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Author: Yatskievych, George

Source: *Lundellia*, 23(1) : 19-27

Published By: The Plant Resources Center, The University of Texas at Austin

URL: <https://doi.org/10.25224/1097-993X-23.1.19>

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# THE STATUS OF THE NON-NATIVE FERN *CHEILANTHES VIRIDIS* (PTERIDACEAE) IN THE UNITED STATES.

George Yatskievych

Billie L. Turner Plant Resources Center, University of Texas at Austin, Main Bldg, Rm 127, 110 Inner Campus Dr,  
Stop F0404, Austin, TX 78712-1711, U.S.A.  
Email: [george.yatskievych@austin.utexas.edu](mailto:george.yatskievych@austin.utexas.edu)

**Abstract:** *Cheilanthes viridis* (Pteridaceae), green cliffbrake, is reported as new to the floras of Texas and Louisiana. This African native has long been cultivated as an ornamental fern and likely escaped to become naturalized in eastern Texas and adjacent Louisiana. The expanding distribution of the taxon in Florida, Georgia, Louisiana, South Carolina, and Texas is discussed. Classification and taxonomy are also reviewed.

In 2016, Andy Newman, an observant contributor to the iNaturalist website (<https://www.inaturalist.org>), posted an image of a large colony of an unusual fern from a public greenway in the Houston, Texas, area. iNaturalist is a website at which citizen scientists and others post images that are then discussed and crowd-curated as to taxonomic identity. Mr. Newman's report engendered a lively discussion that resulted in the confirmation of these plants as *Cheilanthes viridis* (Forssk.) Sw. Over the next four years, additional reports have been added to the iNaturalist site, which currently contains about a dozen records from Texas. The present account thus does not represent the results of the author's personal explorations so much as an attempt to confirm and summarize data on the status of this plant in the continental United States, and to present a discussion on its taxonomy.

## DISTRIBUTION WORLDWIDE AND IN THE UNITED STATES

*Cheilanthes viridis* has a broad distribution in the South African region extending northward to Tropical East Africa and adjacent countries. Roux (2009) listed the following countries in mainland Africa from which *C. viridis* has been documented: Angola, Botswana, Burundi, Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Malawi, Mozambique, Namibia, Rwan-

da, Somalia, South Africa, Sudan, Swaziland, Tanzania, Uganda, Zambia, and Zimbabwe. He noted that the native range of the species extends to the Comoro Islands, Madagascar, Mascarene Islands, and Socotra. The range extends farther northward into mainland Yemen and the island of Socotra (Miller, 1996). In Macaronesia, the taxon supposedly is a disjunct native in the Cape Verde Islands (Lobin et al., 1998), but is considered introduced in the Azores and Madeira (Vieira, 2002; Aldasoro et al., 2004). It has also become widely naturalized elsewhere, including eastern Australia (Bostock, 1998), New Zealand (Webb et al., 1995), Bangladesh and India (Fraser-Jenkins et al., 2017), Hawaii (Wilson, 2002), and the southeastern United States and Texas (discussed below).

In Brazil, *Pellaea flavesceus* was described as an endemic native species by Fée (1869), but this taxon recently was shown to be identical to *C. viridis* (Prado et al., 2013), based on molecular and other data. Prado et al. were unable to decide whether the Brazilian populations should be regarded as an intercontinental disjunction (Moran and Smith, 2001) or an early introduction into the Brazilian flora. As the species has become established from escapes in other areas far removed from its native range, this is not outside the realm of possibility.

There are a number of specimens in herbaria from the continental United States dating to the 1930s, but all are from plants



FIG. 1. Portion of a large colony of *Cheilanthes viridis* growing at edge of grove of *Ilex vomitoria*, with grasses, *Rudbeckia*, and *Monarda*; Bastrop County, Texas.

in cultivation in gardens or greenhouses. The earliest voucher to document *Cheilanthes viridis* growing spontaneously dates to 1985 from Georgia. Other reports are all more recent and likely represent independent escapes. The oldest herbarium specimens representing plants in the wild include: South Carolina, 1992; Florida, 1999, Texas, 2019; and Louisiana, 2020. Thus far, specimens from outside of cultivation have only been collected in these five states. Botanists in other southeastern states, as well as in southern California, should be on the lookout for additional naturalized populations. The species was treated for Florida by Wunderlin and Hansen (2000), who did not cite specimens or comment that this represented the first report of the taxon for North America. The Georgia occurrence was included by Weakley (2012) in his regional floristic treatment of southeastern states.

Ecologically, the North American populations of *C. viridis* occur in a variety of habitats. Plants tend to grow terrestrially in acidic, often sandy (but sometimes loamy) soils or epipetrically from crevices of sandstone outcrops. In Louisiana, plants in the sole population documented thus far grow associated with timbers of an old bridge over a stream in a forested area. Insolation varies from full to partial shade. At least in Texas, the species may be limited ecologically by periods of prolonged drought and latitudi-

nally by excessively cold winter freezes. Existing populations in the United States occur in areas of U.S.D.A. Plant Hardiness Zone 8A and higher (<https://planthardiness.ars.usda.gov>), which includes much of the southeastern United States north to the southern half of Arkansas, and northward along the Eastern Seaboard through eastern South Carolina. Thus, it seems likely that the species has not yet fully occupied its potential climatic niche. Where they occur, plants are frequently relatively abundant and can form dense populations along the margins of wooded areas (Fig. 1). These areas are subjected to at least moderate seasonal drought-stress.

It is unclear whether the species should be considered an invasive exotic. On the one hand, the dense stands of plants that can develop over time almost certainly impact other herbaceous plants and seedlings of woody plants negatively. On the other hand, the species is still known from relatively few populations and tends to be localized in a fairly small proportion of available habitat. Landowners should observe the species to monitor potential future spread. Although green cliffbrake is no longer widely grown in gardens and in greenhouses, it is still available commercially from various plant nurseries. Thus, the potential for new escapes from cultivated materials continues to exist.

As noted below, the species has been subdivided into a number of infraspecific taxa, two of which have escaped in the United States. The South Carolina material was determined as var. *macrophylla* by David Lellinger in 1992. All of the specimens studied from other states thus far are referable to var. *viridis*.

REPRESENTATIVE SPECIMENS (VAR. *VIRIDIS*): **UNITED STATES. Florida:** Hernando Co.: About 4.3 miles SW of U.S. Hwy. 98 junction with Interstate 75, on E side of highway; 1.05 miles NW of Harris Hill Rd./ Lockhart Rd. intersection, 28.464269°, -82.268425°, disturbed pine-oak-hickory forest with *Quercus virginiana*, *Q. laurifolia*, *Asplenium platyneuron*, 18 Apr 2018, P. Diamond 2375 (USF). Hillsborough Co.:

Ca. 0.75 mi. SE of Howard's Prairie. T32S, R21E, Sec. 36, SW¼ of NE¼, ditchbank in relatively sandy soils, with some young *Quercus nigra* and *Q. laurifolia*, Apr 2002, *M. M. James s.n.* (USF); Lithia, several plants in wet woods, 29 Aug 1999, *C. Watson s.n.* (USF). Sumter Co.: From intersection of Durden Road and Coit Road travel E 1.6 mi. on Coit Road, walk ca. 245 ft. N to site; plants are ca. 295 ft. E of Withlacoochee River, hydric hammock, moist soils, with *Oplismenus* spp., *Nephrolepis cordifolia*, and *Mitchella repens*, shade under *Quercus* sp., *Magnolia grandiflora*, T23S, R22E, Sec. 20, Lacoochee Quad, 28° 27' 52.66" N, 82° 8' 10.904" W, 23 Oct 2015, *E. Williamson s.n.* (USF). Leon Co.: Frequent (naturalized plants of varying ages) in shaded, moist loamy soil of Governor's Park Hidden Woods (old-growth beech-magnolia-oak remnant with many exotics), S of Waldo Palmer Ln off Mahan in Tallahassee, 30.45017° N, 84.23278° W, 11 Dec 2012, *L. C. Anderson & W. Baker 25357* (FSU, 2 sheets). **Georgia:** Coffee Co.: On small ledge of indurated sand/clay of Altamaha Formation (Altamaha "Grit"), 220 ft., ca. 1 mi. due NW of falls on Rocky Creek; ca. 1 mi. S of GA Hwy 107 and 1.5 mi. W of Jeff Davis Co. line, Broxton NE Quad, 28 June 1989, *F. Snow & E. Carter s.n.* (DUKE, UGA); Vicinity of Broxton, crevices and shallow soil accumulations, small outcrop of Altamaha Grit sandstone, 2 May 1992, *J. Allison & F. Snow 6463* (UGA). DeKalb Co.: Tucker, residential lot, solitary plant, [escape], 1.5 ft., sandy loam, SW aspect, slope 0–5%, pine-hardwood habitat, understory loblolly pine, sweetgum, post oak, hickory, yellow poplar, dogwood, sweetshrub, *Potentilla*, 1000 ft., 1 June 1985, *L. Lacher s.n.* (UGA). Lowndes Co.: Kinderloun Plantation, 1.98 air miles SW of farm headquarters (heading 211.72°), edge of mixed hardwood-pine woods and old field, plants local in disturbed clayey loam, 30.77136° N, 83.39382° W, 23 Sep 2009, *R. Carter & W. W. Baker 19620* (VSC). **Louisiana:** Calcasieu Par.: Approx. 6.5 aerial miles SSE of DeQuincy, 10 mi. W of Gillis and 2.5 E of LA Hwy 27; 30.373633°; -93.367524°; growing on a

wooden creosote bridge crossing Little River in a secondary growth small stream forest with surrounding land being utilized for short rotation pine cultivation, 15 July 2020, *C. Doffitt & B. Gregory 3720* (BRIT, LSU, TEX).

REPRESENTATIVE SPECIMENS (VAR. *MACROPHYLLA*): **UNITED STATES. South Carolina:** Richland Co.: Fairly abundant on sandy ground (escaped?) below office building on W side of Marion Ave, opp. Moncrief Hospital, Fort Jackson Army Installation, 16 Feb 1992, *J. B. Nelson 12091* (TENN, USCH); Fort Jackson Army Installation, persisting after cultivation (?) below TRADOC Mgt Bldg along Jackson Blvd, near main HQ, 26 June 1992, *J. B. Nelson & D. Kennemore 13065* (USCH).

#### STATUS IN TEXAS

Records of *Cheilanthes viridis* are mainly from the Houston metropolitan area in Harris and Montgomery counties. An online report from Travis County could not be relocated in the field during a search by the author in 2019. However, the single population known from Bastrop County remains extant and, in fact, is increasing. It seems likely that the fern will continue to attempt to colonize new sites and expand its range outside of its known naturalized distribution in the state.

In the Houston area, plants currently seem to be most abundant in the Spring Creek Greenway and adjacent Jesse H. Jones Park and Nature Center in Harris County; and in and around the William Goodrich Long State Forest in Montgomery County. However, there is no reason to believe that the species has not become established elsewhere in East Texas, especially on privately owned properties that are inaccessible to naturalists.

*Cheilanthes viridis* is fairly distinctive within the fern flora of Texas. The only species with which it could be confused is the native *Pellaea atropurpurea* (L.) Link (purple cliffbrake). That species differs in its concolorous rhizome scales; somewhat more dimorphic fronds; pinnules that are discrete

and a bluer green color; and rachis rounded adaxially (non-sulcate), but with two parallel rows of dense, short, crispate trichomes adaxially. *Pellaea atropurpurea* also tends to have ascending rhizomes and a preference for calcareous substrates. It is widespread in temperate North America and southward through Mexico to Guatemala. For a recent treatment of this species in Texas that includes discussion, drawings, and photographs, see Diggs and Lipscomb (2014).

The following treatment serves to circumscribe the morphology of *Cheilanthes viridis* as it occurs in Texas and to contrast with the features listed above for *P. atropurpurea*:

***Cheilanthes viridis* (Forssk.) Sw., Syn. Fil. 127. 1806.**

*Pteris viridis* Forssk., Fl. Aegypt.-Arab. 186. 1775.

TYPE: **YEMEN**. Montium Hadiensium, *P. Forsskal* s.n. (lost). A lectotype or neotype has yet to be designated.

*Pteridella viridis* (Forssk.) Mett. ex Kuhn in Decken, Reis. Ost-Afr. 3(3 [Bot.]): 16. 1879.

*Pellaea viridis* (Forssk.) Prantl, Bot. Jahrb. Syst. 3: 420. 1882.

*Allosorus viridis* (Forssk.) Kuntze, Revis. Gen. Pl. 2: 806. 1891.

*Adiantum viride* (Forssk.) Vahl, Symb. Bot. 3: 104. 1894.

*Oeosporangium viride* (Forssk.) Fras.-Jenk. & Pariyar, Annot. Checkl. Ind. Pterid. 1: 263. 2016.

*Hemionitis viridis* (Forssk.) Christenh., Global Fl. 4: 22. 2018.

For additional synonymy, see Roux (2009).

**Rhizomes** short-creeping, usually unbranched, 4–6 mm in diameter, internodes very short, scaly distally; scales 3–4 mm long, linear-lanceolate, sometimes with abruptly broadened, auricular bases, apices attenuate, margins irregularly and minutely toothed; bicolorous, central stripe narrow and brown to broad and nearly black, matte to slightly shiny, marginal bands hyaline. **Fron**ds appearing tufted, to 70 cm, erect to

arching. **Stipe** ca.  $\frac{1}{2}$  as long to about as long as lamina, castaneous, adaxially slightly flattened proximally grading to shallowly sulcate distally, margins of sulcus lighter brown; with scattered scales near base, these grading from similar to rhizome scales to linear,  $\pm$  concolorous, and entire, also with appressed to somewhat tortuous 1-seriate, multicellular trichomes 0.3–0.6 mm long; glabrescent medially and distally but often with minute (0.1–0.4 mm) glandular trichomes in sulcus. **Lamina** to 40 cm, narrowly to broadly lanceolate-triangular in outline (basal pinnae usually largest and basal-basiscopically somewhat enlarged), 2-pinnate to 2-pinnate-pinnatifid or 3-pinnate,  $\pm$  monomorphic (fertile pinnules sometimes slightly narrower than vegetative ones), herbaceous to slightly chartaceous, rachis, costae, and costules sulcate adaxially, castaneous to nearly black color passing into pinnule bases; ultimate segments (except terminal ones) short-stalked, generally relatively planar (except when drought-stressed), the costules with minute (0.05–0.3 mm),  $\pm$  spreading, gland-tipped, unicellular to multicellular trichomes concentrated adaxially; lateral pinnules variously oblong-ovate to narrowly triangular-lanceolate, bases broadly to narrowly cuneate or slightly acuminate, tips bluntly to sharply acute to attenuate; terminal pinnules similar or more commonly with 1–3 proximal lobes; surfaces glabrous or dorsal glandular trichomes from stalk extending slightly onto laminar tissue; margins minutely crenulate; venation easily observed, free, secondary veins mostly branched dichotomously 1–3 times, arched outward, vein endings unthickened, extending between crenulations and into pseudindusium. **Pseudindusium** well-differentiated, not covering sporangia at maturity, a continuous abaxial band at bases of crenulations, hyaline from a green basal region, appearing somewhat corrugated, narrow (0.4–0.5 mm), glabrous, margin entire. **Sporangia** in a continuous, narrow, submarginal, abaxial soral line adjacent to pseudindusium; 32-spored. **Spores** triangular-globose, 35.7–57.6  $\mu$ m in diameter



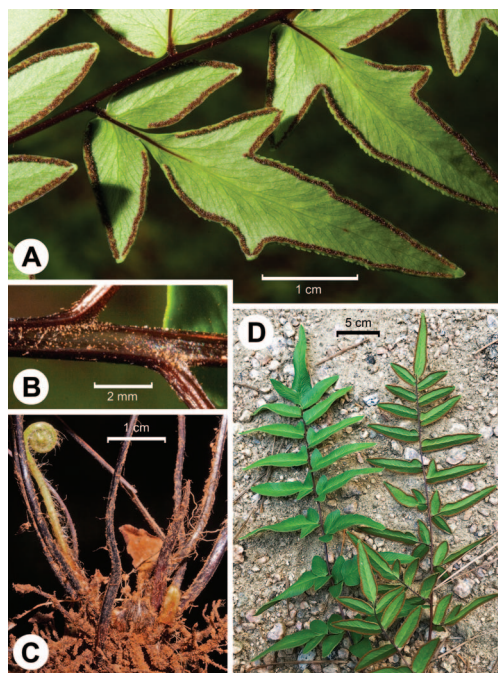


FIG. 2. Selected details of *Cheilanthes viridis* morphology. A. Portion of fertile lamina showing lobed terminal segments, crenulate segment margins, inconspicuous pseudoindusia, and easily visible venation. B. Portion of sulcate adaxial costa and costule. C. Base of plant with horizontal rhizome, fiddlehead, and stipe bases. D. Laminar portions of fertile fronds showing abaxial and adaxial sides. A–C, Bastrop County, Texas. D, Harris County, Texas.

( $\bar{X} = 43.9$ ,  $SD \pm 5.03$ , based on measurements of 20 random spores mounted in glycerine), trilete with relatively prominent scar, surface irregularly and finely cristate-echinate, brown. Figs. 1, 2.

For a detailed line drawing, see Burrows (1990). As noted elsewhere, Texas collections are all referable to var. *viridis*.

#### SPECIMENS EXAMINED: UNITED STATES.

**Texas:** Bastrop Co.: Welch property, on E side of Split Oak Drive N of junction with High Crossing Road (County Road 305); near S end of property; large parcel with formerly grazed prairie openings on reddish sandy soil and groves of *Pinus*, *Juniperus*, *Ilex*, *Quercus*, in partial shade along margin of grove of trees, with *Monarda*, *Clitoria*,

*Coreopsis*, *Rubus*; in dark loamy soil; elev. 500 ft.; 29.95538° N, 097.23573° W, 21 June 2020, G. Yatskievych, K. Welch & J. Curry 20-024 (MO, TEX). Harris Co.: S parcel of Kleb Woods Nature Preserve, on SW side of intersection of Draper Road and Mueschke Road, ca. 6 air miles NNW of Cypress; disturbed clearing in pine woodland; with scattered *Morus*, *Ilex*, grasses, *Elephantopus*; in full sun and partial shade, in sandy loam soil; elev. 268 ft; 30° 04' 13.3" N, 095° 44' 17.9" W, 24 Oct 2019, G. Yatskievych, A. Black & M. Ahlgren 19-075 (MO, TEX). Montgomery Co. William Goodrich Jones State Forest, N of Gravel Pit Trail, 30.23° N, 95.49° W, 22 May 2020, E. Duran s.n. (BRIT, MO, TEX); William Goodrich Jones State Forest (Texas A&M Forest Service), Conroe, 1328 Road FM 1488; in a dry drainage ditch adjacent to service road within fire-maintained, second growth loblolly pine (*Pinus taeda*) forest, S of WG Trail; elev. 227 ft; 30.235685° N, 095.488004° W, 16 June 2020, C. Murnane, A. Clapp, L. Alfaro & A. Saenz s.n. (MERCA, TEX).

#### TAXONOMY AND CLASSIFICATION

As with many species belonging to Pteridaceae subfam. Cheilantheoideae (the cheilanthoid ferns), the generic affiliation of the green cliffbrake has been problematic. It was originally described as *Pteris viridis* by Forsskål (1775), but since then has at times been treated as a member of several diverse genera, including: *Adiantum*, *Allosorus*, *Cheilanthes*, *Hemionitis*, *Oeosporangium*, *Pellaea*, and *Pteridella* (see above). This is a reflection of controversies in the classification of genera of Pteridaceae, rather than a particular issue with the morphology of this species. Most older floristic works on African ferns have treated it as *Pellaea viridis* (Forssk.) Prantl (e.g., Schelpe, 1970). However, Tryon and Tryon (1982), Anthony and Schelpe (1982), and Anthony (1984) restricted the African cohort of *Pellaea* taxa to those with discrete terminal pinnae (vs. fronds with lobed to pinnatifid terminal segments) and reclassified the green cliffbrake and several others to *Cheilanthes*.

Tryon et al. (1990) noted that such revisions to narrow the circumscriptions of cheilanthoid genera such as *Pellaea* had the consequence of rendering *Cheilanthes* more heterogeneous and difficult to define. The name *Cheilanthes viridis* (Forssk.) Sw. has been accepted by most subsequent authors (e.g., Burrows, 1990; Roux, 2009).

Classification of genera in Pteridaceae subfam. Cheilantheoideae remains problematic. As noted by Yatskievych and Gastony (2001) and others, homoplasy is very high within the group. In large measure, this has resulted from adaptations to seasonally dry environments that have occurred repeatedly in different lineages, coupled with a number of taxonomic radiations, resulting in a hyperdiverse assemblage of more than 425 species present on 6 continents (Pteridophyte Phylogeny Group, 2016), and with six main biogeographic centers of diversity (Tryon and Tryon, 1972). Additionally, polyploidy and apomixis are rampant within the subfamily.

Thus far, there has not been a molecular phylogenetic study of cheilanthoid ferns published that is sufficiently comprehensive for taxon or marker sampling to allow adequate resolution of all component lineages across the subfamily. Instead, there mostly has been a number of more restricted studies that have emphasized regional cohorts of taxa or have attempted to circumscribe small, relatively well defined genera within the six major clades in the subfamily (Windham et al., 2009). The initial broad survey of three plastid markers across the entire family Pteridaceae (Schuettpelz et al., 2007) included only 17 cheilanthoid taxa, but placed *C. viridis* sister to a species of *Doryopteris* in a different lineage than the other sampled taxa of *Cheilanthes* and *Pellaea*. Kirkpatrick's (2007) molecular study of non-monophyly among subgroups of *Pellaea* similarly placed *C. viridis* at some distance on her trees from the core lineage of *Pellaea*. To date, the only regional study that has focused on African cheilanthoid taxa (Eiserhardt et al., 2011) involved sequence data from five plastid marker regions to examine phylogeny in the context of taxo-

nomic radiations within the Cape Floristic Province. This study sampled 22 species present in South Africa within a matrix of 175 total in-group taxa. The study hypothesized three different species radiations in South Africa. *Cheilanthes viridis* was one of seven morphologically diverse taxa in their African Clade 3, which was sister to a largely South American group that included members of the genera *Doryopteris*, *Lytoneuron*, and *Ormopteris*. The study was inconclusive as to the generic-level classification of African taxa of Pteridaceae, but it did provide data to dispute traditional circumscriptions of cheilanthoid fern genera in Africa.

Given the difficulties in circumscribing monophyletic generic groups within the cheilanthoid ferns and in differentiating lineages within the subfamily morphologically, pteridologists have tended to be relatively polarized in the number of genera they have been willing to accept. In the 20<sup>th</sup> Century, the two main competing systems of classification were those of Rodolfo Pichi Sermolli (1977), who accepted about 40 genera (in three families), and Rolla Tryon, who accepted between 12 and 16 genera in a single tribe or subfamily of Pteridaceae at various times (Tryon and Tryon, 1982; Tryon et al., 1990). Setting aside a small number of misclassified genera in each system, Tryon's taxonomic philosophy still encompassed far fewer, more broadly circumscribed genera than that of Pichi Sermolli. More recent taxonomists, with the benefit of molecular data and many more collections, have been as polarized. The pteridological community-based consensus classification of the Pteridophyte Phylogeny Group (2016) accepted 23 genera of cheilanthoid ferns. At the opposite extreme, Maarten Christenhusz (in Christenhusz et al., 2018) reduced the entire suite of cheilanthoid ferns to a single genus, *Hemionitis*. However, the trend among most specialists has been to further dissect genera more finely (e.g., George et al., 2019) rather than combining them into larger taxonomic units. Regardless of the philosophy followed, morphological circumscription of mono-

phyletic groups within the cheilanthoid ferns remains problematic despite decades of study by some of the world's most eminent pteridologists.

That said, Prado et al. (2013) noted that the members of the *Cheilanthes viridis* complex need to be accommodated in some genus other than *Pellaea* or *Cheilanthes*, as they are phylogenetically distant from the types of those genera. Thus far, an existing generic name has not been located for this group, and it seems likely that the *Cheilanthes viridis* complex eventually will be segregated into a newly named genus following more detailed study.

Green cliffbrake is one of nearly 50 African species attributed to *Cheilanthes* by one or more authors (Roux, 2009). The majority of this group is endemic to South Africa, but the native range of *C. viridis* is broader, extending into the Middle-East. Within the group, taxonomic relationships are poorly understood, and morphologically defined species groups are discordant with those defined in the molecular analysis of regional taxa (Eiserhart et al., 2011). Additionally, many of the presently accepted species appear to represent cryptic complexes involving multiple ploidies and sexual vs. apomictic life histories. Ultimately, resolution of the various entities comprising the *C. viridis* complex will require intensive studies of variation in cytology and population genetics, combined with re-analysis of morphological variation. Likely, a molecular-based framework will be needed to confirm that the delineated taxa share a close ancestry and are not the result of convergence.

Morphologically, *C. viridis* has been divided into three or more varieties, some of which (such as var. *obscura* N.C. Anthony) are now referred to other species and others are generally regarded as trivial variants (such as *P. viridis* var. *canonica* (Kunze) Verdc., with less well-developed sulci and relatively small pinnules). Those that remain associated with *C. viridis* differ in details of rachis and pinnule morphology and vestiture, as well as quantitative details of plant and pinnule size. However, a

number of authors have noted common intermediates for all of the characters said to separate them (Burrows, 1990; Verdcourt, 2002; Crouch et al., 2011). The nominate infrataxon, var. *viridis*, is morphologically variable, but defined by the following character trends: laminae generally 2–3-pinnate (occasionally more divided in its native range), stipes relatively shallowly sulcate (Fig. 2B) and glabrescent distally; basal pinnae tending to be more developed basiscopically than acroscopically; and branch points of costae and costules bearing inconspicuous, gland-tipped trichomes that sometimes extend slightly onto the pinnule bases. Compared with var. *viridis*, plants attributed to var. *macrophylla* (Kunze) Schelpe & N.C. Anthony have laminae that are 1–2-pinnate and tend to be more consistently broadly deltate-triangular in outline, with ultimate segments that tend to be somewhat larger. Plants attributed to var. *glauca* (Sim) Schelpe & N.C. Anthony tend to differ from var. *viridis* as follows: laminae 2–4-pinnate, stipes more deeply sulcate with better-developed, lighter-colored, winglike margins and more persistently scaly; basal pinnae tending to be more equally developed basiscopically and acroscopically; and branch points of costae and costules lacking gland-tipped trichomes.

Plants attributed to var. *viridis* occur throughout the species' range. Plants attributed to var. *macrophylla* and var. *glauca* have been documented from scattered points within the African portion of the range. Crouch et al. (2011) noted that var. *viridis* and var. *macrophylla* tend to occur in shadier wooded sites, whereas var. *glauca* tends to be found in sunnier open places. The var. *viridis* comprises an uncommon, 64-spored, putatively sexual phase and more abundant, 32-spored, putatively apomictic populations. Chromosome counts to assign ploidies to these variants have not been made. The distributions of the races also have not been mapped, although it is notable that 64-spored sporangia correspond to the majority of specimens determined as var. *macrophylla* and a small minority of those determined as var. *viridis*,



whereas all of var. *glauca*, most of var. *viridis*, and a minority of specimens of var. *macrophylla* are 32-spored. It should be noted that North American specimens studied thus far, which include only the Texas and Louisiana populations, have all produced 32-spored sporangia.

#### ACKNOWLEDGMENTS

Chris Hoess first brought this taxon to the author's attention. He and others contributed to discussions on *Cheilanthes viridis*, including Pete Diamond, Eric Keith, and David Lorence. Chris Doffitt, Eric Duran, Beau Gregory, Connor Murnane, and Anita Tiller kindly assisted with the collection and processing of specimens. Thanks to the Texas A&M Forest Service and Kleb Woods Nature Preserve for granting permission for samples to be collected on their lands. Kindra Welch and John Curry generously hosted a visit to their family's property in Bastrop County. Megan Ahlgren and Adam Black were equally generous with their time and knowledge during a collecting trip to Kleb Woods Nature Preserve in Harris County. The manuscript benefited from the incisive edits and comments of two expert reviewers: Barney Lipscomb and Robbin Moran. The SEINet, iDigBio, and iNaturalist web sites continue to be a motherlode of online data and images for everyone interested in natural history, including this botanist.

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