



## Molecular biology of mosses

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The Editors are pleased to present a special issue on the molecular biology of mosses. When we received the proposal for the special issue, we first thought about how we would title it. Based on the research background of the editors, we thought about whether to include *Physcomitrium* (*Physcomitrella*), Bryophytes—mosses, liverworts, and hornworts—or more broadly flagellated plants, i.e., photosynthetic eukaryotes that have not lost (sperm) motility (see, iMOSS, international molecular moss science society iMOSS web page, <http://imoss.org>). Thanks to the huge efforts made by the plant community to gather data on the genome sequences and expressed genes in various plants, it is now no longer necessary to focus on only one type of a model plant to study. The moss, *Physcomitrium patens* began to attract attention in the late 1990s as a model for mosses and as the first bryophyte whose whole genome was revealed (Schaefer and Zryd 1997; Rensing et al. 2008). In the last decade, the liverwort, *Marchantia polymorpha*, has also attracted attention as an additional model, with the report of its genome sequence in 2017 (Bowman et al. 2017), and this plant is now being actively studied. Towards completion of the picture in bryophytes, last year, the genome of the hornwort was finally published (Zhang et al. 2020; Li et al. 2020). In addition to this, the genome sequences of

many more bryophytes are expected to be reported in the near future. Therefore, we decided to use the term "moss" for this special issue because it is broad enough not to limit the issue to articles dedicated only to *P. patens*, but excludes articles that would concern other bryophytes and flagellated plants, including charophytes, that would deserve more than a single special issue.

Including the two articles that have been already published in the May and June issue (Lyapina et al. 2021; Terada et al. 2021, respectively), we published a total of 16 articles in this special issue. This includes 4 review articles and 12 research articles. Of these, 11 articles used *P. patens*, and 5 articles included mosses besides *P. patens*, indicating that *P. patens* continues to be the most popular model for moss research. As a review in the field of development, Hata and Kyozyuka describe the developmental evolution of stem cell regulation, comparing stem cell research in *P. patens* and *A. thaliana* (Hata and Kyozyuka 2021). Bibeau et al. reviewed the current quantitative cell biology of *P. patens*, which combines cell biology and mathematical models (Bibeau et al. 2021). A comprehensive review of the hormone biosynthesis and signaling studies conducted in *P. patens* is provided by Guillory and Bonhomme (Guillory and Bonhomme 2021). Finally, Kume et al. provide a review of the hypergravity responses and experiments in space, focusing on the responses of *P. patens* and other mosses to extreme environmental conditions (Kume et al. 2021).

From the 12 research articles, three studies concern the developmental biology field, including the regulation by miR171-GRAS module of plant meristem formation in *P. patens* (Beheshti et al. 2021), the role of a subgroup of DEAD-box RNA helicases on both gametophytic and sporophytic development in *P. patens* (Perroud et al. 2021), and a study on the conserved function of VASCULAR RELATED NAC-DOMAIN transcription factors during secondary wall formation in the peat moss *Sphagnum palustre* (Terada et al. 2021). Further, Trogu et al. reported the results of a multiplex gene editing technique for seven *PHY* genes using Multiplex CRISPR-Cas9 mutagenesis (Trogu et al. 2020), and Furumizu and Sawa reported the molecular evolution

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of the subfamily X of Leucine-rich repeat receptor-like kinases using genomic information from a broad range of land plants, including hornworts, mosses and a liverwort (Furumizu and Sawa 2021). Studies on abiotic or biotic stress responses in *P. patens* include the functional analysis of the structural maintenance of chromosome protein complex, SMC5/6 complex, on DNA double strand break repair caused by genotoxic stress (Holá et al. 2021), the conserved and species-specific plant defense mechanisms to a fungal pathogen using a transcriptomic approach (Reboledo et al. 2021), and the comprehensive identification of small secreted peptides, some of which participate in immune responses such as to chitosan treatment (Lyapina et al. 2021). Ríos-Meléndez reported the results of physiological and transcriptomic analyses of the moss *Pseudocrossidium replicatum*, which has high desiccation tolerance (Ríos-Meléndez et al. 2021).

In addition, Utsunomiya et al. newly reported the proteins that play a critical role in chloroplast division (Utsunomiya et al. 2020), and Takahashi et al. reported the novel function of a pentatricopeptide repeat protein involved in chloroplast biogenesis (Takahashi et al. 2020). While the two studies were conducted using the *P. patens*, Sadamitsu et al. reported the complete chloroplast genome sequence of the moss *Takakia lepidozoides*, one of the earliest moss lineages, and found numerous cases of RNA editing in the plastid genome (Sadamitsu et al. 2021).

In addition to *P. patens*, molecular biological approaches to other moss species are steadily progressing and expanding. In the future, research to elucidate new functions and mechanisms of mosses will continue, with *P. patens* most likely leading the way as a model for mosses. The study of the divergent mosses, estimated to be about 13,000 species, will reveal the diversity of their environmental adaptability, new developmental mechanisms, and evolutionary significance. Research on biotechnological applications is also being conducted in *P. patens* as well as in other mosses, for example, as a plant factory to produce useful substances (Campos et al. 2020; Decker and Reski 2020). Hence, we expect to see a broad development of basic and applied sciences using mosses in the future.

A more comprehensive understanding of mosses will also allow for more detailed comparative studies with hornworts and liverworts (Frangedakis et al. 2021; Kohchi et al. 2021). Furthermore, research focusing on the various valuable secondary metabolites produced by bryophytes, which consist of about 20,000 species, will reveal more about the diversity and attractiveness of bryophytes as a whole (Horn et al. 2021). Such research will not only focus on bryophytes but will also advance our understanding of the differences and similarities between bryophytes and their sister groups, the charophytes and green algae. In turn, this research will help us to understand what changes have occurred in the process

of plant adaptation from aquatic to terrestrial environments and to what extent mosses and other terrestrial plants will be able to adapt to environments that will continue to change in the future.

Understanding the mechanisms of response and adaptation of land plants, including bryophytes, to the terrestrial environment is expected to significantly contribute to basic science and the discovery and application of new knowledge. We hope that the research on mosses in this special issue will be connected with research in other biological fields and contribute to the wisdom of humanity that will help ensure and maintain the stability of living organisms, including us humans, and the global ecosystem that surrounds them. In this way, we believe that moss and plant research are not unrelated to the problems of human society and all the living things and environments on earth.

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## References

- Beheshti H, Strotbek C, Arif MA, Klingl A, Top O, Frank W (2021) PpGRAS12 acts as a positive regulator of meristem formation in *Physcomitrium patens*. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01125-z>
- Bibeau JP, Galotto G, Wu M, Tüzel E, Vidali L (2021) Quantitative cell biology of tip growth in moss. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01147-7>
- Bowman JL, Kohchi T, Yamato KT, Jenkins J, Shu SQ, Ishizaki K, Yamaoka S, Nishihama R, Nakamura Y, Berger F, Adam C, Aki SS, Althoff F, Araki T, Arteaga-Vazquez MA, Balasubramanian S, Barry K, Bauer D, Boehm CR, Briginshaw L, Caballero-Perez J, Catarino B, Chen F, Chiyoda S, Chovatia M, Davies KM, Delmans M, Demura T, Dierschke T, Dolan L, Dorantes-Acosta AE, Eklund DM, Florent SN, Flores-Sandoval E, Fujiyama A, Fukuzawa H, Galik B, Grimaneli D, Grimwood J, Grossniklaus U, Hamada T, Haseloff J, Hetherington AJ, Higo A, Hirakawa Y, Hundley HN, Ikeda Y, Inoue K, Inoue SI, Ishida S, Jia QD, Kakita M, Kanazawa T, Kawai Y, Kawashima T, Kennedy M, Kinose K, Kinoshita T, Kohara Y, Koide E, Komatsu K, Kopsischke S, Kubo M, Kyozuka J, Lagercrantz U, Lin SS, Lindquist E, Lipzen AM, Lu CW, De Luna E, Martienssen RA, Minamino N, Mizutani M, Mochizuki N, Monte I, Mosher R, Nagasaki H, Nakagami H, Naramoto S, Nishitani K, Ohtani M, Okamoto T, Okumura M, Phillips J, Pollak B, Reinders A, Rovekamp M, Sano R, Sawa S, Schmid MW, Shirakawa M, Solano R, Spunde A, Suetsugu N, Sugano S, Sugiyama A, Sun

- R, Suzuki Y, Takenaka M, Takezawa D, Tomogane H, Tsuzuki M, Ueda T, Umeda M, Ward JM, Watanabe Y, Yazaki K, Yokoyama R, Yoshitake Y, Yotsui I, Zachgo S, Schmutz J (2017) Insights into land plant evolution garnered from the *Marchantia polymorpha* genome. *Cell* 171:287. <https://doi.org/10.1016/j.cell.2017.09.030>
- Campos ML, Prado GS, dos Santos VO, Nascimento LC, Dohms SM, da Cunha NB, Ramada MHS, Grossi-de-Sa MF, Dias SC (2020) Mosses: versatile plants for biotechnological applications. *Biotechnol Adv* 41:107533. <https://doi.org/10.1016/j.biotechadv.2020.107533>
- Decker EL, Reski R (2020) Mosses in biotechnology. *Curr Opin Biotechnol* 61:21–27. <https://doi.org/10.1016/j.copbio.2019.09.021>
- Frangedakis E, Waller M, Nishiyama T, Tsukaya H, Xu X, Yue Y, Tjahjadi M, Gunadi A, Van Eck J, Li F-W, Szóvényi P, Sakakibara K (2021) An agrobacterium-mediated stable transformation technique for the hornwort model *Anthoceros agrestis*. *New Phytol* 232:1488–1505. <https://doi.org/10.1111/nph.17524>
- Furumizu C, Sawa S (2021) Insight into early diversification of leucine-rich repeat receptor-like kinases provided by the sequenced moss and hornwort genomes. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-020-01100-0>
- Guillory A, Bonhomme S (2021) Phytohormone biosynthesis and signaling pathways of mosses. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01172-6>
- Hata Y, Kyozuka J (2021) Fundamental mechanisms of the stem cell regulation in land plants: lesson from shoot apical cells in bryophytes. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01126-y>
- Holá M, Vágnerová R, Angelis KJ (2021) Kleisin NSE4 of the SMC5/6 complex is necessary for DNA double strand break repair, but not for recovery from DNA damage in *Physcomitrella* (*Physcomitrium patens*). *Plant Mol Biol*. <https://doi.org/10.1007/s11103-020-01115-7>
- Horn A, Pascal A, Lončarević I, Volpatto Marques R, Lu Y, Miguel S, Bourgaud F, Thorsteinsdóttir M, Cronberg N, Becker JD, Reski R, Simonsen HT (2021) Natural products from bryophytes: from basic biology to biotechnological applications. *Crit Rev Plant Sci* 40:191–217. <https://doi.org/10.1080/07352689.2021.1911034>
- Kohchi T, Yamato KT, Ishizaki K, Yamaoka S, Nishihama R (2021) Development and molecular genetics of *Marchantia polymorpha*. *Annu Rev Plant Biol* 72:677–702. <https://doi.org/10.1146/annurev-arplant-082520-094256>
- Kume A, Kamachi H, Onoda Y, Hanba YT, Hiwatashi Y, Karahara I, Fujita T (2021) How plants grow under gravity conditions besides 1 g: perspectives from hypergravity and space experiments that employ bryophytes as a model organism. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01146-8>
- Li FW, Nishiyama T, Waller M, Frangedakis E, Keller J, Li Z, Fernandez-Pozo N, Barker MS, Bennett T, Blazquez MA, Cheng SF, Cumming AC, de Vries J, de Vries S, Delaux PM, Diop IS, Harrison CJ, Hauser D, Hernandez-Garcia J, Kirbis A, Meeks JC, Monte I, Mutte SK, Neubauer A, Quandt D, Robison T, Shimamura M, Rensing SA, Villarreal JC, Weijers D, Wicke S, Wong GKS, Sakakibara K, Szovenyi P (2020) *Anthoceros* genomes illuminate the origin of land plants and the unique biology of hornworts. *Nat Plants* 6:259–272. <https://doi.org/10.1038/s41477-020-0618-2>
- Lyapina I, Filippova A, Kovalchuk S, Ziganshin R, Mamaeva A, Lazarev V, Latsis I, Mikhalchik E, Panasenko O, Ivanov O, Ivanov V, Fesenko I (2021) Possible role of small secreted peptides (SSPs) in immune signaling in bryophytes. *Plant Mol Biol* 106:123–143. <https://doi.org/10.1007/s11103-021-01133-z>
- Perroud P-F, Demko V, Eugene Ako A, Khanal R, Bokor B, Pavlovič A, Jásik J, Johansen W (2021) The nuclear GUCT domain-containing DEAD-box RNA helicases govern gametophytic and sporophytic development in *Physcomitrium patens*. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01152-w>
- Reboledo G, Agorio A, Vignale L, Alberto Batista-García R, De León IP (2021) Transcriptional profiling reveals conserved and species-specific plant defense responses during the interaction of *Physcomitrium patens* with *Botrytis cinerea*. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01116-0>
- Rensing SA, Lang D, Zimmer AD, Terry A, Salamov A, Shapiro H, Nishiyama T, Perroud P-F, Lindquist EA, Kamisugi Y, Tanahashi T, Sakakibara K, Fujita T, Oishi K, Shin-I T, Kuroki Y, Toyoda A, Suzuki Y, Hashimoto S-I, Yamaguchi K, Sugano S, Kohara Y, Fujiyama A, Anterola A, Aoki S, Ashton N, Barbazuk WB, Barker E, Bennetzen JL, Blankenship R, Hyun Cho S, Dutcher SK, Estelle M, Fawcett JA, Gundlach H, Hanada K, Heyl A, Hicks KA, Hughes J, Lohr M, Mayer K, Melkozernov A, Murata T, Nelson DR, Pils B, Prigge M, Reiss B, Renner T, Rombauts S, Rushton PJ, Sanderfoot A, Schween G, Shiu S-H, Stueber K, Theodoulou FL, Tu H, Van de Peer Y, Verrier PJ, Waters E, Wood A, Yang L, Cove D, Cumming AC, Hasebe M, Lucas S, Mishler BD, Reski R, Grigoriev IV, Quatrano RS, Boore JL (2008) The *physcomitrella* genome reveals evolutionary insights into the conquest of land by plants. *Science* 319:64. <https://doi.org/10.1126/science.1150646>
- Ríos-Meléndez S, Valadez-Hernández E, Delgado C, Luna-Guevara ML, Martínez-Núñez MA, Sánchez-Pérez M, Martínez-y-Pérez JL, Arroyo-Becerra A, Cárdenas L, Bibbins-Martínez M, Maldonado-Mendoza IE, Angel Villalobos-López M (2021) *Pseudocrossidium replicatum* (Taylor) R.H. Zander is a fully desiccation-tolerant moss that expresses an inducible molecular mechanism in response to severe abiotic stress. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01167-3>
- Sadamitsu A, Inoue Y, Sakakibara K, Tsubota H, Yamaguchi T, Deguchi H, Nishiyama T, Shimamura M (2021) The complete plastid genome sequence of the enigmatic moss, *Takakia lepidozoioides* (Takakiopsisida, Bryophyta): evolutionary perspectives on the largest collection of genes in mosses and the intensive RNA editing. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-021-01214-z>
- Schaefer DG, Zryd JP (1997) Efficient gene targeting in the moss *Physcomitrella patens*. *Plant J* 11:1195–1206. <https://doi.org/10.1046/j.1365-313X.1997.11061195.x>
- Takahashi A, Sugita C, Ichinose M, Sugita M (2020) Moss PPR-SMR protein PpPPR\_64 influences the expression of a *psaA-psaB-rps14* gene cluster and processing of the 23S–4.5S rRNA precursor in chloroplasts. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-020-01090-z>
- Terada S, Kubo M, Akiyoshi N, Sano R, Nomura T, Sawa S, Ohtani M, Demura T (2021) Expression of peat moss VASCULAR RELATED NAC-DOMAIN homologs in *Nicotiana benthamiana* leaf cells induces ectopic secondary wall formation. *Plant Mol Biol* 106:309–317. <https://doi.org/10.1007/s11103-021-01148-6>
- Trogu S, Ermert AL, Stahl F, Nogué F, Gans T, Hughes J (2020) Multiplex CRISPR-Cas9 mutagenesis of the phytochrome gene family in *Physcomitrium* (*Physcomitrella*) *patens*. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-020-01103-x>
- Utsunomiya H, Saiki N, Kadoguchi H, Fukudome M, Hashimoto S, Ueda M, Takechi K, Takano H (2020) Genes encoding lipid II flippase MurJ and peptidoglycan hydrolases are required for chloroplast division in the moss *Physcomitrella patens*. *Plant Mol Biol*. <https://doi.org/10.1007/s11103-020-01081-0>
- Zhang J, Fu XX, Li RQ, Zhao X, Liu Y, Li MH, Zwaenepoel A, Ma H, Goffinet B, Guan YL, Xue JY, Liao YY, Wang QF, Wang QH, Wang JY, Zhang GQ, Wang ZW, Jia Y, Wang MZ, Dong SS, Yang JF, Jiao YN, Guo YL, Kong HZ, Lu AM, Yang HM, Zhang SZ, Van de Peer Y, Liu ZJ, Chen ZD (2020) The hornwort genome and early land plant evolution. *Nat Plants* 6:107–118. <https://doi.org/10.1038/s41477-019-0588-4>