University, Montréal, Canada
  - 2018. Smithsonian Tropical Research Institute, Panama
  - 2018. Field Museum, Chicago, USA
  - 2018. Mer Bleue workshop, McGill University
  - 2017. University of Alberta, Canada.
  - 2017. Museum of Nature, Ottawa, Canada
  - 2017. Université de Montréal, Montréal, Canada
  - 2016. Duke University, USA
  - 2016. L'Institut de biologie intégrative et des systèmes. Université Laval
  - 2015. Université Laval, Canada
  - 2015. RBGE, Scotland
  - 2014. Instituto de Investigaciones Científicas (INDICASAT), Panama
  - 2014. Muséum National d'Histoire Naturelle, Paris, France
  - 2014. Eastern China Normal University, Shanghai, China
  - 2014. Smithsonian Tropical Research Institute, Panama
  - 2013. Department of Plant Sciences, University of Cambridge, UK
  - 2013. Department of Syst. Botany, University of Göttingen, Germany
-

## TEACHING EXPERIENCE

- Université Laval, Canada  
*Microbial Ecology* : April 2021, 2023
- Eagle Hill Institute, Maine, USA  
*Hornwort biology and systematics*: March 2021, 2022
- Université Laval, Canada  
*Biodiversity of Plants and Algae I*: Fall 2016-2022
- Smithsonian Tropical Research Institute, Panama  
*A 2-week intensive course on bryophyte taxonomy and evolution*: August 2017
- Smithsonian Tropical Research Institute, Panama  
*A class on symbiosis and bryophyte diversity*: February 2016
- Royal Botanic Garden, Edinburgh, Scotland  
*Bryology section of the master's program at RBGE*: February 2014, 2015.

---

## AD-HOC REVIEWER

**American Journal of Botany; Annals of Botany; Australian Journal of Systematic Botany; Biological Journal of the Linnean Society; Bryologist; Fieldiana; Frontiers in Plant Sciences; Journal of Biogeography; Journal of Bryology; Journal of Experimental Botany; Nature; Nova Hedwigia; Phytokeys; Phytotaxa; Plant and Cell Physiology; Proceedings of the Royal Society B; Systematics and Biodiversity.**

## SYMPOSIUM ORGANIZATION

- Co-organization of the symposium of the Canadian Society of Plant Biologists. June 2023.
- Chair of the conference entitled: “**Bryophytes, lichens, and northern ecosystems in a changing world**”. –July 6-9, 2021.
- Co-organization of the symposium entitled: “**Future Arctic: A global initiative on bryophyte and lichen Arctic research: from species to ecosystems**” Canada. Co-organizer: L. Rochefort– May 24-26, 2017.
- Co-organization of the symposium entitled: “**Biology, genomics and evolution on the complex thalloids, including *Marchantia***” RBGE, Scotland – July 14-15, 2015.
- Co-organization of the symposium entitled: “**Bryophyte biology, genomics and evolution on the occasion of the 200th anniversary of the Munich Herbarium**” Germany. Co-organizer: S.S. Renner – March 22 2013.

---

## INTERVIEWS

1. **TVN-2, Panama 2022**: [https://www.tvn-2.com/contenido-exclusivo/panameno-seleccionado-desarrollar-investigacion-canada\\_1\\_1000837.html](https://www.tvn-2.com/contenido-exclusivo/panameno-seleccionado-desarrollar-investigacion-canada_1_1000837.html)
2. **Telemetro Reporta, Panama 2021**: <https://www.youtube.com/watch?v=EFwyyp4bNSY>
3. **BBC mundo 2018**: <http://www.bbc.com/mundo/noticias-43811164>
4. **La Prensa, Panama 2018**: [https://www.prensa.com/impres/vivir/Hongos-plantas-misterios\\_0\\_5064993515.html](https://www.prensa.com/impres/vivir/Hongos-plantas-misterios_0_5064993515.html)

5. **La Prensa, Panama**, 2017: [https://www.prensa.com/impresa/panorama/Cientifico-panameno-seducido-Artico\\_0\\_5159484062.html](https://www.prensa.com/impresa/panorama/Cientifico-panameno-seducido-Artico_0_5159484062.html)

---

FIELD EXPERIENCE:

- Canada (Hudson Bay, James Bay, boreal forest and subarctic); Colombia (Nariño); Costa Rica; Dominican Republic; India (East and West Himalayas: Shimla and Darjeeling); Mexico; Panamá; USA (especially Southern Appalachians, California); Venezuela (Mérida); Germany (Hessen).

---

**Full publication list (72 publications).** Students and postdocs\*

1. Escolástico–Ortiz, D.A. \*, Charlotte Blasi, Jean-Philippe Bellenger and **J.C. Villarreal A.** Submitted. Differentially abundant bacteria drive the N<sub>2</sub>-fixation of a widespread moss in the forest-tundra transition zone. *Environmental Microbiology*
2. Escolástico–Ortiz, D.A. \*, Lars Hedenäs, Dietmar Quandt, Dörte Harpke, Juan Larraín, Michael Stech & **Juan Carlos Villarreal A.** 2023. Cryptic speciation shapes the biogeographic history of a northern distributed moss. *Botanical Journal of the Linnean Society* 201(1): 114-134.
3. Bell–Doyon, P. \*, V. Bellavance\*, L. Bélanger, M.J. Mazerolle, **J.C. Villarreal A.** 2022. Bacterial, Fungal, and Mycorrhizal Communities in the Soil Differ between Clearcuts and Insect Outbreaks in the Boreal Forest 50 Years after Disturbance. *Forest Ecology and Management* 523(1): 120493
4. Cargill D.C., Sahut Chantanaorrapint., Rui- Liang Zhu, AK. Asthana, Ian Li, Karen S. Renzaglia, **Juan Carlos Villarreal A.** 2022. Resolving relationships within the hornwort genus *Anthoceros*. *Bryophyte diversity and evolution*.
5. Peñaloza-Bojacá, G., Adriel M. Sierra\*, Hannes Becher, Karen S. Renzaglia, **Juan Carlos Villarreal A.** 2022. Historical Biogeography of the austral hornwort genus *Phaeomegaceros* (Dendrocerotaceae, Anthocerotophyta) *Bryophyte diversity and evolution*.
6. Claudio M. Monteza–Moreno, Lilisbeth Rodríguez–Castro\*, Pedro L. Castillo–Caballero, Edgar Toribio, Kristin Saltonstall. 2022. Arboreal camera trapping sheds light on seed dispersal of the world’s only epiphytic gymnosperm: *Zamia pseudoparasitica*. *Ecology and Evolution* 12(3): e8769.
7. Marta Alonso–García\*, Raquel Pino–Bodas, **Juan Carlos Villarreal A.** 2022. Co–dispersal of symbionts in the lichen *Cladonia stellaris* inferred from genomic data. *Fungal Ecology* 60 : 101165.
8. Jairo Patiño, Irene Bisang, Bernard Goffinet, Lars Hedenäs, Stuart McDaniel, Silvia Pressel, Michael Stech, Claudine Ah–Peng, Ariel Bergamini, Richard T Caners, D Christine Cargill, Nils Cronberg, Jeffrey Duckett, Sarah Eppley, Nicole J Fenton, Kirsten Fisher, Juana González–Mancebo, Mitsuyasu Hasebe, Jochen Heinrichs, Kristoffer Hylander, Michael S Ignatov, Javier Martínez–Abaigar, Nagore G Medina, Rafael Medina, Dietmar Quandt, Stefan A Rensing, Karen Renzaglia, Matthew Renner, Rosa M Ros, Alfons Schäfer–Verwimp, **J.C. Villarreal**, Alain Vanderpoorten. 2022. Unveiling the nature of a miniature world: a horizon scan of fundamental questions in bryology. *Journal of Bryology* 44(1): 1–34
9. Alonso, M.\* & **J.C. Villarreal.** 2022. Bacterial community of reindeer lichens differs between northern and southern lichen woodlands. *Canadian Journal of Forest Research* 52(5).

10. Breinholt, J.W., Sarah B. Carey, ...20 authors, **J.C. Villarreal**, Evelyn Webb Williams & J. Gordon Burleigh. 2021. A target enrichment probe set for resolving the flagellate plant tree of life. *Applications in Plant Sciences* 9(1) : e11406
10. Rahmatpour, N., D.A. Hauser, J.M. Nelson, P.Y. Chen, **J.C. Villarreal A.**, M.Y. Ho, F–W. Li. 2021. A novel thylakoidless isolate fills a billion year gap in the evolution of Cyanobacteria. **Current Biology** 31(13): 2587–2867. Cover of the journal.
11. Bell–Doyon\*, S.B. Selva & T. R. McMullin. 2021. Calicioid fungi and lichens from an unprotected intact forest ecosystem in Québec. *Écosciences* 28(2) : 127–136.
12. Alonso, M.\* , F. Grewe, S. Payette & **J.C. Villarreal**. 2021. Population genomics and genetic diversity of a reindeer lichen species in Eastern Canada lichen woodlands. *American Journal of Botany* 108(1) 159–171.
13. **Villarreal, A., J.C.**; M. Renaudin, A. Beaulieu–Laliberté\* & J.P. Bellenger. 2021. *Stigonema* associated with boreal *Stereocaulon* possesses the alternative vanadium nitrogenase. *The Lichenologist* 53 : 215–220
14. Alonso, M.\* , **J.C. Villarreal**, K. McFarland & B. Goffinet. 2020. Population genomics and phylogeography of a clonal bryophyte with spatially separated sexes and extreme sex ratios. *Frontiers in Plant Science* 11:495.
15. Frangedakis, E., M. Shimamura, **J.C. Villarreal**, F–W. Li, M. Tomaselli, M. Waller, K. Sakakibara, K. Renzaglia, P.Szövényi 2020. The Hornworts: Morphology, evolution and development. *The New Phytologist* 229: 735-754.
16. Bouchard, R.\* , G. Peñaloza–Bojacá\*, S. Toupin\*, Y. Guadalupe\*, J. Gudiño, N. Salazar, F.W. Li & **J. C. Villarreal A.** 2020. Contrasting bacteriome of the hornwort *Leiosporoceros dussii* in two nearby sites with emphasis on the hornwort–cyanobacterial symbiosis. *Symbiosis* 81: 39-52
17. Bell–Doyon, P.\* & **J.C. Villarreal A.** 2020. New Notes on the Ecology of the Epiphytic gymnosperm and Panamanian endemic *Zamia pseudoparasitica*. *Neotropical Naturalist* 2: 1–7
18. Lavoie, C.\* , M. Renaudin\*, R. Troy McMullin, J. Gagnon, C. Roy, M.–E. Beaulieu, J. P. Bellenger & **J. C. Villarreal A.** 2020. Extremely low genetic diversity of *Stigonema* associated with *Stereocaulon* in eastern Canada. *The Bryologist*, 123(2):188–203
19. Li, FW, .... (25 authors)...**J.C.Villarreal**, P. Szövényi. 2020. *Anthoceros* genomes illuminate the origin of land plants and the unique biology of hornworts. *Nature Plants* 6: 259–272.
20. T. Dawes\*, **J.C. Villarreal** , P. Szövényi, I. Bisang, F–W. Li, D.A. Hauser, D. Quandt, D.C. Cargill & L.L. Forrest. 2020. Molecular data shows a recent European origin of the model species *Anthoceros agrestis*. *Plant Systematic and Evolution* 306:49.
21. Bell–Doyon, P.\* , J. Laroche, K. Saltonstall, **J.C. Villarreal A.** 2020. Specialized bacteriome uncovered in the coralloid roots of the epiphytic gymnosperm, *Zamia pseudoparasitica*. *Environmental DNA* 2(4) : 418-428.
22. OneKP Initiative. A Phylogenomic View of Evolutionary Complexity in Green Plants. 2019. *Nature* 574: 679–685.
23. Peñaloza–Bojacá, G.\* , **J.C. Villarreal A.** and A. Silva. 2019. Phylogenetic and morphological circumscription of the genus *Dendroceros* Ness (Dendrocerotaceae; Anthocerotophyta), with the addition of two new subgenera. *Systematics and Biodiversity* 17:7, 712-727.
24. Bell, D.....23 authors, **J. C. Villarreal A.**... S. Graham. 2019. Organellomic datasets confirm a cryptic consensus on (unrooted) land–plant relationships, and provide new insights into bryophyte molecular evolution. *American Journal of Botany* 107(1): 91-115.



25. Nelson, J.M., D.A. Hauser, J.A. Gudiño, Y.A. Guadalupe\*, J.C. Meeks, N. Salazar, **J.C. Villarreal**, F.–W. Li. 2019. Complete genomes of symbiotic cyanobacteria clarify the evolution of vanadium nitrogenase. *Genome Biology and Evolution* 11 (7): 1959–1964, <https://doi.org/10.1093/gbe/evz137>
26. Garrido A., Jose Gudiño Ledezma, Armando A. Durant–Archibold, Noris Salazar Allen, **J.C. Villarreal A.**, and Mahabir P. Gupta. 2019. Chemical profiling of the gametophyte and sporophyte from the Panamanian hornwort *Leiosporoceros dussii* (Leiosporocerotaceae) by HSSPME–GC–MS. *Natural Products Communications* 14(8) : doi:10.1177/1934578X19868875
27. Sierra, A.M.\*, J. Bechteler, D. Cardoso D, C. Zartman & **J.C. Villarreal A.** 2018. Divergence time analyses suggest a Miocene origin of the narrow Amazonian endemic rheophytic *Ceratolejeunea temnantha* (Spruce) Reiner–Drehwald (Porellales, Lejeuneaceae). *Bryophyte Diversity and Evolution*. 40(2): 55–67.
28. Renzaglia, K.S., **J.C. Villarreal A.** & D. Garbary. 2018. Morphology supports the setaphyte hypothesis: mosses plus liverworts form a natural group. *Bryophyte Diversity and Evolution*. 40(2): 11–17.
29. **Villarreal, A., J.C.**, Monique Turmel; Maurane Bourgouin–Couture\*, Jérôme Laroche, Noris Salazar–Allen, Fay–Wei Li, Shifeng Cheng, Karen Renzaglia & Claude Lemieux. 2018. Genome wide organellar analyses from the hornwort *Leiosporoceros dussii* show low frequency of RNA editing. *Plos One*13(8): e0200491.
30. Lewis, L.R., Ickert–Bond, S., Biersma, E.M, Convey, P., Goffinet, B., Hassel, K., Kruijer, K., La Farge, C., Metzgar, J., Stech, M., **J.C. Villarreal**, McDaniel, S.F. 2017. Future directions and priorities for Arctic bryophyte research. *Arctic Science* 3: 475–497.
31. Lang, D., —**J.C. Villarreal**, —50 authors.2017. The *P. patens* chromosome–scale assembly reveals moss genome structure and evolution. *The Plant Journal* 93: 515–533.
32. Li, F.–W., **J.C. Villarreal**, Szövényi, P. 2017. Hornworts: an overlooked window into carbon concentrating mechanism. *Trends in Plant Science* 22(4): 275–277.
33. **Villarreal, J.C.**, Duckett, J.G., Pressel, S. 2017. Morphology, ultrastructure and phylogenetic affinities of the single–island endemic *Anthoceros cristatus* Steph.(Ascension Island). *Journal of Bryology* 39(3) :226–234, DOI: 10.1080/03736687.2017.1302153
34. Renzaglia, K.S., **J.C. Villarreal**, Piatkowsky, B.T., Reagan, J.L. & Merced, A. 2017. Hornwort stomata: architecture and fate shared with 400 million year old fossil plant without leaves. *Plant Physiology* 174(2) : 788–797. <https://doi.org/10.1104/pp.17.00156>
35. Long, D.G., Forrest, L.L., **J.C. Villarreal** & Crandall–Stotler. 2016. The genus *Aitichisoniella* Kashyap (Marchantiopsida, Cleveaceae) new to China, and its taxonomic placement. *Journal of Bryology* 38: 308–311.
36. Long, D.G., Forrest, L.L., **J.C. Villarreal** & Crandall–Stotler. 2016. Taxonomic changes in Marchantiaceae, Corsiniaceae and Cleveaceae (Marchantiidae, Marchantiophyta). *Phytotaxa* 252(1): 077–080.
37. **Villarreal, J.C.**, Crandall–Stotler, B.J., Hart, M.L., Long, D.G. & Forrest, L.L. 2016. Divergence times and the evolution of morphological complexity in an early land plant lineage (Marchantiopsida) with a slow molecular rate. *New Phytologist* 209(4):1734–46. doi: 10.1111/nph.13716
38. Söderström, L. —40 authors, **J.C. Villarreal**. 2016. World Checklist of hornworts and liverworts. *Phytokeys* 59: 1–828.
39. Chantanaorrapint, S., Penjor P & **J.C. Villarreal**. 2015. Taxonomic notes on *Phaeoceros himalayensis*, with the lectotypification of *Anthoceros himalayensis*. *Phytotaxa* 231(2): 193–196.

40. Forrest, L.L., D.G. Long, P.M. Hollingsworth, D.C. Cargill & **J.C. Villarreal**. 2015. On *Monocarpus* (Monocarpaceae, Marchantiopsida), an isolated salt-pan complex thalloid liverwort allied to the Sphaerocarpaceae. *Australian Systematic Botany* 28: 137–144.
41. Li, F.-W., M. Melkonian, C.J. Rothfels, **J.C. Villarreal**, D.W. Stevenson, S.W. Graham, G. K.-S. Wong, K.M. Pryer & S. Mathews. 2015. Phytochrome diversity in green plants and the origin of canonical plant phytochromes. *Nature Communications* 6: 7852  
doi:10.1038/ncomms8852.
42. **Villarreal, J.C.** & K. Renzaglia. 2015. The hornworts: important advancements in early land plant evolution. *Journal of Bryology* 37(3): 157–170.
43. **Villarreal, J.C.**, D.C. Cargill, A. Hagborg, L. Söderström & M. von Konrat. Notes on Early Land Plants. 61. 2015. Taxonomic changes in hornworts. *Phytotaxa* 208: 092–096.
44. Li, F.-W., M. Melkonian, C.J. Rothfels, **J.C. Villarreal**, D.W. Stevenson, S.W. Graham, G. K.-S. Wong, K.M. Pryer & S. Mathews. 2015. Origin and evolution of phototropins in plants. *Frontiers in Plant Sciences* 6: 637. <http://dx.doi.org/10.3389/fpls.2015.00637>
45. **Villarreal, J.C.**, N. Cusimano & S.S. Renner. 2015. Biogeography and diversification rates in hornworts – the limitations of diversification modeling. *Taxon* 64: 229–238.
46. Brown, R.C., B.E. Lemmon, M. Shimamura, **J.C. Villarreal** & K.S. Renzaglia. 2015. Spores of relictual bryophytes: diverse adaptations to life on land. *Review of Palaeobotany and Palinology* 216: 1–17.
47. Sustaita, D., C.L. Owen, **J.C. Villarreal** & M.A. Rubega. 2014. Morphometric tools for distinguishing between sexes of California populations of the loggerhead shrike. *Southwestern Naturalist* 59:560–567.
48. Wicket, N., —42 authors, D.W. Stevenson, **J.C. Villarreal**, J.A. Leebens-Mack. 2014. A phylotranscriptomics analysis of the origin and early diversification of land plants. *Proceedings of the National Academy of Sciences, USA*. 111 (45) E4859-E4868.  
<https://doi.org/10.1073/pnas.1323926111>
49. Mastasci, N., —40 authors, D.W. Stevenson, **J.C. Villarreal**, G.K. Wong. 2014. Data access for the 1000 (1KP) project. *Gigascience* 3:17.  
<http://www.gigasciencejournal.com/content/3/1/17>
50. Laenen, B., —**J.C. Villarreal**, —15 authors. Extant diversity of bryophytes emerged from successive post-Mesozoic diversification bursts. 2014. *Nature Communications*. 5: 6134.  
DOI: 10.1038/ncomms6134
51. Li, F.-W., **J.C. Villarreal**, —32 authors, D.W. Stevenson, K.M. Pryer. 2014. Horizontal gene transfer of a chimeric photoreceptor, neochrome, from bryophytes to ferns. *Proceedings of the National Academy of Sciences, USA* 111: 6672–6677, DOI: 10.1073/pnas.1319929111.
52. **Villarreal, J.C.**, L.L. Forrest, E. Cooper & D.G. Long. 2014. Phylogenetic affinities and conservation status of the liverwort *Telaranea murphyae* in Britain. *Journal of Bryology* 36: 191199.
53. **Villarreal, J.C.** & S.S. Renner. 2014. A review of molecular clock calibrations and substitution rates in liverworts, mosses, and hornworts, and a timeframe for a taxonomically cleaned-up genus *Nothoceros*. *Molecular Phylogenetics and Evolution* 78: 25–35.
54. **Villarreal, J.C.** & S.S. Renner. 2013. Correlates of monoicy and dioicy in hornworts, the apparent sister group to vascular plants. *BMC Evolutionary Biology* 13: 239.
55. Bainard, J. & **J.C. Villarreal**. 2013. Genome size increases in recently diverged hornwort clades. *Genome* 56: 431–435.

56. Desiró A., J.G. Duckett, S. Pressel, **J.C. Villarreal** & M. Bidartondo. 2013. Fungal symbioses in hornworts: A chequered story. *Proceedings of the Royal Society, B*. 280: 20130207.
57. **Villarreal, J.C.**, L.L. Forrest, N. Wickett & B. Goffinet. 2013. The plastid genome of the hornwort *Nothoceros aenigmaticus*: Phylogenetic signal in inverted repeat expansion, pseudogenization and intron gain. *American Journal of Botany* 100: 467–477.
58. **Villarreal, J.C.** & S.S. Renner. 2012. Hornwort pyrenoids: carbon-concentrating mechanisms evolved and were lost at least five times during the last 100 million years. *Proceedings of the National Academy of Sciences, USA* 109: 18873–18878. DOI: 10.1073/pnas.1213498109.
59. Johnson, M., —36 authors, **J.C. Villarreal**,— & K. Wong. 2012. Evaluating methods for isolating total RNA and predicting the success of sequencing phylogenetically diverse plant transcriptomes. *PLoS One* 7(11): e50226.
60. **Villarreal, J.C.**, L.L. Forrest, K. McFarland & B. Goffinet. 2012. Chloroplast, mitochondrial and nuclear microsatellites from the Southern Appalachian hornwort, *Nothoceros aenigmaticus* (Dendrocerotaceae). *American Journal of Botany* 99: e88–e90. DOI: 10.3732/ajb.1100392.
61. **Villarreal, J.C.**, L.V. Campos & B. Goffinet. 2012. Parallel evolution of endospory in hornworts: the case of *Nothoceros renzagliensis*, sp. nov. *Systematic Botany* 37: 31–37.
62. Garcia, C., C. Sergio, **J.C. Villarreal** & F. Lara. 2012. The genera *Dendroceros* Nees and *Megaceros* Campb. in São Tomé e Príncipe (Africa, Gulf of Guinea) and description of a new species, *Dendroceros paivae*. *Cryptogamie, Bryologie et Lichenologie* 33: 3–21.
63. Sérusiaux, E., **J.C. Villarreal**, T. Wheeler & B. Goffinet. 2011. Recent origin, active speciation and dispersal for the lichen genus *Nephroma* (Peltigerales) in Macaronesia. *Journal of Biogeography* 38: 1138–1151.
64. **Villarreal, J.C.**, D.C. Cargill, A. Hagborg, L. Söderström & K.S. Renzaglia. 2010. Hornwort diversity: Patterns, causes and future work. *Phytotaxa* 9: 150-166.
65. **Villarreal, J.C.**, B. Goffinet, R.J. Duff & D.C. Cargill. 2010. Phylogenetic delineation of the genera *Nothoceros* and *Megaceros*. *The Bryologist* 113: 106-113.
66. **Villarreal, J.C.**, B. Goffinet & D.C. Cargill. 2010. *Phaeomegaceros squamuliger* subspecies *hassellii* (Dendrocerotaceae, Anthocerotophyta), a new taxon from the Southern Hemisphere. *Nova Hedwigia* 91: 349-360.
67. Duff, R.J., **J.C. Villarreal**, D.C. Cargill & K.S. Renzaglia. 2007. Progress and challenges in developing a phylogeny and classification of the hornworts. *The Bryologist* 110: 214-243. 58.
68. **Villarreal, J.C.**, G. Hässel de Menéndez & N. Salazar Allen. 2007. *Nothoceros superbus* (Dendrocerotaceae), a new species of hornwort from the Neotropics. *The Bryologist* 110: 279-285.
69. **Villarreal, J.C.** & K.S. Renzaglia. 2006. Structure and development of *Nostoc* strands in *Leiosporoceros dussii* (Anthocerotophyta): a novel symbiosis in land plants. *American Journal of Botany* 93: 693-705. (Journal cover). DOI:10.3732/ajb.93.5.693
70. **Villarreal, J.C.** & K.S. Renzaglia. 2006. Sporophyte structure in the Neotropical hornwort *Phaeomegaceros fimbriatus*: implications for phylogeny, taxonomy and character evolution. *International Journal of Plant Sciences* 167: 413-427.
71. Dauphin, G., T. Pócs, **J.C. Villarreal** & N. Salazar Allen. 2006. Nuevos Registros de Hepáticas y Anthocerotófitas para Panamá. *Tropical Bryology* 27: 73-85.
72. Cargill, D.C., R.J. Duff, **J.C. Villarreal** & K.S. Renzaglia. 2005. Generic concepts in hornworts: historical review, contemporary insights and future directions. *Australian Systematic Botany* 18: 716.