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Applications in Plant Sciences

APPLICATION ARTICLE

The PteridoPortal: A publicly accessible collection of over three million records of extant and extinct pteridophytes

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Abstract

Premise: Pteridophytes—vascular land plants that disperse by spores—are a powerful system for studying plant evolution, particularly with respect to the impact of abiotic factors on evolutionary trajectories through deep time. However, our ability to use pteridophytes to investigate such questions—or to capitalize on the ecological and conservation-related applications of the group—has been impaired by the relative isolation of the neo- and paleobotanical research communities and by the absence of large-scale biodiversity data sources.

Methods: Here we present the Pteridophyte Collections Consortium (PCC), an interdisciplinary community uniting neo- and paleobotanists, and the associated PteridoPortal, a publicly accessible online portal that serves over three million pteridophyte records, including herbarium specimens, paleontological museum specimens,

For affiliations refer to page 8.

and iNaturalist observations. We demonstrate the utility of the PteridoPortal through discussion of three example PteridoPortal-enabled research projects.
Results: The data within the PteridoPortal are global in scope and are queryable in a flexible manner. The PteridoPortal contains a taxonomic thesaurus (a digital version of a Linnaean classification) that includes both extant and extinct pteridophytes in a common phylogenetic framework. The PteridoPortal allows applications such as greatly accelerated classic floristics, entirely new "next-generation" floristic approaches, and the study of environmentally mediated evolution of functional morphology across deep time.
Discussion: The PCC and PteridoPortal provide a comprehensive resource enabling novel research into plant evolution, ecology, and conservation across deep time, facilitating rapid floristic analyses and other biodiversity-related investigations, and providing new opportunities for education and community engagement.

KEYWORDS
Advancing Digitization of Biodiversity Collections (ADBC) program, *Equisetum*, ferns, flora of Colombia, flora of Venezuela, fossil classification, iNaturalist, lycophytes, tubers, Symbiota

Pteridophytes—spore-bearing vascular plants—are a diverse and disparate set of plants, today comprising approximately 11,000 extant species of ferns (including horsetails and whisk ferns) and 1300 species of lycophytes (Schuettpelz et al., 2016). The pteridophyte macrofossil record extends back to the late Silurian (Gensel, 2008), and pteridophytes were ecologically dominant for hundreds of millions of years as the first plants to evolve roots or leaves (Schneider et al., 2002), to move into drier habitats, and to form forests (Bateman et al., 1998; Stein et al., 2012). While much of extant pteridophyte diversity is the result of relatively recent radiations (Schuettpelz and Pryer, 2009; May et al., 2021), at least 14 extant lineages have independent histories extending back over 200 million years (Smith et al., 2010; Rothfels et al., 2015; Testo and Sundue, 2016); these lineages provide separate examples of routes to evolutionary success.

Pteridophytes are distinguished from other plants by being vascular, dispersing by spores, and by their life cycle: both the sporophyte and gametophyte phases are free-living and nutritionally independent (Taylor et al., 2005; Haufler et al., 2016). Also, because they reproduce and disperse without biotic intermediates, they are less sensitive to biotic factors that might obscure the relationship between their geographic ranges and underlying abiotic conditions. Finally, the high dispersal potential of their spores reduces the effect of historical contingency on taxon ranges.

Their deep evolutionary history and tight connection to abiotic factors make pteridophytes an ideal system for studying evolutionary and ecological processes through time. In addition, they have an excellent macrofossil record in both temporal range and quality. Pteridophytes tend to grow close to depositional environments with greater fossilization potential, and thus their fossil record is denser, at least for the first few hundred million years of land plant evolution, than for groups like the seed plants, where much of the morphological innovation is postulated to have occurred in drier habitats where the chance of fossilization is low (Looy et al., 2014). Also, pteridophytes have an added advantage for paleobotanical studies in that their reproductive organs frequently have a long-persistent association with their leaves and stems, which greatly facilitates whole-plant reconstructions.

Finally, pteridophytes are an ideal group in which to link fossil and extant data sources. They tend to be more morphologically conservative than seed plants (Phipps et al., 1998; Bomfleur et al., 2014; Sundue and Rothfels, 2014; May et al., 2021), allowing researchers to integrate data from fossil and extant specimens to a degree not possible in other groups. These features—the strong connection between pteridophytes and the abiotic environment in conjunction with their extensive fossil record—allow us to correlate their occurrences with abiotic conditions not only as those conditions vary geographically in the present, but also as they vary temporally, extending into the deep past.

Understanding pteridophyte diversity, including their spatial and temporal distribution and phylogenetic relationships, is important for understanding the evolution and persistence of terrestrial ecosystems, their associated biodiversity and ecosystem services, and their potential responses to global change. Comprehensive records documenting these lineages and their changes over time are available in the form of professionally curated natural history specimens in herbaria and paleontological museums. However, these neo- and paleobotanical collections are often housed in separate facilities and studied by separate communities of researchers; there is no centralized source of these data, and available resources, such as the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and iNaturalist (https://www.inaturalist.org/), are not specifically oriented towards pteridophytes and therefore lack some of the specialized functionality necessary to capitalize on the research potential of this group.

METHODS

In response to the fragmentation of the pteridological research community and the lack of a central repository of pteridophyte occurrence data, we formed the National

Science Foundation (NSF)–funded Pteridophyte Collections Consortium (PCC) in 2018 as an initiative to integrate these communities by databasing and imaging herbarium and fossil pteridophyte specimens and making these data available in a publicly accessible online digital resource: the PteridoPortal (https://www.PteridoPortal.org). Led by University of California, Berkeley, and eight collaborating institutions (Field Museum of Natural History, University of Florida, University of Michigan, Missouri Botanical Garden, New York Botanical Garden, University of North Carolina at Chapel Hill, University of Vermont, and Yale University), the PCC now comprises 63 contributing collections (Appendix S1).

The PteridoPortal is powered by Symbiota (Gries et al., 2014), a biodiversity data mobilization software that facilitates central, web-based access to datasets managed by multiple collections and using a range of data formats. Symbiota provides both back-end data management tools (so that an institution can manage its holdings directly in a data portal), as well as tools for importing static “snapshot” datasets from other sources, for example, Darwin Core Archive files (i.e., data files with the fields standardized according to the Darwin Core format) prepared for GBIF (Wieczorek et al., 2012). The PteridoPortal is a thematic portal that consists largely of such subsetted “snapshots” of data, rather than a portal in which institutions manage their individual collections. This structure allows us to leverage other digitization projects not directly focused on pteridophytes, while also customizing features of the site—such as the taxonomic thesaurus—to fit the needs of our community.

We demonstrate the usefulness of the PteridoPortal through three empirical studies: one utilizing the PteridoPortal to accelerate the production of a pteridoflora for Venezuela; one applying PteridoPortal tools to create a “next-generation” floristic study of Colombia; and a third that synthesizes extant and fossil collection data from the PteridoPortal to derive new hypotheses on the evolution of tubers in the horsetails (Equisetaceae).

RESULTS

As of 7 October 2024, the PteridoPortal includes over 2,345,000 extant and almost 30,700 fossil specimens (Table 1; a by-family breakdown is available in Appendix S2). The NSF funding to establish the PCC was limited to non-federal U.S. institutions; the holdings of these collections, however, are often global in scope, and volunteer institutions, such as the Smithsonian National Museum of Natural History (US and NMNH; herbarium acronyms per Index Herbariorum [Thiers, 2025]) in the United States, Naturalis Biodiversity Centre (L) in the Netherlands, the Royal Botanical Garden Edinburgh (E) in Scotland, and the United Herbaria of the University and ETH Zurich (ZT and Z) in Switzerland, generously allowed their data to be served on the PteridoPortal, further increasing the global representation of this resource (Figure 1). In addition, we serve over a million research-grade iNaturalist observations (GBIF.org, 2024a, b, c, d, e, f, g). The iNaturalist records constitute a sizeable proportion of the available records for some countries with particularly active iNaturalist communities (such as the United States, Canada, Australia, and South Africa); however, for most of the globe the available records are almost exclusively specimen-based (Figure 1).

TABLE 1 PteridoPortal holdings as of 7 October 2024.

Record type	Extant	Fossil
Total specimen records	2,345,687	30,699
Fully transcribed specimens[a]	1,915,110	21,309
Georeferenced specimens[b]	769,205	15,503
Imaged specimens[c]	2,093,134	23,703
iNaturalist observations	1,064,775	NA

[a]Specimens for which the core metadata have been completely transcribed (but they may or may not be georeferenced or have an associated image).

[b]Specimens that have coordinates available, either as part of the original label data or subsequently derived as part of focused georeferencing efforts.

[c]Specimens including an image of the specimen in addition to the label data.

The PteridoPortal provides users with a broad range of tools for interacting with and downloading the data. For example, users can search records through parameters such as collector, locality, date of collection, taxonomic identification, or catalog number. Filtering tools allow for the selection of specimens from cultivated material, nomenclatural types, and those with associated images, coordinates, and/or genetic data. Taxonomic searches are linked to the PteridoPortal's underlying taxonomic thesaurus, which is a hierarchical classification of global pteridophytes, including full synonymy. The classification for extant pteridophytes is based on the Checklist of Ferns and Lycophytes of the World (https://www.worldplants.de/world-ferns/ferns-and-lycophytes-list), generously provided by Michael Hassler. For example, if one searches for “*Athyrium acrocarpum*,” the PteridoPortal will return all records identified as *Athyrium acrocarpum* (Rosenst.) Copel. in the family Athyriaceae of suborder Aspleniineae, as well as records identified under the synonymous names *Asplenium acrocarpum* (Rosenst.) Heiron. or *Diplazium acrocarpum* Rosenst. (Figure 2A). Similarly, if one searches for “*Athyrium*,” the PteridoPortal will include in the results any specimens identified as a species of *Hypochlamys* Fée, *Pseudathyrium* Newman, *Pseudocystopteris* Ching, or *Solenopteris* Zenker.

A major contribution of the PteridoPortal is the incorporation of 2792 fossil taxa within the taxonomic thesaurus, resulting in a classification of pteridophytes from their origin to the present day that places both extinct and extant species in a single cohesive evolutionary context. We derived this list of taxa by downloading all pteridophyte records from GBIF (in January 2020) and manually reconciling their classification to a coherent set of ranks following the framework of Taylor et al. (2009). One particular challenge in adding fossil taxa to the

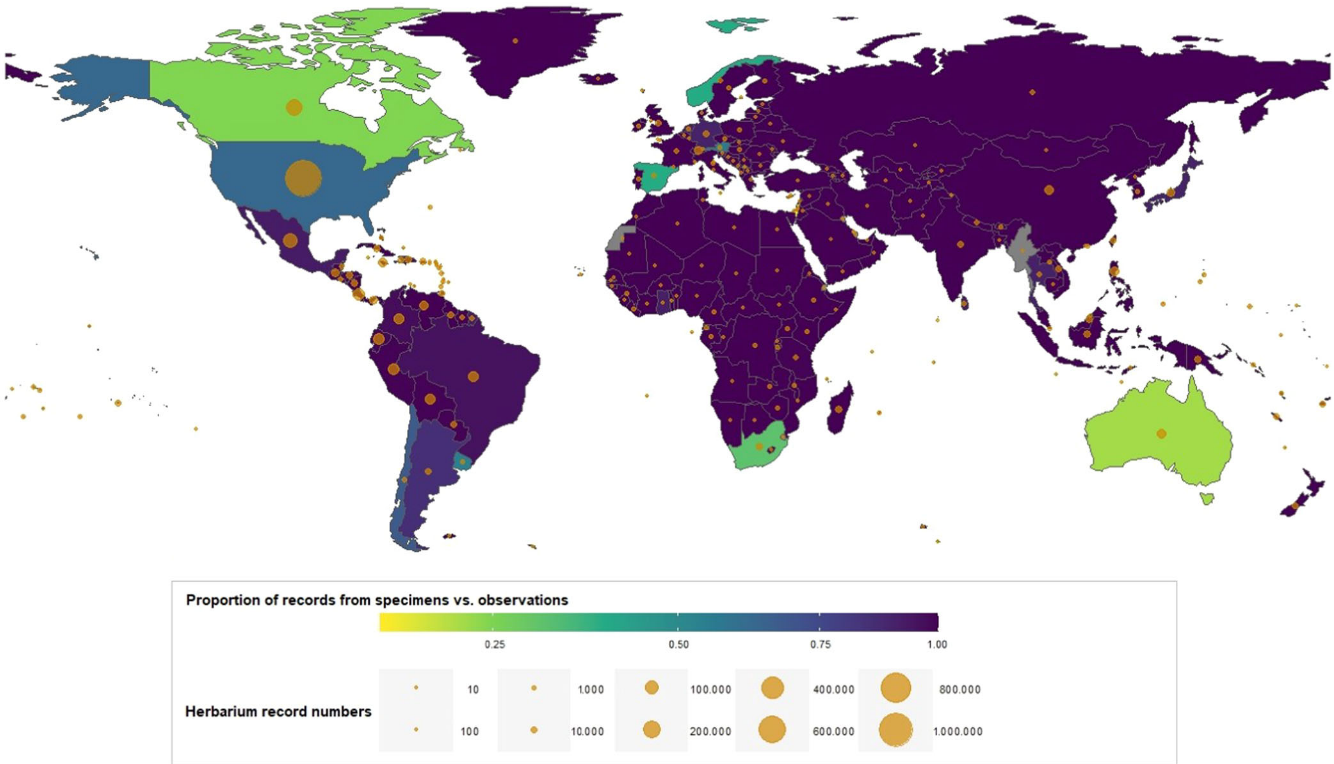

FIGURE 1 Global representation of PteridoPortal records. Circles are proportional to the number of records from each county, and countries are colored by the proportion of their records that are specimen-based (i.e., from herbarium or paleontological museums) versus observation-based (i.e., from iNaturalist). Countries with smaller proportions of records derived from specimens (those in light green) tend to be those with very active iNaturalist communities, such as Canada, South Africa, and Australia. Countries in gray lack iNaturalist records.

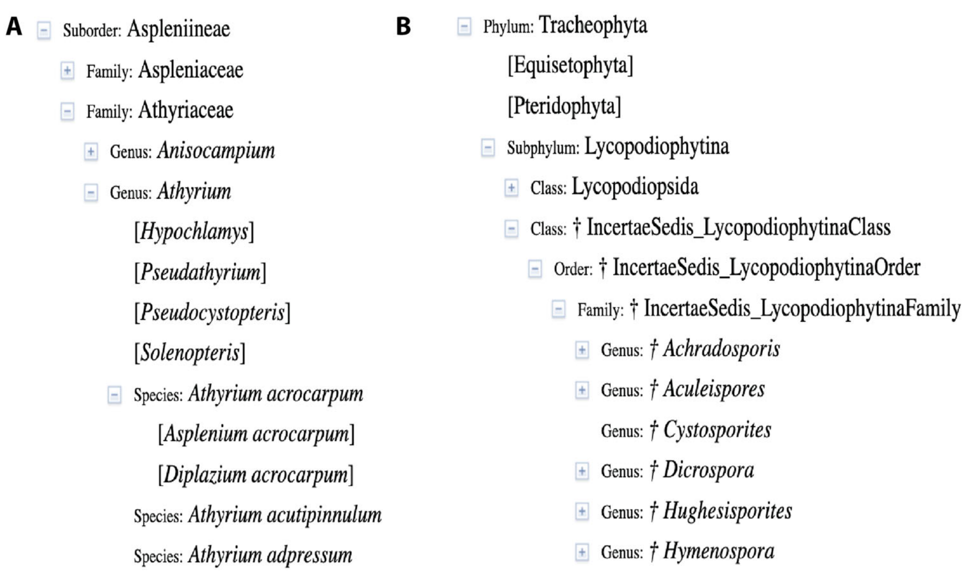

FIGURE 2 Structure of the taxonomic thesaurus. (A) The nested classification for a portion of the Athyriaceae. Taxa treated as synonyms are within square brackets and map automatically to the accepted taxon that they are nested beneath. (B) Nested classification of a portion of Lycopodiopsida showing the application of the incertae sedis placeholder taxa to accommodate unknown higher classifications of lower-rank taxa. Extinct taxa are indicated with a "†".

thesaurus is the presence of taxa whose higher-level taxonomic relationships are unknown. For example, the genus *Dicrospora* M. R. Winslow is used to refer to lycophyte megaspores of uncertain affinity; they are believed to be produced by a member of the Lycopodiophytina, but we do not know to which family, order, or class they belong (Quetglas et al., 2024). To accommodate situations like this within the thesaurus, we created a series of placeholder "incertae sedis" taxa, formatted as "† IncertaeSedis_highertaxonRank" (where the "†" is used to indicate an extinct taxon; see Figure 2B). For example, "† IncertaeSedis_LycopodiophytinaFamily" is a family-level placeholder taxon for genera, like *Dicrospora*, that are thought to be in the Lycopodiophytina, but whose intermediate taxonomic affinities (class, order, and family, in this case) are unknown. This classification allows users to seamlessly query all data in the PteridoPortal—extant or fossil—within a common taxonomic framework.

In addition to searching by taxonomic affiliation or other record features, a user can query the data using Symbiota's mapping functions. Using these functions, a user can draw a polygon on a map and capture all the records within that polygon. This mapping tool is useful for data visualization, providing a convenient representation of the distribution of georeferenced taxon occurrences in space. The results of any PteridoPortal search can be displayed as a list or table and downloaded, with or without a list of URLs for the associated specimen images. In addition, for any query, the PteridoPortal will produce a species list, which can be built from either the names on the specimens or according to the synonymy relationships in the taxonomic thesaurus.

The taxonomic thesaurus also provides users with a tool for resolving questions of pteridophyte classification. The "taxonomic explorer" tool displays the full taxonomic tree for any taxon of interest, as well as any relevant synonymy relationships. Selecting any accepted taxon in the taxonomic explorer will bring the user to a dedicated taxon page that includes a representative photograph of that taxon, a selection of specimen images of that taxon from the PteridoPortal database, a description of that taxon's morphology from the Flora of North America (Flora of North America Editorial Committee, 1993), and links to outside resources relating to that taxon, such as the International Plant Names Index or the IUCN Red List (Croft et al., 1999; IUCN, 2024).

Another important feature of the PteridoPortal is its checklist functionality. These checklist tools allow a user to query the portal for records from a particular geographic region and then to manually vet the resulting species list and to select a set of records (specimens and/or iNaturalist observations) that support the occurrence of each species in that region. This approach provides a transparent and verifiable way to document the pteridophyte diversity of a region; the inclusion of a particular species can be confirmed or refuted by examining its purported voucher specimen(s). Checklists can alternatively be uploaded from an existing list of taxa. This provides a straightforward way to archive and share previously generated taxonomic checklists, and it also provides a platform for identifying which species need voucher specimens to adequately document a species' occurrence. As specimens are re-identified as part of research and curational work, checklist managers can use built-in tools to view those changes, which may prompt them to modify their checklists accordingly.

In addition to these core Symbiota tools, the PteridoPortal features new functionality. Most notably, the PCC project spearheaded the development of the Symbiota paleo module, which provides the basic data structures necessary to store, share, and access paleontological specimen data. This paleo module is now part of Symbiota's base code and is thus available to other Symbiota portals and for future augmentation and development (e.g., by the Paleo Data Working Group, NSF Award #2324690). Finally, beyond tools for querying and summarizing the data, the PteridoPortal includes mechanisms for members of the public to add to the resource by, for example, submitting data corrections to the specimen host institution, or by participating in label transcription through the crowdsourcing functionality.

DISCUSSION

The PteridoPortal in education and outreach

The PteridoPortal's crowdsourcing module, built on Symbiota's platform, serves as a powerful tool for education and public engagement in biodiversity science. This feature not only accelerates the digitization of specimen data but also provides unique opportunities for STEM education and community science participation (Monfils et al., 2017). By allowing users worldwide to contribute to label transcription, the PteridoPortal transforms the digitization process into an interactive learning experience, fostering a deeper understanding of biodiversity collections and their scientific value (Cook et al., 2014).

The educational impact of this crowdsourcing initiative extends beyond data entry. It offers hands-on experience with real scientific data, enhancing participants' skills in data management, species identification, and digital literacy (Ellwood et al., 2015). Many institutions have integrated these activities into their curricula, offering class credit for student participation, thereby bridging the gap between traditional classroom learning and practical scientific contribution (Monfils et al., 2017; von Konrat et al., 2024). This approach not only motivates students but also exposes them to career paths in biodiversity informatics and collection management. Furthermore, the gamification aspect, exemplified by the scoreboard feature, adds an element of friendly competition that has proven highly engaging, as evidenced by the remarkable contributions of individuals like Jeffrey Greenhouse, who has transcribed over 47,820 PteridoPortal specimens. Such initiatives have shown to increase public awareness of the importance of natural history collections and foster a sense of stewardship for biodiversity (Sforzi et al., 2018), while simultaneously advancing scientific research and data accessibility.

The PteridoPortal in research

The goal of the PCC in creating the PteridoPortal is to facilitate research on pteridophytes by compiling and disseminating biodiversity data on extant and extinct pteridophyte taxa. Below we discuss three examples of ongoing research utilizing the PteridoPortal—two based on extant specimen data and one primarily utilizing the paleontological collections—to demonstrate the potential of this resource.

Accelerated large-scale floristics and monography: The Pteridoflora of Venezuela

The utilization of the PteridoPortal in the Pteridoflora of Venezuela project (Alan R. Smith, in prep.) provides a clear example of how this resource can accelerate the invaluable and laborious process of large-scale "classical" floristics. The Pteridoflora of Venezuela project had its genesis in the late 1970s, and has been proceeding, in fits and starts, since then. Early products included a publication covering the state of Falcón (van der Werff and Smith, 1980) and a preliminary conspectus of the pteridophytes for the whole country (Smith, 1985). Beginning in about 2000, and with the advent of molecular work that greatly increased our understanding of fern relationships, the project vision expanded to encompass a full-blown modern pteridophyte flora with reworked keys and discussion of the taxonomy and distribution of the species within Venezuela. This effort was greatly accelerated by the development of the PteridoPortal, which provided easy access to specimens in critical herbaria throughout the United States, including during the peak of the COVID pandemic, when travel was severely curtailed.

Over an approximately five-year period, Smith was able to access and identify most (perhaps >80%) of the specimens in the largest herbaria. From his home institution at the University and Jepson Herbaria (UC/JEPS) and at other remote locations, he looked at, assessed, and recorded in excess of 100 images and associated metadata per day, searching by taxon, country, state, and sometimes by collector and collection number. He estimates that he saw and identified more than 50,000 records of Venezuelan pteridophytes during this period, a scale of study that would not have been possible without the PteridoPortal, even if travel restrictions were not limiting (Alan R. Smith, personal communication).

Many specimens in the PteridoPortal were correctly identified, but there were also misidentified and undetermined specimens, undescribed taxa were sometimes unearthed, and many taxonomic changes have been made. Thus, the PteridoPortal, in addition to providing a direct source of occurrence data at a massive scale, produced taxonomic and distributional insights that would otherwise have gone undetected.

Next-generation biodiversity documentation: Leveraging online resources to document the pteridophyte diversity of Colombia

The Ferns of Colombia (FOCO) project is a collaborative effort led by Alejandra Vasco, Weston Testo, and Michael Sundue to accelerate lineage discovery and document fern diversity in the American tropics. Unlike traditional floristic projects that compile vetted data into an off-line manuscript, FOCO operates as a database-driven flora using PteridoPortal as its core. The FOCO team continuously updates the flora, and at any point, they can export it as a country-wide checklist, providing a snapshot of the current data, complete with specimen voucher details and the herbaria where those specimens reside. This approach eliminates the need to maintain a separate document and avoids transcribing records into a working manuscript.

The FOCO team uses checklists exported from PteridoPortal to accomplish project tasks. For instance, they compare the current PteridoPortal records with a published checklist for Colombia (Bernal et al., 2020) to identify potential discrepancies. These flagged discrepancies—often resulting from misidentified specimens, nomenclatural innovations, or the discovery of new records—help them address issues and update the flora accordingly. Checklists also prove useful in the field. Before an expedition, participants export a checklist for the Colombian department (a political unit approximately equivalent to a state) they plan to visit. Each species in the export is accompanied by an image of a specimen. Collectors receive PDF versions of these guides, which they keep on their phones and use as "rapid field guides." These guides facilitate identifications, serve as teaching aids, and help focus attention on rare and under-collected species. The FOCO team also prioritizes efforts when sampling specimens for DNA extraction during herbarium visits by using the checklist tool. PteridoPortal records help them determine which species are poorly represented in herbaria, allowing them to prioritize these during their visits. Additionally, they search through digitized images for well-preserved specimens that are expected to yield high-quality DNA. An unexpected consequence of hunting for rarities is that they often discover rarely collected species and become aware of species to be on the lookout for in the field. They have even "rediscovered" some very rare species this way, including *Amauropelta strigillosa* (A. R. Sm. & Lellinger) Salino & T. E. Almeida, *Pteris semidentata* Fée, and *Diplazium nicotianifolium* C. Chr.

Data transcription of new collections is also handled efficiently by adopting PteridoPortal as the central data repository. For example, new records are born digitally, transcribed only once from the collector's field notebook into a Darwin Core–compatible spreadsheet, which is then uploaded to the PteridoPortal to both populate the digital records and generate specimen labels.

To achieve a comprehensive representation of the Colombian fern flora, FOCO has invited new partners into the PteridoPortal, including the Fundación Jardín Botánico Joaquín Antonio Uribe de Medellín (JAUM) and the Royal Botanic Garden Edinburgh (E), both of whom joined in 2023. The FOCO team curates data from many partnering institutions to eliminate aberrant records caused by incorrect identifications and nomenclatural confusion from homonyms. These are identified by comparing data from published checklists to the holdings reported in specific herbaria. Of particular help in this case are the PteridoPortal tools that flag inconsistent identifications of duplicate specimens housed in different herbaria. These corrections are communicated through the comment tool supported by PteridoPortal or through bulk editing facilitated by Darwin Core–formatted spreadsheets.

In conclusion, the FOCO project takes full advantage of PteridoPortal to document fern diversity in Colombia. These tools streamline the process of collecting, curating, and sharing data and demonstrate the benefits of real-time biodiversity documentation.

Tracing the evolutionary ecology of belowground tubers in *Equisetum* in deep time

The digitized paleo- and neobotanical specimens of the PteridoPortal can support the study of the evolution of morphology and development in deep time. An example is the study of the evolutionary ecology of the belowground rhizome tubers of *Equisetum* L. Recently, Lee (2025) conducted an extensive review of the anatomy, morphology, paleobiogeography, and phylogenetic distribution of tubers in equisetaleans, utilizing both in-person examination of fossil and extant specimens and the examination of digitized records in the PteridoPortal. The major findings of this review include: (1) among extant taxa, tubers are exclusively present in species of subgenus *Equisetum*; (2) fossil tuberous *Equisetum/Equisetites* are solely known from the Northern Hemisphere; (3) the fossil record is predominantly from mid- to high paleolatitudes; (4) the abundance and geographic distribution of tubers rapidly expands at the onset of the Cretaceous, coinciding with the estimated divergence between the subgenera *Equisetum* and *Hippochaete* (Milde) Baker; and (5) the oldest occurrence of tuberous equisetaleans—from the latest Triassic to earliest Jurassic—coincides with the origin of the *Equisetum* crown group, which suggests that tubers may be plesiomorphic or have evolved more than once within the group.

Equisetum tubers are grossly underrepresented in herbaria; in an analysis of ~1400 digitized *Equisetum* herbarium specimens in the PteridoPortal, less than 1% included tubers, corroborating the findings from an in-person UC/JEPS collection analysis (Lee, 2025). This poor representation of tubers in herbaria is likely due to their occurrence at soil depths often >50 cm, and to a collection bias towards aboveground organs (Tribble et al., 2021). Conversely, tubers are relatively well represented in paleobotanical collections (Lee, 2025), likely due to the mesic-to-hydric habitat of Equisetaceae taxa favoring fossilization and to the water dispersal of tubers (Mukula, 1963). An analysis of 558 digitized fossil specimens in the PteridoPortal shows that ~10% of fossil specimens bear tubers, all from Cretaceous and Cenozoic occurrences of mid- to high latitudes of North America. This finding corroborates the results from an in-person examination of equisetalean specimens in NMNH (Lee, 2025). The similar estimates of tuberous specimen frequency derived from digitized PteridoPortal specimen data and from in-person examinations of NMNH specimens—NMNH has among the widest geographic and stratigraphic representation among paleontological museums—shows the efficacy of using the PteridoPortal for morphological studies and its impact in reducing geographic and/or socio-economic barriers and improving accessibility to natural history collections.

In addition to corroborating the published record and the results of the in-person NMNH study, the PteridoPortal analysis found 13 unpublished stratigraphic occurrences of tuberous *Equisetum* in North America across three museums (Lee, 2025), a result that emphasizes the degree to which natural history collections remain unpublished and difficult to access. Beyond these 13 new records, the PteridoPortal provided a valuable opportunity for quality control: equisetalean tubers and tuber-bearing rhizomes can resemble other plants, such as diaspores and reproductive axes, resulting in incorrect label data and erroneous reports in the literature (Lee, 2025). In this case, for example, some of the Early Cretaceous tuber-bearing *Equisetum* specimens (e.g., YPM PB 174529-32) appear to represent angiosperm reproductive axes bearing capsule- or schizocarp-like fruits in opposite arrangements, a finding that would not have been possible without access to the specimen images.

The individual specimen records of the PteridoPortal also allow for the estimation of the relative frequency of tuberous specimens within an assemblage; this information is omitted in descriptions of paleofloras, which typically report only the presence/absence of taxa or specific organs. The frequency information permits exploration of potential ecological patterns in deep time. *Equisetum* specimens in floras that are disproportionately tuberous include the Albian Winthrop flora in Washington (43% of digitized specimens bearing tubers; $N = 7$), the Cenomanian Dakota flora from Utah (100%; $N = 9$), and the Campanian Kaiparowits flora from Utah (50%; $N = 10$). Additionally, the frequency of tuberous *Equisetum* specimens from the Renova Formation from Montana changes from 90% in the late Eocene ($N = 10$) to 17% in the early Oligocene ($N = 12$). Tuberous *Equisetum* occurrences are more abundantly represented during the mid- to Late Cretaceous, Paleocene–Eocene, and Miocene intervals compared to poorer representation during the Oligocene and Pliocene (Lee, 2025). Notably, the geologic intervals with higher frequency of tuberous specimens roughly coincide with elevated atmospheric CO_2 levels (Caldeira and Rampino, 1991; Lowenstein and Demicco, 2006; Wang et al., 2014).

These frequency changes through geological time may be related to an interesting feature of tuber development. In *Equisetum*, tuber production is suppressed by high nitrogen (NH_4^+) concentrations (Andersson and Lundegårdh, 1999; Nakatani and Fujii, 2013), a response also seen in some tuberous angiosperms, where it is triggered by a high N:C ratio (Mantell and Hugo, 1989; Zierer et al., 2021). Assuming a similar control of tuberization in *Equisetum*, the abundance of tuberous *Equisetum* during hothouse intervals may have been facilitated by elevated atmospheric CO_2, which can result in a higher plant tissue C:N ratio (Gifford et al., 2000; De Graaff et al., 2006). Currently, however, the sample size of tuberous *Equisetum* fossils is not sufficient to determine whether the observed pattern is biologically and ecologically meaningful or merely represents preservational or other biases. The tuberization process is less well understood in pteridophytes, and other biotic and environmental factors, such as photoperiod, plant productivity, and hormone levels, also control tuber development in angiosperms (Mantell and Hugo, 1989; Zierer et al., 2021).

While the current data are inconclusive as to the role of climate in the development of tubers in *Equisetum* across geological time, the PteridoPortal analysis raises an interesting, testable hypothesis on the ecological evolution of a belowground storage organ in an ancient pteridophyte lineage. Furthermore, this study demonstrates the utility of the PteridoPortal in providing easily accessible, large-scale, content-rich data across both neo- and paleontological timescales, and in the ability of those data to investigate questions—such as the environmental drivers of tuber frequency—that would not otherwise be possible.

CONCLUSIONS

We are excited to further develop the PteridoPortal resource and grow the PCC, with the goal of promoting and facilitating the synthesis of neo- and paleontological studies of pteridophytes. We will continue to expand the core resource itself, through ongoing digitization by PCC members and through the incorporation of specimen data from other collections; we invite and encourage all prospective contributors to reach out to us. Other clear opportunities are to increase the fossil representation in the PteridoPortal, augment and refine our classification of extinct pteridophytes, update the classification of extant pteridophytes to the upcoming revised Pteridophyte Phylogeny Group classification (PPG II), and develop new tools for reviewing and incorporating externally generated specimen annotations (such as re-identifications and data quality flags).

AUTHOR CONTRIBUTIONS

A.Ka. was the PCC Project Manager; J.G. was the PCC Portal Manager; C.J.R., C.V.L., and D.M.E. were the PCC lead institution PIs and co-PIs; A.L., A.P., A.W., C.N., C.St., D.E.G., E.B.S., E.M., G.W., G.Y., I.M., K.M.P., K.P., K.W., L.S., L.Z., M.A.S., M.D.W., M.L., M.L.P., M.P., M.V., M.v.K., P.G., P.S., R.J.B., R.K.R., S.H., S.M.I., T.L., and T.Re. were the PCC collaborating PIs and co-PIs; A.Kl., A.V., C.A.M., C.M.T., C.Sm., D.F., E.A., E.J., E.S., G.H., H.L., I.G., J.B., J.S., J.T., Ke.D.P., L.C.M., L.H., M.R.K., R.L., R.M., S.O., T.A.R., T.W., and Y.R. were PCC contributors and Senior Personnel; E.G., and Ka.D.P. provided Symbiota development; M.H. provided the core taxonomic thesaurus; and A.R.S., A.V., C.J.R., C.V.L, J.L., M.A.S., P.F.-P., and W.T. drafted the manuscript. All authors critically revised and/or reviewed the manuscript, and all authors approved the final version.

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DATA AVAILABILITY STATEMENT

The PteridoPortal is publicly accessible at https://www.pteridoportal.org.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. PteridoPortal contributors.

Appendix S2. Per-family counts of PteridoPortal records from herbaria, iNaturalist, and paleontological collections (data as of December 2024).

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