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Authors
Schuettpelz, Eric
Rouhan, Germinal
Pryer, Kathleen M
et al.

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POINT OF VIEW

Are there too many fern genera?

Eric Schuettpelz,[1] Germinal Rouhan,[2] Kathleen M. Pryer,[3] Carl J. Rothfels,[4] Jefferson Prado,[5] Michael A. Sundue,[6] Michael D. Windham,[3] Robbin C. Moran[7] & Alan R. Smith[8]

1 *Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A.*
2 *Muséum national d'Histoire naturelle, Institut Systématique Evolution Biodiversité (ISYEB), CNRS, Sorbonne Université, EPHE, Herbier national, 57 rue Cuvier, CP39, 75005 Paris, France*
3 *Department of Biology, Duke University, Durham, North Carolina 27708, U.S.A.*
4 *University Herbarium and Department of Integrative Biology, University of California, Berkeley, California 94720-2465, U.S.A.*
5 *Herbário SP, Instituto de Botânica, São Paulo, SP, CP 68041, 04045-972, Brazil*
6 *The Pringle Herbarium, Department of Plant Biology, University of Vermont, Burlington, Vermont 05405, U.S.A.*
7 *The New York Botanical Garden, 2900 Southern Blvd., Bronx, New York 10458-5126, U.S.A.*
8 *University Herbarium, University of California, Berkeley, California 94720-2465, U.S.A.*
Author for correspondence: *Eric Schuettpelz, schuettpelze@si.edu*

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A global consortium of nearly 100 systematists recently published a community-derived classification for extant pteridophytes (PPG I, 2016). This work, synthesizing morphological and molecular data, recognized 18 lycophyte and 319 fern genera in 51 families, 14 orders, and 2 classes. Using monophyly as a defining criterion, while affirming the importance of stability in names and circumscriptions, the contributors produced a summary statement of then-current taxonomic hypotheses to serve as a resource for the scientific community and a framework for future research. The authors explicitly emphasized that their proposed classification was not intended to be the final word on pteridophyte taxonomy, nor was it to be imposed on anyone.

Taxonomy, like every scientific discipline, is constantly evolving. Although changes in classification can be frustrating for some users, they are often necessary to accommodate new discoveries and shifting interpretations of available data. Given the current pace of discovery, we were not surprised to read about a forthcoming classification for vascular plants (Byng & Christenhusz, in prep., as cited in Christenhusz & al., 2018). However, we were surprised and dismayed to learn of the authors' decision to dismiss, rather than improve upon, the community-derived effort for ferns (PPG I, 2016). The newly proposed taxonomic framework will instead be based on a classification by Christenhusz & Chase (2014) that recognized just 212 fern genera. Apparently, the new treatment will include even fewer genera—for example, the thirteen genera in subfamily Cheilanthoideae (sensu PPG I, 2016) will be reduced to one (Christenhusz & al., 2018)—and will simultaneously require an unprecedented number of nomenclatural changes. To this end, Christenhusz & al. (2018) made a total of 1282 nomenclatural changes for ferns, including 1107 new combinations, 20 new combinations with a change in status, and 155 replacement names. While some (42) of these changes are also required by the PPG I (2016) classification (e.g., those for *Alsophila* R.Br. and *Ptisana* Murdock), most (1240) were driven by the broad generic concepts favored by Christenhusz & Chase (2014) and Christenhusz & al. (2018). Most prominently, 308 species were moved to *Grammitis* Sw., 468 to *Hemionitis* L., and 388 to *Thelypteris* Schmidel. These 1164 transfers alone resulted in new names for 11% of fern species. The rationale presented for this profusion of names is that Christenhusz & Chase (2014) is ultimately more "in line with historical treatments" (Christenhusz & al., 2018). But, in fact, this treatment, and those based on it, largely ignore more than a century of intellectual progress.

In *Species plantarum* and *Genera plantarum*, Linnaeus (1753, 1754, respectively) recognized a mere 15 fern genera. Linnaean fern genera were so-called "form genera", based, for the most part, on variation in four characters: frond dimorphism (monomorphic, hemidimorphic, or dimorphic); blade dissection (simple, pinnate, bipinnate, or decompound); sorus position (marginal or abaxial); and sorus shape (round, linear, or funnelform). With advances in microscopy, phytochemistry, cytology, and molecular approaches over the centuries, we now have access to many more characters and a much greater proportion of fern diversity is available for study in natural history collections. We also now appreciate that all ferns share a common ancestor (Pryer & al., 2001), recognize the importance of classifications that reflect evolutionary relationships, and have the analytical tools to infer those relationships. Nearly all of the generic concepts put forward by Linnaeus (1753) for ferns are now known to be polyphyletic, forged from a variety of disparate elements. For example, the 58 species placed in Linnaeus's *Polypodium* are today recognized in 34 genera in 13 families, widely distributed across the leptosporangiate fern phylogeny (PPG I, 2016).

The substantial increase in fern genera, from the 15 recognized by Linnaeus (1753) to the 319 recognized in PPG I

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(2016), was not abrupt. Instead, it resulted from the gradual accumulation of new collections and new data, which in turn led to a greater appreciation of fern diversity and to an improved ability to distinguish taxa (Fig. 1). In the first taxonomic work focused exclusively on ferns, Swartz (1806) recognized 38 genera, more than twice as many as were recognized by Linnaeus (1753). About 20 years later, the number had again more than doubled, to 79 (Desvaux, 1827). By the middle of the 19th century, when extraordinary numbers of new plants were being discovered and described (Bebber & al., 2012), the number of recognized fern genera rose to 134 (Hooker, 1842), 143 (Smith, 1842a, b, c, d, 1843), 176 (Presl, 1836, 1843, 1845, 1847, 1851), and then 181 (Fée, 1852). The clear outlier during this time was the classification of Hooker (1846–1864), which recognized just 68 morphologically heterogeneous genera. Though a definite improvement over the taxonomy of Linnaeus, Hooker's (1846–1864) treatment discounted the work of most of his pteridological predecessors and even represented a reversal of his own earlier opinions (Hooker, 1842). Again taking up the example of *Polypodium* L., Hooker (1846–1864) greatly expanded that genus to include 409 species previously assigned to 30 genera. The radical nature of this realignment (and the reason that it was such an outlier compared to other treatments published in the 1800s) stemmed from a clear bias toward consolidation (lumping) without adequate justification: "the above generic synonyms of what we bring here under the genus Polypodium are by no means all that might be included" (Hooker, 1846–1864, vol. 4 [1862]: 163). Today, the 409 species placed in Hooker's *Polypodium* are assigned to 22 genera in 6 families, widely scattered across the leptosporangiate fern phylogeny. As time passed, new approaches, new data, and new insights again led to global acceptance of greater numbers of genera, with 216 recognized by Christensen (1938), 251 by Ching (1940), 308 by Copeland (1947), 404 by Crabbe & al. (1975), and 435 by Pichi Sermolli (1977). The compilation edited by Kramer & Green (1990), published just prior to the molecular phylogenetic revolution, takes a more conservative approach, recognizing just 217 genera. This reduction was achieved by consolidating a large number of previously accepted genera, many of which were subsequently recognized as distinct in molecular analyses. For example, the Kramer & Green (1990) treatment of the genus *Polypodium* subsumed eight genera, of which five are maintained as distinct by PPG I (2016).

The higher-level classification of ferns by Smith & al. (2006) was the first to incorporate inferences from molecular data in addition to morphology and established a new standard in fern taxonomy (an analysis of research papers published in 2006 found it to be the most highly cited paper in all of botany, earning it a top spot in the inaugural Google Scholar list of classic papers). This classification recognized 278 genera—significantly more than Kramer & Green (1990), but many fewer than Pichi Sermolli (1977). It was followed by a linear sequence (Christenhusz & al., 2011) that took into account subsequent advances in our understanding of phylogenetic relationships and increased the generic count to 288. The community-based PPG I (2016) classification, published a decade after Smith & al. (2006), continued this trend, recognizing 319 fern genera.

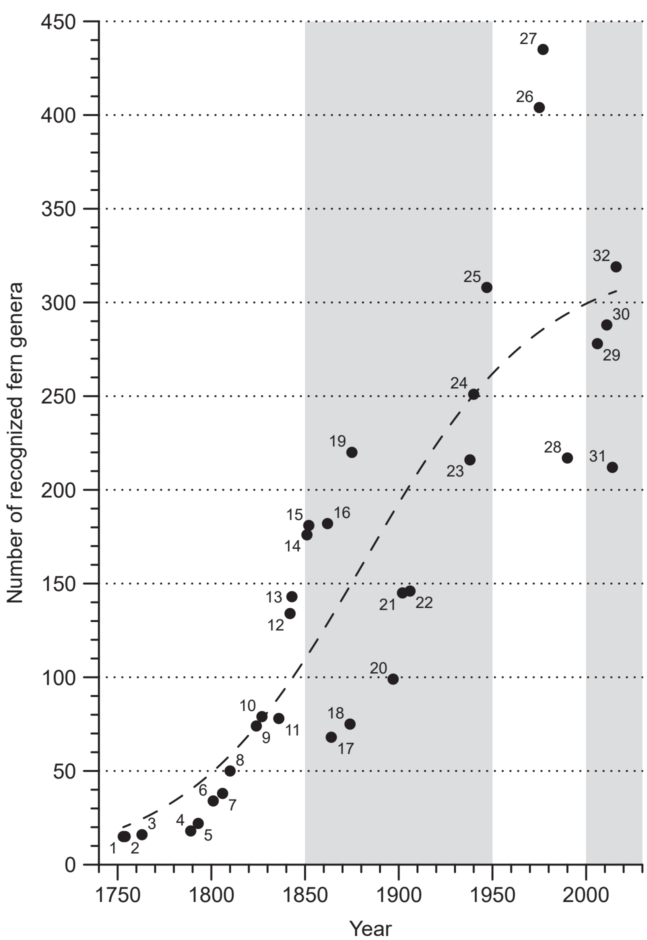

Fig. 1. Number of fern genera recognized in major classifications of extant ferns through time. Although the definition of "fern" has itself evolved, we have made every effort to maintain consistency with the current definition (sensu Pryer & al., 2004). Classifications published in multiple parts are plotted based on the date of completion. **1,** Linnaeus, 1753 (15 genera); **2,** Linnaeus, 1754 (15 genera); **3,** Adanson, 1763 (16 genera); **4,** Jussieu, 1789 (18 genera); **5,** Smith, 1793 (22 genera); **6,** Swartz, 1801 (34 genera); **7,** Swartz, 1806 (38 genera); **8,** Willdenow, 1810 (50 genera); **9,** Kaulfuss, 1824 (74 genera); **10,** Desvaux, 1827 (79 genera); **11,** Endlicher, 1836 (78 genera); **12,** Hooker, 1842 (134 genera); **13,** Smith, 1842a, b, c, d, 1843 (143 genera); **14,** Presl, 1836, 1843, 1845, 1847, 1851 (176 genera); **15,** Fée, 1852 (181 genera); **16,** Moore, 1857–1862 (182 genera); **17,** Hooker, 1846–1864 (68 genera); **18,** Hooker & Baker, 1874 (75 genera); **19,** Smith, 1875 (220 genera); **20,** Christ, 1897 (99 genera); **21,** Engler & Prantl, 1902 (145 genera); **22,** Christensen, 1906 (146 genera); **23,** Christensen, 1938 (216 genera); **24,** Ching, 1940 (251 genera); **25,** Copeland, 1947 (308 genera); **26,** Crabbe & al., 1975 (404 genera); **27,** Pichi Sermolli, 1977 (435 genera); **28,** Kramer & Green, 1990 (217 genera); **29,** Smith & al., 2006 (278 genera); **30,** Christenhusz & al., 2011 (288 genera); **31,** Christenhusz & Chase, 2014 (212 genera); **32,** PPG I, 2016 (319 genera). The dashed line indicates the best-fit logistic curve, corresponding to an expectation of an initial "discovery" phase that gradually tapers off to an equilibrium. The equilibrium estimate from the data is 324 genera (standard error of 44 genera), remarkably close to the 319 recognized in PPG I (2016).

The classifications of Smith & al. (2006), Christenhusz & al. (2011), and PPG I (2016) were products of an increased understanding of fern phylogeny, synthesizing a diversity of research publications in molecular phylogenetics. Such publications refined (and continue to refine) the collective knowledge of relationships within ferns (e.g., Pryer & al., 1995, 2001, 2004; Korall & al., 2006; Qiu & al., 2007; Schuettpelz & Pryer, 2007; Christenhusz & al., 2008; Rai & Graham, 2010; Kuo & al., 2011; Lehtonen, 2011; Rothfels & al., 2012, 2015b; Testo & Sundue, 2016; Wei & al., 2017; Shen & al., 2018), with some contributions favoring the recognition of new genera (e.g., Sundue & al., 2010; Hirai & al., 2011; Li & al., 2012; Grusz & Windham, 2013; Cochran & al., 2014; Mynssen & al., 2016; Zhang & al., 2016) and others arguing for consolidation (e.g., Wang & al., 2010; McKeown & al., 2012; Zhang & al., 2012; Wei & Zhang, 2014; Zhang & al., 2015; Tsutsumi & al., 2016; Chen & al., 2018). In aggregate, since Smith & al. (2006), there has been a distinct trend towards better supported and more explicitly justified classifications, and a strong, albeit not universal, consensus as to the families and genera recognized.

A notable exception to the emerging consensus was the scheme put forward by Christenhusz & Chase (2014) only three years after the publication of Christenhusz & al. (2011). In a reversal reminiscent of Hooker (1842 versus 1846–1864), the authors chose to accept only 212 broadly defined genera. Instead of basing their classification on a synthesis of the available literature, they presented an idiosyncratic treatment that purported to aim for a stable familial and generic classification of ferns, while simultaneously altering the recognition or circumscription of 26 families and at least 93 genera (relative to Christenhusz & al., 2011). Contrary to the assertion in Christenhusz & al. (2018) that the Christenhusz & Chase (2014) classification is "in line with historical treatments of genera", its 212 genera make it a clear outlier (Fig. 1). Instead, it is the community-driven PPG I (2016) that appears to be in step with the historical trajectory of fern classifications.

Through time, the overall increase in the number of recognized fern genera has paralleled a concomitant increase in the number of described species. Today, it is widely accepted that there are approximately 10,500 fern species, with remarkably similar estimates provided in Christenhusz & Chase (2014) and PPG I (2016). The 212 genera recognized by Christenhusz & Chase (2014) and 319 genera recognized by PPG I (2016) thus translate to averages of 50 or 33 species per genus, respectively. Both averages are considerably higher than those for other groups of plants and animals (Table 1), with the Christenhusz & Chase (2014) number being particularly extreme. While patterns of diversity vary among taxa, and norms vary among taxonomic communities as to how to allocate diversity to Linnaean ranks, these comparisons suggest that the PPG I (2016) classification is again more consistent with historical trends in classification (even beyond ferns) than is that of Christenhusz & Chase (2014).

Historical trajectory and broader comparisons aside, we agree with the stated aims of Christenhusz & Chase (2014) and Christenhusz & al. (2018) that taxonomic stability is an important consideration in classification. However, it seems we have some fundamental differences in philosophy with regard to how best to achieve such stability. Taxonomy and nomenclature exist to facilitate communication; if names are constantly changing, the result is confusion. That said, phylogenetic analyses often reveal evolutionary histories that conflict with traditional taxonomic concepts, exposing instances of evolutionary convergence and situations in which taxa were defined based on shared ancestral (as opposed to shared derived) characteristics. When such conflicts arise, systematists who use monophyly to circumscribe taxa have two options: split non-monophyletic taxa into more narrowly defined taxa, or lump them with others to yield more broadly defined taxa. There are numerous secondary criteria to evaluate when making such decisions, including diagnosability, homogeneity, predictability, and hierarchical equivalency in terms of both age and diversity, but when the taxa involved are genera, stability might be the most important consideration. Changing a genus name not only alters the taxon into which a species is placed, but also the species name itself (and sometimes also the specific epithet). Depending on the weight of all the evidence, it may sometimes be preferable to divide a genus, whereas in other cases less "damage" is done by subsuming one genus into another. Christenhusz & al. (2018) seem to believe that broadly defined genera are, in almost every case, the best path to stability, but this argument is undermined by the exceptional number of nomenclatural acts required to accommodate their concepts.

Taxonomic splitting and lumping can both pose problems with regard to diagnosability. More broadly defined taxa may unite disparate lineages without obvious morphological synapomorphies. Likewise, more narrowly defined taxa might only be definable with cryptic or microscopic characters. Although recognizing fewer genera may seem simpler from a pragmatic standpoint (fewer names for users to learn), such an approach is not necessarily more useful. To be sure, *Hemionitis* sensu Christenhusz & al. (2018) is a clade (one that is recognized in PPG I, 2016, as subfamily Cheilanthoideae), but for us that is its sole virtue as a taxonomic entity. The concept of *Hemionitis* favored by Christenhusz & al. (2018) is so morphologically heterogeneous as to be effectively undiagnosable, and is in no way consistent with their focus on "similarities rather than differences" and "morphologically well-defined" taxa. In fact, some genera resolved well outside of subfamily Cheilanthoideae (e.g., *Cosentinia* Tod. and *Pityrogramma* Link; Gastony & Rollo, 1998) are distinguishable from members of this clade only with the microscopic characters that Christenhusz & al. (2018) reject because they are not conducive to field identification. Although recent efforts to define monophyletic groups among the cheilanthoids have indeed destabilized traditionally recognized genera such as *Cheilanthes* Sw., *Doryopteris* J.Sm., and *Pellaea* Link, there is no greater act of destabilization than synonymizing all three under the genus *Hemionitis*, which has always been narrowly defined and requires 468 nomenclatural innovations to effectuate. Christenhusz & al. (2018) "suggest that the entire subfamily should be merged into a single genus, as all the taxa are recently evolved and hybrids across the clade are known" but these false assertions provide a striking illustration of why "generalists" (i.e., those who often lack detailed knowledge

Table 1. Average number of species per genus as calculated for various lineages across the tree of life.

Taxon	Species	Genera	Species per genus (average)	Reference
Millipedes	7,753	1,868	4	Shear, 2011
Birds	10,699	2,312	5	Gill & Donsker, 2018
Mammals	6,399	1,314	5	Burgin & al., 2018
Hemichordates	137	26	5	Cameron, 2016
Orthopterans	23,855	4,418	5	Ingrisch, 2011
Tapeworms	4,810	833	6	Caira & Jensen, 2017
Anthozoans	6,142	954	6	Crowther, 2011
Fishes	34,674	5,184	7	Eschmeyer & al., 2018
Crustaceans	66,914	9,522	7	Ahyong & al., 2011
Centipedes	3,233	431	8	Bonato & al., 2016
Thrips	5,864	767	8	Mound, 2011
Nematodes	24,783	2,829	9	Hodda, 2011
Reptiles	10,639	1,198	9	Uetz & al., 2017
Spiders	43,579	4,191	10	Dunlop & Penney, 2011
Springtails	8,130	762	11	Janssens & Christiansen, 2011
Sponges	8,346	722	12	Hooper & al., 2011
Scorpions	1,947	151	13	Prendini, 2011
Gymnosperms	1,079	83	13	Christenhusz & Byng, 2016
Beetles	386,500	29,500	13	Slipinski & al., 2011
Mosses	12,800	901	14	Crosby & al., 2000
Amphibians	7,810	549	14	AmphibiaWeb, 2018
Hymenopterans	153,088	8,423	18	Aguiar & al., 2013
Hornworts	220	12	18	Söderström & al., 2016
Liverworts	7,266	386	19	Söderström & al., 2016
Angiosperms	295,383	13,164	22	Christenhusz & Byng, 2016
Ferns	10,578	319	33	PPG I, 2016
Ferns	10,535	212	50	Christenhusz & Chase, 2014

or interest in a taxonomic group) such as Christenhusz & al. (2018) should not pursue major nomenclatural realignments. Rather than being recently evolved, this subfamily encompasses a diversity of deeply isolated elements, with a crown age for the clade estimated at 80–110 million years (Schuettpelz & Pryer, 2009; Testo & Sundue, 2016). Likewise, intergeneric hybridization is effectively unknown within the subfamily; the only reported case of intergeneric hybridization (a supposed hybrid between *Cheilanthes* and *Hemionitis*; Mickel, 1987, 1992) has been shown to involve two morphologically disparate but closely related species that are phylogenetically isolated from both *Cheilanthes* and *Hemionitis* (Pryer & al., 2016). It is interesting to note that Christenhusz & al. (2018) made no move to synonymize fern genera that have been unequivocally shown to hybridize, such as *Dryopteris* Adans. and *Polystichum* Roth (Wagner & al., 1992) or *Cystopteris* Bernh. and *Gymnocarpium* Newman (Rothfels & al., 2015a; see also Lehtonen, 2018).

Concerns very similar to those noted for subfamily Cheilanthoideae could be raised regarding the lumping of all grammitid (subfamily Grammitidoideae) genera into a single genus *Grammitis* with over 900 species or the lumping of about 1000 thelypterid (subfamily Thelypteridoideae) species into *Thelypteris*. Recognizing greater numbers of smaller genera fosters more precise and efficient communication, promotes additional research, and facilitates herbarium curation. Moreover, a finer separation enables a focus on key evolutionary attributes—morphological disparity that would be difficult to perceive when genera are defined too broadly. In other words, a comprehensive, scientifically based context (e.g., morphological, evolutionary, molecular, phytogeographical, or paleobotanical) is needed in taxonomic studies; the recircumscription of taxa should not be based on whimsy (e.g., naming dozens of ferns based on obscure characters and place names from Ende's *The neverending story* and Tolkien's *The Lord of the rings*).

What is particularly alarming about the Christenhusz & al. (2018) publication, given their purported desire for taxonomic stability (and previously in Christenhusz & Chase, 2014), is that stability in fern systematics was (and still is) finally within reach. With the ability to include evidence from molecules in addition to morphology, fern classifications beginning with Smith & al. (2006) have steadily moved towards a consensus, with each new classification (Christenhusz & al., 2011; PPG I, 2016; and myriad more narrowly focused examples) building on the earlier works and differing almost exclusively in those areas where new information had become available. Prior to Christenhusz & al. (2018), the sole exception to this trend was Christenhusz & Chase (2014). The claim that "the classification of ferns has been contentious in recent times" (Christenhusz & al., 2018) is wholly disingenuous—it has seemingly only been contentious to those authors. PPG I (2016) and other recent synthetic classifications have simply made explicit a consensus that already exists in the international fern community.

Despite occasional short-term reversals, the number of fern genera recognized in global classifications rose steadily for the first 200 years following the publication of *Species plantarum* (Linnaeus, 1753), most likely due to the increased availability of collections. Today, discoveries are still happening, driven largely by the availability of more powerful tools with which to study our collections, but it would appear we are beginning to see an asymptote (Fig. 1). The number of genera recognized in the PPG I (2016) classification is not an outlier, but rather a continuation of the historical trajectory. While Christenhusz & al. (2018) advocate for much broader generic concepts in ferns, our historical survey (Fig. 1) and data for lineages across the tree of life (Table 1) suggest that such broad concepts are out-of-step with past and present treatments. Classifications serve many purposes and will always be subjective, but most systematists would concur that a classification that is phylogenetically based, reflects finer-level relationships, and synthesizes the available data and taxonomic opinions ultimately best serves both specialists and generalists. Ferns are not out-of-line in this respect. Our analyses of trends within ferns and our comparisons to other groups indicate that fern genera are not too narrowly defined; if anything, there might not yet be enough fern genera.

■ AUTHOR CONTRIBUTIONS

Conceptualization: ES. Investigation: ES, GR, KMP & MDW. Writing (original draft): ES, CJR, JP & MAS. Writing (review and editing): ES, GR, KMP, CJR, JP, MAS, MDW, RCM & ARS. Visualization: ES & KMP. Supervision: ES.

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