

## The Fern Genera *Vittaria* and *Trichomanes* in Indiana

GEORGE YATSKIEVYCH<sup>1</sup>

Department of Biology

Indiana University

Bloomington, Indiana 47405

MICHAEL A. HOMOYA

Indiana Department of Natural Resources

Indianapolis, Indiana 46204

DONALD R. FARRAR

Department of Botany

Iowa State University

Ames, Iowa 50011

When Deam's *Flora of Indiana* (4) was first published in 1940, it included 57 species of pteridophytes in 24 genera. Ten years later, Clevenger (2) reported 61 total species, still in 24 genera. Today a taxonomically conservative count would yield ca. 73 species in 26 genera. Two self-evident reasons account for the increased number of pteridophytes now recognized to grow in Indiana. The first is that our understanding of species limits among temperate North American ferns has changed dramatically since the publication of Deam's flora, with an increasingly large number of taxonomic and evolutionary studies on these plants (e.g., 12, 21). In addition, new distributional records have resulted from continuing field work by a number of collectors in the state (e.g., 10, 13). The realization that our knowledge of Indiana's fern flora remains incomplete and inexact for many taxa has prompted this report, which concerns three taxa in two genera newly found in the state in recent years.

### **Vittaria**

The genus *Vittaria* (Vittariaceae) comprises ca. 50 primarily epiphytic tropical species (20), of which *V. lineata* J. Smith, whose range presently extends to northern Florida, was once thought to be the only extratropical member. It is now known that gametophytes of a *Vittaria* species exist independently of the sporophyte generation and are distributed as far north as northern Ohio and southwestern New York (8, 18). These gametophytes were originally thought to belong to the filmy fern genus *Hymenophyllum* (23), but were later assigned to *Vittaria* (22). The biology and biogeography of these plants have since been studied in some detail (5-9), although the distribution and habitat requirements of Indiana populations have previously not been published upon.

The Appalachian *Vittaria* gametophytes, as they are commonly known, were first reported for Indiana from a single locality in Crawford County (11). Two subsequent reports (9, 16) made brief mention of records from Martin and Perry Counties, without citation of localities or vouchers. Specimens from all presently known stations in the state are listed in Table 1.

Plants are found at sites where temperature and edaphic conditions remain relatively constant year-round. Non-calcareous substrate is essential for establishment and growth. Elsewhere, *Vittaria* gametophytes have been found growing on a variety of substrate types, including sandstone, quartzite, schist, gneiss, slate, shale, coal, and rarely wood (7), but in Indiana they have thus far been found associated only with the massive Pennsylvanian and (to a lesser extent) Mississippian-age sandstone outcrops in the Crawford Upland Section of the Shawnee Hills Natural Region (15). In places where continuous outcrops form series of bluffs or cavernous rock-houses, populations are found under moist overhangs where high humidity and stable, cool temperatures prevail. Normally such

TABLE 1. Specimens documenting the distribution of *Vittaria* and *Trichomanes* in Indiana. Vouchers are accessioned either at the Deam herbarium of Indiana University (IND) or the herbarium of the Department of Botany, Iowa State University (ISC).

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*Vittaria* sp. (gametophytes):

Crawford Co. ca. 1 mi. east of Perry Co. line on State Hwy. 62, 12 July 1969, *Farrar 1263 1264* (ISC), 10 Nov. 1981, *Farrar 81-11-10-2, 81-11-10-3* (ISC), 10 May 1986, *Yatskievych & McCrory 86-50* (IND); 1 mi. west of West Fork on State Hwy. 37, 8 May 1971, *Wagner 71087* (ISC); Yellow Birch Ravine, ca. 1 mi. southeast of Taswell on rd. to Mifflin, 11 Sep. 1983, *Yatskievych & McCrory 83-283* (IND); bluffs southeast of Mifflin and southwest of Otter Creek, 1 May 1976, *Gastony 1102* (IND), 14 Sep. 1982, *Yatskievych & Gastony 82-238* (IND); Hemlock Cliffs, west of Grantsburg, 13 Nov. 1981, *Farrar 81-11-13-1, 81-11-13-2* (ISC), 14 Sep. 1982, *Yatskievych & Gastony 82-237* (IND).

Martin Co. East Fork White River, 4.2 mi. north of Shoals, 11 Nov. 1981, *Farrar 81-11-11-3* (ISC); west bank of East Fork White River, ca. 1 mi. south of Shoals, 16 Jan. 1983, *Yatskievych & McCrory 83-21* (IND); small southern tributary of Plaster Creek, just west of Jackman Hill Rd., ca. 5 mi southwest of Shoals; 14 Oct. 1984, *Yatskievych & McCrory 84-185* (IND).

Perry Co. Penitentiary Rocks, near Mt. Pleasant, 13 Nov. 1981, *Farrar 81-11-13-4, 81-11-13-5* (ISC); Abbot's Hollow, ca. ½ mi. west of Branchville, 17 Oct. 1982, *Yatskievych & McCrory 82-258* (IND.); Rich Cave Hollow, off Jubin Creek, ca. 1½ mi. north of Branchville, 17 Oct. 1982, *Yatskievych & McCrory 82-259* (IND); Rockhouse Hollow, ca. 3 mi. northwest of Derby, 12 Nov. 1986, *Homoya, Guindon, and Springarn 86-11-12-105* (IND).

*Trichomanes boschianum* (sporophytes):

Crawford Co. Yellow Birch Ravine, 22 May 1977, *Swayne & Swayne 77-Ind-9* (IND).

Martin Co. Plaster Creek watershed, 31 May 1984, *Homoya, Engle, Huffman & Hutchison s.n.* (IND).

*Trichomanes* sp. (gametophytes):

Crawford Co. ca. 1 mi. E of Perry co. line on State Hwy. 62, 12 July 1969, *Farrar 1265* (ISC).

Martin Co. East Fork White River, ca. 1.3 mi. northeast of Shoals, 2 May 1965, *Farrar 1007, 1008, 1009* (ISC); ca. 5 mi. southeast of Shoals, 50-100 ft. from end of box canyon, 2 May 1965, *Farrar 1010* (IND, ISC), *1011, 1012* (ISC).

Montgomery Co. Shades State Park, small tributary to Sugar Creek, 16 July 1968, *Farrar 1178* (ISC).

Perry Co. State Hwy. 62, 1 mi. west of junction with State Hwy. 145, 10 Nov. 1981, *Farrar 81-11-10-1* (ISC).

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localities exhibit at least partial zonation with respect to light intensity, the *Vittaria* gametophytes occupying sites receiving less light than most mosses and liverworts require, and more light than some species of green and blue-green algae.

Appalachian *Vittaria* gametophytes occur in long-lived colonies of various densities and sizes, often discontinuously occupying the uneven contours of their substrate. Individual plants start out as few-celled filaments, but soon grow into irregularly lobed ribbon-like thalli, mainly one cell thick, and enlarging by numerous marginal meristems (Figure 1a). Plants are roughly differentiated into two parts (7). Short basal areas, anchored by hairlike unicellular rhizoids are appressed to and often partially buried in the substrate. Elongate aerial portions are oriented at right angles to the direction of the light. Degree of lobing is variable and depends at least in part on light intensity.

Most populations produce gametangia, although these are not easily observed. Antheridia are normally produced only on young thalli, often while still in the filamentous stage. Archegonia occur amidst rhizoids on the appressed basal lobes of mature plants. Farrar (7) reported three young abortive sporophytes of presumed apogamous origin in a population from Ohio, but sporophyte production has not been observed at any other locality, including those in Indiana. Reproduction is thus accomplished entirely asexually, by fragmentation of existing thalli and by production of filamentous, spindle-shaped gemmae (Figure 1b), the latter formed from specialized gemmiferous cells located along the margins of terminal lobes of mature gametophytes. Each gemmifer normally produces one to several pairs of gemmae, each from two to twelve cells in length. The individual gemmae are easily disarticulated from the gemmifers and are probably dispersed by water, wind, and insects or other small inhabitants of the sites. Irregular gemma for-

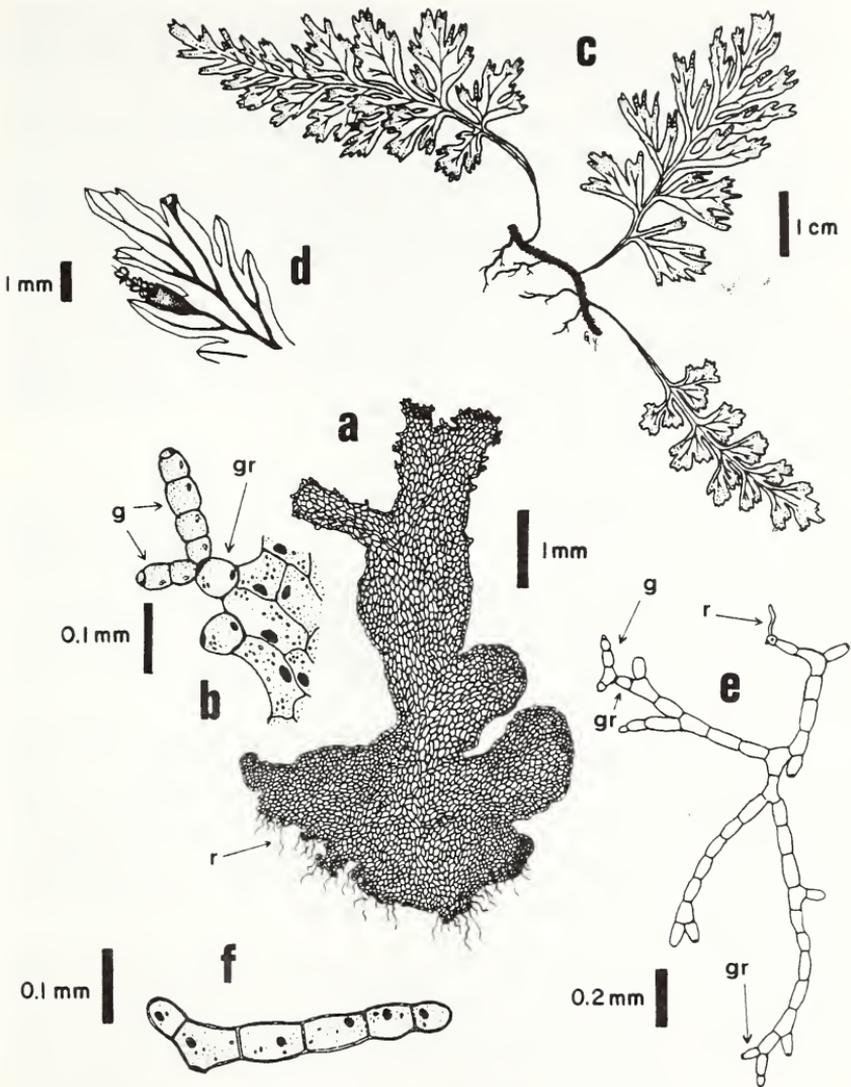


FIGURE 1. a. Independent *Vittaria* sp. gametophyte, b. Detail of terminal lobe of *Vittaria* gametophyte showing two gemmifers, one with a pair of gemmae, c. *Trichomanes boschianum* sporophyte, d. Pinna of *Trichomanes* sporophyte with mature sorus (sporangia on exserted receptacle) and developing sorus, e. Portion of independent *Trichomanes* sp. gametophyte, f. Detached gemma of *Trichomanes* gametophyte. g = gemma, gr = gemmifer, r = rhizoid.

mation involving the production of chains of gemmifers or T-shaped gemmae has also been reported (7), but is rarely observed in field-collected material from Indiana.

The specific identity of the Appalachian gametophyte remains problematic. Determination of fern species in general relies almost entirely on characters of the sporophyte generation and gametophytes of most *Vittaria* species are morphologically essentially

indistinguishable. Attempts to generate apogamous sporophytes of Appalachian *Vittaria* from axenic gametophyte cultures show promise, but to date have not successfully yielded mature sporophytes (1).

Wagner and Sharp (22) first suggested that the independently reproducing gametophytes represented a reduced northern variety of the Florida shoestring fern, *V. lineata*. Gastony (11) presented cytological evidence in support of this view, based on a comparison of ploidy levels for single accessions of sporophytes and independent gametophytes. Farrar (7), however, cited minor morphological discrepancies between the gemmae of the Appalachian gametophyte and those of cultured gametophytes of *V. lineata*. More recently, preliminary electrophoretic data from comparisons of enzyme banding patterns have suggested that the independently reproducing gametophytes are a genetically (and therefore taxonomically) distinct taxon from *V. lineata* and three other neotropical shoestring ferns (8). Further experimental work will be necessary to confirm whether the Appalachian *Vittaria* gametophyte represents a reduced temperate offshoot of *V. lineata*, its geographically closest living relative, or whether this odd fern originated from some other, perhaps now otherwise extinct species.

### Trichomanes

The primarily tropical filmy fern family Hymenophyllaceae contains ca. 600 species in 2 major genera, *Hymenophyllum* and *Trichomanes*, of approximately equal size (20). Only two extratropical species of *Hymenophyllum* are currently known from North America. Sporophytes of *H. tunbrigense* (L.) J. Smith are known from a single locality in Pickens County, South Carolina, and independent gametophytic colonies of this species occur in an adjoining four county area (5, 8). *Hymenophyllum wrightii* Bosch occurs both as sporophytes and (more commonly) as independent gametophytes in coastal Alaska and British Columbia (19).

In the United States, five species of *Trichomanes* are restricted to southern Florida (17). Only two species exist as sporophytes further north. The southeastern *T. petersii* A. Gray is found as far north as Arkansas and Tennessee (8), while the more widespread *T. boschianum* Strum ex Bosch has been collected as far north as Ohio and Indiana. Sporophytes of *T. boschianum* have thus far been found at only two Indiana sites, in Crawford and Martin County (13, 14, Table 1). Both populations are small, consisting of few plants showing obvious signs of cold damage. No spore production has been observed at either site.

Populations grow in sheltered, moist (but not wet) sites near the bases of sandstone bluffs and are to be sought in localities adjacent to, but receiving slightly more light, than those previously described for *Vittaria* gametophytes. The plants possess delicate pinnate-pinnatifid fronds with variously lobed to lacerate pinnae (Figure 1c) to 15 mm long (shorter in Indiana plants). Sporangia (when formed) are clustered on hairlike receptacles that are exerted from the marginal, tubular sori (Figure 1d). Superficially, the plants resemble very young sporophytes of *Dryopteris* and *Athyrium*, which are common on sandstone bluffs in southern Indiana, but the filmy fern may be distinguished from these by its slender, hairy (not scaly), creeping rhizomes, winged stipes, and thin, translucent fronds (usually only one cell thick between the veins).

Independent colonies of *Trichomanes* gametophytes occur nearly throughout the range of sporophytes of the genus in the eastern United States and have also been found as far north as central Vermont (9). They largely co-occur with the *Vittaria* gametophytes, but also inhabit somewhat more open sites on the sides of shady boulders. In Indiana, for unknown reasons, the plants are less abundant than the *Vittaria* gametophytes. They have, thus far, been collected in Crawford, Martin, Montgomery, and Perry Counties (Table 1).

Gametophytes of *Trichomanes* form small cottony tufts composed of an intertwined

network of branching filaments (Figure 1e). They greatly resemble in appearance a filamentous green alga, but are distinguished morphologically by the presence of short rhizoids, multicellular, spindle-shaped gemmae (Figure 1e, f) similar in appearance to those produced by *Vittaria*, and by their unicellular, flask-shaped gemmifers (Figure 1e) that remain attached to the filaments after the gemmae are shed. Gametangia are rarely present on the independent *Trichomanes* gametophytes.

As with the Appalachian *Vittaria*, the taxonomic identity of the independently reproducing *Trichomanes* gametophytes is problematic. Preliminary data from enzyme electrophoresis (8) suggest that these plants are not conspecific with either *T. boschianum* or *T. petersii*, the two sporophyte-producing filmy fern species whose ranges overlap with those of the sporophyte-less colonies, and whose gametophytes are morphologically indistinguishable from them. Further experimental work will be necessary to address whether the independently reproducing *Trichomanes* gametophytes are a species otherwise extinct, or if they represent a temperate range disjunction for an otherwise tropical species.

### Discussion

The genera *Vittaria* and *Trichomanes* have received relatively little attention from Indiana botanists. The independent gametophytes are certainly among the most unusual members of the state's flora, and the sporophytic *T. boschianum* is one of the rarest plant species in the state.

For these sporophytes, severity of winters appears to be the major biogeographic limiting factor. Both Indiana sites are at the climatic extreme, as evidenced by the small size and apparent frost injury of the plants. In contrast, the greatest biogeographic barrier to the spread of both taxa of independent gametophytes appears to be their inefficiency to disperse over long distances. The relatively large (to over 0.5 mm long), filamentous gemmae of these plants are less easily transported by wind currents than the much smaller spores produced by most fern sporophytes, and their thin, unarmored cell walls provide little protection from desiccation, thus making gemmae relatively poor long distance dispersal units. Their slow dispersal rate is evidenced by their spotty occurrence in areas of apparently suitable natural habitats and by the failure of independent gametophytes to colonize altered or recently created habitats such as old quarries and shady roadcuts, even when these lie adjacent to existing populations.

That gemmae of the independent *Trichomanes* gametophytes are somewhat better adapted to dispersal than those of the Appalachian *Vittaria* is attested to by their greater success at recolonization of available habitat north of the Wisconsin and Illinoian glacial boundaries. Since the retreat of the Pleistocene glaciers, *Vittaria* has succeeded in spreading to only two known stations (in northern Ohio and southwestern New York) significantly north of the glacial limits (3, 9, 18). In contrast, independent *Trichomanes* colonies have been reported from a number of stations in previously glaciated areas from Ohio to New Hampshire, as well as the Montgomery County site in Indiana (8, 9).

The distributions of *Vittaria* and *Trichomanes* in Indiana, as circumscribed in this report, should be treated as preliminary, since all suitable localities in the state for these plants have yet to be surveyed. Hopefully the information presented here will stimulate botanists in Indiana to search further for these uncommon ferns, particularly in counties from which they have not previously been reported. Many details of the biology and evolution of the independently reproducing gametophytes have not been studied exhaustively, and provide fertile topics for future research on these interesting and diminutive members of the state's flora.

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#### Note

<sup>1</sup> Present address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri, 63166.