

**EAST ASIAN-EASTERN NORTH AMERICAN DISJUNCTION
IN THE *ONOCLEA SENSIBILIS* SPECIES COMPLEX:
VICARIANCE OR PERIPATRY?**

K. Berry

Science Department, Hoehne Re-3 School District, Hoehne, CO, U.S.A., keith.berry@hoehnesd.org

**ВОСТОЧНО-АЗИАТСКАЯ – ВОСТОЧНО-СЕВЕРОАМЕРИКАНСКАЯ
ДИЗЪЮНКЦИЯ В ВИДОВОМ КОМПЛЕКСЕ *ONOCLEA SENSIBILIS*:
ВИКАРИАНТНОСТЬ ИЛИ ПЕРИПАТРИЯ?**

К. Бэрри

Департамент науки, Школьный округ Хёне Ре-3, Хёне, Колорадо, США, keith.berry@hoehnesd.org

Abstract. Disjunction between East Asian and eastern North American plants has been recognized since the time of Darwin. Although there is considerable evidence for congruent vicariance associated with late Neogene/Quaternary cooling among angiosperms, similar studies among specific fern families (e.g., Osmundaceae Martinov) have appeared incongruous with this pattern. Pteridologists continue to debate whether long-distance dispersal of wind-blown spores could have produced intercontinental disjunctions among ferns. To date, however, state-of-the-art historical biogeographical approaches have not been applied to this problem. In this investigation, multiple chloroplast gene (*rbcL*, *atpA*, *atpB*, and *matK*) sequences for ferns in the family Onocleaceae Pic. Serm. are drawn from GenBank, including those from the recently sequenced chloroplast genome of the East Asian fern *O. sensibilis* L. var. *interrupta* Maxim., and used to create molecular phylogenies using Bayesian (BEAUTi and BEAST) techniques. Using contemporary approaches for relaxed molecular clock divergence time estimation with fossil calibration, divergence time estimates for East Asian and eastern North American populations in the *Onoclea sensibilis* species complex are consistently reconstructed as the Pliocene (ca. 5 – 3.4 Ma), and the best-fitting historical biogeographic model is a DIVA-like (exclusively vicariant) model using BIOGEOBEARS in RASP4, with a low probability of peripatry. Accordingly, these molecular and fossil data appear congruent with the pattern observed among angiosperms, despite the propensity for long-distance dispersal of wind-blown spores in pteridophytes. The lack of evidence for peripatry in this lineage may be related to the presence of short-lived green spores in onocleoid ferns; however, this hypothesis requires further investigation.

Keywords: ferns, biogeography, *Onoclea sensibilis*, vicariance, peripatry, disjunction

INTRODUCTION

Beginning with Asa Gray (1859, 1878), numerous botanists have puzzled over the pattern of disjunction between East Asian and eastern North American floras (Li, 1952; Barrington, 1993; Kato, 1993; Xiang et al., 2000; Wolf et al., 2001; Moran, 2008; Xiang et al., 2015; Li et al., 2016). Using ribulose 1, 5-biphosphate carboxylase/oxygenase large subunit (*rbcL*) gene sequences for reconstruction of angiosperm phylogeny and molecular clock divergence time estimation coupled with fossil calibration, Xiang et al. (2000) concluded that congruent vicariance associated with climatic cooling during the late Neogene and Quaternary was the best explanation for disjunction between East Asian and eastern North American angiosperms. Among those ferns first described by Gray (1859) as exhibiting an East Asian-eastern North American disjunction were varieties of *Osmunda cinnamomea* L. and *Onoclea sensibilis* L. (Li, 1952). Although it is postulated that climatic cooling during the late Neogene and Quaternary was also responsible for vicariance in *O. sensibilis*, long-distance dispersal by wind-blown spores has not yet been ruled out (Barrington, 1993; Kato, 1993; Wolf et al., 2001; Xiang et al., 2015). Moreover, preliminary investigations within specific fern clades, such as Osmundaceae Martinov, using similar *rbcL* and fossil evidence have suggested that the East Asian-eastern North American disjunctions in *O. cinnamomea* and *O. claytoniana* L. (syn. *Claytosmunda claytoniana* (L.) Metzgar et Rouhan) were incongruent with the pattern observed among angiosperm

lineages, as separate episodes of evolutionary divergence coupled with biogeographic disjunction have been dated to the Paleogene rather than the late Neogene/Quaternary: 35 Ma (Eocene) and 25 Ma (Oligocene), respectively (Yatabe et al., 1999). Furthermore, intercontinental disjunctions among fern species are frequently explained by long-distance dispersal of wind-blown spores rather than by vicariance (Wolf et al., 2001; Sessa et al., 2017).

The chloroplast genome of East Asian *Onoclea sensibilis* var. *interrupta* Maxim. was recently sequenced by Du et al. (2021). Therefore, it is now possible to more accurately test the vicariance hypothesis in the *O. sensibilis* species complex using a variety of chloroplast genes coupled with fossil calibration on relaxed molecular clock divergence time estimates. In this investigation, the fossil record of *O. sensibilis* is compared to this chloroplast gene-based phylogeny and subjected to Biogeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts (BIOGEOBEARS; Matzke, 2014) in Reconstruct Ancestral State in Phylogenies v. 4 (RASP4; Yu et al., 2020) to determine the best-fitting historical biogeographic model, either vicariance or peripatry following the procedures outlined by Matzke (2014) (see also Sessa et al., 2017).

MATERIAL AND METHODS

Multiple chloroplast gene sequences, including *rbcL*, ATP synthase alpha and beta chains (*atpA*, *atpB*), and maturase K (*matK*), were drawn from GenBank to form a concatenated dataset. Sequences were aligned using Muscle v. 3.8.31 (Edgar, 2004) and subsequently manually checked for alignment. GenBank-to-Tree Analysis Using New Technology (GB-to-TNT; Goloboff et al., 2012, 2016) was used to create FASTA files, which were uploaded into Bayesian Evolutionary Analysis Utility (BEAUTi) and Bayesian Evolutionary Analysis Sampling Trees (BEAST), v. 2.6.5 (Bouckaert et al., 2019). In accordance with contemporary studies of so-called “living fossils” of ferns and other vascular plants, such as Wood et al. (2020) and Du et al. (2021), the following priors were established in BEAUTi: a lognormal relaxed molecular clock with GTR + I + G model of nucleotide substitution with four rate categories and a birth-death speciation prior. As in the recent study on fern phylogeny by Du et al. (2021), a log normal age distribution of the stem node of *Onoclea* was set at 56 Ma (late Paleocene), the age of the oldest, best preserved fossils attributed to the *O. sensibilis* lineage (Rothwell, Stockey, 1991). As there are different opinions regarding the first appearance of the *O. sensibilis* lineage, however, a separate analysis was run with an offset of 83.6 Ma (the Santonian/Campanian boundary), when fossils attributed to *O. sensibilis* first appear in both the fossil record of North America and Asia (Lloyd, 1971; Vakhrameev, 1991). Following a few preliminary runs with an MCMC chain length of 10,000,000 (10% burn-in), TRACER v. 1.7.2 (Rambaut, 2018) was used to refine the analysis and to evaluate convergence. For the final analyses, MCMC chain lengths of 20,000,000 (10% burn-in) were used, as convergence was observed.

Following specification of these priors in BEAUTi, BEAST was run, and two maximum clade credibility trees (one for each stem age prior) were reconstructed using TreeAnnotator v. 2.6.4 (Rambaut, Drummond, 2021). Upon reviewing the results in Tracer v. 1.7.2 to confirm convergence, a burn-in of 50% of the trees with a posterior probability of 0.95 was selected along with node heights. Although a less stringent criterion for maximum clade credibility construction could have been selected on the basis of Tracer results, this more stringent criterion ensured that only trees with convergent results were considered in construction of the maximum clade credibility tree. Maximum clade credibility trees were analyzed using TreeView v. 1.4.4. (Rambaut, 2018), and node labels and the 95% highest posterior density (HPD) intervals were applied to the nodes. Continental distributions for terminal taxa were coded as follows: (A) North America, (B) Europe, and (C) Asia.

BEAST trees were uploaded into the program RASP4 (Yu et al., 2010, 2015, 2020) to use BIOGEOBEARS (Matzke, 2014) to find the best-fitting historical biogeographic model. This was done by following procedures outlined by Matzke (2014) and Sessa et al. (2017), such as by selecting the model with the highest weight for the Akaike Information Criterion for small samples (AICc) and by conducting a Likelihood Ratio Test (LRT) for determining whether the null hypothesis that historical biogeographic models that are exclusively vicariant (e.g., DIVA-like) or peripatry-accommodating (e.g., DIVA-like + J) conferred equal likelihoods on the data.

Morphological characters were mapped to the molecular phylogeny generated in this study using parsimony in Mesquite v. 3.61 (Maddison, Maddison, 2008). Morphological character states were drawn from Gastony and Ungerer (1997) and Xing and Kato (2013) and verified by comparison with specimens in the United States National Herbarium (USNH), Pteridophyte Collections Consortium (PCC), and

the study conducted by Rothwell and Stockey (1991) on fossils attributed to *O. sensibilis* from the early Paleogene.

DATA AND RESULTS

Regardless of whether a 56 Ma (late Paleocene) age prior or an 83.6 Ma (early Campanian) age prior was used for stem *Onoclea*, BEAST trees converged on a crown node age from slightly less than ~3.5 Ma (mid to late Pliocene) (ESS > 1,000) to an age of ~5 Ma (early Pliocene) (ESS > 1,000), respectively (Fig. 1). According to BIOGEOBEARS (Fig. 2), the best-fitting model was the DIVA-like (exclusively vicariant) model (AICc = 0.53), as opposed to DIVA-like + J (peripatry-accommodating) model (AICc = 0.005) and other models, such as Dispersal-Extinction Cladogenesis (DEC) and DEC + J models. As the test statistic for the Likelihood Ratio Test (LRT) was 0.73 and the p-value 0.39, however, these values were insufficient to reject the null hypothesis that the DIVA-like (exclusively vicariant) and DIVA-like + J (peripatry-accommodating) models conferred equal likelihoods on the data. With regard to the *O. sensibilis* crown node, however, the probability of vicariance being responsible for the East Asian-eastern North American disjunction in *O. sensibilis* was high in both the DIVA-like and DIVA-like + J models (P = 1 and P = 0.92, respectively, with an average P = 0.96). Accordingly, vicariance is more likely than peripatry to have been responsible for divergence between *O. sensibilis* and *O. sensibilis* var. *interrupta*.

Mapping morphological characters to the molecular phylogeny revealed that *O. sensibilis* var. *interrupta* evolved fertile pinnae nearly equal to length to sterile pinnae independently of the outgroup taxon, *Pentarhizidium orientale* (Hook.) Hayata. These patterns of character evolution are illustrated in Figure 3. The best preserved fossils of *O. sensibilis* from western North America exhibit fertile pinnae much shorter than the sterile pinnae, which is reconstructed as plesiomorphic for the *O. sensibilis* lineage.

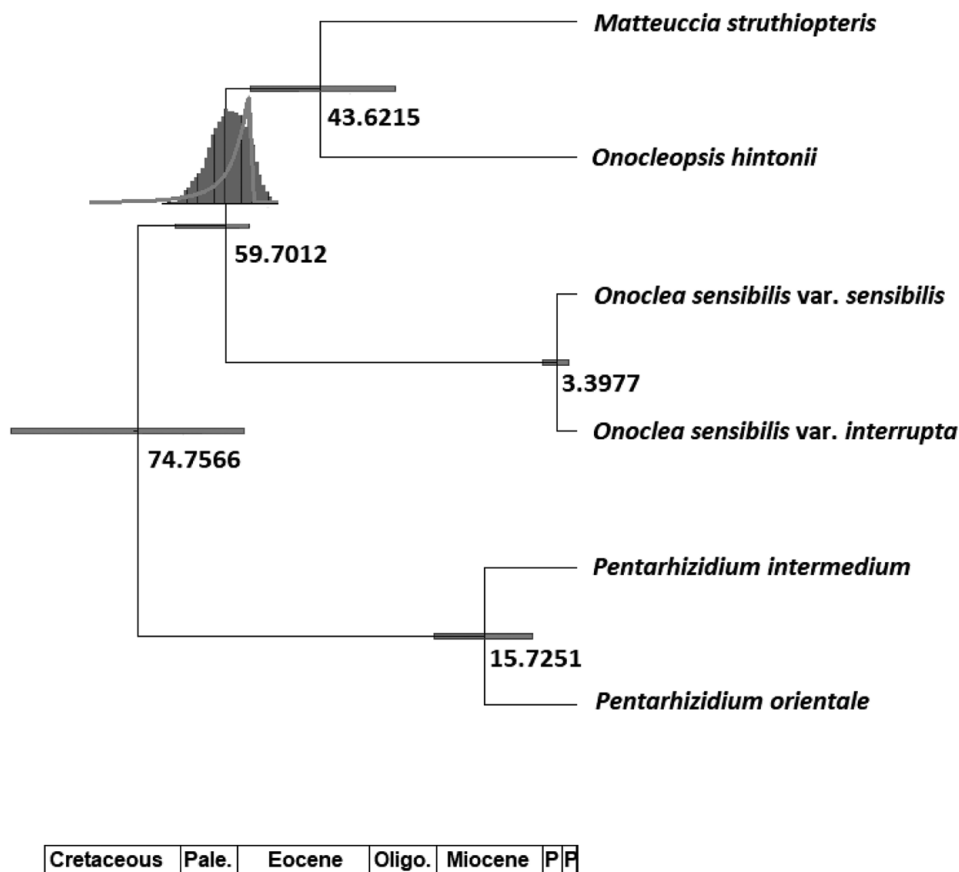


Figure 1. Chloroplast gene-based phylogeny with divergence time estimates mapped to nodes. Note prior and posterior age distribution for the stem node of *Onoclea sensibilis*, which was estimated to be 56 Ma on the basis of well-preserved *O. sensibilis* fossils (Rothwell, Stockey, 1991; Du et al. 2021). Divergence time estimates were calibrated with fossils described in the text, such as the best preserved *O. sensibilis* fossils used to calibrate the stem node (probability distribution), as in Du et al. (2021), and the youngest *O. sensibilis* fossils from the vicinity of Beringia (Wolfe, Tanai, 1980; Fletcher et al., 2021).

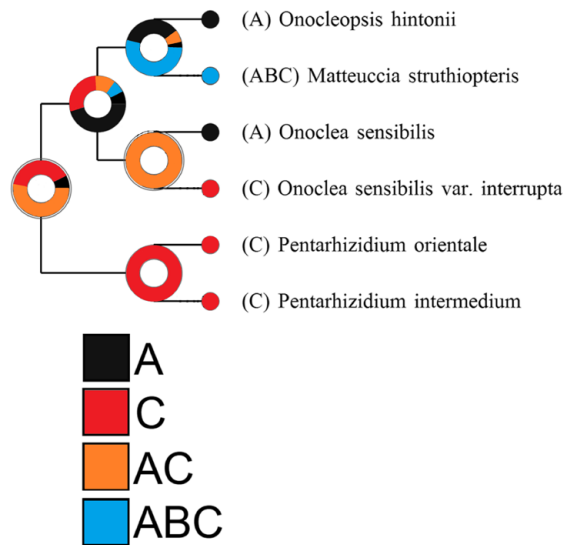


Figure 2. Results of the best-fitting historical biogeographic model based on results from BIOGEOBEARS in RASP4. Vicariance between *O. sensibilis* and *O. sensibilis* var. *interrupta* is reconstructed as having occurred during the Pliocene (Fig. 1).

DISCUSSION

Although it is widely accepted that vicariance associated with climatic cooling during the late Neogene and Quaternary was responsible for the East Asian-eastern North American disjunction among angiosperms on the basis of combined molecular and fossil datasets (Xiang et al., 2000), this hypothesis has garnered less support among pteridologists on the basis of divergence time estimates in Osmundaceae, as disjunction in *O. cinnamomea* and *O. claytoniana* has been dated to the Paleogene rather than the Neogene/Quaternary (Yatabe et al., 1999). Considering that East Asian-eastern North American disjunction in *O. cinnamomea* was among the first examples identified by Gray (1859, 1878), the observation that evolutionary divergence in this lineage has not been dated to the same period as the angiosperms leads one to question whether the causes of disjunction among ferns and angiosperms are ascribable to the same phenomena. This is particularly the case given the fact that pteridophytes demonstrate a propensity for long-distance dispersal of wind-blown spores (Wolf et al., 2001).

The results of this investigation lend support to the concept that climatic cooling associated with vicariance contributed to the pattern of East Asian-eastern North American disjunction observed in the *Onoclea sensibilis* species complex, another example first identified by Gray (1859, 1878). Fossil evidence, which was not incorporated into the BEAUTi and BEAST prior specifications, lend additional support to this hypothesis. First, fossils of *O. sensibilis* are known from mid-Miocene strata in the vicinity of Beringia, but not from the Miocene/Pliocene boundary strata from the same region (Wolfe, Tanai, 1980; Fletcher et al., 2021). Second, fossils attributed to *O. sensibilis* var. *interrupta* are recognized from the Pleistocene of Japan (Yamakawa, Konishi, 2013). Therefore, the fossil record appears to bolster the results of this investigation, which suggests divergence in the *O. sensibilis* species complex occurred near the Miocene/Pliocene transition, when *O. sensibilis* was either scarce or absent from the vicinity of Beringia (Figs. 1, 3), the terrestrial connection between East Asia and North America. Both ~5 Ma and ~3.3 Ma represent episodes of significant global climatic cooling in the Pliocene, particularly in the Northern Hemisphere (Xiang et al., 2000; Balantine et al., 2006; Dolan et al., 2015; De la Vega et al., 2020). However, it is important to acknowledge that temporal correlation does not necessarily imply causation.

Among the more salient criticisms historically leveled at DIVA or DIVA-like historical biogeographic models is that dispersal is penalized a priori, which tends to bias the results toward vicariance rather than peripatry (Lieberman, 2000); however, this criticism has been accommodated by development of the DIVA-like + J and similar classes of peripatry-accommodating models (Matzke, 2014). As long-distance dispersal and peripatry have been well supported by other recent investigations using BIOGEOBEARS (Sessa et al., 2017), the results of this historical biogeographic analysis appear to support the conclusion that vicariance is more likely than peripatry to explain disjunction in the *Onoclea sensibilis* species complex.

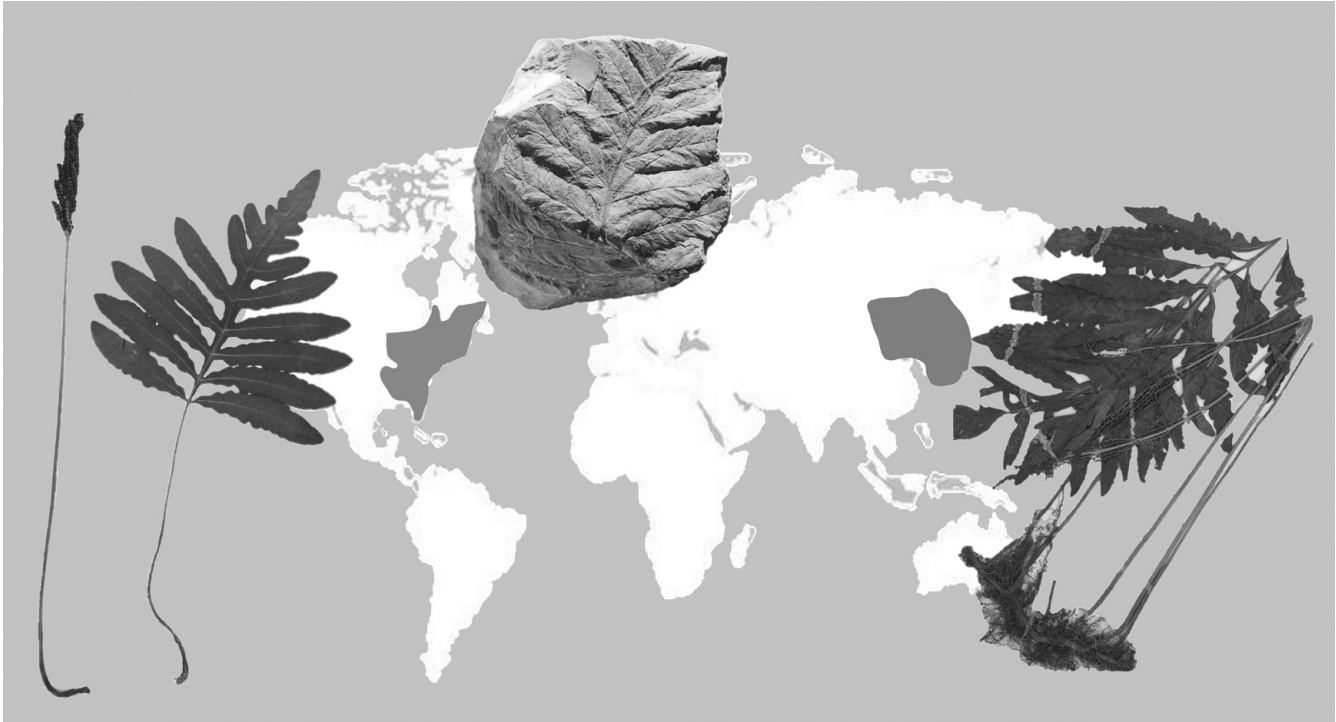


Figure 3. The biogeographic distribution of *Onoclea sensibilis* L., with East Asian and eastern North American varieties. Specimens of *Onoclea sensibilis* var. *sensibilis* (left: Southwest Missouri State University 89556) and *O. sensibilis* var. *interrupta* (right: Chicago Field Museum 1534245). Images courtesy of Pteridophyte Collections Consortium (PCC 2021), CC-by-NC. *O. sensibilis* fossil (NMNH P-45), which is found in both western North America and in the vicinity of Beringia, is illustrated above. Note the differences in dimensions of fertile vs. sterile pinnae, which were mapped to the molecular phylogeny using Mesquite v.3.61.

An additional consideration that may be important to note is the fact that *Onoclea sensibilis* and other onocleoid ferns exhibit short-lived, green spores (Lloyd, Klekowski, 1970). Short-lived, chlorophyllous spores are presumed to preclude long-distance dispersal of wind-blown spores (Mountier et al., 2018). Accordingly, long-distance dispersal by wind-blown spores seems a less likely explanation for evolutionary divergence than vicariance in this instance; however, this hypothesis requires further investigation.

CONCLUSION

Although it is well established that vicariance is the best explanation for the East Asian-eastern North American disjunction among angiosperms, this hypothesis has garnered less support among fern studies. With respect to the ferns first identified by Asa Gray as exhibiting an East Asian-eastern North American disjunction, *Onoclea sensibilis* is regarded to be the most likely to conform to this pattern on the basis of fossil evidence. The results of this investigation support this hypothesis, as vicariance is the best-fitting historical biogeographic model to account for molecular and morphological divergence between extant species. Relaxed molecular clock dating places vicariance in the Pliocene, a pattern that agrees with the fossil record of this group. Accordingly, the pattern of disjunction observed in the *O. sensibilis* species complex is congruent with that observed among angiosperms, suggesting that climatic cooling during the late Neogene/Quaternary underlies the East Asian-eastern North American disjunction in vascular plants.

ACKNOWLEDGMENTS

I would like to thank the editor, Lena Golovneva, for assistance in improving the manuscript and figures. I would also like to thank two anonymous reviewers for their helpful suggestions. There are no funding sources to report, and I declare no conflicts of interest.

REFERENCES

- Ballantine, A. P., Rybczynski, N., Baker, P. A., Harrington, C. R., White, D. 2006. Pliocene Arctic temperature constraints from the growth rings and isotopic composition of fossil larch. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 188–200. <https://doi.org/10.1016/j.palaeo.2006.05.016>
- Barrington, D. S. 1993. Ecological and historical factors in fern biogeography. – *Journal of Biogeography*, 20: 275–279. <https://doi.org/10.2307/2845635>
- Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchéne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Poppinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M. A., Wu, C.-H., Xie, D., Zhang, C., Stadler, T., Drummond, A. J. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. – *PLoS Computational Biology*, 15: 1–28.
- De la Vega, E., Chalk, T. B., Wilson, P. A., Bysani, R. P., Foster, G. L. 2020. Atmospheric CO₂ during the mid-Piacenzian warm period. – *Nature Scientific Reports*, 10: 1–8. <https://doi.org/10.1038/s41598-020-67154-8>
- Dolan, A. M., Haywood, A. M., Hunter, S. J., Tindall, D. J., Pickering, S. J. 2015. Modelling the enigmatic late Pliocene glacial event – marine isotope stage M2. – *Global and Planetary Change*, 128: 47–60.
- Du, X.-Y., Lu, J.-M., Zhang, L.-B., Wen, J., Kuo, L.-Y., Mynssen, C. M., Schneider, H., Li, D.-Z. 2021. Simultaneous diversification of Polypodiales and angiosperms in the Mesozoic. – *Cladistics*, 37: 1–22. <https://doi.org/10.1111/cla.12457>
- Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. – *Nucleic Acids Research*, 32: 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Fletcher, T. L., Telka, A., Rybczynski, N., Matthews, J. V., Jr. 2021. Neogene and early Pleistocene flora from Alaska, USA and Arctic/Subarctic Canada: new data, intercontinental comparisons and correlations. – *Palaeontologia Electronica*, 21: 1–62. <https://doi.org/10.26879/1121>
- Gastony, G. J., Ungerer, M. C. 1997. Molecular systematics and a revised taxonomy of the onocleoid ferns (Dryopteridaceae: Onocleaceae). – *American Journal of Botany*, 84: 840–849. <https://doi.org/10.2307/2445820>
- Goloboff, P. A., Catalano, S. A. 2012. GB-to-TNT: facilitating creation of matrices from GenBank and diagnosis of results in TNT. – *Cladistics*, 28: 503–513. <https://doi.org/10.1111/j.1096-0031.2012.00400.x>
- Goloboff, P. A., Catalano, S. A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. – *Cladistics*, 32: 221–238. <https://doi.org/10.1111/cla.12160>
- Gray, A. 1859. Diagnostic characters of new species of phanogamous plants collected in Japan by Charles Wright, botanist of the U.S. North Pacific Exploring Expedition, with observations upon the relations of the Japanese flora to that of North America, and of other parts of the north temperate zone. – *Memorial of American Academy of Arts and Sciences, Nature Sciences*, 6: 377–453. <https://doi.org/10.2307/25057953>
- Gray, A. 1878. Forest geography and archaeology, a lecture delivered before the Harvard University Natural History Society. – *American Journal of Science and Arts*, 16: 85–94, 183–196. <https://doi.org/10.2475/ajs.s3-16.93.183>
- Kato, M. 1993. Biogeography of ferns: dispersal and vicariance. – *Journal of Biogeography*, 20: 265–274. <https://doi.org/10.2307/2845634>
- Li, C., Lu, S., Ma, J., Gai, Y., Yang, Q. 2016. Phylogeographic history of the woodwardioid ferns, including species from Himalaya. – *Palaeoworld*, 25: 318–324. <https://doi.org/10.1016/j.palwor.2014.10.004>
- Li, H.-L. 1952. Floristic relationships between eastern Asia and eastern North America. – *Transactions of the American Philosophical Society*, 42: 371–429. <https://doi.org/10.2307/1005654>
- Lieberman, B. S. 2000. *Paleobiogeography: using fossils to study global change, plate tectonics, and evolution*. New York: Kluwer Academic, 208 p.
- Lloyd, R. M. 1971. Systematics of the onocleoid ferns. – *University of California Publications in Botany*, 61: 1–93.
- Lloyd, R. M., Klekowski, E. J., Jr. 1970. Spore germination and viability in Pteridophyta: evolutionary significance of chlorophyllous spores. – *Biotropica*, 2: 129–137. <https://doi.org/10.2307/2989770>
- Maddison, W. P., Maddison, D. R. 2008. *Mesquite: a modular system for evolutionary analysis*. Version 3.61. <http://www.mesquiteproject.org> (accessed 6 August 2021)
- Matzke, N. J. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. – *Systematic Biology*, 63: 951–970. <https://doi.org/10.1093/sysbio/syu056>

- Moran, R. C. 2008. Diversity, biogeography, and floristics. – *Biology and Evolution of Ferns and Lycophytes*. Cambridge: Cambridge University Press, p. 367–394.
<https://doi.org/10.1017/CBO9780511541827.015>
- Mountier, C. F., Case, B. S., Perrie, L., Brownsey, P., Paterson, A. M., Curran, T. J., Buckley, H. L. 2018. Patterns of range size in New Zealand ferns and lycophytes. – *New Zealand Journal of Ecology*, 42: 248–261. <https://doi.org/10.20417/nzjecol.42.22>
- Rambaut, A. 2018. FigTree v.1.4.: Tree Figure Drawing Tool. – Institute of Evolutionary Biology, University of Edinburgh.
- Rambaut, A., Drummond, A. J. 2021. TreeAnnotator v. 2.6.4. – Institute of Evolutionary Biology, University of Edinburgh.
- Rothwell, G. W., Stockey, R. A. 1991. *Onoclea sensibilis* in the Paleocene of North America, a dramatic example of structural and ecological stasis. – *Review of Palaeobotany and Palynology*, 70: 113–124.
[https://doi.org/10.1016/0034-6667\(91\)90081-D](https://doi.org/10.1016/0034-6667(91)90081-D)
- Sessa, E. B., Juslén, A., Väre, H., Chambers, S. M. 2017. Into Africa: molecular phylogenetics and historical biogeography of sub-Saharan woodferns (*Dryopteris*). – *American Journal of Botany*, 104: 1–10.
<https://doi.org/10.3732/ajb.1600392>
- Vakhrameev, V. A. 1991. Jurassic and Cretaceous floras and climates of the Earth. Cambridge: Cambridge University Press, 318 p.
- Wolf, P. G., Schneider, H., Ranker, T. A. 2001. Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? – *Journal of Biogeography*, 28: 263–270.
<https://doi.org/10.1046/j.1365-2699.2001.00531.x>
- Wolfe, J. A., Tanai, T. 1980. The Miocene Seldovia Point Flora from the Kenai Group, Alaska. – *United States Geological Survey Professional Paper*, 1105: 1–52. <https://doi.org/10.3133/pp1105>
- Wood, P., Besnard, G., Beerling, D. J., Osborne, C. P., Christian, P.-A. 2020. Phylogenomics indicates the “living fossil” *Isoetes* diversified in the Cenozoic. – *PLoS ONE*, 15: 1–28.
<https://doi.org/10.1371/journal.pone.0227525>
- Xing, F. W., Kato, M. 2013. Onocleaceae. – *Flora of China*, Vol. 2–3 (Pteridophytes). St. Louis: Missouri Botanical Garden Press, p. 408–410.
- Xiang, J.-Y., Wen, J., Peng, H. 2015. Evolution of the eastern Asian-North American biogeographic disjunctions in ferns and lycophytes. – *Journal of Systematics and Evolution*, 53: 2–32.
<https://doi.org/10.1111/jse.12141>
- Xiang, Q.-Y., Soltis, D. E., Soltis, P. S., Manchester, S. R., Crawford, D. H. 2000. Timing the eastern Asian-eastern North American floristic disjunction: molecular clock corroborates paleontological estimates. – *Molecular Phylogenetics and Evolution*, 15: 462–472. <https://doi.org/10.1006/mpev.2000.0766>
- Yamakawa, C., Konishi, S. 2013. Fossil fern fronds from the early Pleistocene Kobiwako Group in Minakuchi, Shiga Prefecture, central Japan. – *Journal of Fossil Research*, 45: 61–69.
- Yatabe, Y., Nishida, H., Murakami, N. 1999. Phylogeny of Osmundaceae inferred from *rbcL* nucleotide sequences and comparison to the fossil evidence. – *Journal of Plant Research*, 112: 397–404.
<https://doi.org/10.1007/PL00013894>
- Yu, Y., Blair, C., He, X. J. 2020. RASP 4: Ancestral state reconstruction for multiple genes and characters. – *Molecular Biology and Evolution*, 37: 604–606. <https://doi.org/10.1093/molbev/msz257>
- Yu, Y., Harris, A. J., Blair, C., He, X. J. 2015. RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. – *Molecular Phylogenetics and Evolution*, 87: 46–49.
<https://doi.org/10.1016/j.ympev.2015.03.008>
- Yu, Y., Harris, A. J., He, X. J. 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. – *Molecular Phylogenetics and Evolution*, 56: 848–850.
<https://doi.org/10.1016/j.ympev.2010.04.011>